# THE EVOLUTION
# OF
# PSYCHOLOGICAL DIVERSITY
# IN
# ANTHROPOIDS

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PhD Psychology
The University of Edinburgh
2012

# Contents

# Acknowledgements

This work was supported in part by the Great Britain Sasakawa Foundation (No. 3591) and by the Moray Endowment Fund Award. The idea behind the analysis in Chapter 3 came from a suggestion by Vincent Careau. Bonaventura Majolo, Julia Ostner, Jim King, and Alexander Weiss provided some of the data analyzed in Chapters 2 and 4. Gary Lewis, Timothy Bates, and Ian Deary were helpful in securing access to the data analyzed in Chapter 5.

I would like to thank Jarrod Hadfield, Gary Lewis, and Timothy Bates for helpful advice on modelling and Miho Inoue-Muryama, Hideki Sugiura, Eiji Inoue, and Takafumi Suzumura for their support in conducting field work. This work has made use of the resources provided by the Edinburgh Compute and Data Facility (ECDF).

I am indebted to my supervisors, Alexander Weiss and Timothy Bates, for their support, and to Michael Huffman, Goro Hanya, and Koichiro Zamma for introducing me to primatology. I also thank the members of the Differential Club for their camaraderie; among them Gary Lewis, Ana María Fernández, Stuart Ritchie, Andrea Zammit, Virginia Xythali, Marieke Gartner, Iva Čukić, Ulrika Alm Bergvall, Vanessa Wilson, Clare Mitchell, Sebastian Sandoval Similä, Despina Archontaki, David Hill, Jason Major, Abdo Abuhassàn, Aja Louise Murray, Rhona Kennedy, Dana Neomagus, Clare Nicholson, Sophie Drennan, Kaisa Wilson, Caimei Liu, Milan Valášek, Carmen Lefèvre, and Tom Booth.

I thank Christopher for the clonal repeatability, Maria for the meeps, Mana for the monkey chasing, Dorita for the butterflies, and Jan for encouragement toward the birds.

For everything else, and much more besides, I thank Sarah.

# Published works

Material included in this work has appeared in published form:

- Adams MJ (2011) Evolutionary genetics of personality in nonhuman primates. In M Inoue-Murayama, A Weiss, & S Kawamura (Eds.), *From Genes to Animal Behavior: Social Structures, Personality, Communication by Color*. pp. 137–164. Tokyo: Springer. DOI: 10.1007/978-4-431-53892-9_6 **(Chaps. 1, 2).**
- Adams MJ, Careau V, Weiss A, & Réale D (under revision) Fast–slow life histories and personality differences among modern human cultures. *Evolution and Human Behavior*. **(Chap. 3).**
- Adams MJ, King JE, & Weiss A (2012) The majority of genetic variance in orangutan personality and subjective well-being is nonadditive. *Behavior Genetics*. **(Chap. 4).**
- Weiss A & Adams MJ (in press) Differential behavioral ecology. In C Carere & D Maestripieri (Eds.), *Animal Personalities: Behavior, Physiology, and Evolution*. Chicago: The University of Chicago Press. **(Chap. 1).**
- Weiss A & Adams MJ (2010) Personality, temperament, and behavioral syndromes. In GF Koob, M Le Moal, & RF Thompson (Eds.), *Encyclopedia of Behavioral Neuroscience*, volume 3, pp. 47–53. Oxford: Academic Press. **(Chap. 1).**
- Weiss A, Adams MJ, & Johnson W (2011) The Big None: no evidence for a general factor of personality in chimpanzees, orangutans, or rhesus macaques. *Journal of Research in Personality 45:* 393–397 DOI:10.1016/j.jrp.2011.04.006 **(Chap. 1).**

- Weiss A, Adams MJ, Widdig A, *&* Gerald MS (2011) Rhesus macaques *(Macaca mulatta)* as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology 125:* 72–83 DOI: 10.1037/a0021187 **(Chap. 2).**

and in the following forms in preparation:

- Adams MJ. Orchid hypotheses: developmental evolution of risk and resilience. **(Chap. 6).**
- Adams MJ, Majolo B, Ostner J, *&* Weiss A. Comparative personality structure of macaques. **(Chap. 2).**
- Adams MJ, Penke L, *&* Weiss A. Natural selection on personality has a genetic basis. **(Chap. 5)**
- Adams MJ, Penke L, *&* Weiss A. Testing selection on cognitive traits in a pedigree sample without using individual fitness. **(Chap. 5).**
- de Ruiter JR, Adams MJ, *&* Inoue-Murayama M. Population differentiation of 5-HTTP, DRD4, and AR-Q genes and blood proteins in wild long-tailed macaques. **(Chap. 1).**

# Declaration

I hereby declare that I am the author of this thesis and that the work presented herein is my own. This work has not been submitted for any other degree or professional qualification.

# Abstract

Differential psychologists rightly identified evolutionary theory as a unifying framework for explaining the origins and persistence of individual differences in a wide array of human psychological characteristics. Psychological diversity occurs on multiple levels, including between species, populations, generations, and individuals. Each level reveals the outcome of evolutionary processes at different temporal scales. I embrace a range of methods and results from quantitative and population genetics, developmental evolution, and phylogenetically-grounded comparative psychology to explore how personality evolves in humans and non-human primates. At the level of species, I compared personality structure derived from rater assessments for four species of macaques and found a consistent, core set of personality dimensions (Dominance, Confidence, and Friendliness) describing these species. At the population level, I studied the relationship in humans between fertility/longevity trade-offs and the average personality of a country and found that Neuroticism and Agreeableness exhibit adaptively plasticity to life-history conditions. At the level of families, I estimated the quantitative genetic structure of personality in orang-utans and found that, like humans, a large portion of the phenotypic variance was explained by non-additive genetic effects. I examined between generation changes in personality by testing whether personality traits in humans are genetically correlated with fitness and found that in modern environments personality evolves very slowly. Finally, I translated current conceptual models of biological reactivity and stress response into mathematical models of developmental evolution and determined that evolution would select highly resilient phenotypes but that variation could be maintained by skew in the distribution of underlying genetic factors. From these results I broadly conclude that primate personality structure is generally conserved among species, mean personality levels change only very slowly between human generations, and that this evolution results in a genetic basis of personality that is characterized by epistasis. The evolution of individual differences has much to gain from the rigorous application of evolutionary methodology.

# Chapter 1

# The evolution of the psyche

*Personality is what a man really is.* — Gordon Allport

## 1.1 Variety

In the time of Carl Linnaeus, the Swedish naturalist and taxonomist, the essentialist species concept ruled (Hull, 1975; Mayr, 1983). Under this rubric, an individual organism is simply the manifestation of a static and unchanging (and unchangeable) essence, a timeless type. A species was at its core about similarity and the only meaningful difference was that which marked the boundaries between species. This essentialism served as the basis for the chief object of the naturalists' attention: the identification and classification of species. Taking a species as a category made it possible to treat all members of that species as interchangeable (Hull, 1965). Individuals from different species could then compared for the purpose of classifying species together with other species at the level of the genus. Higher level classifications, such as those in the Linnaean hierarchy (Simpson, 1961) followed the same architectural rule. Classification required discovering the shared essence between similar types of organisms and marking out the taxonomic characters that could best be used to group and differentiate them. Yet the unit of variability was the species.

Variation between individuals of the same species was accidental in nature and a meaningless deviation (Beddall, 1957; Mayr, 1983). This is not to say that Linnaeus or his forerunners, contemporaries, and successors were unaware of within-species variability. Linnaeus wrote of variation within a species attributable to living in a specific (climatic, edaphological) environment, the varieties of domesticated plants and animals, and geographic races. Mayr (1983) notes that while the term 'variety' was in widespread use among biologists of this time it was applied inconsistently and distinctions such as that between inherited and non-inherited characteristics, continuous and discontinuous variation, and individual- versus population-level variability were lost.

This changed with Charles Darwin. Darwin's name is cemented together with evolution but his key insights into the mechanism of natural selection and speciation required first overturning essentialism and adopting population thinking (Mayr, 1983). Species are not unchanging types but are instead populations composed of individuals (Hull, 1967; Ghiselin, 1974; Mayr, 1983). Tellingly, Darwin started *The Origin of Species* not with geology or geography but with variation, and not variation in nature but variation in domesticated animals and cultivated plants. After noting the great variety within a domesticated species, Darwin pointed out that the entire enterprise of animal and plant breeding—particularly for the study system he focussed his attention on, fancy pigeons—requires the breeder to attend to individual differences for it is from these differences that they decide which individuals to breed together.[1] This is selection. Individual variability, plus the transmission of this variability from parents to offspring, was exactly that required by natural selection to act. For Darwin (1859, p 102) "mere individual differences" were sufficient for natural selection to do its work.

From the modern perspective on the reconciliation of the studies of evolution and inheritance (Huxely, 1974) along with theoretical results from population genetics (Crow & Kimura, 1970; Rice, 2004), we are in a much better position to demarcate the scale on which biological—including (my interest here) psychological—diversity is generated. While evolutionary psychology is 'evolutionary' in so far as it seeks ultimate, adaptive explanations for psychological traits, the relative importance of various evolutionary processes for the trait of interest is highly dependent upon the timescale necessary to understand the trait's evolution. Different aspects of our psyche evolved at different times (Gosling & Graybeal, 2007). For example, psychological adaptations for living in groups have been evolving for the last 52 million years, starting when our ancestors transitioned from solitary foraging to social groups (Shultz, Opie, & Atkinson, 2011). Adaptations for complex combinatorial and referential

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[1] As will be seen, this was not the end of the influence of animal breeding on evolutionary biology.

language, a trait that debatably distinguishes us from other primates (Hauser, Chomsky, & Fitch, 2002), could, in contrast, be appropriately studied by only looking at tens or hundreds of thousands of years of our evolution (Lieberman, 2007). The particular timescale then dictates both the theory and the data necessary to answer the question at hand. Likewise, if a particular evolutionary process is thought to be important in explaining variation in a trait, that will also determine the time scale necessary for that process to have an appreciable effect. Comparing diversity at the species level, for instance, could entail understanding mutational input that gives rise to species differences. Mutation, however, would play a smaller role in genetic differences between an island and a mainland population accrued over only a few generations. Evaluating various approaches to studying the evolution of psychological traits and their appropriateness as frameworks for analyzing the evolution of individual differences therefore requires marking out which processes each approach emphasizes and over what timescales they consider the human mind to have evolved.

### Evolutionary psychological perspectives on individual differences

A number of approaches have been taken to study the evolution of human behavior including: sociobiology; human behavioral ecology; Evolutionary Psychology[2]; approaches inspired by gene and population genetic perspectives, including memetics and gene-culture coevolution (Laland & Brown, 2002); and, in the last decade, evolutionary genetic driven research (Penke, Denissen, & Miller, 2007; Keller, Howrigen, & Simonson, 2011). Each of these approaches finds its origins in workers from different disciplines (Laland & Brown, 2002) and therefore differ in the way that questions are posed and answered. These research traditions have differing interpretations of the evolutionary standing of individual differences.

#### Sociobiology

Sociobiology took as its starting point the ethological approach to the study of behavior, pioneered by Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, and combined it with theoretical perspectives on evolutionary processes such as kin selection and reciprocal altruism and methods from evolutionary game theory (E. O. Wilson, 1975; Segerstråle, 2000;

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[2] Or EP. Note the capitalization. Here I will use EP to denote a specific theoretical and methodological orientation within evolutionary psychology *sensu lato*.

Laland & Brown, 2002). When studied, individual variation was looked at in terms of genetic differences between individuals (Williams, 1966) or in terms of alternative behavioral strategies or types (R. Dawkins, 1978; Maynard Smith, 1982). Coming from the ethological tradition, the focus was on the optimal behavior of an individual given its environment and the distribution of strategies employed by the individual's competitors. Like with Darwin, the availability of variation for selection to work with was assumed.

Sociobiologists originated and promoted many concepts that are still central to evolutionary studies of human behavior (Laland & Brown, 2002). Kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971) were foundational to the study of the evolution of social behavior (West-Eberhard, 1975) and cooperative behavior in humans (Bowles & Gintis, 2003). While frequently challenged (Fehr & Fischbacher, 2003), these concepts are still central to debates over human nature (West, El Mouden, & Gardner, 2011).

### Human behavioral ecology

Like sociobiology, human behavioral ecology focused on optimal behavior given environmental conditions but broke from sociobiology by relying more heavily on data to test hypotheses (Laland & Brown, 2002). While sociobiology talked about human universals, research informed by behavioral ecology paid much closer attention to within- and between-population variability (Borgerhoff Mulder, 2001). The chief working assumption of this school is that humans exhibit great behavioral flexibility in response to environmental conditions and that behavior can be tuned and selectively deployed to maximize fitness (E. A. Smith, 2000; Laland & Brown, 2002; G. R. Brown, Dickins, Sear, & Laland, 2011). A conditional response gives the organism flexibility to adjust its strategy and choose between alternative behaviors as the situation or strategies of other individuals change (Gross & Repka, 1998). For example, mating preferences may relate to resource availability such as when males with more resources choose females with higher residual reproductive value (Voland & Engel, 1990) or when females who control resources shift mating preferences to emphasize physical attractiveness of mates (Moore, Cassidy, Law Smith, & Perrett, 2006). A focus on individual flexibility leaves little room to consider stable individual differences in behavior (that is, personality). However, human behavioral ecology has indirectly had an influence on the study of personality evolution through its examination of trade-offs in human life-history traits (Voland, 1998, see also Chap. 3).

### Cultural evolution

The evolution of human behavior has also been studied from the subfields of memetics and gene–culture coevolution. These approaches take culture to be either the main focus or as an alternative but equally important inheritance mechanism for behavior (Laland & Brown, 2002). Memetics studies the evolutionary dynamics of cultural or behavioral units ('memes') but does not require individual differences in dispositions to explain variation in behavior (R. Dawkins, 1978). Instead, individuals would behave differently because each person would contain a different set of memes that inform and direct their behavior (R. Dawkins, 1978; Lehmann, Aoki, & Feldman, 2011). Gene–culture coevolution, in contrast, sees both genetic and cultural inheritance as necessary to explain the evolution of complex human behavior (Lumsden & Wilson, 1981; Boyd & Richerson, 1985; Feldman & Laland, 1996; Odling-Smee & Feldman, 2003). The foundation of this approach is that a cultural behavior functions against a particular genetic background (the classic, and dogged, example being the coevolution of dairy farming and lactose persistence; Feldman & Laland, 1996) and that the capacity for culture is itself a behavioral adaptation (Laland & Brown, 2002). Coevolutionary approaches see individual variation as a product of both inherited genetic and inherited environmental factors (Feldman & Otto, 1997).

### Evolutionary Psychology™

Evolutionary Psychology (EP) also takes as its subject evolved universal traits in humans (Tooby & Cosmides, 1990b; D. M. Buss, 1995). EP differed from sociobiology and human behavioral ecology by making the psychological mechanism, rather than the behavioral output, the unit of inquiry (Cosmides & Tooby, 1987). Taking a cognitive psychology approach that the mind is highly modular (Fodor, 1983), EP posits that the mind is composed of a host of individual mechanisms that evolved for producing a domain-specific set of adaptive behaviors (D. M. Buss & Greiling, 1999), and it is this theoretical orientation that differentiates this particular school from the broader enterprise of evolutionary psychology. Individual variation, in this view, is produced by a universal response to the unique environment encountered by each individual (similar to the human behavioral ecology view of adaptively flexible behavior) or by non-adaptive genetic noise that produces a departure from the evolved species optimum (Tooby & Cosmides, 1990a). Selection will reduce variation around this optimum and minimize adaptive individual differences so that, from a functional point of view, all humans are basically the same. In this view, many of the individual differences noted by psychologists are the result of neutral genetic variation plus random fluctuations that occur during development. Because selection will weed out fitness-related variants, adaptive psychological traits will be notable for their low heritability. The non-zero heritability of many individual differences traits (Turkheimer, 2000) is thus evidence for their non-adaptiveness (Tooby & Cosmides, 1990a). In this view, while this neutrality is not adaptive now, it can serve as the raw variation with which selection will produce future psychological adaptations.

The other important tenet of EP, one which grounds it methodologically, is the contention that human psychological mechanisms must be understood in the context of the *past* environment in which they evolved (Tooby & Cosmides, 1990b). Inquiry proceeds by discovering the environment of evolutionary adaptedness (EEA; Bowlby, 1969, 1973), "a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and fitness-consequences" (Tooby & Cosmides, 1990b, pp 386–387). Although Tooby and Cosmides distance themselves from associating the EEA with a specific time and place, they believe that most psychological adaptations of interest will have evolved during the Pleistocene (approximately 2.5 mya - 11 kya; Gibbard & Kolfschoten, 2004) when anatomically modern humans evolved (Lahr & Foley, 1998). The concept of the EEA is particularly informative of the type of methodology needed to investigate psychological adaptations. If the current environment differs substantially from that in which the behavior evolved, it will not appear to be fitness enhancing and may even appear maladaptive (Symons, 1987). Thus the attention is on past rather than contemporary evolution.

### Differential psychology

Evolutionary differential psychology differs from EP in basic precepts and overall methodological orientation. The primary theoretical departure is that personality and other psychological variation is conceived of, in part, as adaptive individual differences (D. M. Buss, 1991; D. M. Buss & Greiling, 1999; Penke, Denissen, & Miller, 2007). In this view, selection actually results in personality variation. In contrast to the cognitive psychology and information processing orientation of EP (Laland & Brown, 2002), evolutionary differential psychology as a field within psychology is methodologically aligned with individual differences, developmental, psychometric, and behavior genetic approaches. Scholars taking this approach also draw thoroughly from life-history theory and evolutionary genetics (Hawley & Buss, 2011).

Work in this area is represented by two main branches. The first is in clarifying, evolutionarily, what personality is 'for' (D. M. Buss, 1991; MacDonald, 1995; D. M. Buss & Greiling, 1999; Denissen & Penke, 2008a) and how continuous variation in a personality trait might relate to fitness trade-offs (Nettle, 2006; D. M. Buss, 2009b; Figueredo et al., 2011). Because of its origins in psychometrics and psychological measurement, a related research pursuit is to develop questionnaires that take an evolutionarily-informed approach to personality assessment (Figueredo, Vásquez, Brumbach, & Schneider, 2007; Denissen & Penke, 2008a). The second strand concerns reconciling what is known about the genetics of personality with evolutionary genetic principles (Penke, Denissen, & Miller, 2007; D. M. Buss, 2009b; Gangestad, 2011; Keller et al., 2011; Miller, 2011). One of the main tenets underlying this school of thought is that selective neutrality is an unlikely explanation of personality variation because fitness differences between alleles of personality-related genes would have to be extraordinarily small to not be able to overcome genetic drift given assumed ancestral human population sizes (Keller et al., 2011). If $N_e$ is the effective population size and $s$ is the selection coefficient of a mutation, random genetic drift will overcome selection when $|2N_e s| \approx 1$ (Ohta, 1992). Keller and Miller (2006) calculated that if we assume a human effective population size of $N_e \approx 10000$ (Tenesa et al., 2007), then for drift to dominate the selection coefficient would have to be so small that it would not result in a single difference in reproductive success over a dozen generations or more.

This last point emphasizes the incorporation by the differential approach of specific quantitative principles from evolutionary quantitative and population genetics into evolutionary–psychological theorizing. Using this framework, evolutionary differential psychology has also studied the evolution of mental disorders (Keller & Miller, 2006; Crespi, Summers, & Dorus, 2007; Penke, Denissen, & Miller, 2007; Keller, 2008; Nettle, 2008; Nichols, 2009). Again, the main focus of the inquiry is to understand how variation in genes underlying mental disorders persists in the face of the negative consequences for individual fitness.

### Comparative personality psychology

Another approach that grew primarily out of psychology is personality research on nonhuman animals (Gosling & Graybeal, 2007). This approach offers a comparative perspective on the evolution of individual differences in behavior. The realization by scientists that nonhuman primates are individually recognizable and behaviorally distinct began in early laboratory colonies and preceded the formal study of their personality (Crawford, 1938; Yerkes, 1939). Later contributions came from researchers such as Itani (1957) who considered introversion and extraversion in Japanese macaques, and Goodall (1986a), who described the personalities of the chimpanzees she studied at Gombe. Rather than being simple anthropomorphism, the assumption that primate personality should resemble our own has a strong phylogenetic basis (Weiss & Adams, 2008). Without evidence to the contrary, we assume that closely related species will be more similar to each other than more distantly related species (Darwin, 1859, ch. 13). Thus, how individuals within a nonhuman primates differ behaviorally should resemble how humans differ from each other.

One new goal of psychologically-informed animal personality research is to determine a whole personality structure rather than study only single behavioral dimensions. Such studies have been primarily carried out on nonhuman primates, including rhesus macaques (Stevenson-Hinde & Zunz, 1978; Bolig, Price, O'Niell, & Suomi, 1992; Capitanio, 1999; Weiss, Adams, Widdig, & Gerald, 2011), langurs (Konečná et al., 2008), chimpanzees (King & Figueredo, 1997; Weiss, King, & Hopkins, 2007; Weiss et al., 2009), orang-utans (Weiss, King, & Perkins, 2006), and gorillas (Gold & Maple, 1994). While the personality structure of other species such as fallow deer (Bergvall, Schäpers, Kjellander, & Weiss, 2011) have been studied comprehensively the close phylogenetic relationship of nonhuman primates makes them particularly informative of human studies for genetics (Weiss, King, & Figueredo, 2000), health (Capitanio, Mendoza, & Baroncelli, 1999) and longevity (Weiss, Adams, & King, 2011), and mental well-being (King & Landau, 2003; Weiss et al., 2006; Brüne, Brüne-Cohrs, McGrew, & Preuschoft, 2006; Weiss, Adams, Widdig, & Gerald, 2011).

### Behavioral syndromes

The evolution of individual differences in behavior is also being studied in parallel under the heading of behavioral syndromes (Sih, Bell, Johnson, & Ziemba, 2004; Sih, Bell, & Johnson, 2004). Researchers in this field tend to be ethologists rather than psychologists and typically study nonprimate animals. A behavioral syndrome is a correlated suite of behaviors that is consistent across contexts (Sih, Bell, Johnson, & Ziemba, 2004) and is a more general concept that encompasses personality (Stamps & Groothuis, 2010a; but see Uher, 2011a). While personality refers to the interindividual differences in behavior that are stable across situations, behavioral syndromes can also exist at the population level. Because of its origins in biology and its use of study organisms with shorter lifespans, research on behavioral syndromes tends to take a more selectionist approach to studying the evolution of behavior. Rather than reconstructing the ancestral environment, the selectionist approach attempts to empirically determine the strength and shape of phenotypic selection using contemporary populations (Lande & Arnold, 1983; Endler, 1986; Kingsolver et al., 2001; Réale & Dingemanse, 2011). This approach is particularly relevant to the study of individual differences because it allows hypotheses about the maintenance of variation in a behavioral trait to be directly tested (Réale & Dingemanse, 2011, and Chap. 5).

In carrying out the studies in this work, I draw primarily on evolutionary differential psychology and comparative personality psychology but combined with the selectionist common in behavioral syndromes research. The primary reason is that these approaches take the adaptiveness of a particular individual difference as something to be tested rather than assumed a priori. The second reason is that these subdisciplines rely more heavily on methodology from population and evolutionary quantitative genetics to test evolutionarily informed hypotheses against data.

## 1.2 Evolutionary psychology as framework

D. M. Buss (2009b, p 359) described evolutionary psychology as a "metatheoretical paradigm" for understanding the orgins, function, and structure of psychological traits. While some branches of evolutionary studies of human behavior (e.g., Evolutionary Psychology *sensu stricto*) offer a specific theory of human nature (e.g., that adaptive evolution has fashioned the mind out of specialized modules: Fiddick, Cosmides, & Tooby, 1995; Cosmides & Tooby, 1997), as an overarching metatheory evolutionary psychology offers a framework for asking questions, determining what evidence constitutes an answer, and organizing results. In terms of practice, grounding psychological studies in evolutionary biology provides a set of tools and procedures for understanding the trait of interest. On a theoretical level, evolutionary reasoning can help guide our thinking and answer questions in psychology that may not at first strike one as directly related, such as under what conditions we should expect personality traits to be stable.

To understand what constitutes suitable questions and acceptable answers in evolutionary psychology, we can turn back to Darwin's (1859) original formulation. Evolution by natural selection is a result of

1. variation among individuals,
2. resemblance between parents and offspring,
3. differential survival and reproductive success among individuals, and
4. the variation among individuals being the cause of differences in fitness.

Selection is the result when these four assumptions hold: differences in reproductive success (fitness) means that variation in the offspring will be a subset of that in the parents, which over many generations leads to adaptation. Evolutionary biology has since also identified the extent to which other processes influence the evolution of a trait (Mayr, 1983; Hartl & Clark, 2007). Darwin did not have much to say about the cause of new variation (Darwin, 1859, p 325), but we now know that variation arises from mutations in the genome. Evolution can also proceed from random differences in fitness, which produces genetic drift through random sampling of alleles. The variation within a population can be effected by the immigration and emigration of individuals. These processes (selection, mutation, migration, and drift) have complex but precisely determined relationships with each other (Hartl & Clark, 2007). Mutation and migration tend to increase variation within a population while drift and selection reduce it. Mutation and drift will increase between population differences while migration between populations will make them more similar. Selection's effect on between-population variation depends on whether selection pressures are uniform. When they are, selection will make populations more similar but differing selective environments will result in divergence between populations. These processes also apply if the populations represent different species, with the exception that there could be no migration. Evolutionary psychology thus comes down to understanding how the interaction of these processes has shaped and continues to shape our psychological character.

The practice of evolutionary psychology, rather than being limited to specific phenotypes that on the surface seem related (surely, *surely!*) to fitness and reproductive success (e.g., attractiveness, mating strategy), should instead be broadened to (and, at its core, be) the application of an evolutionary analysis of selection, mutation, migration, and drift with regard to any psychological trait. Because selection is the dominant process over long periods of evolutionary time (Hartl & Clark, 2007), the evolution of personality first requires understanding what personality is an adaptation *to*. Other aspects of the growth and development of an organism (Stamps, 2007; Stamps & Groothuis, 2010a) can also act as constraints (Hansen & Houle, 2008; Merilä, 2009) on the selection of personality. Comparisons of personality in closely related species can also be informative of how differences in social ecology might shape personality. Looking at personality in nonhuman primates is likewise informative of which aspects of personality are ancestral versus derived (Gosling, 2001; Gosling & Graybeal, 2007; Weiss & Adams, 2008). Such complementary avenues of exploration show how evolution can be a proper metatheory and framework for understanding the origins of individual differences in behavior.

### Personality from the comparative perspective

Early biographers such as Plutarch (46 AD-120 AD) ascribed personality characteristics to their subjects but the study of human personality as a science has a shorter history. Research in human personality originated from Galton's (1892) study of human individual differences, which also led to the development of modern psychometrics, statistics, behavior genetics, and intelligence research. The insight that personality descriptors may be found in natural languages and can be used to construct personality inventories came later (Allport & Odbert, 1936) and is still one of the most popular ways of studying human personality (McCrae & Costa, 1995). These data are most commonly analyzed using factor or principal components analysis (Gorsuch, 1983), which involve examining covariances among variables to determine whether groups of variables cluster, i.e., are indicative of one or more latent underlying constructs (factors or components). Current trait explanations of personality take personality traits to be relatively stable, underlying behavioral dispositions that interact with external influences to produce behavior (McCrae & Costa, 1995).

### Personality structure

The study of human personality via ratings was and is still not without debate. The most serious charge by critics was that personality traits did a poor job of predicting behavior and were inconsistent across situations (Mischel, 1968). In fact, like early (and some contemporary) ethologists and behavioral ecologists (M. S. Dawkins, 2007), Mischel favored using behavioral measures. This challenge was later answered by research showing that personality measures were related to behavior if behavior was aggregated over time (Epstein, 1979). Personality researchers also showed that self-ratings and observer-ratings were correlated (McCrae, 1994), that personality was mostly stable in adulthood (Costa & McCrae, 2002), and that personality predicted a broad range of important outcomes (Ozer & Benet-Martínez, 2006; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007; Deary, Weiss, & Batty, 2010). Other debates, many of which are still ongoing, revolved around the number of personality dimensions needed to explain human personality differences (Costa & McCrae, 1992a, 1992b; H. J. Eysenck, 1992, 1992; K. Lee, Ogunfowora, & Ashton, 2005; Block, 2010).

In much contemporary research, the Five Factor Model (FFM; Digman, 1990) has become the dominant model of human personality and the basis for the human and nonhuman primate personality research pursued herein. Five Factor Theory contends that human personality consists of five normally-distributed dimensions or domains: neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness (Costa & McCrae, 1992c). Individuals on the low end of neuroticism are emotionally stable, well-adjusted, and exhibit low levels of negative affect; individuals on the high end tend to be emotionally unstable, have problems with adjustment, and have high levels negative affect. Individuals high in extraversion are more sociable, assertive, active, and experience more positive affect whereas those low in extraversion do not seek out others' company and are independent, less active, and experience less positive affect. Individuals scoring higher in openness to experience tend to be curious, to value new experiences and feelings, and to be unconventional whereas individuals scoring on the low tend to be less curious, prefer the familiar to the novel, and are more conventional in their outlooks and behavior. Individuals higher in agreeableness tend to be helpful, trusting, and more inclined to cooperate rather than compete. On the other hand, individuals lower in agreeableness tend to be less inclined to help others, suspicious and cynical, and more competitive. Finally, individuals ranking high in conscientiousness will be reliable, organized, directed, and self-disciplined whereas those lower in conscientiousness will often be less reliable, disorganized, directionless, and lacking in self-discipline.

The five personality dimensions appear to be a human universal because they replicate across cultures (McCrae, 2002; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007) and show cross-cultural consistency in genetic structure (Yamagata et al., 2006). However, some personality instruments do not show complete measurement equivalence where items making up a personality scale have equivalent relationships to each other across samples. One study (Nye, Roberts, Saucier, & Zhou, 2008) found that the five personality dimensions showed configural equivalence (the items showed similar structure across cultures) but not metric (similar loadings) or scalar equivalence (similar means and loadings). However, this study used a shorter personality instrument (Saucier, 1994) and simulation has shown that if scalar equivalence is a large problem for cross-culture studies then consistent factor structures are unlikely to be recovered (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005).

Debates about structure also extend to higher levels. There is some evidence that the five human personality dimensions intercorrelate. One formulation of this creates two higher order factors: Stability out of agreeableness, conscientiousness, and (reversed) neuroticism; and Plasticity from extraversion and openness (Digman, 1997; DeYoung, 2006; DeYoung, Peterson, & Higgins, 2002). It has also been proposed that a single higher-order personality factor (the general factor of personality or GFP) underlies first- or second-order structures of a variety of personality measures (Musek, 2007; Rushton & Irwing, 2008). Critics have challenged the psychometric validity of the GFP and suggested that it is an artifact arising from, for example, common method variance (Riemann & Kandler, 2010), self-presentation bias (Bäckström, Björklund, & Larsson, 2009), or blends of orthogonal factors (Ashton, Lee, Goldberg, & Vries, 2009). One way to potentially clarify these debates is to explore personality structure in species that are closely related to humans.

### Nonhuman primates

Personality dimensions similar to those identified in humans have been found in nonhuman primates (Gosling, 2001; Freeman & Gosling, 2010). Most studies of nonhuman primates focus on single dimensions or behavioral traits such as anxiety (e.g., Barros, Major, Huston,

& Tomaz, 2008; Rogers, Shelton, Shelledy, Garcia, & Kalin, 2008), impulsivity (e.g., Fairbanks, 2001; James et al., 2007), and aggression (e.g., Anestis, 2006; Kitchen & Beehner, 2007). A minority of studies, however, have attempted to determine a full personality structure for nonhuman primates using methods imported from human personality research (Freeman & Gosling, 2010). Freeman and Gosling (2010) identified 14 different personality dimensions or traits that have appeared in these studies. In structural studies that use a large number of personality items or behaviors to define a whole personality structure the most commonly identified dimensions were Sociability, Fearfulness, and Playfulness.

Our closest living relatives, chimpanzees, who shared a common ancestor with us approximately six or seven million years ago (Steiper & Young, 2006; Chatterjee, Ho, Barnes, & Groves, 2009), have five human-like personality factors in addition to dominance, a broad factor that describes individual differences in social assertiveness (King & Figueredo, 1997). This might be expected given that, like humans, chimpanzees live in complex social groups, have a slow life-history strategy, and exhibit many human-like behaviors, characteristics, and abilities. Among others, these include theory of mind, moral behaviors, empathy, cooperative hunting, culture, and warfare (Goodall, 1990). Orang-utans, who shared a common ancestor with humans and chimpanzees sometime around 15–18 million years ago (Steiper & Young, 2006; Chatterjee et al., 2009), are less similar still in terms of personality (Weiss et al., 2006). While they share with humans and chimpanzees separate extraversion, agreeableness, and neuroticism dimensions they differ from both of these species in several respects. Like chimpanzees but unlike humans, orang-utans can be characterized in terms of a dominance dimension. However, while both humans and chimpanzees have independent openness and conscientiousness dimensions, items describing curiosity and goal-related behaviors covary as a single dimension in orang-utans called intellect (Weiss et al., 2006). This suggests that there is at least some phylogenetic patterning in personality structure (Weiss & Adams, 2008; Weiss, Adams, Widdig, & Gerald, 2011, and see Chap. 2).

Given their phylogenetic similarity to humans, we might expect nonhuman primate personality to incite similar debates about how to measure it. This turns out to be the case. The charge of anthropomorphism, ascribing human-like traits such as personality to nonhuman animals (Schilhab, 2002), has long plagued studies of nonhuman primate behavior (Goodall, 1990; Uher, 2008a; Wynne, 2009). However, there are no empirical studies that show anthropomorphism being detrimental to the study of animal behavior. In fact, results from numerous studies contradict what one would expect if anthropomorphism had a strong influence on animal personality ratings (Gosling, 2001; Kwan, Gosling, & John, 2008; Uher & Asendorpf, 2008; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012). The most striking evidence against nonhuman personality domains being anthropomorphic projections is their external validity. For example, rater-assessed chimpanzee personality dimensions correlated with recorded behaviors (Pederson, King, & Landau, 2005; Uher & Asendorpf, 2008). Personality in nonhuman primates also relates to immune functioning (Capitanio et al., 1999; Maninger, Capitanio, Mendoza, & Mason, 2003) and brain structure (Blatchley & Hopkins, 2010). Rhesus macaques that were rated higher on sociability had an increased antibody response compared to individuals low on sociability (Maninger et al., 2003). In chimpanzees, individuals who scored higher on dominance and conscientiousness (Blatchley & Hopkins, 2010) had a greater percentage of gray matter in the cingulate cortex, a brain region that in humans has been linked to emotional processing (Drevets et al., 1997; Coryell, Nopoulos, Drevets, Wilson, & Andreasen, 2005).

However, even among researchers who accept the pertinence of nonhuman primate personality, there is still room for debate. Assessing primate personality differs in terms of the *what* and the *how* of measurement (Itoh, 2002; Koski, 2011; Freeman, Gosling, & Schapiro, 2011). Behaviors can either be recorded through naturalistic observation or elicted via behavioral tests. These behaviors can then be assessed either by trait ratings (by knowledgeable raters on adjectival items) or by behavioral codings (objective measurement of specific behaviors). Each combination of methods has its advantages and disadvantages (Freeman et al., 2011). While coding naturalistic behaviors is easier to implement and can be performed by researchers who have less familiarity with individual animals, they are time consuming and only capture behaviors in single contexts. Trait ratings can be collected on a large number of individuals at once and smooth over temporal variability but rely on impressions of the same individual animals that may differ between raters. Testing allows behaviors to be studied under controlled conditions but requires manipulating subjects and are more difficult to conduct outside of laboratory and captive settings (Freeman et al., 2011).

Whether using trait adjectives or behavioral codings, personality scales can also be differentiated based on the origins of the adjectives or behaviors they are composed from (Gosling, 2001; Uher, 2008a; Freeman et al., 2011). Analogously with cross-culture studies of human personalitiy, etic approaches are those where a personality scale developed for one species is used to assess another. In contrast, emic approaches describe the development of a scale based solely on observations of the species that is to be studied. While etic approaches, such as studies of chimpanzees, orang-utans, and rhesus macaques using nearly-identical questionnaires (King & Figueredo, 1997; Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011) have the advantage of yielding results that allow between-species comparisons to be easily made, Uher (2008a, 2008b) criticized such studies as being "top-down" and possibly imposing a personality structure of one species (namely humans) on to that of another (nonhuman primate). As an alternative, Uher proposed a "bottom-up" approach of developing behavioral repertoires based on what is known about the behavior and ecology of a species. Among its advantages, this approach promises to be much more sensitive to the specific contexts in which behavior is expressed and, more importantly, to describe new, species-specific personality dimensions that are missed when behavioral descriptors from one species are appropriated wholesale to study another.[3] Weiss and Adams (2008) defended their approach, noting that while being "top-down" it has developed "bottom-up" over time, and questioned the suitability of behavioral repertoire approaches for comparative personality research and its disregard for phylogenetic relationships between organisms.

### Guideposts of evolutionary theory

Debates about the structure and assessment of personality can be guided by evolutionary theory. In measuring nonhuman primate personality, which side of the dispute a researcher finds themselves on can seemingly be explained by whether or not the default assumption is that species that are genetically closely related will also be behaviorally similar. The importance here is not what turns out to be the case (for separating homologous, phylogenetically shared versus analogous, convergently evolved traits has to be determined empirically) but simply what the *default* assumption is. And when it comes to cognitive and behavioral phenotypes, the most parsimonious explanation is for similarity (de Waal, 2009). Telling apart homologous and analogous features requires comparing multiple species with known phylogenetic relationships.

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[3] What these new, as-yet-unheralded personality dimensions might be is still forthcoming, as far as I can tell.

Perhaps one problem is in thinking that evolution is omnipotent. Tooby and Cosmides (1989, p 175) write, for example, that "[b]ecause selection acts on the consequences of behavior, the behavioral output of the psyche will be *easily* shaped by adaptive demands over evolutionary time" (emphasis mine). While we might be vulnerable to the dazzling variety of nature, the evidence points to strong constraints on evolutionary processes (Merilä, 2009). Thus, in determining personality structure, it is prudent to assume phylogenetic similarity until we find evidence to the contrary.

A phylogenetically-informed comparative approach is highly relevant to broad debates about human personality. For example, if we assume that the human GFP is substantial rather than artefactual, it is useful to determine whether it characterizes nonhuman primates as well. A study of chimpanzee, orang-utan, and rhesus macaque personality found no evidence for a single, higher-order factor (Weiss, Adams, & Johnson, 2011). While assessments of nonhuman primate personality are probably less likely to suffer from desirability biases that have been proposed as explanations for a human GFP (Bäckström et al., 2009), this result leaves open the possibility that, if it exists, the covariance among personality dimensions leading to a GFP is a uniquely human trait. This puts constraints on when a human GFP evolved, that is, after the speciation of humans and chimpanzees. Some arguments for a GFP tie it in with life history traits (Figueredo et al., 2011) and thus base its probable existence in evolution rather than psychometrics. In this case, a consistent theory of the GFP would have to show why it did not evolve in socially and behaviorally similar species.

If comparative studies of primate personality reveal personality dimensions to be adaptations to specific social or ecological factors, evolutionary psychology may be able to answer Fiske's (1994) question "Why these five?" For example, if conscientiousness turns out to unique to humans, chimpanzees, and another socially or ecologically but not phylogenetically similar species, then this will help explain under what circumstances conscientiousness tends to evolve as an independent personality dimension. Comparative perspectives can also be used to assess the utility of new personality models. As a test of validity, attempts to reconceptualize personality structure, such as circular trait arrangements (e.g., Tiliopoulos, Pallier, & Coxon, 2010), should offer the hypothesis that chimpanzee personality items will show a more human-like structure than other species. Evolutionary theory can also guide debates about situations versus traits (Epstein, 1979; Mischel & Shoda, 1995; D. M. Buss, 2009a) and trait stability over the lifespan (McCrae et al., 2000; Costa & McCrae, 2002; Roberts, Walton, & Viechtbauer, 2006; Costa & McCrae, 2006) by answering questions like *Why do we find behavioral variability at all?* (Wolf, Sander van Doorn, Leimar, & Weissing, 2007) and *How do we expect personality to develop?* (Stamps, 2007; Stamps & Groothuis, 2010a).

### Personality as an adaptation to the social environment

Understanding the adaptiveness of a trait requires understanding to what aspect of the environment the trait is adapted. Instead of thinking about environments of evolutionary adaptedness, Irons (1998) proposed the "adaptively relevant environment" (ARE) as a more practically workable concept. Irons thought that, in its formulation, the EEA concept overemphasized the amount of stasis in ancestral environments. The EEA concept also yields a human nature that is adapted to past conditions and maladapted to the present (Symons, 1987). However, 10000 years of evolution would encompass hundreds of generations, which has shown to be an ample amount of time for evolution to affect change (Irons, 1998), a point born out by evidence of recent selection across the entire human genome (Hawks, Wang, Cochran, Harpending, & Moyzis, 2007). Rather than seeing the environment as monolithic, the ARE concept suggests that phenotypes will instead adapt to specific aspects of the environment, which may in turn show different amounts of stability over evolutionary time. In other words, not all aspects of the environment are relevant for every trait.

The independence of personality dimensions from each other thus suggests that each might have a separate adaptively relevant environment. Human personality is primarily an adaptation to the social environment (D. M. Buss, 1995; Penke, Denissen, & Miller, 2007; D. M. Buss, 2011). In terms of fitness, personality relates primarily to reproductive success rather than survival (B. Smith & Blumstein, 2008). Humans thus require adaptations to compete for, attain, and retain mates and cooperate with allies and with kin in the acquisition of material resources and status (D. M. Buss, 1995, 2009b). Primate social structure may have solved problems such as foraging and predator defense (Strier, 2003) that creates individual differences in behavior in other species (Sih, Bell, & Johnson, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). The relevant environment for a primate's personality is the behavior of conspecifics.

Personality dimensions have been explained as alternative, continuously distributed strategies for achieving reproductive success in variable environments (MacDonald, 1995, 1998; Nettle, 2006). Synthesizing various conceptions of the five personality dimensions, Denissen and Penke (2008a) found support for the Five-Factor Model of personality using questionnaire items related to motivational reactions that had been formulated to tap into evolutionarily-relevant behaviors. They formulated extraversion as reward in social situations, agreeableness as a tendency to cooperate during resource conflicts, conscientiousness as the ability to choose among multiple competing goals, neuroticism as sensitivity to punishment with regard to social exclusion, and openness as reward sensitivity for cognitive activity. Thus, the five factors relate to the basic social tasks that humans need to deal with: making social affiliations, being included in the social group, cooperating with others, pursuing goals, and transmitting culture. Because features of social organization are phylogenetically conserved (Thierry, Iwaniuk, & Pellis, 2000; Shultz et al., 2011), it is likely that personality dimensions in other primate species are also adaptations to similar social tasks.

### Life-history

Life history refers to organisms' patterns of growth, development, maturation, and reproduction (Stearns, 1992). These traits typically reflect a trade-off between reproductive and somatic effort (Fisher, 1958; Stearns, 1992; Bulmer, 1994). Dall, Houston, and McNamara (2004) reconceptualized personality as alternative behavioral strategies and Wolf et al. (2007) placed personality in the context of life-history evolution. An individual's optimal behavior depends both on its own condition and behavioral history as well as on the behaviors of others in the population. For example, an animal with poor body condition and, therefore, a low potential for reproductive success, would do better to invest in foraging, even if this increases predation risk. Likewise, the advantage of behaviors like aggression depends both on how others are behaving and on population density. Normally, aggression leads an individual to out-compete its neighbors for resources, but at low population densities with moderate competition, high aggression might be counter-productive, leading to lower fitness (Dingemanse, Both, Drent, & Tinbergen, 2004; Sih, Bell, Johnson, & Ziemba, 2004).

One model of the life-history trade-off between growth and reproduction is offered by $r/K$ theory (Pianka, 1970). Unstable environments lead to species that are $r$-selected, that is, characterized by reproductive effort. These $r$-selected species (e.g., rabbits) have short generation times, a lower probability of offspring survival, and small body size. On the other hand, stable environments lead to species that are characterized by somatic effort or $K$-selected. Individuals within $K$-selected species (e.g., elephants) possess traits indicative of somatic effort, namely larger body size, high parental investment, and greater longevity.

Rushton (1985) argued that $r$- and $K$-selection could also be applied at the individual or group level, which he dubbed differential K theory. Life-histories tend to be coordinated affairs and although humans are $K$-selected species (with slow development, long lives, small family sizes, and high offspring investment), some humans are "more K than others" (Rushton, 1985, p 441). Humans show a trade-off between the life-history traits of fertility and longevity (Doblhammer & Oeppen, 2003; Korpelainen, 2003; Maklakov, 2008; Penn & Smith, 2007; Pettay, Kruuk, Jokela, & Lummaa, 2005; Thomas, Teriokhin, Renaud, De Meeus, & Guegan, 2007; Westendorp & Kirkwood, 1998) and this trade-off also links in with cognitive traits such as intelligence (Rushton, 1985). To test whether human personality dimensions were also related to how K-selected individuals were, Figueredo et al. (2005, 2007) conducted two analyses. In the first they showed that factor analysis of either the phenotypic or genetic covariance among questionnaire items concerning altruism, reproductive effort, parenting effort, and other aspects of life history revealed a single factor, which they named K. Figueredo et al. also conducted a second factor analysis on the covariance among K and the five human personality factors and found a single higher order factor. These findings are certainly suggestive. However, these studies are limited in that they are cross-sectional and do not rule out the possibility that correlations may have arisen because personality and outcome measures were assessed using the same method, i.e., questionnaires (see Campbell & Fiske, 1959).

While the $r/K$ distinction has become shorthand for talking about coordinated, individual differences in human life-history traits, the terminology is theoretically problematic. The terms $r$-selected and $K$-selected, coined by MacArthur and Wilson (1967), come from a simple model describing the evolution of a trade-off between fecundity and development (MacArthur, 1962), the dynamics of which are

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{1.1}$$

where $N$ is the population size, $r$ is the rate of population growth, and $K$ is the population carrying capacity. Together, these variables yield $dN/dt$, or the change in population size overtime. The equation shows that population size grows fastest when the population is far from carrying capacity. While theoretical analysis led to the implications of $r$- versus $K$-selected species, the model is really about how life-histories evolve under density-dependent selection (Reznick, Bryant, & Bashey, 2002). If discussions of human life history and personality are not about population growth rates and carrying capacity there is no reason to tie the discussion to MacArthur's (1962) and Pianka's (1970) formulations. Giving equation 1.1 a generous squeeze is unlikely to provide any insight about the evolution of human personality. Thus, if differential K theory (Rushton, 1985) is about life-history trade-offs, particularly with regards to stable and unstable environments (Brumbach, Figueredo, & Ellis, 2009; Figueredo et al., 2011), it is more useful to talk about the specific trade-offs involved rather than to hang onto an equation that has since been supplanted by other models (Stearns, 1992; Reznick et al., 2002).

A more useful formulation that has a strong theoretical and empirical basis for the co-adaption of personality with life-history traits is the trade-off between developmental growth and mortality (Stamps, 2007; Biro & Stamps, 2008). As growth rate is known to vary consistently between individuals in many different species, individuals that require an increased food intake benefit from a personality style suitable for high foraging rates, e.g., by being bold, aggressive, or explorative. The maintenance of variation in both productivity and behavioral traits require and reinforce each other. Behaviors on balance either provide energy (e.g., foraging) or consume it (e.g., courtship) and thus consistencies individuals have in time allocated to different behaviors have to be compatible with life-history productivity (Biro & Stamps, 2010). For example, Careau, Bininda-Emonds, Thomas, Humphries, and Réale (2009) found that in rats exploratory behavior was negatively related to basal metabolic rate. When resources are scarce, it is beneficial to use energy at a low rate when resting but to explore the environment to increase the chances of finding food resources. On the other hand, when resources are plentiful, less time is needed exploring and having a high metabolic rate allows the organism to "spend" its energy more quickly to reproduce faster. These behavioral and physiological processes come together to form a consistent pace of life (Careau, Réale, Humphries, & Thomas, 2010). It has also been theorized that such life-history trade-offs are what generates personality (Wolf et al., 2007). The trade-off between current and future reproduction can maintain variation in a population because no one strategy can dominate

(Rueffler, Dooren, & Metz, 2004). Wolf et al. (2007) built simulations to show that when such life-history differences exist, concomitant behavioral strategies emerge to support the required level of risk taking necessary to support short-term or long-term fitness. Multiple objectives ultimately result in fitness trade-offs, but in humans and other primates these trade-offs may go beyond life-history traits.

### Personality and fitness outcomes

While laymen would be inclined to see one end of each personality domain as a desirable state of affairs, when considered within the framework of evolution, it is easy to imagine the advantages and disadvantages presented by various levels of each of the five domains. Nettle (2006, 2006) has outlined possible benefits and costs to the high end of each domain which I briefly detail. While high neuroticism could offer benefits such as increased vigilance, it might also carry costs including poorer interpersonal relationships which are critical in social species. Extraversion, while possibly leading to benefits such as mating success, might also cost in terms of harm from risk taking behaviors. High openness to experience, while being related to benefits such as increased creativity, carries the possible costs of having unusual or even harmful beliefs. High agreeableness may benefit individuals by making them more valued partners in coalitions, though it may also lead to individuals being at greater risk from social cheaters. Finally, while conscientiousness may benefit individuals by helping them meet long-term goals, it can potentially cost them the benefits of more immediate fitness gains.

There is evidence supporting the existence of these trade-offs (Nettle, 2011a). While neuroticism is linked to stress and mental illness (Fanous, Gardner, Prescott, Cancro, & Kendler, 2002; Kendler, Gatz, Gardner, & Pedersen, 2006), individuals high in neurotoicism are also more likely to accurately detect threats in the environment (Haselton & Buss, 2000; Nesse, 2005). Individuals high in extraversion have more sexual partners but are also more prone to accidents (Nettle, 2005). Openness is linked with increased creativity (McCrae, 1987) and may therefore be attractive to potential mates (Miller, 2001). On the downside, people high in openness to experience are more predisposed to a range of mental illnesses (Saulsman & Page, 2004; Gurrera et al., 2005). Individuals who are high in agreeableness enjoy strong inter-personal relationships (Asendorpf & Wilpers, 1998) but may also overinvest in social relationships at their own personal expense (Nettle, 2011a).

Apart from these trade-offs, personality has also been linked to actual differences in reproductive success (see Chap. 5). While the relationships differ between populations, individuals higher in extraversion tend to have higher fitness (Alvergne, Jokela, & Lummaa, 2010; Jokela, Alvergne, Pollet, & Lummaa, 2011). Jokela et al. (2011) also found that in the US individuals low in openness and neuroticism had higher fitness while Alvergne et al. (2010) determined that in a high-fertility population in Senegal women's fitness was maximized at intermediate levels of neuroticism. Another study conducted in Australia found individuals whose extraversion and neuroticism scores were at opposite extremes (one high, one low) had the highest fitness (Eaves, Martin, Heath, Hewitt, & Neale, 1990). Personality, like many other phenotypes under selection in contemporary populations (Stearns, Byars, Govindaraju, & Ewbank, 2010), continues to adapt. Examining fitness correlates and trade-offs is important to understanding how selection can maintain variation in personality and also shows that, instead of having "stone age minds" in our "modern skulls" (Cosmides & Tooby, 1997), our psychological makeup continues to adapt to our environment.

### Maintenance of genetic variation

The assumption for selection to proceed that offspring resemble their parents means that the study of heritability is highly relevant to understanding the evolution of a trait through a population's response to selection pressures. When a population experiences selection, how does it respond? Say we go into the wild and find a troop of apes that differ in extraversion. We measure their personalities and find, as it happens, that only individuals who are a value of $S$ below the population mean in extraversion are having children. For the moment, do not worry about why this might be the case. How sociable should we expect these offspring to be? Here, $S$ is the selection differential (the amount that the parents producing offspring deviate from the average trait value) and we want to know by how much the offspring will also differ from the parental average (or the response to selection, $R$). We are asking to solve $R = x \times S$ and the value of $x$ should have something to do with the resemblance between parents and their offspring.

Heritability captures this resemblance between relatives. Heritability ($h^2$) is the proportion of the difference in phenotypes attributable to differences in inherited genes and thus ranges from 0.0 to 1.0. Narrow sense heritability is the ratio between additive genetic variance ($V_{\mathrm{A}}$) and the phenotypic variance ($V_{\mathrm{P}}$):

$$h^2 = V_A / V_P. \tag{1.2}$$

Because parents and offspring share genes but not whole genotypes, the genetic causes of resemblance are from the independent (additive) effects of genes (Falconer & Mackay, 1996). Alternatively, heritability can be defined as the resemblance between parents and offspring from a linear regression of offspring ($z_O$) on mid-parent ($z_P$) phenotype:

$$\beta_{z_O, z_P} = \frac{cov(z_O, z_P)}{var(z_P)}. \tag{1.3}$$

In practice the second definition can be used as a way to estimate the first (and more complex estimation techniques are available; see Lynch & Walsh, 1998) but the second definition is more general because it does not lay claim to the *cause* of parent–offspring resemblance, which may be down to genetic and (inherited) environmental factors (Rice, 2004).

In the age of molecular genetics, heritability may seem like an old fashioned or even outdated concept (Visscher, Hill, & Wray, 2008). It may also appear quirky to put so much focus on *genes* (without naming specific ones) rather than on *genotypes*. Would we not like to know the specific genes that interact with each other and with the environment to determine an individual's personality? For answering evolutionary questions, however, heritability gets at those differences in genes that are required for the change of phenotypes through both random drift and natural selection and are therefore fundamental to the debate over how phenotypic differences are maintained in populations. Heritability relates to selection ($S$) and response ($R$) through the breeder's equation (Falconer & Mackay, 1996)

$$R = h^2 S \tag{1.4}$$

However, something else follows from the application of this equation. If some individuals are outbreeding others, genes from individuals with higher fitness will have greater representation in the next generation. This leads to a reduction in the genetic variance by selection. A basic question in evolutionary biology is, therefore, if selection tends to reduce genetic variance, why do so many traits have such high levels of genetic variance? This turns out to be a question that is difficult to resolve precisely because it has so many possible solutions (Barton & Turelli, 1989; Barton & Keightley, 2002). To evaluate the alternatives, it is first necessary to take stock of what is known about the genetic structure of personality.

### Quantitative genetics

Across animal species, the heritability of behavioral traits tends to be lower than that of morphological traits (Mousseau & Roff, 1987; Stirling, Réale, & Roff, 2002). A review of the literature suggested that approximately 50% of the variance of all five human domains was heritable with little to no variance being accounted for by the shared family environment (Bouchard & Loehlin, 2001). While there is some variation in heritability estimates of personality, ranging from about .4 to .8 depending on the population and whether personality is assessed with self- or peer-reports (Riemann, Angleitner, & Strelau, 1997) and whether nonadditive genetic effects are included (Eaves, Last, Young, & Martin, 1978; Keller, Coventry, Heath, & Martin, 2005). Additive genetic effects are those that contribute to the phenotype independent of their genetic background. Nonadditive genetic effects arise from interactions either between the two alleles at the same locus (dominance genetic variance) or between genes at different loci (epistatic genetic variance). There is evidence that a substantial proportion of the genetic variance in personality traits is caused by nonadditive genetic effects (Eaves, Heath, Neale, Hewitt, & Martin, 1998; Keller et al., 2005; Rettew, Rebollo-Mesa, Hudziak, Willemsen, & Boomsma, 2008; Rushton, Bons, & Hur, 2008).

Additive and nonadditive genetic variance estimates are of similar magnitude in other animal species (van Oers, Jong, Noordwijk, Kempenaers, & Drent, 2005). There have also been several recent studies on the genetics of personality in nonhuman primates. Weiss et al. (2000) estimated the heritability of the six factors of chimpanzee personality. Of these factors, only dominance was found to be significantly heritable ($h^2 = .63$). The estimate for conscientiousness was .21; while not detectably greater than .00, this suggests low to moderate heritability. The remaining traits showed little or no heritability. Importantly, this study of zoo-housed chimpanzees also established that very little of the differences in personality could be accounted for by differences among zoos. A later study using a different estimation technique confirmed the high heritability of dominance ($h^2 = .66$) and established the high genetic correlation with subjective well being ($r_A = 1.00$, Weiss, King, & Enns, 2002). However, it is not yet known to what extent nonhuman primate personality can be explained by nonadditive genetic variance.

The heritability of facets of personality and other related traits has also been investigated in nonhuman primates. Williamson et al. (2003) estimated the heritability of fearfulness and anxiety in rhesus macaques. Several aspects of their responses, such as a tendency to explore novel environments (latency to leave the protection of their mother in a Free Play Test) or to approach novel objects (in this case, a kiwi fruit) had estimated heritabilities of 1.0. These high estimates of heritability in these types of traits were confirmed in a later study with a similar measure of vigilance with $h^2 = .98$ (Rogers et al., 2008). Latency to approach strangers (measured as a Social Impulsivity Index) is also heritable in vervets, but only moderately so ($h^2 = .34 \pm .11$; Fairbanks et al., 2004). There was no effect from the maternal environment which, given how it was estimated, includes nonadditive genetic variance from dominance and epistatic effects as well as the influence of maternal care and the mother's genotype. The Social Impulsivity Index consisted of two subscales measuring approach–avoidance and aggressiveness that were themselves highly genetically correlated ($r_A = .78 \pm .12$), suggesting that both facets are influenced by a similar set of genes. The lack of a maternal effect in vervet impulsivity is also consistent with the small influence of shared environment, such as maternal care experienced by siblings, on personality in humans (Bouchard, 1994; Rowe, 1994).

### Molecular genetics

Molecular genetic research in humans and nonhuman primates supports the findings of quantitative geneticists that personality traits have a genetic basis. Various candidate genes related to neuronal and hormone functions have been linked to behavior (Inoue-Murayama, 2009). Many of these genes are involved in signal transduction between neurons; and mutations to these genes effect either the function or expression proteins involved in the release, reception, or metabolization of neurotransmitters like dopamine and serotonin. Associations include genes encoding the serotonin transporter with anxiety (Lesch et al., 1996), dopamine receptors with impulsivity (Noble et al., 1998) and novelty seeking (Benjamin et al., 1996), and the androgen receptor with psychoticism (Turakulov, Jorm, Jacomb, Tan, & Easteal, 2004). Although these associations do not always replicate, meta-analyses have confirmed the association of serotonin transporter with anxiety-related traits (Sen, Burmeister, & Ghosh, 2004) and the dopamine receptor with novelty seeking (Munafò, Yalcin, Willis-Owen, & Flint, 2008). In some cases, a failure to replicate may be the result of insufficient power, as the small effect size of a single gene requires large sample sizes to detect (Sen et al., 2004). The evolutionary functional significance of these variants is unclear but homologous genes have also been studied in nonhuman primates (Lesch et al., 1997; Inoue-Murayama et al., 2000; Seaman, Chang, Deinard, Quiñones, & Kidd, 2000) and these genes may have a similar physiological role. Between and within species variants in these genes have been identified in promoter, exon, and untranslated regions and include single nucleiotide polymorphisms, indels, and tandem repeats (Inoue-Murayama, 2009). Like humans (Lesch et al., 1996), several macaque species (Lesch et al., 1997; Wendland et al., 2006; Chakraborty et al., 2010; de Ruiter, Adams, & Inoue-Murayama, submitted) have tandem repeat variants in the promoter region of the serotonin transporter gene (*5-HTT*), referred to as the serotonin transporter polymorphic linked region (*5-HTTLPR*), which influences the expression level of the serotonin transporter protein. In rhesus macaques the short allele predisposes individuals to alcohol consumption (Barr et al., 2003), has a neuroendocrine response to stress moderated by rearing condition (Barr et al., 2004), and correlates with higher scores for behavioral measures of social anxiety and threat response (Champoux et al., 2002; Watson, Ghodasra, & Platt, 2009). In vervet monkeys, a repeat polymorphism in the dopamine D4 receptor (*DRD4*) was linked to differences in novelty seeking (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007). This locus is also variable in several species of macaques (Wendland et al., 2006; de Ruiter et al., submitted). In chimpanzees, trytophan hydroxylase 2 (*TPH2*), a gene controlling serotonin production, is associated with neuroticism (Hong et al., 2011).

In addition to the direct effects of specific genes, studies have also uncovered gene × environment interactions. Experimental studies of genotyped rhesus macaques suggests that the effects of genetic polymorphisms on behavioral indicators of personality differs as a function of early environmental stressors (Champoux et al., 2002; Newman et al., 2005; Kraemer, Moore, Newman, Barr, & Schneider, 2008). Studies of humans have found similar interactions between the effect of a gene on behaviors related to stress reactivity and the environment in which an individual develops (Caspi & Moffitt, 2006; Caspi, Hariri, Holmes, Uher, & Moffitt, 2010; Belsky & Beaver, 2011) though several other studies failed to support this finding (Gillespie, Whitfield, Williams, Heath, & Martin, 2005; Surtees et al., 2006; Risch et al., 2009). One possible explanation for this inconsistency is that multiple genes contribute to the behavioral phenotype under study so effects are easily masked by the joint effects of other genes (Belsky & Beaver, 2011).

A recent meta-analysis for genome-wide association studies of personality turned up few consistent associations (Moor et al., 2012). Openness to experience was related to a SNP near the *RASA1* gene, which is involved in cell signalling and differentiation, and conscientiousness was associated with a SNP in the intron of *KATANAL2*, a gene involved in neuronal migration and pruning. This meta-analysis had 80% power to detect effects explaining as little as .23% of the variance. Thus, genes affecting personality must have very small effect sizee, be at very low frequency, not be captured by current SNP platforms, or have effects are primarily epistatic. While the last possibility is supported by the large proportions of nonadditive genetic variance for personality, these alternative explanations for GWAS findings are not mutually exclusive.

### Evolutionary processes maintaining variation

The maintenance of heritable variation in traits is a long standing problem in biology (Barton & Turelli, 1989; Barton & Keightley, 2002). It is a puzzle because under directional or stabilizing selection, the eventual heritable variance of in any given trait should be negligible (Barton & Turelli, 1989; Falconer & Mackay, 1996). Processes that maintain additive genetic variation in a trait may come through direct action on the trait or through indirect action on a genetically correlated trait (Robertson, 1967). All genetic differences ultimately arise through mutation, so it is possible for genetic variance to be maintained by a balance between its introduction by mutation and its removal by selection (Lande, 1979) or by random drift (Barton & Turelli, 1989). In biology, most of the debate involves theoretical considerations about the distribution of mutation effect sizes, the number of loci influencing the trait, and the extent of pleiotropy (T. Johnson & Barton, 2005). Pleiotropy, where a gene has an effect on multiple traits, is effective at maintaining polygenic variation when the population is near the fitness optimum because each trait may have different, possibly opposing, effects on fitness (Turelli, 1985; Turelli & Barton, 2004). Selection on a trait may also be balanced by mutation when the trait is influenced by a large number of genes (Turelli, 1984; Barton & Keightley, 2002).

Evolutionary psychologists have in turn given many explanations for the persistence of variation in human personality. These explanations have been grouped into three categories: adaptive, non-adaptive, and maladaptive differences (D. M. Buss & Greiling, 1999). In evolutionary genetic terms, the categories can be rephrased. When speaking of adaptive or maladaptive differences, one is interested in traits that are causally related to fitness, without regard for 'where' the variation is coming from (genes or the environment). Non-adaptive sources of difference include neutral variation that, while it may correlate with fitness, does not cause fitness differences; and so-called "by-products of adaptive variation" (D. M. Buss & Greiling, 1999, p 209) that come about through the correlated selection of some other trait.

When Tooby and Cosmides (1990a) placed personality squarely within a modern evolutionary framework, they argued that individual variation was the result of neutral evolution. The neutral theory states that most mutations have neither beneficial nor deleterious fitness consequences (Kimura, 1983, 1986) leading to a balance between the input of new variation by mutation and its removal by drift (Lynch & Hill, 1986). Most of the variation in the traits that psychologists consider as personality would evolve by drift if behavioral tendencies that are stable across situations are not adaptive; this is because such general tendencies would not be solving any particular problem and thus be causally unconnected with fitness, that is, evolving neutrally. While the effective population size in humans is large enough that drift is inadequate at reducing genetic variance in neutral traits, all the evidence connecting personality to differences in health, longevity, and reproductive success contradicts the required complete selective neutrality (Penke, Denissen, & Miller, 2007). Furthermore, even extremely small selection differences can have an effect over a few hundred generations (Keller & Miller, 2006; Penke, Denissen, & Miller, 2007; Miller, 2011). MacDonald (1995, 1998) and Nettle (2006) argued instead that variation is maintained by balancing selection for personality differences as alternative behavioral strategies. The fitness tradeoffs (see above) could maintain variation because no single strategy is optimal.

Penke, Denissen, and Miller (2007) argued for balancing selection as the most likely explanation for the maintenance of genetic variation in personality. Balancing selection includes processes like heterogeneity in selection pressures across space and time (Hedrick, Ginevan, & Ewing, 1976), frequency-dependent selection where the fitness of an allele (or behavioral strategy) depends on its frequency in the population (Maynard Smith, 1982), and agonistic plieotropy where a gene has opposing effects on two or more components of fitness (Hedrick, 1999). Models show that these processes are capable of maintaining genetic variability (Barton & Keightley, 2002). Given theory and evidence about fitness trade-offs for personality (MacDonald, 1998; Nettle, 2006), Penke, Denissen, and Miller (2007) found balancing selection to be a plausible explanation and made the prediction that personality genes would be found at intermediate frequencies and have moderate effects. This was a reasonable prediction at the time given the number of studies with candidate genes for behavior that were found at intermediate frequencies (Lesch et al., 1996; Chang, Kidd, & Kidd, 1996; Spinelli et al., 2007). However, it is inconsistent with evidence from GWAS studies indicating that personality-related genes will have to have very small effects, because alleles with moderate or large effects would have been detected under the power of current studies (Gangestad, 2011; Miller, 2011; Penke, 2011).

Demographic processes may also be involved with creating variability in the environment to which personality is adapted. Del Giudice (2012) theorized that, given their relationship to life-history variables and mating strategies, personality dimensions should show differential fitness effects depending on the sex ratio of the population. The sex ratio determines much about the competition for mates, because there is more competition for the rarer sex (Weir, Grant, & Hutchings, 2011). Theory and evidence suggest that, when males are the more frequent sex, there will be selection for high agreeableness and conscientiousness. The opposite selection pressure should prevail when females are more frequent. Given reasonable estimates for the average size of human demes, or the population of potential reproductive partners, of about 500 (Birdsell, 1973; Eller, Hawks, & Relethford, 2009), the sex ratio will fluctuate just by chance (Del Giudice, 2012). This sets up a potentially strong and repeated source of temporal heterogeneity in selection for personality.

Several alternative processes can be joined together that could explain genetic variance of personality and we should therefore be wary of thinking that a single process will suffice (Figueredo et al., 2011). Personality might be under both directional and stabilizing selection which would create a difference between maximum and mean fitness (Gangestad, 2011). This could presumably be combined with frequency-dependent selection, particularly if this applies to a large number of genes at once (Penke, 2011). Most theoretical models focus on variation in single genes, but variation can also be maintained depending on the structure of the phenotype. For example, phenotypes that are the product of partially independent processes (for example, different populations of neurons influencing the same behavior) can be maintained more easily by selection (Reeve & Dugatkin, 1998). This is plausible given that personality domains are composed of lower order facets and have each been linked to multiple brain regions (DeYoung et al., 2010). There is also some evidence that copy-number variants (CNV), large segmental duplications in the genome, relate to several psychatatric disorders (reviewed in Gangestad, 2011) and thus may influence personality as well. CNVs have much greater mutation rates than nucleotide point mutations (Sebat et al., 2007) which means that mutation on a trait influenced by CNVs could balance against stronger selection pressures (Gangestad, 2011). However, while all of this is plausible, we currently lack data to rigorously test these hypotheses (Miller, 2011). For psychological phenotypes where a large number of putative genes have been identified, such as schizophrenia, it is possible to conduct more detailed analyses like look for molecular signatures of selection (Crespi et al., 2007).

### Species ecology and genetic variants

Wendland et al. (2006) proposed that the presence of polymorphisms in *5-HTT* and the monoamine oxidase A (*MAOA*) gene, which produces an enzyme that breaks down serotonin, are related to interspecific differences in aggression in macaques. Macaque species can be classified in terms of the dominance and reconciliation styles (Thierry, 2000). Among seven macaque species, those with intolerant and nepotistic societies had multiple alleles at the loci linked to *5-HTT* and *MAOA* while more tolerant species were monomorphic at these regions. Contrary to this, (Chakraborty et al., 2010) found long/short *5-HTT* variants in samples from wild populations of bonnet and Arunachal macaques, species which have a relaxed dominance style. Like rhesus macaques, bonnet macaques are successful in a wide range of habitats, leading Chakraborty et al. (2010) to propose that within-species behavioral flexibility underpinned by genetic variation may be a factor contributing to ecological success. Spinelli et al. (2007) proposed that the relatively high frequencies for the long and short *5-HTTLPR* alleles have been maintained by balancing selection. In long-tailed macaques, another ecologically successful species with an intermediate dominance style, de Ruiter et al. (submitted) found evidence for directional selection on a short version of the serotonin transporter promoter. Selection occured in isolated island populations with reduced predation and smaller groups size. Variation in the expression of the serotonin transporter may thus arise under particular ecological conditions. Even once we identify genes that influence personality, it will still be a challange to work out their exact evolutionary origins.

### Personality development

While we are starting, very slowly, to pick apart the genetics of personality, we are still left with about half of the phenotypic variance coming from environmental effects (Bouchard & Loehlin, 2001). From an evolutionary perspective, it is pertinent to ask why personality develops the way it does (Draper & Belsky, 1990; Stamps & Groothuis, 2010b, 2010a). Across animal species, an individual's experiences during growth can have strong effects on its behavior as an adult (Stamps & Groothuis, 2010a). For example, fish exposed to predators during development change their levels of exploration and boldness (Dingemanse et al., 2009). For humans, much of the research focus is on the developmental effects of stress (Belsky, 1997; Ellis, Boyce, Belsky, Bakermans-Kranenburg, & Ijzendoorn, 2011). For optimizing fitness, it is beneficial to be sensitive to environmental cues during development because of uncertainty in the exact environment the individual will encounter (Bulmer, 1994; West-Eberhard, 2003). This will lead to coordinated responses among life-history traits, physiology, and behavior (Réale et al., 2010). Developmental reaction norms define the value of a phenotype that will develop under various environmental conditions (Pigliucci, 2001). While studies showing how behavioral phenotypes develop differently under different environments have established the presence of these reaction norms, studies showing interactions between genes and environment suggest that reaction norms may differ between individuals (Suomi, 2006). One theoretical question to address however, is why individuals should differ in their reaction norms.

While personality undergoes change through out the lifespan (McCrae et al., 2000), the personality of adults is relatively stable compared with the amount of change experienced during childhood and adolesence (Soto, John, Gosling, & Potter, 2011). Chimpanzees show similar age related changes as humans, namely that over the lifespan extraversion and openness decrease while agreeableness and conscientiousness increase (King, Weiss, & Sisco, 2008). This suggests that great apes and perhaps other primates share common maturational processes for the development of personality.

### Happiness is ancestral

Happiness was once perceived as the result of virtuous action (Aristotle, Nicomachean Ethics Book X). However, we now know happiness, also known as subjective well-being (SWB) is related to personality and that people who are lower in neuroticism and higher in extraversion and agreeableness are generally happier (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008). SWB is furthermore underpinned by genetic variation (Nes, Røysamb, Tambs, Harris, & Reichborn-Kjennerud, 2006; Bartels & Boomsma, 2009; Caprara et al., 2009; Nes, Czajkowski, & Tambs, 2010) that is shared with the Five-Factor Model domains of neuroticism (in the form of Emotional Stability), extraversion, and conscientiousness (Weiss, Bates, & Luciano, 2008) This is not surprising in light of the fact that high neuroticism is also genetically co-morbid with depression (Fanous et al., 2002; Kendler et al., 2006) and neuroticism, agreeableness, conscientiousness, and extraversion explain all of the genetic variation in borderline personality disorder (Kendler et al., 2008; Distel et al., 2009). In addition to being a key part of mental health (Keyes, 2005) and protecting against psychopathology (Diener & Seligman, 2002; Furnham & Cheng, 1999), SWB is also related to longevity (Danner, Snowdon, & Friesen, 2001) and positive life events such as health and relationship status (Diener, Suh, Lucas, & Smith, 1999; Lyubomirsky, King, & Diener, 2005). SWB is therefore part of a healthy physical and psychological life.

While we are starting to understand the genetic and environmental etiology of the nexus of SWB and personality, the ultimate origins of happiness, and why it is genetically correlated with personality and affective disorders rather than just an indicator of present fortunes, remain speculative. Evolutionary accounts of happiness (D. M. Buss, 2000), and psychopathology (Keller & Miller, 2006) are beginning to address these questions of ultimate origins. The mechanisms that produce distress, happiness, and emotions like jealousy or anger are adaptations that allow individuals to solve particular social problems (D. M. Buss, 2000; Nesse, 2004; Andrews & Thomson, 2009). A complementary, non-adaptive factor in the prevalence of anxiety and depression is that the modern environment differs dramatically from that to which our capacities for positive and negative affect are optimally adapted (D. M. Buss, 2000; Nesse, 2004). This does not explain, however, why individuals differ in their “set points” of well being (Diener et al., 1999). Nesse (2004) suggested that it is not the baseline level but only the individual’s capacity to change their affective state as situations demand that is adaptive, but this is inconsistent with the general robustness of baseline happiness to changes in life circumstances (Lykken & Tellegen, 1996) and does not resolve why human happiness shares a common genetic cause with personality (Weiss et al., 2008). An alternative explanation is that evolution has selected for adaptive individual differences in personality and affect. Like personality, selection may maintain variation in SWB because there is no single optimal trait value and the relationship between happiness and fitness differs across environments and contexts (Penke, Denissen, & Miller, 2007). In these scenarios, the stable aspects of positive and negative affect and their correlation with personality would be part of the alternative behavioral strategies that humans follow.

Nonhuman primates can also be characterized in terms of individual differences in positive and negative affect (King & Landau, 2003) and psychopathology (Lilienfeld, Gershon, Duke, Marino, & de Waal, 1999; Brüne et al., 2006). Chimpanzees (King & Landau, 2003; Weiss et al., 2009), orang-utans (Weiss et al., 2006), and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) can all be reliably assessed in terms of SWB. In all three species, SWB correlates with personality. Chimpanzees who are higher in dominance, extraversion, and conscientiousness are also rated as being happier (King & Landau, 2003). High SWB in orang-utans is related to lower neuroticism and higher extraversion and agreeableness (Weiss et al., 2006). Orang-utans who are happier also, like humans, live longer (Weiss, Adams, & King, 2011). For rhesus macaques, higher confidence and friendliness and lower anxiety were both concurrently and prospectively related to SWB (Weiss, Adams, Widdig, & Gerald, 2011). Chimpanzee SWB also shares a genetic cause with the dominance domain, leading the researchers to propose an underlying 'covitality' factor to explain the common basis (Weiss et al., 2002). The genetic basis of chimpanzee happiness in personality led researchers to look for, and find, the same relationship in humans (Weiss et al., 2008). This shows the importance of evolutionarily-informed, cross-species comparisons for guiding reserach about human individual differences.

## 1.3 Origins and destinations

Differential psychologists have rightly identified evolutionary theory as a unifying framework for explaining the origins and persistence of individual differences in a wide array of human psychological characteristics. Workers are integrating evidence from behavior genetics, life-

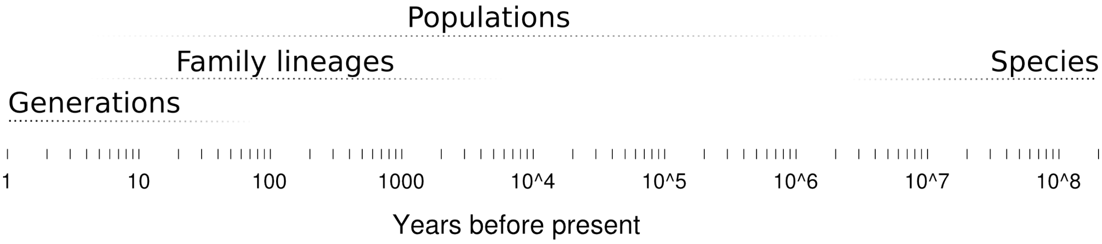

Figure 1.1: Schematic of temporal scales over which psychological diversity is generated: mean level differences between generations from selection and drift; divergence among lineages of related individuals, population differentiation from adaptation, drift, and migration; and speciation.

history theory, genomics, and neuroscience to show how variation is likely adaptive (Hawley & Buss, 2011). The basis of evolutionary psychology in evolutionary theory can do more than prompt questions. It also provides a readymade and comprehensive set of tools for testing our hypothesis against our data. Here I embrace a range of methods and results from quantitative and population genetics, developmental evolution, and phylogenetically-grounded comparative psychology to explore how personality evolves on a range of time scales.

Psychological diversity is generated over a range of different time scales (Figure 1.1). The evolutionary processes of mutation, selection, drift, and migration have differing effects at each temporal level. At the broadest level, socioecological differences lead to differences in behavioral adaptations among species. Primate cladogenesis and speciation covers millions to tens of millions of years of evolution (Fleagle, 1999). Behavior has been found to provide as strong a phylogenetic signal as morphological traits (Queiroz, 1993) and social structure tends to be conserved between species (Thierry et al., 2000; Shultz et al., 2011).

For this bout of evolutionary psychology, I selected anthropoids as the group of organisms to study (Fig. 1.2). The Infraorder Anthropoidea includes monkeys, apes, and humans. I selected this clade because it has the best coverage using a comprehensive personality instrument and because it includes two groups (humans and macaque monkeys) that are well understood from a behavioral perspective. I sought to better integrate comparative, adaptationist, and selectionist approaches to evolutionary psychology. I studied the phylogenetic patterns of personality in four species of macaques and the genetic basis of personality and subjective well-being in orang-utans. In humans, I studied the plasticity of personality to life

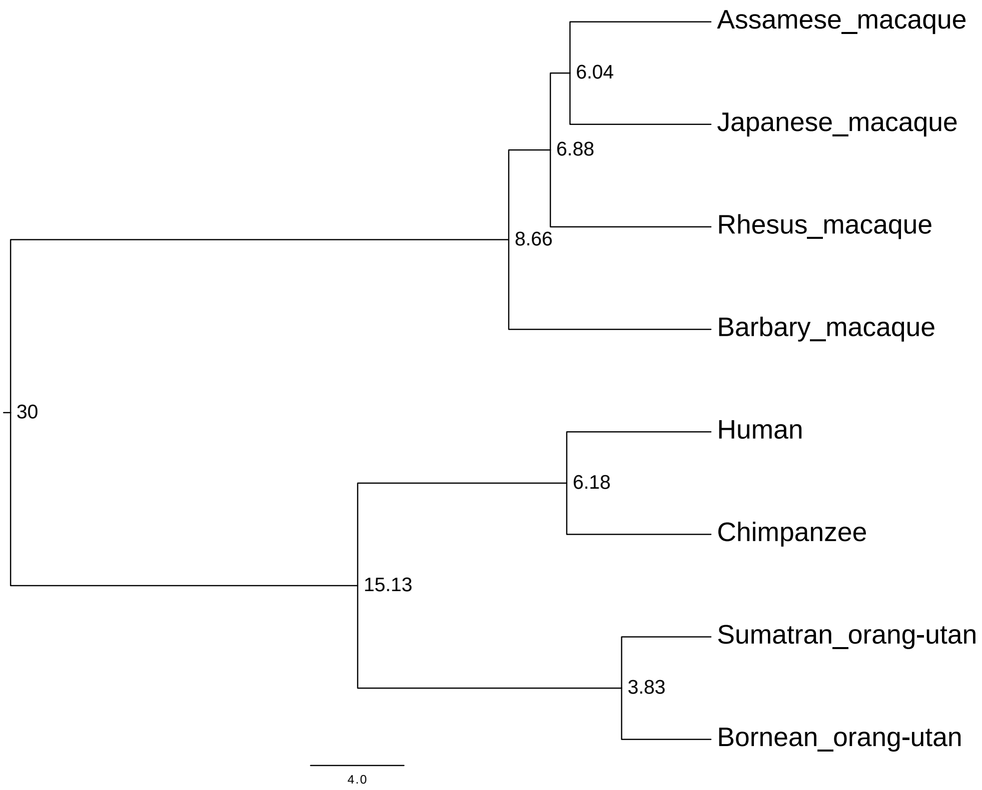

Figure 1.2: Phylogeny of species considered in the studies. Node labels give time to common ancestor in millions of years. Tree and branch lengths from consensus tree inferred using 10kTrees `http://10ktrees.fas.harvard.edu/` (C. Arnold et al., 2010).

history and how personality is continuing to adapt to the environment. Finally, I undertook a theoretical analysis to explore what aspects of personality development could maintain genetic variation.

### Comparative personality structure

Species that are more closely related to each other or who are have similar socioecologies should therefore be more similar in personality structure (Weiss & Adams, 2008). Because of the long time scales involved, differentiation will occur primarily through the processes of mutation and selection. Mutation provides the raw input on top of which selection shapes adaptive characters. In chapter 2 I will explore psychological variation at the species level via the phylogenetic patterning of personality in macaques and other primates. Macaques are a genus of Old World monkeys that shared a common ancestor with humans approximately

27 million years ago (Andrews, 1986). A study of rhesus macaques found that their personality could be described using six personality dimensions (Weiss, Adams, Widdig, & Gerald, 2011). Rhesus macaques differed from chimpanzees (King & Figueredo, 1997) and orang-utans (Weiss et al., 2006) that had been measured using the same personality instrument. In contrast to these two ape species that, like humans, had independent extraversion and agreeableness dimensions, rhesus macaques had a single friendliness dimension that captured aspects of behavior related to social affiliation and cooperativeness. Rhesus macaques also differed from humans, chimpanzees, and orang-utans by having two dimensions related to neuroticism-like aspects of behavior. Weiss, Adams, Widdig, and Gerald (2011) proposed that primate personality dimensions could be defined in terms of the blending or splitting of lower level personality facets. I sought to test the feasibility of this idea by studying how rhesus macaque personality generalized to other macaque species. Along with several collaborators, I collected data on rater impressions of personality for three additional macaque species to determine which of these aspects of personality structure distinguished macaques from apes. Macaques species share a common social structure based around female phylopatry, where females stay in their natal troop and males migrate between troops, where the social organization centers around lineages of related females. I therefore predicted that the personality domain friendliness, related to social affiliation, might generalize to the other species of macaques. Macaque species do however differ in the gradient of their dominance hierarchy, ranging from species that are extremely nepotistic to those that are more egalitarian (Thierry, 2000). In the nepotistic species, the outcomes of agonistic interactions between two individuals almost always favor one individual over the other. In egalitarian societies, reversals between winners and losers are common. I therefore predicted that the species might differ in the composition of their dominance and confidence dimensions. Specifically, species with rigid hierarchies might show more differentiation in these personality domains because of the need to persue alternative 'winner' and 'loser' strategies.

Because of heterogeneity in the linguistic and cultural backgrounds of the raters, I formalized an analysis technique that was flexible with regards to the 'meaning' of any one particular item for a particular personality dimension. Across studies of nonhuman primates, categories of personality dimensions often have similar and overlapping item loadings (Freeman & Gosling, 2010). For example, dimensions variously called dominance and fearfulness often resemble each other in terms of item content depending on the species studied. It can thus be helpful to conceptualize items as having a continuous rather than a binary membership in a personality dimension (King & Weiss, 2011). Formalizing these relationships allowed me to determine the core set of items that consistently described personality dimensions across species.

### Adaptive plasticity to life-history conditions

Within species, populations can also come to differ from one another. If selection pressures are consistent across populations, then selection will tend to make populations more alike one another. However, if selection differs across environments, this will cause populations to diverge. Random genetic drift and mutation will also cause populations to diverge from each other as well whereas migration between populations will help maintain homogeneity. On shorter time scales, environmental differences might also cause populations to differ from one another in phenotypes that are adaptively plastic to local conditions. Mean level personality traits differ between human populations (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005) but the causes of this variation have not yet been determined (Allik & McCrae, 2004). Because personality relates to differences in life-history traits, it is possible that personality will show some adaptive tuning to the life-history conditions experienced during development. In this case, the organism is attempting to achieve a more optimal personality given the life-history conditions that it will experience as an adult. Humans show a trade-off between longevity and fertility (Westendorp & Kirkwood, 1998). It is therefore possible that personality levels will differ in response to the local longevity–fertility conditions experienced during ontogeny. Furthermore, because national populations differ in their average life-history conditions (Borgerhoff Mulder, 1998), some of the cross-cultural differences in average personality differences could be explained by shifts in population-level life-history. Average personality in a country relates to socioeconomic factors (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005) which are in turn strongly related to fertility and mortality trends (Chesnais, 1992). I therefore estimated whether within-country shifts in life-history across a generation were related to parallel changes in personality while controlling for socioeconomic factors and unknown (cultural/ecological/genetic) sources of resemblance between neighboring countries

(Chap. 3).

### Genetic structure of orang-utan personality and subjective well-being

Within populations, diversity also exists between lineages of related individuals. Put in other words, family members tend to resemble each other. Family resemblance is the basis of heritability estimates and understanding the genetic and environmental influences on individuals differences. Personality has been found to be heritable in humans (Bouchard & Loehlin, 2001) and chimpanzees (Weiss et al., 2000), so I aimed to estimate whether similar amounts of genetic variation was present in orang-utans. Second, extended-family studies of human personality have uncovered a large proportion of nonadditive genetic variance (Keller et al., 2005). It has been argued that this is consistent with 'recent' selection on human personality (Rushton et al., 2008). After reviewing evidence that higher proportions of nonadditive than additive genetic variance is in fact consistent with long-term selection on a trait, I sought to test whether the presence of nonadditive genetic variance was a unique aspect of the genetic structure of human personality or whether it might be present in other primates. In chapter 4, I estimate the heritability of and genetic and environmental correlations among personality and SWB dimensions in a sample of captive orang-utans linked by an extended pedigree. I also devised a quantitative genetic model that would, as far as possible, remove rater effects on personality and that handled heterogeneity in the varying number of items in the personality questionnaires that the sample was assessed with.

### Contemporary selection on personality

The smallest, most basic increment of evolutionary change in a quantitative trait is the change in its mean between generations from selection. While there have been several studies of the fitness correlates of human personality (Eaves et al., 1990; Alvergne et al., 2010; Jokela et al., 2011), they have relied on an untested assumption that the genetic relationship between personality and fitness is the same as the phenotypic relationship (M. B. Morrissey, Kruuk, & Wilson, 2011). A genetic relationship is necessary to establish because selection works through the differential transmission of genes to the next generation. In chapter 5, I use two genetically-informative samples from the US and Scotland to estimate the genetic covariance between lifetime reproductive success and personality. In this analysis, I take a selectionist (as oppposed to adaptationist) approach to the study of the evolution of personality. This approach does not assume that a species is perfectly adapted to its environment and instead seeks to test how selection pressures continue to shape the trait (Réale & Dingemanse, 2011).

### Developmental evolution of individual differences

To understand personality evolution, it is necessary to understand its development (Draper & Belsky, 1990; Stamps & Groothuis, 2010a). Theory and evidence point to individuals differing in their developmental responses to early life stress (Boyce & Ellis, 2005; Ellis, Essex, & Boyce, 2005). Surprisingly, a U-shaped relationship was found between early-life stress and the sensitivity of the stress response system later in life. While individuals experiencing a moderate amount of stress had low reactivity, individuals who experienced both the highest and the lowest amount of stress developed the most active response systems. Boyce and Ellis (2005) and Del Giudice, Ellis, and Shirtcliff (2011) have theorized that evolution has tuned the stress response system to show this kind of plasticity in order to have the optimal response later in life. While this theory is consistent with the evidence, it is unclear whether genetic variability could be maintained or whether we should expect the population to settle on a single, optimal reaction norm. Thus, this theoretical evolutionary analysis has the potential to support or refute the plausibility of evidence for gene × environment interactions for robustness (Caspi & Moffitt, 2006). In chapter 6 I formalize the evolutionary development model proposed by Boyce and Ellis (2005) and analyze how the system evolves as a function of genetic and environmental factors.

# Chapter 2

# Building blocks of macaque personality

> . . . there are an infinite number of personality traits one can define and measure, but evolutionarily analyzable order will tend to be found only in those causally related to adaptive function.
>
> Tooby and Cosmides (1990a, p. 25)

## 2.1 Evolutionary patterns of primate personality

Nonhuman primate personality has been examined from a number of stances but integrating these different views is still a major challenge (Clarke & Boinski, 1995; Itoh, 2002; Uher, 2008a; Uher & Asendorpf, 2008; Freeman & Gosling, 2010; Freeman et al., 2011). These methods include, broadly, impressionistic ratings using adjectives describing personality; observational measures and codings of differences in the presence, frequency, and duration of behaviors; and impressionistic ratings of behavior–situation units (Uher, 2008a). While methodological differences can shroud comparisons among species, Gosling and John (1999) found broad support for the basic personality dimensions related to sociality, anxiety, and cooperativeness in a number of other animals, from octopuses to chimpanzees. While species-specific dimensions outside of those that differentiate humans exist (Uher, 2008a, 2008b) and while personality should encompass not only people but also behaviors and situations (Funder, 2009; Uher, 2011b), descriptions of stable, between-human personality differences as rendered in factor models usefully orient explorations of nonhuman primate personality structure. Studying multiple species with the same instrument also aids phylogenetic comparisons of personality structure by revealing the historical patterning of the emergence and modification of personality dimensions (Weiss & Adams, 2008).

### Models

One of many models for human personality describes personality differences in five independent dimensions (Digman, 1990): generally speaking, differences in sociability and assertiveness are called extraversion; variation in trust and cooperation are grouped as agreeableness; conscientious describes differences in discipline, planning, and self control; variation in curiosity and creativity are captured by openness; and a dimension called neuroticism differentiates individuals in terms of anxiety, emotional stability, and stress response. Reasonably, it is referred to as the Five-Factor Model. A single individual is characterized by a stable density distribution along each of these dimensions (Fleeson, 2001). The Five-Factor Model is robust across cultures (McCrae, 2002; Allik & McCrae, 2004; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007, see Chap. 3) and emerges whether people are measured on items that are adjectival descriptors (Digman, 1990) or cognitive-affective reactions to situations (Denissen & Penke, 2008a).

This factor-model description of human personality has served as the starting point of several investigations of nonhuman primate personality. Chimpanzees share with humans the broad dimensions of the Five-Factor Model, with the addition of dominance, which describes differences in competitive facility (King & Figueredo, 1997). As a personality trait in primates, dominance should be distinguished from social dominance or rank as the latter is an outcome rather than an aspect of personality (Hinde, 1978; A. H. Buss, 1988; Gosling & John, 1999). The chimpanzee dimensions agreeableness and openness were given identical names to their human homologues or analogues. While the labels differ, the remaining three traits map human equivalents, surgency onto extraversion, emotionality onto neuroticism, and dependability onto conscientiousness. While chimpanzee conscientiousness is more narrowly defined than its counterpart in humans (it does not include facets related to trustworthiness and duty) the conscientiousness personality dimension seems to be a derived character in humans and chimpanzees, as it has not appeared as a “pure” construct in any other species investigated (Gosling & John, 1999; Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011). Chimpanzees can also be differentiated from each other in their behavioral signatures, including propensities to set upon or affiliate with conspecifics, anxiety and arousal in stressful situations, curiosity toward novel foods and objects, impulsivity, goal pursuit, and physical and sexual activity (Pederson et al., 2005; Uher, Asendorpf, & Call, 2008; Uher & Asendorpf, 2008).

Gorillas likewise can be differentiated in their behavioral repertoires, similar to chimpanzees (Uher et al., 2008). Gorillas have also been described under the rubric of the human Five-Factor Model using the dimensions extraversion, understanding (i.e., agreeableness), fearfulness (i.e., neuroticism), and dominance (Gold & Maple, 1994). Salient in their absence from gorilla personality are homologues of human and chimpanzee openness and conscientiousness. Do gorillas really not differ in levels of curiosity and self control or did researchers not include items that load on these traits (Gosling & John, 1999; Weiss et al., 2006)?

The importance of being more thorough was demonstrated by Weiss et al.'s (2006) study of orang-utan personality using a similarly broad instrument previously applied to chimpanzees (King & Figueredo, 1997). Orang-utans can be described with the dimensions dominance, extraversion, agreeableness, neuroticism, and a blend of openness and conscientiousness that was dubbed intellect. Given that gorillas are more closely related to chimpanzees and humans than orang-utans, it likely that a openness dimension was present in the ancestor of great apes and that gorillas can be characterized by openness, too. A nonhuman personality instrument can only capture what it is designed to measure (Uher, 2008a).

A variety of models using impressionistic ratings have emerged to describe rhesus macaque personality. Some early studies revealed alternatively three dimensions of fear, hostility, and affiliation (Chamove, Eysenck, & Harlow, 1972); or excitability, sociability, and confidence (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980). Later studies derived four dimensions of either tense–fearful, aggressive, solitary, and curious–playful (Bolig et al., 1992) or sociability, confidence, excitability, and equability (Capitanio, 1999). Rhesus macaques can even be described in as many as six dimensions: confidence, friendliness, dominance, anxiety, openness, and activity (Weiss, Adams, Widdig, & Gerald, 2011). These results demonstrate the vagaries of measuring personality with instruments that have been incompletely adapted from studies of other species (Uher, 2008a). That said, despite the various labels and differing numbers of components, many of these dimensions describe the same constructs. The primate dimensions of

- extraversion are captured by affiliation/sociability/solitary,
- agreeableness by hostility/aggressive/friendliness,
- neuroticism by fear/excitability/tense–fearful/confidence–anxiety,
- openness by curious–playful/openness,
- and dominance by confidence/dominance (Gosling & John, 1999; Weiss, Adams, Widdig, & Gerald, 2011).

This lumbering development matches the slow growth and refinement in characterizing broad dimensions of human personality chronicled by Digman (1990). We will not get there all in one go.

Using behavioral codings, Rouff, Sussman, and Strube (2005) identified three dimensions of overall behavioral variation and four of between-individual differences in the personalities of lion-tailed macaques. The components that differentiated individuals (as opposed to behavioral occasions irrespective of the individual exhibiting them) map roughly onto the rhesus macaque dimensions friendliness, dominance, activity/confidence, and anxiety. While methodological and sample-size differences between these studies makes for a knotty comparison, they suggest that several broad features are conserved in the genus *Macaca*. It also shows that basic dimensions can shine through even if the instrument or ethogram are not specifically designed to find them. For instance, Rouff et al. (2005) chose behaviors that defined neuroticism-like, bipolar facets, namely Anxious–Relaxed and Reactive–Unreactive. Each pole of these facets, however, did not group together. Reactive clustered with the confidence-like component while Relaxed and Unreactive loaded on the anxiety-like component. This tallies with the claim that primate neuroticism can become uncoupled into two independent dimensions describing free-floating anxiety (the anxiety dimension) versus situationally-determined anxiety (the confidence dimension) (Weiss, Adams, Widdig, & Gerald, 2011). Further work on lion-tailed, rhesus, and other macaque species is needed to clarify personality structure within this genus.

Whole personality structures have been educed in other Old World monkeys. Vervet monkey personality consists of three dimensions: social competence, playful–curious, and opportunistic self-serving (McGuire, Raleigh, & Pollack, 1994), which map to the great ape domains of dominance, openness, and agreeableness, respectively (Gosling & John, 1999). Konečná et al. (2008) have extended the search for nonhuman primate personality structure to colobines. They investigated male Hanuman langur personality using both impressionistic descriptors and behavioral codings. Male langur behavior exhibits a three-dimensional structure consisting of dominance, involvement, and activity. Impressionistic ratings also revealed three dimensions called agreeableness, confidence, and extraversion. High agreeableness was expressed behaviorally by low dominance, high confidence by high dominance and involvement and by low activity, and high extraversion by elevated activity. Again, these dimensions broadly match those found in other primate species while the absence of other distinct dimensions (such as Openness) have reasonable ecological explanations (e.g., langurs are opportunistic foragers).

Over the years other, more specific aspects of personality and temperament have been examined in nonhuman primates (Clarke & Boinski, 1995; Freeman & Gosling, 2010). Factor models and behavioral profiles by no means cover all the facets of primate personality that have been discovered. But attempts to describe all the features of between-individual personality differences are starting to pay dividends by distinguishing the separate threads we need to weave the historical patterns of primate personality evolution.

### Building blocks

Gosling and John (1999) showed that dimensions analogous (and perhaps *homologous)* to the five human factors appear in other species with the addition of two dimensions, dominance and activity. While dominance is a salient dimension across many species, there initially little evidence for activity as a separate dimension. Further research has shown that activity is commonly found in behavioral-ecological investigations of personality (Réale et al., 2007) and in nonhuman primates (Freeman & Gosling, 2010), such as wild langurs (Konečná et al., 2008) and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). Furthermore, in humans, while this dimension is subsumed under extraversion in adults, it can emerge as a separate feature in adolescent males (John, Caspi, Robins, Moffitt, & Stouthamer-Loeber, 1994).

As it is possible for traits that normally vary together to become uncoupled during devel-

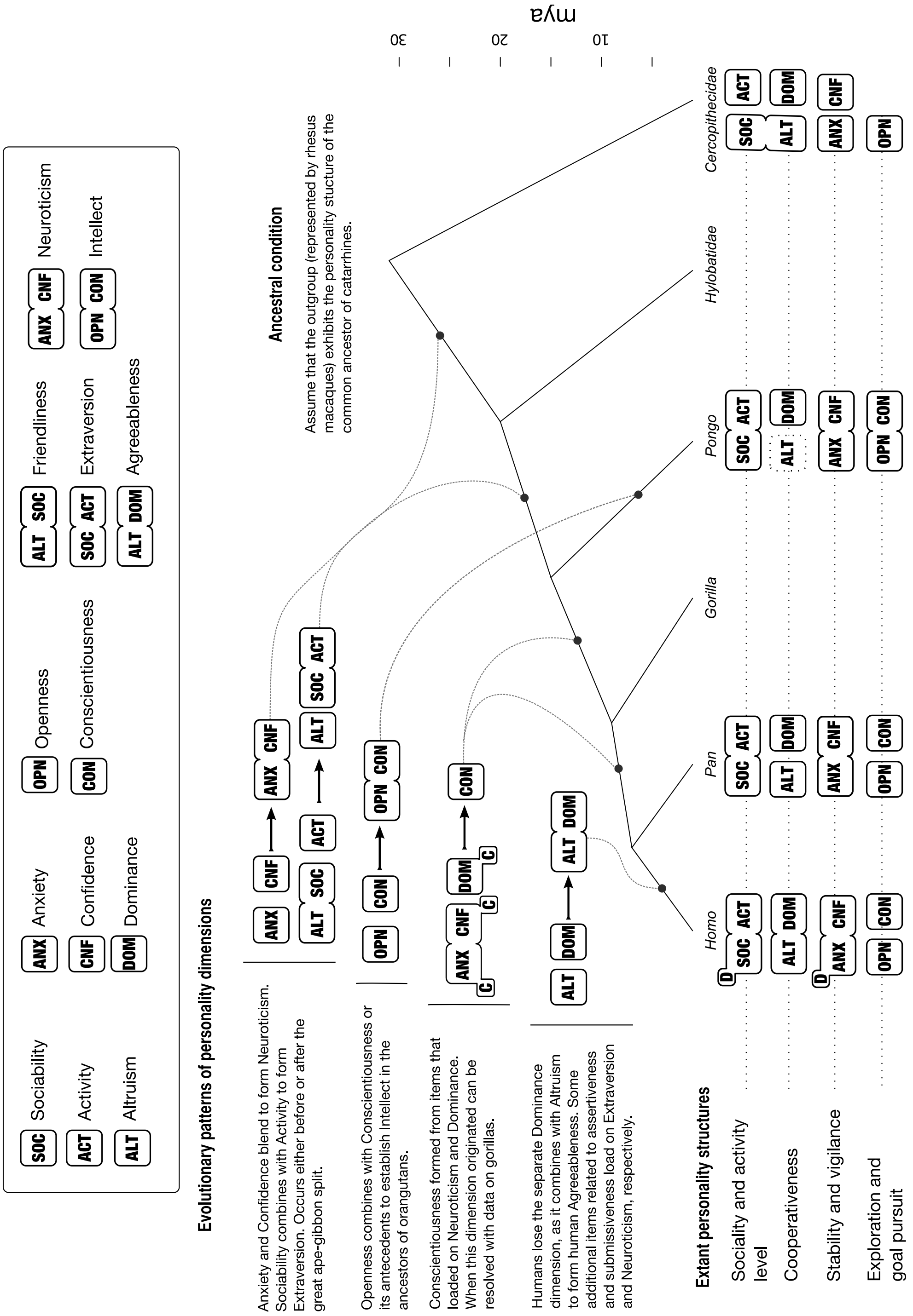

Figure 2.1: Cladogram of hypothetical patterns of personality structure evolution in catarrhine primates. The schematic describes personality structures as a combination of ‘basic’ or ‘blended’ dimensions. Figure by Weiss, Adams, Widdig, and Gerald (2011) and reproduced under a Creative Commons Attribution Unported Licence.

opment (Groothuis & Carere, 2005), we can consider the developmental evolution and phenotypic integration of personality dimensions. Correlated variation in the rudimentary personality structures of humans, chimpanzees, orang-utans, and rhesus macaques can be described with a set of eight "basic" and five "blended" personality traits (Weiss, Adams, Widdig, & Gerald, 2011). The basic traits are called Sociability, Activity, Altruism, Anxiety, Confidence, Dominance, Openness, and Conscientiousness (Fig. 2.1). The other traits are combinations of these components. In humans, chimpanzees, and orang-utans Sociability and Activity positively covary to form extraversion while Anxiety and Confidence negatively covary as neuroticism. In rhesus macaques, Sociability instead fluctuates with Altruism and is denoted as friendliness. Meanwhile, in humans, Altruism and Dominance negatively covary in the dimension that describes cooperative behavior, namely agreeableness, while orang-utans have an interesting blend of openness and conscientiousness called intellect. Identifying and hypothesizing about these different basic traits follows the suggestion of Réale et al. (2007) to start defining possible categories of correlated suites of behavior beyond those already considered in work on behavioral syndromes (namely, shyness–boldness, exploration–avoidance, activity, aggressiveness, and sociability). These basic traits may be the result of opportunities for adaptive behavioral variation for meeting the social, ecological, and developmental challenges faced by big-brained, gregarious, and long-lived mammals. Factor models for each species are the first step in hypothesizing the building blocks constituting primate personality structures.

Personality traits have also been posited to cluster together at higher levels. Noting intercorrelations among the five human personality dimensions, Digman (1997) proposed two higher-order factors which he labelled $\alpha$ (comprising agreeableness, conscientiousness, and (reversed) neuroticism) and $\beta$ (extraversion and openness). DeYoung et al. (2002) offered a more firm interpretation of these two higher order factors. *Stability* describes a refractory ability in situations that are emotionally, socially, and motivationally demanding and draws on the shared variance of agreeableness, conscentiousness, and emotional stability (i.e., neuroticism). *Plasticity* reflects exploration, engagement, and flexibility with(in) the environment and thus ties in with extraversion and openness. Genetically-informed designs in humans have also recovered these two higher-order factors (Jang et al., 2006), suggesting they may be a stable feature of personality. Building on this, several researchers proposed and found evidence for a single higher order factor, dubbed the general factor of personality (Musek, 2007; Rushton & Irwing, 2008), or GFP, that describes variance common to the five personality dimensions with positive loadings from extraversion, agreeableness, openness, and conscientiousness and a negative loading from neuroticism. A hierarchical structure also found the GFP sitting atop Stability and Plasticity (Musek, 2007)

The existence of a GFP and other higher-order factor structures has been criticized on methodological grounds. The GFP has been explained away psychometrically as a result of biases in self-presentation (Bäckström et al., 2009), common method variance inherent in assessing personality dimensions using only one instrument that evaporates when using multi-trait multimethod approaches (Riemann & Kandler, 2010), or the result of the preponderance of items that load in the same direction even though the personality dimensions are orthogonal (Ashton et al., 2009). Even if two higher order factors are substantial, the shared variance seems to be incorporating at least some biases that creep in during personality evaluation (McCrae et al., 2008). Weiss, Adams, and Johnson (2011) took a comparative approach to addressing the existence of a GFP by testing whether a single, higher-order factor was a good fit to personality data on chimpanzees, orang-utans, and rhesus macaques. The answer was a resounding 'no'. Like in humans, intercorrelations among the nonhuman primate personality dimensions were only weak, questioning whether, even if it exists, a higher order factor is worthy of the title 'general'.

### Affect

Like behavioral domains, basic differences in subjective well-being (or, simply put, happiness) have been found in nonhuman primates, including chimpanzees, orang-utans, and rhesus macaques (King & Landau, 2003; Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011). Subjective well-being captures the balance of positive and negative moods as well as one's overall satisfaction with life (Diener et al., 1999). Across species, subjective well-being has a shared basis in personality variation. In nonhuman primates, subjective well-being assesses affect and positive functioning in social relationships and goal achievement. In humans, happiness is positively related to extraversion, agreeablenss, and conscientiousness and negatively related to neuroticism (DeNeve & Cooper, 1998; Steel et al., 2008). Chimpanzees rated higher in subjective well-being are also higher in dominance, extraversion, and conscientiousness (King & Landau, 2003). Subjective well-being in orang-utans is related to lower neuroticism and higher extraversion and agreeableness (Weiss et al., 2006). Rhesus macaques that were higher in subjective well-being were also higher in confidence, friendliness, and activity; and lower in anxiety (Weiss, Adams, Widdig, & Gerald, 2011). Furthermore, in rhesus macaques high confidence, high friendliness, and low anxiety were also prospectively related to subjective well-being assessed more than a year later.

Genetic variation in human personality overlaps completely with personality (Weiss et al., 2008) and chimpanzee personality also genetically covaries with the dominance personality dimension (Weiss et al., 2002), although there were not any detectable shared basis between personality and subjective well-being in orang-utans (Chap. 4). However, in both humans (Diener & Chan, 2011) and orang-utans (Weiss, Adams, & King, 2011), individuals who are happier live longer lives. Personality and subjective well-being thus seems to form a common nexus of 'covitality' in primates (Weiss et al., 2002).

### Patterns

The presence of a GFP in humans, because it is linked to self-assessed life-history strategies, could be explained as the result of directional selection on human personality (Figueredo & Rushton, 2009, but see Sec. 4.7). Whether the GFP is substance or artifact in humans, its absence in closely related species of primate, indicates that, if it is an actual feature of human personality, it may be unique to the human lineage. Weiss, Adams, and Johnson (2011) note that given chimpanzees', orang-utans', and rhesus macaques' phylogenetic proximity to humans, a shared genetic basis of behavior, slow life-histories, and the similar social environments that they inhabit, an artefactual explanation of the GFP is more parsimonious. However, testing all of the possible alternative evolutionary explanations for why humans exhibit a GFP but these other three species do not would require examining nonhuman primates that are more human-like in some aspect of their socioecology (for example, cooperative breeding in marmosets or monogamy in gibbons). Therefore the identification of personality domains in nonhuman primates suggests a phylogenetic patterning (Weiss & Adams, 2008; Weiss, Adams, Widdig, & Gerald, 2011; King & Weiss, 2011), namely that more closely related species are more similar to each other and that differences in personality structure can be framed as shared or derived evolutionary characteristics.

The relative invariance of personality structure in a nonhuman primate species across habitats, rearing environments, social groups, and observers' culture (King, Weiss, & Farmer, 2005; Weiss et al., 2007, 2009) means that the presence or absence of a particular personality dimension can be informative of behavioral evolution (Weiss & Adams, 2008; King & Weiss, 2011). In this way, personality structure can, like any trait or set of traits, characterize evolutionary lineages (Harvey & Pagel, 1991; Gosling & Graybeal, 2007). For example, the presence of a conscientiousness domain in humans and chimpanzees but not in orang-utans or rhesus macaques suggests that this dimension is an evolutionary derived feature in the human–chimpanzee lineage relative to the ancestral condition (Fig. 2.1; Weiss, Adams, Widdig, & Gerald, 2011). Likewise, if we take rhesus macaques as representative of the ancestral condition, this implies that human, chimpanzee, and orang-utan neuroticism and extraversion are derived from multidimensional ancestral variants where neuroticism comes from an integration of confidence and anxiety and extraversion of friendliness and activity. These differences may be the result of adaptation to differences in social organization and complexity, where chimpanzees and orang-utans live in fission-fusion societies whereas rhesus macaques live in stable troops organized around matrilines (Wrangham, 1987; Melnick & Pearl, 1987; Strier, 2003). The lack of a clear, distinct dominance domain is the feature that separates human personality structure the most from that of other primates. While several species differences do exist, the overall pattern suggests that personality structure is also highly conserved among primates. Both humans and chimpanzees exhibit a conscientiousness domain despite wide ranging differences in social structure (Boehm, 1999) which makes parallel evolution a less than parsimonious explanation (King & Weiss, 2011) and suggests that personality structure may be conserved despite divergence in social and ecological traits.

As these broad brush strokes are being applied, a complete picture is beginning to emerge. Studying personality in species that have different phylogenetic relationships to each other can be used to determine at what point along each lineage different features of personality structure could have evolved (Fig. 2.1) However, it is necessary to examine more closely related clades of nonhuman primates to understand which features of personality structure uniquely define each group and whether there are signs of conservation in personality structure. Here, I compare the personality structure of four species from the same genus, namely macaques, to determine which aspects of rhesus macaque personality structure can be used to define these species more broadly. The friendliness domain in rhesus macaques seems to combine features of ape extraversion and agreeableness, so my first goal was to see whether this domain also characterized other macaques. Earlier studies of rhesus macaques (Stevenson-Hinde & Zunz, 1978; Bolig et al., 1992; Capitanio, 1999) did not find any dimension resembling openness, which was found when rhesus macaques were assessed with a broader instrument (Weiss, Adams, Widdig, & Gerald, 2011) that had uncovered that domain in chimpanzees and orang-utans. Thus, I wanted to see whether the same broad questionnaire would uncover openness in other species of macaques. Finally, rhesus macaques have three separate domains (dominance, confidence, and anxiety) that in apes relate to facets of dominance and neuroticism and I therefore wanted to see whether the separation of these dimensions was shared with other species of the macaque genus.

## 2.2 Study species

Macaques are a genus of Old World monkeys that shared a common ancestor with humans around 29 million years ago (Andrews, 1986; Chatterjee et al., 2009). The genus *Macaca* consists of around two dozen species and as the most geographically distributed primate genus besides humans, reside in a wide range of habitats and ecologies (Melnick & Pearl, 1987; Fleagle, 1999). Fossil (Delson, 1980; Fooden, 1980) and recent molecular evidence (Morales & Melnick, 1998; Tosi, Morales, & Melnick, 2000; Deinard & Smith, 2001; Tosi, Morales, & Melnick, 2003) suggests that macaque species can be clustered into four or five lineages. Macaque societies are based around female phylopatry with male dispersal (Fleagle, 1999) and troops tend to move as cohesive units (Melnick & Pearl, 1987). Macaque species differ in how strict or relaxed their dominance hierarchies are (Thierry, 2000) and also exhibit considerable phylogenetic inertia in their social structure compared with morphological (particularly dietary) adaptations (Thierry et al., 2000).

I examined personality structure in four species of macaque: rhesus macaques (*Macaca mulatta*), Japanese macaques (*Macaca fuscata*), Barbary macaques (*Macaca sylvanus*), and Assamese macaques (*Macaca assamensis*). I collected data on Japanese, Barbary, and Assamese macaques and compared their personality structures to the published rhesus macaque structure (Weiss, Adams, Widdig, & Gerald, 2011) derived using the same personality instrument. The phylogeny for these species is shown in Figure 2.2. These four species shared a common

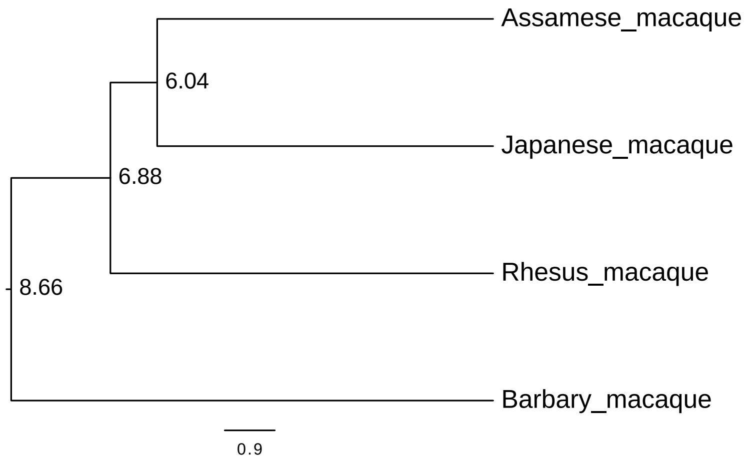

Figure 2.2: Phylogeny of macaque species studied. Node labels give time to common ancestor in millions of years. Tree and branch lengths from consensus tree inferred using 10kTrees `http://10ktrees.fas.harvard.edu/` (C. Arnold et al., 2010).

ancestor approximately 9 million years ago (Chatterjee et al., 2009). The rhesus and Japanese macaques were previously classified together in the *fascicularis* group of macaques, separate from the *sinica* group that contained Assamese macaques and the *silenus-sylvanus* group that included Barbary macaques (Fooden, 1980). However, while molecular evidence shows that the Barbary macaques are an unambiguous outgroup to other macaques, it is ambiguous about the relationship between rhesus, Japanese, and Assamese macaques (Tosi et al., 2003). This ambiguity could be a result of introgression or incomplete lineage sorting or a combination of both processes. Recent molecular evidence indicated that Japanese and Assamese macaques are the most closely related of the two, with the Barbary macaques forming an incontrovertible outgroup to all other macaques (Tosi et al., 2003).

Japanese macaques have traditionally been divided into two subspecies: *Macaca fuscata fuscata* and *Macaca fuscata yakui* (Kuroda, 1940).[1] The subspecies classification is recognized on the basis of differences in pelage, size, and distribution (Fooden & Aimi, 2005). *M. f. yakui* are slightly darker and smaller than *M. f. fuscata* and restricted to Yakushima, an island off the southern coast of Kyushu. However, molecular evidence does not support the separation of Japanese macaques into two subspecies (Marmi, Bertranpetit, Terradas, Takenaka, & Domingo-Roura, 2004). The genetic difference between the Yakushima and other popula-

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[1] In Japanese the native monkeys are generally referred to as *nihonzaru* while *M. f. yakui* are designated *yaku-nihonzaru*, or more simply and affectionately, *yakuzaru*.

tions is the same as between populations of *M. f. fuscata*. For my analysis I will therefore treat Japanese macaques as a single taxon.

## 2.3 Subjects and study sites

The subjects came from a mix of captive, free-ranging, and wild troops.

### Japanese macaques

The Japanese macaque sample consisted of 24 subjects from a free-ranging troop in Japan (Koshima, see Fig. 2.3), 21 subjects from two wild troops on Yakushima, Japan (Umi and Donguri), and 29 subjects from two zoos in Italy and the US. There were 52 females and 22 males and as noted above, the two wild troops from Yakushima were *M. f. yakui* while the other individuals were all *M. f. fuscata*. The mean age of females was 12.3 (SD = 6.8, range = 1–29) and of males was 12.8 (SD = 6.3, range = 3–27). While the ages of the free-ranging and captive individuals were known, the ages of the subjects from wild troops were approximated by the field researchers.

### Barbary macaques

There were 63 (25 females and 38 males) Barbary macaque subjects from three wild troops living in the Atlas Mountains, Morocco (Flat-face, Green, and Large). Exact ages were not known so the subjects were classified into age categories. There were 19 adult and 6 sub-adult females and 31 adult and 7 sub-adult males.

### Assamese macaques

The Assamese macaque sample comprised 60 subjects from a free-ranging troop at the Phu Khieo Wildlife Sanctuary, Thailand. There were 22 females and 38 males. There were 19 adult, 9 juvenile, and 1 infant females; and 18 adult, 9 juvenile, and 4 infant males.

## 2.4 Instruments and raters

Nonhuman primate personality traits can be captured with rater impressions of individuals on adjectives that describe primate behavior, dispositions, and affect. The rater assessments

Figure 2.3: Japanese macaques *(Macaca fuscata)* on Koshima, Miyazaki Prefecture, Japan (August 2009).

are reliable in that they are consistent across raters and time (Stevenson-Hinde et al., 1980; King & Figueredo, 1997; Weiss et al., 2006; Dutton, 2008; King et al., 2008; Uher et al., 2008; Weiss, Adams, Widdig, & Gerald, 2011). Personality dimensions in chimpanzees have been found to generalize across samples living in different environments (King et al., 2005; Weiss et al., 2007) and when using raters from differing cultural backgrounds (Weiss et al., 2009). The personality structures describe differences among the animals and are not merely artifacts of rater biases or projections (Weiss et al., 2012) although genetic modelling revealed that rater effects may either enhance or hide correlations among personality dimensions (Chap. 4). The personality traits defined by rater assessments are also valid. They are related to observed behavior (Stevenson-Hinde et al., 1980; Capitanio, 1999; Pederson et al., 2005; Kuhar, Lukas, Stoinski, & Maple, 2006; Uher & Asendorpf, 2008; Murray, 2011), affect (King & Landau, 2003; Weiss et al., 2006, 2009; Weiss, Adams, Widdig, & Gerald, 2011), neuroanatomical structure (Blatchley & Hopkins, 2010), and genetic polymorphisms (Hong et al., 2011); and are heritable (Weiss et al., 2000, 2002, Chap. 4).

Ratings-based methods of personalitiy assessment have several advantages and disadvantages compared with other methods such as behavioral coding and behavioral tests (Itoh, 2002; Freeman & Gosling, 2010; Freeman et al., 2011). Compared to behavioral coding, ratings can be used to assess a large sample quickly and takes variability in behavior into account. While ratings approaches rely on subjective judgments, they are based on the cumulative knowledge of raters who are familiar with each subject and thus can be deployed at research sites where researchers are observing the subjects for purposes other than personality data collection. While ratings data may make comparisons between individuals more difficult to interpret (Freeman & Gosling, 2010), they are particularly advantageous because the use of a single questionnaire makes it possible to standardize measurement across different study sites and species (King & Weiss, 2011; Weiss & Adams, in press). Describing different species personality structures with the same set of items aids cross-species comparisons.

### Hominoid Personality Questionnaire

While early studies of Japanese macaque behavior were framed in psychological terms including *introversion*, *extraversion* and *individual personality* (Itani, 1957; Imanishi, 1957), the systematic study of personality structure only began with the development of specific questionnaires designed to assess it (Stevenson-Hinde & Hinde, 2011). Work on rhesus macaque personality was conducted using a questionnaire composed of 33 adjectives describing behavior (Stevenson-Hinde & Zunz, 1978). Studies using this questionnaire in captive samples yielded three or four personality domains (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde et al., 1980; Bolig et al., 1992; Capitanio, 1999). To study chimpanzee personality King and Figueredo (1997) developed the Chimpanzee Personality Questionnaire (CPQ) which contained 43 personality descriptor adjectives borrowed from the human literature (Goldberg 1990).

Each adjective was given a definition to place it within the context of primate behavior in general rather than chimpanzee behaviors specifically. For example *fearful* was defined as "Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress." Forty-one of the items were taken from the Big Five subscales (Goldberg, 1990) and two items, *clumsy* and *autistic* were added by King and Figueredo (1997). Weiss et al. (2006) expanded and modified the CPQ for use with orang-utans. Because a previous study of chimpanzees found that neuroticism and openness did not replicate in a different habitat, (Weiss et al., 2006) added three additional items that would potentially describe neuroticism (*anxious*, (not) *cool*, and *vulnerable*) and two that could flesh out openness (*conventional* and *curious*). Together these 48 items composed the Orangutan Personality Questionnaire (OPQ). In another study of chimpanzees, Weiss et al. (2009) added additional items, again derived from the human literature (McCrae & Costa, 1985) to assess conscientiousness (*distractable*, *quitting*, and *thoughtless*) and openness (*individualistic* and *innovative*). This 54-item questionnaire is known as the Hominoid Personality Questionnaire. The HPQ was modified by Weiss, Adams, Widdig, and Gerald (2011) for use in assessing free-ranging and wild monkeys, which involved replacing references in the adjective descriptions to 'enclosure' with the word 'environment'.

### Subjective well-being

The subjective well-being questionnaire contained four items drawn from human subjective well-being measures and was identical to the questionnaire used to assess orang-utans (Weiss et al., 2006), chimpanzees (Weiss et al., 2009), and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). The items assessed the individual monkey's balance of positive and negative *moods*, pleasure derived from *social* interactions, the ability to achieve *goals*, and how 'happy' the raters think they would *be* if they were the target individual.

### Questionnaire translation

The HPQ and subjective well-being questionnaire were translated into Japanese by Miho Inoue-Murayama and checked for equivalence with the original English version via back-translation (Weiss et al., 2009). For this study I used both the English version of the questionnaires from Weiss, Adams, Widdig, and Gerald (2011) as well as a Japanese versions adapted by Akitsugu Konno for use with Japanese macaques.

### Raters and assessment

Raters were zookeepers, field station staff, and researchers who were all familiar with the individual subjects they rated. The raters had between 4 months and 6 years (mean = 22.5 months, SD = 17.9 months) experience with the subjects they assessed.

### Japanese macaques

One rater used the Japanese-language questionnaire while the remaining 7 used the English-language version and ratings were made between February 2009 and February 2010. Each subject was rated by 1–3 raters (mean = 1.4) and each rater assessed between 6 and 24 subjects. Sixteen subjects were missing a rating on at least 1 personality item (mode = 1, range=1–4). Three subjects were missing a rating on a single subjective well-being item while four subjects were not assessed on subjective well-being.

### Barbary macaques

Two raters used the English-language questionnaire and ratings were made between June 2009 and December 2010. The raters assessed 17 and 47 subjects and all but one subject was assessed by a single rater. There were three subjects missing a rating on a single personality item and all subjects had complete subjective well-being assessments.

### Assamese macaques

All eight raters used the English-language questionnaire. Ratings were made between May and December 2009. Each subject was rated by between 1 and 8 raters (mean = 5.6) and each rater assessed between 32 and 58 subjects. Nine subjects were missing a score for a single personality item. No subjects were assessed on the subjective well-being questionnaire.

## 2.5 Personality structure

A personality structure can be derived from ratings data by means of data reduction techniques that compress the high dimensional item data into a smaller number of dimensions. I used principal components analysis (PCA) to determine the dimensions underlying the data. Structures derived from PCA are similar to those derived from principal axis factors (Velicer, 1977) and previous studies of primate personality ratings have found the structures yielded by the two techniques are almost identical (Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011). I ran the PCA using the `principal` procedure in R (Revelle, 2011). To determine the appropriate number of components to extract for each sample I examined the scree plot and conducted a parallel analysis using the `paran` function in R (Dinno, 2010), which determines the number of components by using the eigenvalue expected by chance given the data as a cutoff (Horn, 1965). I ran the PCA on mean scores across raters for the items. For each species I only used items that had intraclass correlation coefficients ICC(3, $k$) $> 0$. I obtained orthogonal components using a varimax rotation and oblique components using a promax rotation.

I calculated personality domain scores using unit-weighting, which assigns items with salient positive or negative loadings ($\geq |.40|$) a component score of either $+1$ or $-1$. Items that did not have a salient loading were assigned a component weight of 0. I used unit-weighting in order to create more generalizable results as scores derived from differentially-weighted loadings vary between samples (Gorsuch, 1983).

To interpret the personality dimensions I interpreted the item content and pattern of loadings primarily in light of the rhesus macaque personality structure derived using the same instrument (Weiss, Adams, Widdig, & Gerald, 2011). I also created unit-weighted domain scores for the Japanese, Barbary, and Assamese macaques based on the rhesus macaque (Weiss, Adams, Widdig, & Gerald, 2011), chimpanzee (King & Figueredo, 1997; Weiss et al., 2009), and orang-utan (Weiss et al., 2006) personality dimensions and examined the correlations with domain scores from each species's structure. This scoring approach had the advantage over calculations of congruence coefficients between components because it did not require the personality structures to contain precisely the same items.

### Item reliabilities

To make good inferences from personality measurements, it is necessary to only rely on items where there is some measure of agreement among raters. Interrater reliability can be calculated by means of intraclass correlation coefficients. I used two intraclass correlation coefficients (Shrout & Fleiss, 1979): ICC(3, 1), which gives the expected correlation of item scores between single raters assessing the same subject, and ICC(3, $k$), which gives the expected correlation among the mean item scores of two groups of $k$ raters.

The ICC for an item is calculated by an analysis of variance from the regression

$$\text{score} = \text{subject} + \text{rater} + e$$

yielding a between-subject mean square (BMS) and an error mean square (EMS). The intraclass correlation coefficients are then

$$\begin{aligned} \mathrm{ICC}(3,1) &= \frac{\mathrm{BMS} - \mathrm{EMS}}{\mathrm{BMS} + (k-1)\mathrm{EMS}} \\ \mathrm{ICC}(3,k) &= \frac{\mathrm{BMS} - \mathrm{EMS}}{\mathrm{BMS}} \end{aligned}$$

and are appropriate when the subjects are considered a random sample from a larger population.

For the rhesus macaque sample, the personality item reliability from single raters (ICC[3, 1]) had a mean of .26 and ranged from -.05 for *autistic* to .63 for *dominant* (Weiss, Adams, Widdig, & Gerald, 2011). The item reliability for mean ratings (ICC[3, *k*]) was .52 and ranged from -.17 for *autistic* to .86 for *dominant*. For this study I calculated the item reliabilities for the Japanese and Assamese samples but could not calculate them for the Barbary macaque sample because only one subject had been assessed by more than one rater. The item reliabilities are given in Table 2.1. For Japanese macaques the mean ICC(3, 1) was .40 and the mean ICC(3, *k*) was .47. The least reliable item was *intelligent* (ICC[3,1] = -.15, ICC[3, *k*] = -.22) and the most reliable item was *active* (ICC[3,1] = .79, ICC[3, *k*] = .85). For the sample of Assamese macaques, the mean ICC(3, 1) was .22 and the mean ICC(3, *k*) was .57. The least reliable item was *autistic* (ICC[3,1] = .05, ICC[3, *k*] = -.23) and the most reliable item was *active* (ICC[3,1] = .61, ICC[3, *k*] = .90).

### Japanese macaques

A parallel analysis suggested a five-component solution (eigenvalues 13.3, 9.1, 7.2, 3.7, and 2.6). However, the adjusted eigenvalue of the last component retained was 1.01, indicating it was only marginally above what would be expected by chance. An examination of the screeplot (Fig. 2.4a) showed that the fifth component had an eigenvalue that did not differ substantially from that of the sixth component. I therefore extracted four components to describe Japanese macaque personality. Item loadings are listed in Table 2.2.

The first component was positively defined by items such as *dominant* and *aggressive* and negatively by items such as *submissive* and *fearful*. These items describe traits related to both Machiavellianism and social potency (Maestripieri, 2007), which in humans are found in the negative pole of agreeableness (Goldberg, 1990), and to reactions within the social environ-

| | Japanese | | Assamese | |
|---|---|---|---|---|
| | ICC(3, 1) | ICC(3, $k$) | ICC(3, 1) | ICC(3, $k$) |
| Fearful | .62 | .69 | .25 | .65 |
| Dominant | .66 | .73 | .58 | .88 |
| Persistent | .41 | .49 | .12 | .43 |
| Cautious | .45 | .53 | .24 | .64 |
| Stable | .45 | .53 | .20 | .58 |
| Autistic | .50 | .58 | .05 | .23 |
| Curious | .32 | .40 | .31 | .72 |
| Thoughtless | .42 | .51 | .10 | .38 |
| Stingy/greedy | .52 | .60 | .19 | .56 |
| Jealous | .39 | .47 | .13 | .46 |
| Individualistic | .05 | .06 | .12 | .43 |
| Reckless | .62 | .69 | .09 | .35 |
| Sociable | .21 | .27 | .29 | .70 |
| Distractable | .11 | .14 | .09 | .35 |
| Timid | .61 | .69 | .39 | .78 |
| Sympathetic | .33 | .40 | .05 | .24 |
| Playful | .72 | .78 | .61 | .90 |
| Solitary | .64 | .71 | .45 | .82 |
| Vulnerable | .47 | .56 | .41 | .79 |
| Innovative | .42 | .50 | .05 | .24 |
| Active | .80 | .85 | .38 | .78 |
| Helpful | .54 | .62 | .18 | .56 |
| Bullying | .54 | .62 | .25 | .65 |
| Aggressive | .53 | .62 | .27 | .68 |
| Manipulative | .50 | .58 | .23 | .63 |
| Gentle | .22 | .28 | .17 | .54 |
| Affectionate | .43 | .52 | .16 | .51 |
| Excitable | .10 | .13 | .22 | .61 |
| Impulsive | .12 | .16 | .21 | .60 |
| Inquisitive | .29 | .36 | .33 | .74 |
| Submissive | .63 | .70 | .51 | .85 |
| Cool | .08 | .11 | .14 | .48 |
| Dependent/follower | .07 | .09 | .42 | .80 |
| Irritable | .42 | .50 | .19 | .56 |
| Unperceptive | .41 | .49 | .14 | .47 |
| Predictable | -.08 | -.12 | .08 | .33 |
| Decisive | .43 | .51 | .32 | .73 |
| Depressed | .34 | .42 | .24 | .64 |
| Conventional | .32 | .39 | .12 | .43 |
| Sensitive | .30 | .38 | .09 | .37 |
| Defiant | .77 | .82 | .15 | .49 |
| Intelligent | -.15 | -.22 | .22 | .61 |
| Protective | .65 | .72 | .36 | .76 |
| Quitting | .38 | .46 | .11 | .40 |
| Inventive | .22 | .28 | .08 | .33 |
| Clumsy | .49 | .57 | .13 | .46 |
| Erratic | .45 | .54 | .08 | .32 |
| Friendly | .23 | .29 | .10 | .38 |
| Anxious | .57 | .65 | .23 | .63 |
| Lazy | .32 | .39 | .33 | .74 |
| Disorganized | .25 | .32 | .16 | .52 |
| Unemotional | .56 | .63 | .19 | .57 |
| Imitative | .51 | .59 | .22 | .61 |
| Independent | .43 | .51 | .27 | .68 |

Table 2.1: Intraclass correlation coefficients for personality items.

ment, similar to human neuroticism (Goldberg, 1990). High-scoring individuals would thus be competent in social interactions and confident when facing challenges within their environment. Low-scoring individuals would be more cautious when confronting such challenges and would readily yield during conflicts. This dimension was similar to the confidence–fearful dimension in rhesus macaques (Stevenson-Hinde & Zunz, 1978). Unit-weighted scores on this domain (Table 2.5) were correlated with the rhesus macaque dimensions of confidence and dominance and was almost identical to the chimpanzee dimension dominance. Scores also correlated postively with scores on orang-utan dominance and intellect and negatively with orang-utan neuroticism. I therefore named this component 'dominance'.

The second component was defined by items related to exploratory behavior, such as *curious*, which in humans makes up openness (McCrae & Costa, 1985). It also contained items related to low conscientiousness and high neuroticism in humans, such as *impulsive* (Goldberg, 1990; Costa & McCrae, 1992c). Individuals scoring high on this dimension would be highly exploratory and also prone to act impulsively. Low scorers would in contrast be less active and playful in their environment. This dimension was extremely similar to the openness dimension in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) and likewise resembled chimpanzee extraversion, openness, and (negatively) conscientiousness (Table 2.5). It also resembled orang-utan extraversion and dominance but not intellect. I named this component 'openness'.

The third component was related to social affiliation, including items such as *social* and *solitary*, and to cooperative behavior, with items like *gentle* and *helpful*. It was thus similar to facets of human extraverison and agreeableness (Goldberg, 1990). It also contained items (*irritable*, *excitable*, and *stable*), related to high and low human neuroticism (Costa & McCrae, 1992c). High scorers would therefore seek out social contact and would act cooperatively in social situations. Low scorers, meanwhile, would shun social engagement. This dimension was extremely similar to friendliness in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) and was similar in resembling chimpanzee extraversion and agreeableness and orang-utan agreeableness (Table 2.5. However, unlike rhesus friendliness, this dimension in Japanese macaques also (negatively) resembled chimpanzee and orang-utan neuroticism. I named this component 'friendliness'.

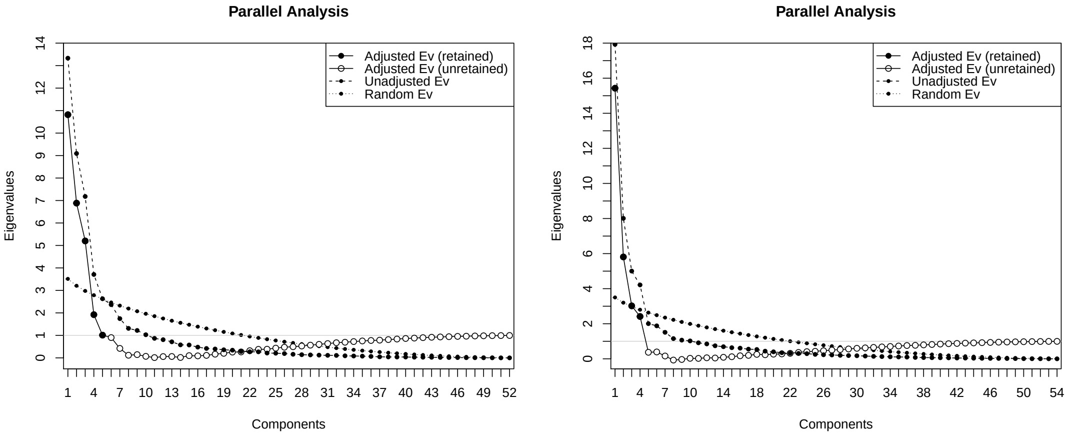
The final component contained items such as *erratic* and *disorganized* that were related to human conscientiousness (Goldberg, 1990). It also contained items related to high neuroticism in humans, such as *anxious* and *depressed* (Costa & McCrae, 1992c). High scorers would therefore be volatile in their behavior and tense while low scorers would be less emotional. This dimension differed from the first component, dominance, in that it seems to describe reactions to less context-specific stressors. In this way it was similar to the anxiety/confidence division seen in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) although this dimension discribed features related to both rhesus macaque confidence and anxiety (Table 2.5). In terms of correlations based on unit-weighted domain scores, it resembled chimpanzee conscientiousness but not neuroticism and resembled both orang-utan neuroticism and (reversed) intellect. I named this domain 'anxiety'.

Because of the results of the parallel analysis, I also tried a five-component solution. I calculated factor congruence coefficients using the psych package in R (Revelle, 2011) and found that the four dimensions were also well described in the five-component solution (congruence coefficients = .90–1.0). The highest loading on the fifth component was (not) *cool* (-.69) and also contained the items *excitable*, *reckless*, *impulsive*, and (not) *stable*. This component had factor congruences of .46 and -.58 with openness and friendliness from the four-component solution and had several salient cross-loadings on the other components. While it resembled rhesus macaque excitability (Stevenson-Hinde & Zunz, 1978) it did not represent a clear separate dimension in Japanese macaques. I therefore stuck with the four-component solution.

### Barbary macaques

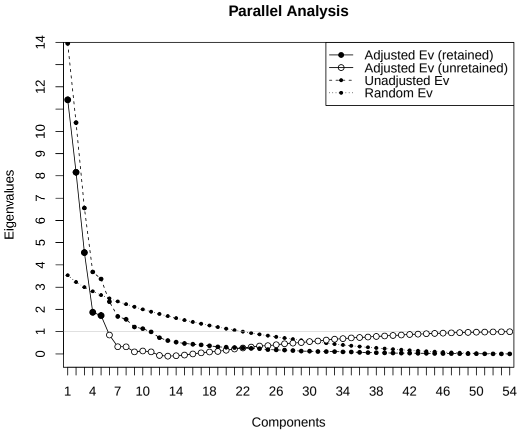
The parallel analysis yielded four components (eigenvalues 17.9, 8.0, 5.0, 4.2) which was supported by an examination of the screeplot (Fig. 2.4b). Item loadings are listed in Table 2.3.

The first component was large and encompassing and explained 32% of the variance in item scores. It was primarily characterized by items (*dependent/follower*, *independent*, *fearful*) related to human neuroticism as well as both the positive (*helpful* and *protective*) and negative (*dominant*) poles of human agreeableness (Goldberg, 1990). The loadings on several items also resembled human conscientiousness, such as *persistent* and *decisive*. After reflecting the component loadings, individuals who score high on this trait would therefore be commanding in a variety of situations while low-scorers would be more cautious and timid. This compo-



(a) Japanese macaques

(b) Barbary macaques



(c) Assamese macaques

Figure 2.4: Scree plots from parallel analysis for personality items in 1) Japanese macaques, b) Barbary macaques, and c) Assamese macaques. Adjusted eigenvalues (EV) show the number of components retained by the analysis as having eigenvalues greater than expected by chance.

| | Dom | Opn | Frd | Anx | $h^2$ |
|---|---|---|---|---|---|
| Dominant | **.93** | .02 | .02 | -.21 | .90 |
| Submissive | **-.89** | .08 | -.13 | -.09 | .82 |
| Timid | **-.87** | .03 | -.06 | .11 | .77 |
| Aggressive | **.86** | .17 | -.20 | .10 | .81 |
| Bullying | **.81** | .27 | -.24 | .06 | .79 |
| Fearful | **-.81** | .17 | -.11 | .34 | .80 |
| Manipulative | **.63** | .11 | .14 | -.27 | .51 |
| Independent | **.63** | .23 | -.28 | .29 | .61 |
| Persistent | **.61** | **.47** | .00 | .06 | .60 |
| Stingy/greedy | **.61** | .26 | -.10 | .32 | .55 |
| Decisive | **.60** | .33 | .25 | -.09 | .54 |
| Cautious | **-.60** | -.17 | .10 | .21 | .44 |
| Vulnerable | **-.55** | .06 | -.23 | **.41** | .53 |
| Dependent/follower | **-.53** | **.46** | .15 | .13 | .53 |
| Quitting | **-.44** | -.19 | -.30 | **.43** | .50 |
| Protective | **.44** | .09 | **.43** | .16 | .41 |
| Innovative | .06 | **.78** | .08 | -.05 | .62 |
| Inventive | .06 | **.77** | .25 | -.11 | .67 |
| Curious | .19 | **.76** | .33 | -.10 | .74 |
| Playful | -.19 | **.75** | .20 | -.06 | .64 |
| Inquisitive | .05 | **.72** | .29 | .04 | .61 |
| Active | .20 | **.70** | .13 | .12 | .56 |
| Impulsive | .26 | **.64** | **-.42** | -.07 | .66 |
| Imitative | -.03 | **.63** | .35 | .38 | .67 |
| Reckless | **.40** | **.60** | -.27 | -.07 | .59 |
| Jealous | **.55** | **.57** | .02 | .03 | .63 |
| Defiant | .39 | **.56** | -.26 | .29 | .62 |
| Distractable | -.37 | **.49** | -.08 | .05 | .39 |
| Individualistic | .04 | **.47** | -.30 | .22 | .36 |
| Conventional | -.04 | **-.46** | .14 | -.21 | .27 |
| Gentle | -.25 | -.01 | **.81** | -.09 | .73 |
| Affectionate | .03 | .30 | **.80** | -.15 | .75 |
| Sympathetic | .03 | .31 | **.71** | -.22 | .65 |
| Friendly | -.16 | **.49** | **.69** | -.17 | .77 |
| Irritable | .36 | .11 | **-.69** | .00 | .62 |
| Sociable | .31 | .37 | **.65** | -.13 | .68 |
| Excitable | .13 | **.44** | **-.60** | .04 | .57 |
| Solitary | -.19 | -.09 | **-.57** | .29 | .45 |
| Helpful | .22 | .34 | **.56** | -.09 | .49 |
| Stable | .26 | -.30 | **.50** | -.31 | .50 |
| Disorganized | -.31 | .07 | -.05 | **.79** | .72 |
| Unperceptive | -.01 | -.01 | -.11 | **.76** | .59 |
| Erratic | .03 | .31 | -.14 | **.76** | .69 |
| Clumsy | -.01 | -.12 | -.10 | **.74** | .58 |
| Autistic | -.20 | .20 | -.09 | **.74** | .64 |
| Depressed | -.32 | -.02 | -.32 | **.70** | .70 |
| Unemotional | .10 | -.21 | .40 | **.68** | .68 |
| Anxious | **-.56** | .09 | -.20 | **.67** | .82 |
| Sensitive | -.19 | -.01 | .14 | **-.60** | .42 |
| Thoughtless | .32 | **.42** | -.02 | **.45** | .49 |
| Lazy | -.32 | -.38 | -.20 | .05 | .29 |
| Cool | .37 | -.20 | .38 | -.02 | .32 |

Table 2.2: Japanese macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings ($\geq |.40|$) are bolded. Dom = dominance, Opn = openness, Frd = friendliness, Anx = anxiety. $h^2$ = communalities.

| | Cnf | Opp | Frd | Opn | $h^2$ |
|---|---|---|---|---|---|
| Dependent/follower | **-.91** | .02 | .03 | .02 | .82 |
| Independent | **.91** | .17 | .18 | -.13 | .90 |
| Dominant | **.90** | .19 | .06 | -.11 | .86 |
| Distractable | **-.90** | .03 | -.08 | .12 | .84 |
| Fearful | **-.90** | -.06 | -.06 | -.2 | .86 |
| Stable | **.89** | -.08 | .19 | .14 | .85 |
| Vulnerable | **-.88** | -.25 | -.23 | -.07 | .90 |
| Timid | **-.86** | -.24 | -.27 | -.04 | .87 |
| Intelligent | **.85** | -.21 | .06 | .04 | .77 |
| Anxious | **-.84** | -.07 | -.23 | -.15 | .79 |
| Submissive | **-.83** | -.24 | -.01 | .12 | .76 |
| Quitting | **-.82** | .08 | -.02 | .04 | .69 |
| Cool | **.82** | -.06 | .22 | .11 | .73 |
| Clumsy | **-.81** | .21 | -.06 | -.06 | .70 |
| Decisive | **.79** | .06 | .09 | -.20 | .67 |
| Manipulative | **.77** | .13 | .11 | -.09 | .64 |
| Persistent | **.76** | **.40** | .23 | .04 | .79 |
| Disorganized | **-.72** | .38 | .20 | .07 | .70 |
| Excitable | **-.71** | .10 | .13 | **-.43** | .71 |
| Unemotional | **.68** | .17 | -.28 | .32 | .67 |
| Cautious | **-.57** | **-.52** | -.25 | -.17 | .69 |
| Thoughtless | **-.53** | .31 | .08 | .22 | .44 |
| Erratic | **-.52** | **.43** | -.23 | -.16 | .53 |
| Protective | **.51** | **-.46** | .23 | .17 | .56 |
| Helpful | **.48** | -.32 | **.48** | .07 | .57 |
| Unperceptive | **-.45** | .23 | **-.43** | .14 | .46 |
| Jealous | .31 | **.73** | .16 | .00 | .65 |
| Impulsive | -.30 | **.72** | .10 | .02 | .61 |
| Stingy/greedy | **.43** | **.70** | .23 | -.19 | .77 |
| Reckless | -.01 | **.68** | .08 | .15 | .50 |
| Gentle | -.17 | **-.66** | .30 | .23 | .61 |
| Predictable | .14 | **-.65** | -.12 | .04 | .45 |
| Sympathetic | .15 | **-.64** | .28 | -.16 | .53 |
| Aggressive | **.59** | **.62** | .03 | .08 | .74 |
| Bullying | **.57** | **.61** | .20 | -.19 | .77 |
| Individualistic | .15 | **.58** | .18 | -.06 | .40 |
| Conventional | .01 | **-.53** | .05 | -.14 | .31 |
| Sensitive | .19 | **-.47** | **.43** | -.23 | .49 |
| Sociable | .28 | .14 | **.83** | -.08 | .78 |
| Friendly | -.06 | -.36 | **.75** | .18 | .73 |
| Solitary | -.36 | -.28 | **-.71** | .13 | .73 |
| Affectionate | -.07 | -.12 | **.70** | -.20 | .54 |
| Depressed | -.35 | -.21 | **-.66** | .13 | .62 |
| Playful | -.20 | .22 | **.62** | .33 | .58 |
| Active | .01 | **.50** | **.62** | .26 | .70 |
| Autistic | -.38 | -.17 | **-.56** | .39 | .64 |
| Lazy | -.23 | -.27 | **-.52** | -.37 | .53 |
| Imitative | -.22 | .23 | -.09 | **.79** | .73 |
| Innovative | .15 | -.03 | -.12 | **.76** | .61 |
| Inventive | .31 | -.04 | -.17 | **.72** | .65 |
| Irritable | -.14 | .30 | -.22 | **-.59** | .50 |
| Inquisitive | -.13 | **.44** | .08 | **.55** | .52 |
| Curious | -.19 | .27 | **.44** | **.52** | .57 |
| Defiant | .36 | .38 | .24 | .13 | .35 |

Table 2.3: Barbary macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings ($\geq |.40|$) are bolded. Cnf = confidence, Opp = opportunistic , Frd = friendliness, Opn = Openness. $h^2$ = communalities.

| | Cnf | Act | Opn | Frd | Opp | $h^2$ |
|---|---|---|---|---|---|---|
| Dependent/follower | **-.86** | .15 | -.15 | .10 | -.23 | .84 |
| Anxious | **-.85** | -.31 | .12 | -.06 | .07 | .85 |
| Vulnerable | **-.82** | -.21 | .05 | -.09 | -.20 | .76 |
| Fearful | **-.80** | .09 | .07 | .03 | -.02 | .66 |
| Timid | **-.80** | -.23 | .03 | -.05 | -.15 | .72 |
| Submissive | **-.80** | -.02 | -.01 | .06 | -.36 | .76 |
| Dominant | **.77** | -.06 | .08 | -.01 | **.51** | .86 |
| Independent | **.74** | -.22 | .21 | -.21 | .05 | .68 |
| Decisive | **.73** | -.12 | .19 | .08 | .37 | .72 |
| Protective | **.71** | -.25 | -.06 | **.41** | .22 | .79 |
| Quitting | **-.64** | -.37 | .08 | -.19 | .06 | .59 |
| Clumsy | **-.59** | -.26 | .36 | .30 | .04 | .64 |
| Intelligent | **.59** | .07 | .02 | **.44** | .13 | .57 |
| Reckless | **-.58** | -.17 | **.56** | -.16 | -.17 | .73 |
| Lazy | .09 | **-.84** | -.16 | -.26 | .09 | .81 |
| Stable | .06 | **-.77** | -.23 | .06 | **-.45** | .85 |
| Unemotional | .06 | **-.76** | -.33 | -.09 | -.16 | .72 |
| Depressed | -.41 | **-.72** | .07 | -.36 | -.10 | .83 |
| Cool | .35 | **-.66** | -.11 | .00 | -.18 | .60 |
| Predictable | -.21 | **-.62** | -.15 | .27 | .08 | .53 |
| Active | -.20 | **.62** | **.48** | .34 | -.11 | .79 |
| Playful | -.27 | **.56** | **.49** | .40 | -.18 | .81 |
| Cautious | -.30 | **-.53** | -.29 | -.27 | -.03 | .53 |
| Persistent | **.45** | **-.46** | **.43** | .18 | .28 | .71 |
| Unperceptive | -.33 | -.35 | .33 | -.15 | -.10 | .37 |
| Thoughtless | .01 | .09 | **.79** | .03 | .08 | .64 |
| Conventional | -.11 | -.36 | **-.73** | -.12 | -.08 | .69 |
| Innovative | .13 | .07 | **.71** | .18 | .02 | .56 |
| Distractable | -.27 | .14 | **.68** | -.02 | .09 | .57 |
| Inventive | .26 | .28 | **.65** | .15 | -.08 | .60 |
| Erratic | -.20 | .15 | **.60** | -.22 | **.41** | .64 |
| Individualistic | **.44** | -.20 | **.56** | -.28 | .08 | .64 |
| Impulsive | .06 | .36 | **.56** | .16 | .52 | .74 |
| Excitable | **-.48** | **.44** | **.53** | -.07 | .18 | .74 |
| Disorganized | **-.44** | .22 | **.47** | .19 | .11 | .51 |
| Helpful | .24 | .06 | .00 | **.90** | .10 | .87 |
| Affectionate | -.10 | .20 | -.03 | **.84** | -.22 | .80 |
| Sympathetic | -.03 | -.25 | .07 | **.83** | -.20 | .80 |
| Sociable | .24 | **.45** | .19 | **.72** | .05 | .81 |
| Friendly | -.20 | .30 | -.08 | **.70** | **-.41** | .79 |
| Solitary | -.20 | **-.53** | -.20 | **-.63** | -.05 | .77 |
| Curious | .06 | **.44** | **.55** | **.63** | .12 | .91 |
| Inquisitive | -.01 | .34 | **.45** | **.62** | .26 | .76 |
| Sensitive | -.07 | .04 | -.08 | **.60** | .14 | .40 |
| Jealous | .25 | -.12 | -.14 | .05 | **.83** | .79 |
| Stingy/greedy | .20 | -.24 | -.22 | .04 | **.82** | .81 |
| Bullying | .31 | .23 | .26 | -.10 | **.78** | .84 |
| Aggressive | .37 | .15 | .29 | -.04 | **.77** | .83 |
| Irritable | -.11 | .29 | .37 | -.19 | **.73** | .79 |
| Manipulative | **-.54** | .03 | .18 | .12 | **.64** | .74 |
| Gentle | -.23 | **-.41** | .08 | .53 | **-.60** | .86 |
| Defiant | .16 | **.44** | **.47** | .03 | **.50** | .69 |
| Imitative | -.39 | .32 | -.12 | -.04 | -.17 | .29 |
| Autistic | -.07 | .11 | -.19 | -.32 | .24 | .21 |

Table 2.4: Assamese macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings ($\geq |.40|$) are bolded. Cnf = Confidence, Act = Activity, Opn = Openness, Frd = friendliness, Opp = Opportunistic. $h^2$ = communalities.

| | Japanese macaque | | | | Barbary macaque | | | | Assamese macaque | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dom | Opn | Frd | Anx | Cnf | Opp | Frd | Opn | Cnf | Act | Opn | Frd | Opp |
| Rhesus | | | | | | | | | | | | | |
| Dom | **.82** | **.58** | -.27 | .03 | **.65** | **.77** | .35 | -.10 | **.68** | .28 | **.50** | .06 | **.91** |
| Cnf | **.89** | -.01 | .20 | **-.49** | **.98** | .29 | .30 | .06 | **.94** | -.04 | -.22 | .09 | .34 |
| Frd | **.45** | .35 | **.84** | -.39 | **.65** | -.02 | **.77** | .02 | .42 | **.54** | .15 | **.93** | .16 |
| Opn | .33 | **.94** | .22 | .19 | -.22 | **.43** | .16 | **.83** | .11 | **.74** | **.82** | **.65** | .39 |
| Anx | -.32 | .33 | **-.46** | **.58** | **-.87** | .09 | -.15 | -.11 | **-.44** | .42 | **.60** | .06 | .39 |
| Act | .20 | **.75** | .25 | .00 | .27 | **.62** | **.70** | **.47** | .01 | **.94** | **.60** | **.54** | .11 |
| Chimpanzee | | | | | | | | | | | | | |
| Dom | **.99** | .36 | .05 | -.20 | **.94** | **.48** | .35 | .03 | **.93** | .20 | .21 | .20 | **.72** |
| Ext | .30 | **.61** | **.75** | -.10 | .24 | .29 | **.98** | .34 | -.02 | **.85** | .39 | **.86** | .01 |
| Agr | .23 | .26 | **.85** | -.31 | .38 | **-.57** | .27 | -.02 | .27 | -.03 | -.15 | **.70** | -.14 |
| Neu | -.07 | .24 | **-.62** | .08 | **-.85** | -.13 | -.07 | -.27 | -.12 | **.83** | **.72** | .32 | .41 |
| Opn | .24 | **.86** | .37 | .06 | .07 | .35 | .08 | **.85** | .20 | **.69** | **.68** | **.75** | .31 |
| Con | -.28 | **-.74** | .34 | **-.54** | .39 | **-.70** | -.09 | -.05 | -.16 | **-.57** | **-.84** | -.25 | **-.72** |
| Orang-utan | | | | | | | | | | | | | |
| Ext | .29 | **.82** | .28 | -.01 | .06 | **.60** | **.75** | **.52** | -.01 | **.95** | **.60** | **.64** | .21 |
| Dom | **.90** | **.57** | -.13 | -.04 | **.70** | **.78** | .34 | -.01 | **.72** | .28 | .38 | .09 | **.94** |
| Agr | .30 | .38 | **.86** | -.26 | **.41** | -.24 | **.72** | .05 | .29 | .40 | .02 | **.90** | .03 |
| Neu | **-.68** | .17 | **-.46** | **.63** | **-.96** | -.15 | -.32 | -.16 | **-.71** | .26 | **.49** | -.09 | .02 |
| Int | **.78** | .20 | .20 | **-.64** | **.96** | .12 | .16 | -.08 | **.91** | -.05 | -.10 | -.06 | .37 |

Table 2.5: Correlations between unit-weighted scores for macaques as defined by the species structures and rhesus macaque and chimpanzee structures. Bold indicates significance at $p < .001$. Dom = dominance, Opn = openness, Frd = Friendliness, Anx = Anxiety, Cnf = confidence, Opp = opportunistic, Act = activity.

nent resembled the rhesus macaque confidence dimensions (Stevenson-Hinde & Zunz, 1978; Weiss, Adams, Widdig, & Gerald, 2011) but also shared some features with rhesus macaque dominance (Weiss, Adams, Widdig, & Gerald, 2011). Unit-weighted domain scores correlated positively with scores on rhesus macaque dominance, confidence, and friendliness and negatively with anxiety (Table 2.5). Scores also correlated positively and negatively with chimpanzee dominance and neuroticism. This component also strongly resembled orang-utan neuroticism (reversed) and confidence and had weaker correlates with both dominance and agreeableness. However, while this component had a high loading from the item *dominant*, it did not resemble rhesus macaque dominance in not having many items related to aggressive behavior, which instead loaded on the second component. I therefore named this component 'confidence'.

The second component was composed of items related to the positive (*gentle*, *sympathetic*) and negative (*jealous*, *aggressive*, *bullying*) poles of agreeableness in humans (Goldberg, 1990). It also had high loadings from human conscientiousness-like items such as *reckless*. Individuals high on this dimension would be aggressive toward conspecifics. Low scorers would be constrained and supportive in social relations. The items in this component resembled rhesus macaque dominance and activity and chimpanzee and orang-utan dominance (Table 2.5). Unit-weighted domains scores also correlated negatively with chimpanzee agreeableness and conscientiousness. Because this component related to forceful behavior but without the controlled Machiavellianism of dominance or confidence, I named this component 'opportunism'.

The third component was similar to human agreeableness (items like *friendly* and *affectionate*) and to human extraversion (*sociable*, *solitary*, *active*). High scorers would seek out social affiliation while low scorers would be more solitary. It thus resembled the sociable–solitary (Stevenson-Hinde & Zunz, 1978; Capitanio, 1999) and friendliness domains (Weiss, Adams, Widdig, & Gerald, 2011) in rhesus macaques, particularly in being a blend of extraversion- and agreeableness-like features. This component did indeed correlate with rhesus macaque friendliness when compared using domain scores (Table 2.5). It also correlated with rhesus macaque activity and orang-utan extraversion and agreeableness. It most resembled chimpanzee extraversion. I named this component 'friendliness'.

The fourth component was characterized primarily by positive loadings on items related to human openness (McCrae & Costa, 1985), such as *innovative* and *curious*. High scorers would therefore be high on exploratory behavior. Domain scores revealed this component to be similar to rhesus macaque and chimpanzee openness but it also shared some features with rhesus macaque activity and orang-utan extraversion (Table 2.5). It did not resemble orang-utan intellect. I therefore named this component 'openness'.

### Assamese macaques

The parallel analysis suggested that five components be retained (eigenvalues = 14.0, 10.4, 5.6, 3.7, and 3.4) which agreed with an examination of the screeplot (Fig. 2.4c). Item loadings for the Assamese macaque structure are listed in Table 2.4.

After reflection the first component was chiefly defined by items related to human neuroticism (Goldberg, 1990), such as negatively by *anxious* and *vulnerable* and positively by *independent*. It also had positive loadings from items *decisive* and *intelligent* and negative loadings from items *quitting* and *reckless* related to human conscientiousness (Goldberg, 1990). The loadings on *dominant* and *submissive* also suggested human agreeableness. Monkeys scoring high on this domain could therefore be described as competent in meeting challenges in their environment. Individuals scoring low on this component would display anxiety across a variety of situations. Items making up this component were similar in nature to the confidence dimensions in rhesus macaques (Stevenson-Hinde & Zunz, 1978; Capitanio, 1999; Weiss, Adams, Widdig, & Gerald, 2011). Domain scores from unit-weighted loadings correlated positively with rhesus macaque dominance and confidence and negatively with anxiety (Table 2.5). It was also highly similar to chimpanzee and orang-utan dominance and correlated positively and negatively with orang-utan intellect and neuroticism. However, like with the Barbary macaques, this component was not strongly characterized by items related to the negative pole of human agreeableness. I therefore named this component ’confidence’.

After reflecting the second component, it had negative loadings from items related to human neuroticism (*stable*, *unemotional*) and to human conscientiousness (*lazy*, *persistent*). It was also defined positively by two items, *active* and *playful*, related to extraversion in humans (Goldberg, 1990). High scorers would therefore be active but stable when engaging with their enviroment while low scorers would be more cautious and less energetic. This component was similar to activity in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) and correlated positively with domain scores on rhesus macaque activity as well as friendliness and openness. Domain scores also correlated positively with chimpanzee neuroticism and openness and negatively with conscientiousness; and highly resembled scores on orang-utan extraversion. Given its similarity to the rhesus macaque domains, I named this component ‘activity’.

The third component had items, such as *innovative* and *inventive*, related to the positive pole of human openness (Costa & McCrae, 1992c). It also had negative markers of human conscientiousness, such as *distractable* and *disorganized*. High scorers would thus be novel yet erratic in their behavior whereas low scorers might be more typical. This domain was therefore similar to both rhesus macaque openness and activity. The domain scores also revealed that it was similar to anxiety in rhesus macaques and was positively correlated with domain scores on chimpanzee neuroticism and openness and negatively with chimpanzee conscientiousness. This component also resembled orang-utan extraversion and neuroticism but not intellect. Given its similarity to the rhesus and chimpanzee domains, I named this

**Japanese macaque**

| | Dom | Opn | Frd |
|---|---|---|---|
| Opn | .26 | | |
| Frd | -.09 | -.09 | |
| Anx | .13 | .17 | -.30 |

**Barbary macaque**

| | Cnf | Opp | Frd |
|---|---|---|---|
| Opp | -.00 | | |
| Frd | .28 | -.11 | |
| Opn | -.04 | .11 | -.08 |

**Assamese macaque**

| | Cnf | Act | Opn | Frd |
|---|---|---|---|---|
| Act | .01 | | | |
| Opn | -.00 | .28 | | |
| Frd | .07 | .21 | -.11 | |
| Opp | .24 | .17 | .27 | -.08 |

Table 2.6: Intercorrelations for components derived via promax rotation. Act = activity, Anx = anxiety, Cnf = confidence, Frd = Friendliness, Opn = openness, Opp = opportunism.

component ‘openness’.

The fourth component showed the same blend of agreeableness- (*helpful*, *affectionate*) and extraversion-like items (*sociable*, (not) *solitary*) as friendliness in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). Domain scores correlated positively with rhesus macaque friendliness, openness, and activity and with chimpanzee and orang-utan extraversion and agreeableness (Table 2.5). I therefore named this component ‘friendliness’.

The last component was defined by items, such as *stingy/greedy*, *bullying*, and *irritable*, that characterize the negative pole of human agreeableness. It was similar in content to the Barbary macaque opportunism dimension and likewise correlated positively with domain scores on rhesus, chimpanzee, and orang-utan dominance and negatively with chimpanzee conscientiousness (Table 2.5). I therefore labeled this component ‘opportunism’.

### Oblique rotations

To examine the correlations among the macaque personality dimensions, I extracted the number of components as above but subjected them to a promax rotation. The dimensions for each species were only weakly intercorrelated, with the maximum not greater than $|.30|$ (Table 2.6).

### Domain reliabilities

I measured the agreement among raters on personality domain scores using the ICC(3, 1) and ICC(3, *k*) reliability coefficients (Shrout & Fleiss, 1979). I calculated domain scores using unit-weighting on each rater’s assessment of the subjects using mean substitution on missing scores. Because only the Japanese and Assamese macaque samples had a sufficient number of raters per subject, I only calculated intraclass correlation coefficients for these two species

| | ICC(3, 1) | ICC(3, $k$) | $\alpha$ |
|---|---|---|---|
| Japanese macaque | | | |
| Dominance | .67 | .74 | .92 |
| Openness | .61 | .68 | .90 |
| Friendliness | .37 | .45 | .87 |
| Anxiety | .73 | .79 | .89 |
| Subjective well-being | .63 | .71 | .94 |
| Barbary macaque | | | |
| Confidence | | | .97 |
| Opportunism | | | .88 |
| Friendliness | | | .87 |
| Openness | | | .77 |
| Subjective well-being | | | .95 |
| Assamense macaque | | | |
| Confidence | .60 | .89 | .94 |
| Activity | .51 | .85 | .90 |
| Openness | .27 | .68 | .88 |
| Friendliness | .38 | .77 | .90 |
| Opportunism | .32 | .72 | .91 |

Table 2.7: Interrater reliabilities (ICC[3, 1] and ICC[3, $k$]), and internal consistencies (Cronbach's alpha) of personality and subjective well-being domains scores.

(Table 2.7). For Japanese macaques, the interrater reliabilities ranged from poor (friendliness) to good (dominance, anxiety). For the Assamese macaques, reliabilities ranged from poor (openness) to excellent (confidence, activity). I also calculated internal reliabilities for personality and subjective well-being domains scores via Cronbach's alpha. Domain scores on the personality dimensions had excellent reliability (Table 2.7).

## 2.6 Subjective well-being

I conducted a principal components analysis on subjective well-being for the two species, Japanese and Barbary macaques, that had been rated on this questionnaire (the Assamese macaques had not been rated on subjective well-being). As all but one of the Barbary macaque sample had been assessed by only one rater, I calculated the item reliabilities only for the Japanese macaque sample. The item reliabilities for scores from a single rater (ICC[3, 1]) were .32 for *moods*, .61 for *social*, .76 for *goals*, and .71 for *be*. The average was .60. The reliabilities from average scores from multiple raters (ICC[3, $k$]) were .40 for *moods*, .40 for *social*, .82 for *goals*, and .77 for *be*. The average was .67. I used all of the items even though the reliability for one item, *moods*, was poor.

A parallel analysis for the average scores of each Japanese macaque on the subjective well-being items indicated that one component should be retained (eigenvalue = 3.4). All the items had a high, positive loading on this single component (Table 2.8), which explained 85% of the variation in the scores. A parallel analysis on the Barbary macaques also indicated a single dimension to describe the subjective well-being scores (eigenvalue = 3.5) and all items loaded positively, explaining 88% of the variance. Domain scores on subjective well-being had acceptable interrater reliability for Japanese macaques (Table 2.7). Internal consistency of the subjective well-being scale was excellent for both Japanese and Barbary macaques.

### Personality correlates

I calculated correlations among personality and subject well-being for Japanese and Barbary macaques using unit-weighted domain scores (Table 2.9). Japanese macaques who were higher on dominance and friendliness and lower on anxiety were higher on subjective well-being. Barbary macaques higher on confidence, opportunism, and friendliness were also rated higher on subjective well-being. This mirrors results for rhesus macaques, where individuals high on confidence and friendliness and lower on anxiety had higher subjective well-being (Weiss, Adams, Widdig, & Gerald, 2011).

| | Moods | Social | Goals | Be |
|---|---|---|---|---|
| Japanese macaque | .90 | .93 | .90 | .95 |
| Barbary macaque | .94 | .94 | .91 | .96 |

Table 2.8: Component loadings for Japanese and Barbary macaque subjective well-being domain.

| | *r* | CI | *p* |
|---|---|---|---|
| Japanese macaque | | | |
| Dominance | .63 | .48, .76 | < .001 |
| Openness | .13 | -.10, .35 | .27 |
| Friendliness | .33 | .11, .52 | .003 |
| Anxiety | -.60 | -.74, -.44 | < .001 |
| Barbary macaque | | | |
| Confidence | .88 | .81, .92 | < .001 |
| Opportunism | .25 | .01, .47 | .05 |
| Friendliness | .59 | .41, .74 | .001 |
| Openness | -.04 | -.29, .21 | .74 |

Table 2.9: Correlations among domain scores on personality and subjective well-being. CI = 95% confidence interval.

## 2.7 Personality domains as fuzzy sets

The examination of item content and unit-weighted domains scores show that macaques appear to be consistent in having distinct friendliness and openness domains while differing slightly in the composition of the other domains. Facets of human agreeableness and neuroticism and chimpanzee dominance and neuroticism appear in the various dominance, opportunism, confidence, and anxiety dimensions in rhesus, Japanese, Barbary, and Assamese macaques. King and Weiss (2011) point out that, although the items making up a domain will vary among species, the domains will still be distinct from other domains within each species. A domain can therefore be conceptualized as a "fuzzy set" of items. Rather than yes/no inclusion, a fuzzy set allows sets to be defined in terms of each item's continuous probability of being included (Zedeh, 1965; Smithson & Verkuilen, 2006). This property of membership is referred to as degree-vagueness. I used fuzzy set theory in an attempt to formalize this conception proposed by King and Weiss (2011).

A membership function is used to assign an object (in this case, a personality item) to a set (a personality domain). The membership function maps the object onto the unit interval, from 0 to 1 (Smithson & Verkuilen, 2006)

$$m_K(i) : H \to [0, 1] \tag{2.1}$$

$H$ is space of HPQ items, $H = \{\textit{fearful}, \textit{dominant}, \textit{persistent}, \ldots, \textit{independent}\}$, and $m_K(i)$ is the mapping function of item $i$ onto personality dimension $K$. Because the loading of an item onto a personality component ($v_i$) is between -1 and +1, one possible mapping function is the absolute value of the loading

$$m_K(i) = |v_i| \tag{2.2}$$

If we take the fuzzy value for membership as a probability, we could invent other membership functions. For example, I have used .4 as the salience cutoff out of tradition. Thus, it might be reasonable to take a loading of .35 to represent an item that, while not 'in' the personality domain, is not entirely out of it either. A membership function

$$m(i) = \text{logit}^{-1}(20 \log(2)(|v_i| - 0.35)) \tag{2.3}$$

for example would map a loading of $|.35|$ onto a membership value of .5, that is a 50% probability of being in the set. A loading of $|.4|$ would map onto 67% probability of membership, while $v_i = |.5| \rightarrow .89$ and $v_i = |.8| \rightarrow .998$. However, for the purposes of this analysis, the only property that will be necessary for the membership function is that the resulting membership value relates monotonically to the loading (that is, the loadings can be compared in terms of being lesser than or greater than), not that they exactly frame our intuitions about the probability that an item belongs to a personality domain. Therefore I will use the simpler membership function defined in Equation 2.2, which also means that the outputs of the set functions are understandable as loadings.

### Items supporting each personality domain

The shared support that each item has for two or more personality domains from different species can be determined by making a fuzzy intersection between the sets, where a set contains information on the membership of each item in a personality domain. A membership of an item in the fuzzy intersection between two personality domains $X$ and $Y$, $X \cap Y$, is

$$m_{X \cap Y} = \min(m_X, m_Y) \tag{2.4}$$

which in effect gets the lowest loading (or, more precisely, the value closest to 0) of each item on the two components. For example, the memberships of each item in Japanese macaque dominance would be

$$D_j = \{\mathit{fearful}/.81,\ \mathit{dominant}/.93,\ \mathit{persistent}/.61,\ \ldots,\ \mathit{independent}/.63\}$$

where *fearful*/.81 denotes that the degree of membership of the item *fearful* in dominance is .81. The set for Barbary macaque confidence would be

$$C_b = \{\mathit{fearful}/.90,\ \mathit{dominant}/.90,\ \mathit{persistent}/.76,\ \ldots,\ \mathit{independent}/.91\}$$

and their fuzzy intersection is

$$D_j \cap C_b = \{\mathit{fearful}/.81,\ \mathit{dominant}/.90,\ \mathit{persistent}/.61,\ \ldots,\ \mathit{independent}/.63\}$$

I named the sets for each domain as $D$ = dominance, $C$ = confidence, $F$ = friendliness, $O$ = openness, $X$ = anxiety, $T$ = activity, and $P$ = opportunism. I used the subscripts $r$, $j$, $b$, and $a$ for rhesus, Japanese, Barbary, and Assamese macaques, respectively. I used $|.30|$ as a lenient cutoff for considering an item saliently included in the fuzzy sets. I used fuzzy set theory to differentiate semantically similar domains (confidence/dominance, dominance/opportunism, confidence/anxiety) and to determine what items described the domains that were found in all species (friendliness, openness).

### Dominance/confidence

I used fuzzy intersection to find items uniquely defining the confidence and dominance domains in rhesus macaques, the dominance in Japanese macaques, and confidence in Barbary and Assamese macques. The fuzzy intersection for confidence-like domains for macaques, $C_M$, was

$$C_M = C_r \cap D_j \cap C_b \cap C_a$$

while for dominance-like domains was

$$D_M = D_r \cap D_j \cap C_b \cap C_a$$

Both the dominance and confidence domains were described by the item *dominant* (Table 2.10). However, the dominance set had a much higher loading than the confidence set on this item (.64 versus .50). The confidence set was defined best by the items (not) *submissive*, (not) *fearful*, and (not) *timid*. It was also different from the dominance set by having higher membership for the items *anxious* and *depressed*. The dominance set was separable from confidence by items related to aggressiveness and Machiavellianism (*manipulative*, *aggressive*, *bullying*).

### Dominance/opportunism

Barbary and Assamese macaques had a domain, opportunism, related to the negative pole of agreeableness that defined items related to dominance in other species. I therefore constructed the intersection

$$P_M = D_r \cap D_j \cap P_b \cap P_a$$

which had the greatest membership for the items *aggressive*, *bullying*, and *stingy/greedy* (Table 2.10). Opportunism thus differs from the more inclusive dominance domain by describing aggression without behavioral aspects related to social potency, such as *dominant*, *manipulative*, and *protective*.

### Confidence/anxiety

In rhesus macaques the separation between confidence and anxiety was described as representing reactions to situation-specific versus more generalized reactions to stressors. I looked at the intersection of anxiety in rhesus and Japanese macaques with confidence in Barbary and Assamese macaques

$$X_M = X_r \cap X_j \cap C_b \cap C_a$$

Both the confidence and anxiety sets were described by the items *anxious*, *vulnerable*, and *fearful* (Table 2.10). Interestingly, both sets included an item related to human conscientiousness: *disorganized* in the case of the confidence set and *quitting* in the case of the anxiety set.

### Friendliness

The fuzzy intersection of the friendliness domains

$$F_M = F_r \cap F_j \cap F_b \cap F_a$$

showed that the items that had good support of friendliness across species were describing both extraversion- (*sociable*, *solitary*) and agreeableness-like (*affectionate*, *friendly*, *helpful*) facets (Table 2.10). I then intersected the macaque friendliness set ($F_M$) with chimpanzee extraversion ($E_{CH}$) and agreeableness ($A_{CH}$) defined using loadings from a study that used the same HPQ items (Weiss et al., 2009):

$$\begin{aligned} F_M \cap E_{CH} &= \{\textit{sociable}/.63,\ \textit{solitary}/-.52,\ \textit{depressed}/-.32, \ldots\} \\ F_M \cap A_{CH} &= \{\textit{affectionate}/.70,\ \textit{sociable}/.56,\ \textit{friendly}/.56,\ \textit{gentle}/.30, \ldots\} \end{aligned}$$

The chimpanzee/macaque extraversion set ($F_M \cap E_{CH}$) and agreeableness set ($F_M \cap A_{CH}$) were both well supported by the item *sociable* but were differentiated by the membership of the other items.

### Openness

A fuzzy intersection between the four openness domains

$$O_M = O_r \cap O_j \cap O_b \cap O_a$$

**Confidence**

$C_r \cap D_j \cap C_b \cap C_a$

| Item | $m(i)$ |
|---|---|
| Submissive | -.76 |
| Fearful | -.73 |
| Timid | -.67 |
| Dominant | .50 |
| Dependent | -.43 |
| Anxious | -.41 |
| Vulnerable | -.40 |
| Depressed | -.32 |
| Disorganized | -.31 |

**Dominance**

$D_r \cap D_j \cap C_b \cap C_a$

| Item | $m(i)$ |
|---|---|
| Dominant | .64 |
| Independent | .63 |
| Vulnerable | -.54 |
| Manipulative | .54 |
| Decisive | .47 |
| Submissive | -.43 |
| Protective | .40 |
| Dependent | -.38 |
| Aggressive | .37 |
| Bullying | .31 |
| Disorganized | -.31 |

**Friendliness**

$F_r \cap F_j \cap F_b \cap F_a$

| Item | $m(i)$ |
|---|---|
| Affectionate | .70 |
| Friendly | .69 |
| Sociable | .65 |
| Solitary | -.52 |
| Helpful | .48 |
| Curious | .33 |
| Depressed | -.32 |
| Gentle | .30 |

**Opportunism**

$D_r \cap D_j \cap P_b \cap P_a$

| Item | $m(i)$ |
|---|---|
| Aggressive | .62 |
| Bullying | .61 |
| Stingy | .61 |
| Defiant | .38 |
| Irritable | .30 |
| Jealous | .30 |

**Anxiety**

$X_r \cap X_j \cap C_b \cap C_a$

| Item | $m(i)$ |
|---|---|
| Anxious | .60 |
| Quitting | .43 |
| Vulnerable | .41 |
| Fearful | .34 |

**Openness**

$O_r \cap O_j \cap O_b \cap O_a$

| Item | $m(i)$ |
|---|---|
| Innovative | .71 |
| Inventive | .65 |
| Curious | .52 |
| Inquisitive | .45 |
| Playful | .33 |

Table 2.10: Membership of items in fuzzy intersections of personality domains for the four macaque species. Membership values have been reassigned their positive and negative valence so that the direction of the loading can be interpreted. $D$ = dominance, $C$ = confidence, $F$ = friendliness, $O$ = openness, $X$ = anxiety, $T$ = activity, and $P$ = opportunism. $K_r$ = rhesus macaque, $K_j$ = Japanese macaque, $K_b$ = Barbary macaque, $K_a$ = Assamese macaque.

was supported by the membership of a common set of items related to exploratory behavior, such as *inventive* and *inquisitive* (Table 2.10).

## 2.8 From items to building blocks to dimensions and taxonomies, and beyond

Observer ratings on 54 personality items could be reduced to the following dimensions in three species of macaque:

- Japanese macaque: dominance, openness, friendliness, and anxiety.
- Barbary macaque: confidence, opportunism, friendliness, openness.
- Assamese macaque: confidence, activity, openness, friendliness, and opportunism.

I compared these dimensions with rhesus macaque dimensions derived from ratings on the same personality questionnaire, which were confidence, openness, dominance, friendliness, activity, and anxiety. There was variation in the number of components, ranging from four to six, that described correlations among the personality items.

The personality structure differed between macaque species in several respects. Aspects related to the great ape personality domains of dominance and neuroticism were found in various configurations in macaques, with different aspects being captured by dominance, confidence, anxiety and opportunism. The dominance facet described behavioral dispositions to intervene decisively in social interactions and the tendency to take actions without interference from other individuals. This facet was not as strongly characterized by items related to aggression and intimidation and was instead better described by the item *protective*, suggesting that one aspects of the dominance facet in macaques is the tendency to intervene on behalf of other individuals (Chapais, 2004). The dominance facet appeared as part of the dominance domain in rhesus and Japanese macaques and as part of confidence domain in Barbary and Assamese macaques.

Appearing as part of the dominance domain in rhesus and Japanese macaques and as a separate dimension in Barbary and Assamese macaques, behaviors relating to aggression were subsumed under the opportunism facet. In addition to aggressive behaviors, this facet was also supported by the membership of the items *defiant*, *irritable*, *stingy/greedy*, *jealous*. This suggests that this facet is not just about aggression but also describes a behavioral pattern that runs counter to the established dominance hierarchy and that the antagonism may be part of lashing out at other individuals.

In contrast to the dominance facet, which described how macaques act, the facets of confidence and anxiety seemed to capture how individuals react to different kinds of situations. The confidence facet, which appeared as its own dimension in rhesus but was combined with the dominance facet in Japanese, Barbary, and Assamese macaques, primarily described an individual's reaction in specific situations involving other animals. The item showing the greatest support, *submissive*, describes whether an individual is likely to yield to others and thus the other items appear to describe the level of anxiety and distress that this provokes. Only in rhesus macaques, however, did this facet vary independently from the dominance facet. The anxiety facet likewise appeared as its own dimension in rhesus and Japanese macaques but was part of the confidence dimensions of Barbary and Assamese macaques and differed from dominance/confidence facets by not tying in specifically with behaviors related to the social order. It was also revealing that the scores on macaque dominance and confidence dimensions correlated highly with scores on orang-utan intellect. Orang-utan intellect has been described as a blend of openness and conscientiousness (Weiss et al., 2006) but the macaque results suggest it may be an ancestral facet related more to decisiveness and independence.

Friendliness was the dimension that was most uniquely characteristic of macaques when compared with apes. Friendliness contained a facet similar to chimpanzee agreeableness in only containing items related to the positive pole of the human trait that Weiss, Adams, Widdig, and Gerald (2011) dubbed altruism but was also characterized by a sociability facet describing the sociable–solitary axis of behavior. Friendliness thus does describe a blended personality domain containing two facets that have become uncoupled in other species and its definition using behavioral adjectives is consistent across four different species of macaques.

Openness was unsurprisingly supported by the membership of a consistent set of items that is likely a general feature of primate personality (Freeman & Gosling, 2010). Rather than it being a limitation of the behavioral repertoire of captive macaques, previous studies of rhesus macaque personality (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde et al., 1980; Bolig et al., 1992; Capitanio, 1999) did not uncover this dimension because the questionnaires used did not contain the relevant items (Weiss, Adams, Widdig, & Gerald, 2011). There was nothing that distinguished macaque openness from the dimension as described in other species. For example, even though the item *playful* is part of chimpanzee extraversion, it often has cross-loadings on to openness (Weiss et al., 2007, 2009).

### Phylogeny and social ecology

While the phylogenetic relationship among rhesus, Japanese, and Assamese macaques is ambiguous, they are more closely related to each other than to Barbary macaques. Barbary macaques may also be the best representatives of the ancestral state of social behaviors for macaques (Thierry et al., 2000). If personality is partly an adaptation to social factors (D. M. Buss, 1996; D. M. Buss & Greiling, 1999) then we might expect Barbary macaque personality structure to also be closest to the ancestral state. If this is the case then the ancestors of macaques would have differed from each other in terms of a combined dominance/confidence dimension related to social assertiveness, an opportunism dimension defined by aggression and impulsivity, a friendliness dimension capturing individual differences in social affiliation, and an openness dimension related to curiosity and exploratory behavior. The appearance of separate dominance and anxiety (in rhesus and Japanese macaques) and activity (in rhesus and Assamese macaques) would then be derived characters.

Although Japanese macaques may be more genetically related to Assamese macaques, they have a greater resemblance to rhesus macaques in terms of social patterns (Thierry, 2000; Thierry et al., 2000). Macaques have been divided into four grades that capture species differences in behavioral patterns of aggression, dominance, reconciliation, and temperament (Thierry, 2000). The grades range from tolerant societies (grade 4) to nepotistic societies (grade 1). Rhesus and Japanese macaques are classified as grade 1 and exhibit highly asymmetrical dominance encounters while Barbary macaques are grade 3 and Assamese macaques are classified as grade 2 or 3 (Thierry, 2000, 2007). Both Barbary and Assamese macaques had a dimension called opportunism that was independent of confidence. What could be going on is that, when the dominance hierarchy is relaxed, there is the opportunity for agonistic behaviors to vary independently from dominance and submissiveness. This makes sense in light of the "degrees of freedom" individuals from these species enjoy in their social network (Butovskaya, 2004). Individuals are less constrained in their friendly interactions and have more frequent affiliative encounters with nonkin. Aggressive encounters likewise occur without involving coalitions, so these behaviors are free to vary apart from each other. On the other hand, when the hierarchy is more strict, the only adaptive strategy is for aggression to covary with other behaviors related to social competence and manipulativeness. Japanese and rhesus macaques have greater kin bias among females (Thierry et al., 2000) so individuals can rely more on kin support during conflicts (Thierry et al., 2008). The dominance asymmetries entailed require individuals to be able to form coalitions (Thierry et al., 2008), so both aggressiveness and social competence are required. For example, male Japanese macaques that could not maintain dominance on their own are able to do so with support from females (Nakamichi, Kojima, Itoigawa, Imakawa, & Machida, 1995) or in coalitions with other males (Kutsukake & Hasegawa, 2005).

Japanese macaques societies, furthermore, are matrilocal (Kawamura, 1958), meaning that females tend to stay within their natal group while males migrate to new groups. Female Japanese macaques form stable coalitions with matrilineal kin (Pereira, 1995). Foraging is restricted by the patchiness of their primary food sources (van Shaik, 1989; Saito, 1996). The limited availability of food and the attendant high within-group feeding competition leads to a strict dominance hierarchy in females (Saito, 1996). When food patches are small and isolated, the frequency of agonistic encounters increases. Females that are able to dominate opponents retain access to more desirable foods. The losers in these agonistic encounters are forced to switch to patches containing less nutritious items. If dominance rank requires maintaining kin coalitions through both fighting ability and social assertiness, than opportunistic and aggressive individuals that lack social support could be at a fitness disadvantage if they persist when they are on the losing side. While the dominance personality trait is not the same thing as rank, they may vary together (Anestis, 2005), and thus in rigid hierarchies it would be adaptive for vulnerable, submissive individuals to also be lower on aggression as well. Otherwise, the overly aggressive individual is likely to suffer consequences to fitness through injury (Parker, 1974). If the dominance gradient is less steep and reversals are likely during aggressive encounters, it could be beneficial for an individual to be aggressive independent of their confidence and social assertiveness and engage in agonistic encounters more opportunistically. When dominance hierarchies are strict, aggression needs to be a coordinated part of social manipulation to be adaptive (Western & Strum, 1983).

If an independent opportunism dimension represents the ancestral condition in macaques, then this appears to have been retained in Assamese macaques, a species with a more relaxed hierarchy (Cooper & Bernstein, 1999; Thierry et al., 2000). As Japanese macaques are more closely related to Assamese macaques, the absence of a separate opportunism dimension in rhesus and Japanese macaques may be parallel evolution. These species, with strict dominance hierarchies, evolved similar but slightly different 'solutions' to blending opportunism with other dimensions. In the case of Japanese macaques, opportunism blended with confidence to form a single dominance dimension. For rhesus macaques, behaviors related to aggression began to covary with other aspects of social assertiveness to form the dominance dimension while neuroticism-like traits remained separate. In both species anxiety split off as its own dimension.

Completing the picture of how these different behavioral facets start or stop covarying over evolutionary time will first require determining which of the macaque personality dimensions derived here generalize to other populations of the same species. The Barbary macaques were assessed by only two raters, so it is possible that rater effects could have a larger influence on the structure than is typical (Weiss et al., 2012). Ecological factors may also play into the expression of individual behavioral tendencies as personality differences. While Japanese macaques are classified as highly hierarhical, some of this could be the result of increased aggression in provisioned populations that were used in the foundational studies of this species (D. A. Hill, 1999). Wild (i.e., non-provisioned) troops of Japanese macaques such as those on Yakushima, where I sampled two troops, show less linear dominance hierarchies because of decreased food competition that results in less frequent aggression (D. A. Hill & Okayasu, 1995). Within Yakushima, the dominance gradients do not differ as a function of the environment (Hanya et al., 2008), so the *M. f. yakui* subspecies may be a good candidate to study the adaptive conditions and evolutionary timeframes over which the opportunism could start to vary independently of the confidence/dominance dimension. Further understanding will involve sampling both closely related species and more distantly related ones that share aspects of social structure (Chapman & Rothman, 2009).

### Covitality

In Japanese and Barbary macaques, ratings that assessed the balance of moods, pleasure from social and affiliative interactions, the ability to achieve goals, and global well-being together described a single subjective well-being domain as that found in humans (Diener et al., 1999), chimpanzees (King & Landau, 2003), orang-utans (Weiss et al., 2006), and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). In Japanese macaques the domain showed good interrater reliability. Japanese macaque subjective well-being was related positvely to dominance and negatively to anxiety while in Barbary macaques it was related to higher confidence. In both Japanese and Barbary macaques, individuals higher in friendliness were also higher in subjective well-being. Thus the relationship between positive affect and high sociability and affiliation and low anxiety mirrored findings in humans (Steel et al., 2008), chimpanzees (King & Landau, 2003; Weiss et al., 2009), orang-utans (Weiss et al., 2006), and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). This lends further support to a nexus of affect, neuroticism, and extraversion being present in the common ancestor of Old World monkeys and great apes. Weiss et al. (2002) dubbed this subjective-well-being–peronality nexus *covitality*. This basic relationship may underlie why different aspects of mental health vary together, such as in the comorbidity of anxiety and depression (Kendler, Gardner, Gatz, & Pedersen, 2007). Healthy psychological function may therefore be more than the absence of mental illness (Keyes, 2005).

### Phenotypic integration and imposition

The results here show that one of the advantages of assessing different species using the same personality inventory can aid the comparison of similarites and differences in personality structure. I have also demonstrated that the conceptualization to use fuzzy set theory in understanding personality structure, first proposed by King and Weiss (2011), can yield insights into the facets that describe different aspects of primate personality that appear in different combinations depending upon the species. The prevelance of personality dimensions range from those found in every species assessed, such as openness, to those that are only found in a limited number of species, such as conscientiousness.

Finding a domain in a limited number of species is important for reasons beyond what it tells us about the phylogenetic patterning of personality dimensions (Fig. 2.1). I did not find any domains resembling chimpanzee or human conscientiousness as items defining these domains instead described openness and opportunism in macaques. From the viewpoint of making phylogenetic comparisons (Gosling & Graybeal, 2007), the absence of a macaque conscientiousness dimension lends more support to the conclusion that conscientiousness is a derived personality domain (Gosling & John, 1999) that is exclusive to chimpanzees and humans (Weiss et al., 2006). Additionally, this result also speaks to the validity of using personality questionnaires on nonhuman primates. For although the personality adjectives used in the HPQ items are drawn from the human literature, they do not impose the five-factor structure on nonhuman primates. If they did, we might expect nonhuman primate personality structure to resemble that of humans even more than it does. That four species of macaques resemble each other and differ from other primates in having an unhumanlike friendliness domain suggests that adjective-based personality questionnaires modified from those used on humans can give an accurate, if crude, rendering of personality structures that are phylogenetically informative. Given that the only workable and evolutionarily consistent default assumption is that closely related species resemble each other, if there is anything that instruments like the HPQ are not picking up in a particular species, attempts to measure other dimensions of behavioral and affective variation should be grounded in the specific behavior of the species under study (Uher, 2008a, 2011b). While one of the advantages of rater impressions for personality assessment is that they smooth over within individual variation (Freeman & Gosling, 2010), individuals may still be consistent (that is, differ from each other) in the amount of variation they show across contexts (Uher et al., 2008; Uher, 2011b). Seasonal variation and the mating season, for example, have strong effects on reconciliation behavior in Japanese macaques (Majolo & Koyama, 2006) and this could provide different contexts for the expression of personality and the evolution of individual differences in behavior.

Strong functional equivalences of adjective-derived personality dimensions across primate species have yet to be firmly established (Uher, 2011b). The analysis of personality dimensions as fuzzy sets can guide the development of models testing the structural equivalence of dimensions across species because it can be used to determine facets that are being described consistently across species even when they are obscured within a species through correlation with other facets. The fuzzy set analysis also revealed that some items may be describing different features of separate personality dimensions (e.g., *dominant* and *vulnerable* are both descriptive of the confidence, dominance, and anxiety facets). Nonhuman primate personality as assessed with the HPQ therefore does not appear to show simple structure, where each item loads on one and only one dimension. Separating out the different 'meanings' of these items will require adjective or coding approaches that are sensitive to the context of the behavior (Uher & Asendorpf, 2008). This will serve as the basis for constructing personality taxonomies that start from individual items or behaviors, determine how they fit together as consistent facets, and how these facets covary within a population or species to compose independent personality dimensions.

This comparative approach to personality dimensions also says something stronger about personality domains as evolutionary characters. Why we should find these particular historical patterning in primates or even whether we have the right "basic" dimensions are big questions. When thinking about the evolution of personality dimensions, it might seem strange at first to consider the evolution of something that describes differences between individuals within a species rather than a species universal trait that can be used to distinguish clades from each other. Extraversion, for instance, describes differences between individuals in their sociality and action. Unlike a new behavior or organ, a personality dimension is not an obvious thing that a single individual has. However, this thinking takes a rather narrow view of what evolution is or how it affects populations. Selection does not act only on the mean level of a trait. Evolutionary change can occur on higher moments (like variance, skew, and kurtosis) of the population distribution of a trait as well as its covariance with other traits (Rice, 2004). The genetic and environmental factors contributing to personality can start and stop covarying as the population evolves. While the identification of basic and blended personality dimensions using adjective ratings method may or may not provide the right answer, I believe it is asking the right question.

# Chapter 3

# Personality and life-history across nations

> . . . the correlations among different presumed forms of development left something to be desired. Yet the nagging correlations persisted. It was somehow true, on the average, that richer countries had higher life expectancy, larger shares of the population in cities, greater literacy, smaller completed family sizes, more durable institutions of parliamentary government, and so on, through a long list of national characteristics not deducible by definition from national income.
>
> Why? Although people confused the idea of "modernization" with an answer, the word came to stand for a question: *Why* do these many characteristics vary together, but only imperfectly?
>
> Charles Tilly (1984, p. 45)

## 3.1 Cultures, personalities, and pace-of-life

While differing in countless ways, cultures can be classified by general styles of thinking and acting (Hofstede, 2001). Culture-level attributes generally do not vary along the same dimensions as individual differences (Na et al., 2010), but cultures can be differentiated by aggregate scores on the personality traits that describe individual differences in cognition, affect, and behaviour (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005). The challenge, however, is not only to describe these differences but to explain why personality profiles of cultures differ and how they are distributed globally

(Allik & McCrae, 2004). One intriguing possibility is that personality traits are related to differences in life histories (LH), or the suite of biological traits involving timing, duration, and investment in growth, reproduction, and survival (Biro & Stamps, 2008; Wolf et al., 2007). Studies of human personality, however, have focused on either reproductive success and fertility (Alvergne et al., 2010; Eaves et al., 1990; Jokela, Kivimaki, Elovainio, & Keltikangas-Jarvinen, 2009; Jokela, Hintsa, Hintsanen, & Keltikangas-Jarvinen, 2010) or longevity (Kern & Friedman, 2008; Friedman, Kern, & Reynolds, 2010) separately and not together as a single LH dimension.

Although trade-offs in LH are categorized along a fast–slow continuum, in mammals they actually occupy two dimensions: the first is between offspring size and offspring count and the second concerns reproductive timing (Bielby et al., 2007). A predicted consequence of position along the fast–slow continuum is the generation and maintenance of personality (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007; Wolf et al., 2007, see Sec. 1.2). To optimize fitness, organisms should behave in tune with their LH strategy, so that a "slow" strategy (e.g., low fertility, high life-expectancy) should be associated with behaviours that consistently favour long-term fitness benefits, such as avoiding risk and being cooperative (Wolf et al., 2007). Conversely, high levels of risk-taking, activity, and aggressiveness may be required to fuel the high productivity of a "fast" LH strategy (Biro & Stamps, 2008). Studies of animals have found empirical evidence in support of the connection between fast-slow LH and personality (Biro & Stamps, 2008; Careau et al., 2009, 2010). The coordination of personality and life-history traits may also be part of a larger pace-of-life syndrome involving additional physiological variables (Réale et al., 2010).

One way that personality could become associated with LH traits at the population level is through adaptive developmental plasticity (Bock, 1980) where personality and LH traits become correlated because they are both sensitive to the same environmental cues during ontogeny (Réale et al., 2010). Humans show some changes in personality as a response to LH events such as an increase in emotionality and fluctuations in sociability after giving birth (Jokela et al., 2009). Personality may be particularly sensitive during ontogeny as major changes in metabolic and other physiological processes, such as growth, are already ongoing (Stamps & Groothuis, 2010b, 2010a). To see whether personality had changed as a results of shifts in LH at the population (country) level, I explored whether average personality scores varied consistently between subjects from different national cohorts that were born under different LH conditions.

On the individual level, human personality dimensions have been theorized to relate to LH strategies (Figueredo et al., 2005). There are co-variations among self-reported parental investment, mating effort, and similar traits that indicate the presence of individual fast-slow LH strategies. The slow LH end of this dimension correlates positively with extraversion, openness, agreeableness, and conscientiousness and negatively with neuroticism (Figueredo et al., 2005; Gladden, Figueredo, & Jacobs, 2009). Personality also correlates with real fitness outcomes. Neuroticism appears to interact with reproductive choices along the LH continuum to determine reproductive success (Alvergne et al., 2010; Jokela et al., 2009). Neuroticism also varies in its relationship with longevity, being protective against accidents among the young (W. E. Lee, Wadsworth, & Hotopf, 2006) but a risk factor for mortality later in life (Friedman et al., 2010). Conscientiousness is furthermore associated with greater longevity in lower-fertility populations even when controlling for education and socioeconomic status(Friedman et al., 2010). Because countries can be distinguished along the same dimensions of personality and fertility/longevity trade-off that separate individuals, it may prove insightful to explore connections between personality and LH strategy at the level of human populations. I therefore investigated whether personality and LH strategy covary between cultures and predicted that nations on the slower end of the LH continuum would have higher average extraversion, openness, agreeableness, and conscientiousness and lower neuroticism.

### Culture-level personality profiles

The assessment of aggregate personality scores at the level of culture has been conducted from several measurement frameworks, including the three dimensions from Eysenck's Personality Questionnaire (EPQ; H. J. Eysenck & Eysenck S., 1975; Barrett & Eysenck, 1984; Lynn & Martin, 1995) and five dimensions from the Revised NEO Personality Inventory (NEO-PI-R; Costa & McCrae, 1992c; McCrae, 2002; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005; McCrae et al., 2010) and the Big Five Inventory (BFI; Benet-Martínez & John, 1998; Schmitt et al., 2007). These studies collected data on adolescents, college-aged students, or adults from 24–51 cultures. Across cultures women were on average higher in all personality dimensions and for both sexes older individuals tended to be lower in extraversion and openness and higher in conscientiousness (Costa, Terracciano, & McCrae, 2001; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005).

The studies based on a five-factor model of personality (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007) found that the 5 dimensional structure replicated across cultures. Furthermore, cultures could be differentiated on the basis of their average, or aggregate, scores along roughly the same 5 dimensions that characterize individuals (McCrae, 2002; McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005). There were several broad geographic patterns. European and American cultures were higher on extraversion (Allik & McCrae, 2004; McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005) and lower in agreeableness (Allik & McCrae, 2004) than Asian and African cultures. South American and East Asian cultures were found to be higher in openness (Schmitt et al., 2007). Personality profiles also show finer-grained geographic structure (Allik & McCrae, 2004; McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005) whereby cultures that are geographically close together share more similar personality profiles (see Sec. 3.3). This similarity may have its source in shared genetic (Cavalli-Sforza, Menozzi, & Piazza, 1994) or cultural history or in a response to similar biological, social, and economic factors (Allik & McCrae, 2004).

The amount of between-culture variation in personality is small compared to that within cultures (McCrae, 2002). Yet culture-level personality profiles relate to cultural differences in beliefs, values, and social and economic variables. Allik and McCrae (2004) found that personality profiles of cultures could be separated along two dimensions: the first had a pole representing high extraversion and openness and low agreeableness; the second dimension was defined by high neuroticism and low agreeableness and conscientiousness. Cultures high in neuroticism had also been assessed to be high in uncertainty avoidance (low tolerance for ambiguity and more strictness in laws and norms) and masculinity (larger difference between the values of men and women) (Hofstede, 2001). Additionally, cultures low in neuroticism were high in interpersonal trust (most people can be trusted; Inglehart, 1997) and subjective well-being (Diener, Diener, & Diner, 1995). Cultures that ranked high on the dimension principally characterized by extraversion were also high on individualism (less group integration) and low on power distance (less accepting of inequality; Hofstede, 2001).

Cultures that were higher on extraversion, openness, and agreeableness also tended to have higher gross domestic product (GDP) per capita, greater longevity, greater school enrollment, and less income inequality (Allik & McCrae, 2004; McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005). Economic development also appears to be confounded with several of the relationships between aggregate personality profiles and belief and value variables (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005). However, whether personality profiles of cultures vary with longevity, fertility, or other life-history-related variables has not been investigated.

### No one was ever fired for basing a study on IBM

To test whether life-history patterns experienced during ontogeny related to personality differences between cultures and between cohorts within cultures, I needed aggregate personality scores that studied at least two different age cohorts. I therefore used mean level personality scores for 51 cultures from McCrae, Terracciano, and 78 Members of the Personality Profiles of Cultures Project (2005); McCrae, Terracciano, and 79 Members of the Personality Profiles of Cultures Project (2005) which consisted of peer assessments by 12156 college students, most of whom were native to their countries. The use of participants that have more homogeneous backgrounds but live in different countries may better recover cultural differences in personality, as in Hofstede's (2001) original series of studies which sampled employees from IBM in different countries. The replication of the corporate structure across countries resulted in the same sorts of people in each position in the company so that between country differences were more likely to be the result of between-culture differences. Each participant completed the Form R of the Revised NEO Personality Inventory (Costa & McCrae, 1992c) on a person they knew well (the target) who was also a native-born citizen of their country. Targets were younger (18–21 years) or older ($>$ 40 years) male and female adults. Each sample is referred to as a culture because some came from separate linguistic (e.g., French- and German-speaking Swiss) or administrative subgroups (e.g., Mainland and Hong Kong Chinese) within a country.

To compare personality scores across cultures, it is necessary to establish a degree of measurement invariance (Byrne & Campbell, 1999). The structural equivalence of the 5 personality dimensions emerges on both phenotypic (McCrae, 2002; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007) and genetic (McCrae, Jang, Livesley, Riemann, & Angleitner, 2001; Yamagata et al., 2006) levels across cultures while the functional equivalence is shown by the consistent relationships with non-personality variables (Sec. 3.1). Scalar equivalence refers to the appropriateness of comparing scores numerically across cultures (e.g., that a 50 on extraversion in Japan is the *same* as a 50 in France). Simulations in which aggregate personality scores of each country were perturbed by a random value, thereby introducing structural inequivalence, resulted in an inability to recover the 5-factor structure (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005; McCrae & Terracciano, 2008). This provided evidence that the data had some scalar equivalence. The personality scores from McCrae, Terracciano, and 78 Members of the Personality Profiles of Cultures Project (2005); McCrae, Terracciano, and 79 Members of the Personality Profiles of Cultures Project (2005) also correlated with similar constructs measured at the country-level in other studies (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007).

## 3.2 The second demographic transition

### Human life histories

Studies of humans have provided empirical support for a fertility–longevity trade-off (Doblhammer & Oeppen, 2003; Korpelainen, 2003; Maklakov, 2008; Penn & Smith, 2007; Pettay et al., 2005; Thomas et al., 2007; Westendorp & Kirkwood, 1998). Since the 19th century, many human populations have experienced the "demographic transition," a rapid change of decreasing reproductive effort and increasing lifespan (Borgerhoff Mulder, 1998; K. Hill & Kaplan, 1999; Stearns & Koella, 1986) that occurred with shifts in social and economic development factors including nutrition, public health, education, social life, and resource consumption (Chesnais, 1992). Researchers have recently placed the demographic transition within LH theory, showing that modern human populations exhibit contrasting strategies that map onto the "fast–slow" LH continuum (Bielby et al., 2007). Several explanations have been given for the interplay between the demographic transition and the attendant social and economic chances. For example, Mace (2008) concluded that low fertility is the the result of changes in parental investment under modern work and lifestyle regimes while Potts (1997) found that economic growth was preceded by fertility-regulation and changes in family size. It has also been argued that changes in economic productivity and fertility are not rigidly linked (Bryant, 2007). While the debate continues, it is possible to explore how differences in LH relate to other broad, basic aspects of behaviour.

### Fast–slow (LH) index

I developed a LH index using total fertility rate and life-expectancy at birth data for 194 countries compiled by the World Resource Institute (http://earthtrends.wri.org) from the UN World Population Prospectus. Total fertility rate estimates the number of children a woman would have over her reproductive life assuming current age-specific fertility rates. Life expectancy is the average number of years an individual is expected to live if the mortality rates in its year of birth are maintained throughout its life. The fetal and early-development stages of the younger and older groups would have occurred between 1980–1985 and 1950–1960, respectively (Fig. 3.1). I therefore calculated average fertility rates and life expectancies over these two periods for each country. I matched each culture with country-level data except for Hong Kong and mainland China where separate estimates were available.

A principal components analysis of LH data for 194 countries yielded a single principal component that explained 92% of the variance in fertility and life expectancy (eigenvalue 1.84) with a negative loading on fertility (-.96) and a positive loading on life expectancy (.96). I therefore standardized both LH variables and generated a unit-weighted score for each country covering the years 1950–1960 and 1980–1985 (Fig. 3.2). These periods correspond to the time of birth and early-development of the 40+ and 18–21-year old cohorts, respectively. Countries scoring low on the LH index are characterized by having ‘fast’ LH strategy while a high index score indicates a ‘slow’ LH strategy.

To characterize the average amount of change in the LH index over time, I ran a fixed-

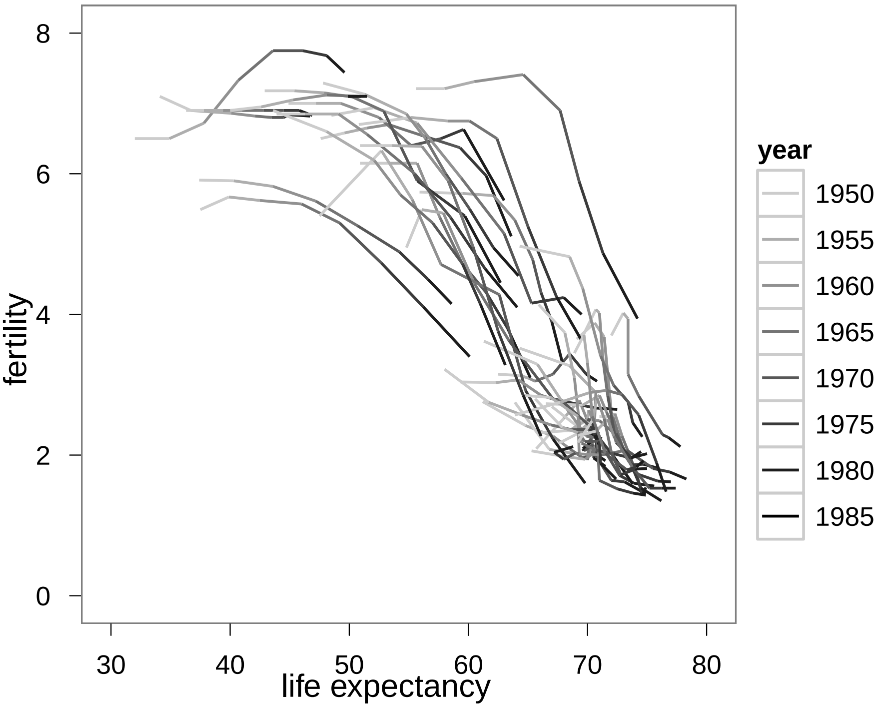


Figure 3.1: Changes in fertility and life expectancy of the 49 countries covered in the study, 1950–1985.

slope, varying-intercept model.[1] The LH index for country $i$ at time $t$ was

$$\mathrm{LH}_{it} = u_0 + \mathrm{time}_t + u_{0i} + e_{it}$$

where $\mathrm{time}_t$ was coded as year (centered at 1950) in 5-year increments, $u_0$ is the mean and $u_{0i}$ is the country-level intercept, and $e_{it}$ is the error term. According to the model, the average LH value in 1950 was $-.74 \pm .06$ SE and LH increased by $.13 \pm .002$ SE every 5 years. Mean differences between countries accounted for 91% of the variance in LH. Among the 49 countries (comprising 51 cultures) with personality data available, the mean change between the older and younger cohorts in fertility was $-1.3 \pm 1.0$ children/woman and in life expectancy was $9.6 \pm 5.0$ years. This translated into a mean change on the LH continuum of $.73 \pm .40$.

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[1] A model with a slope fit for each country did not converge, suggesting homogeneous trajectories between countries.

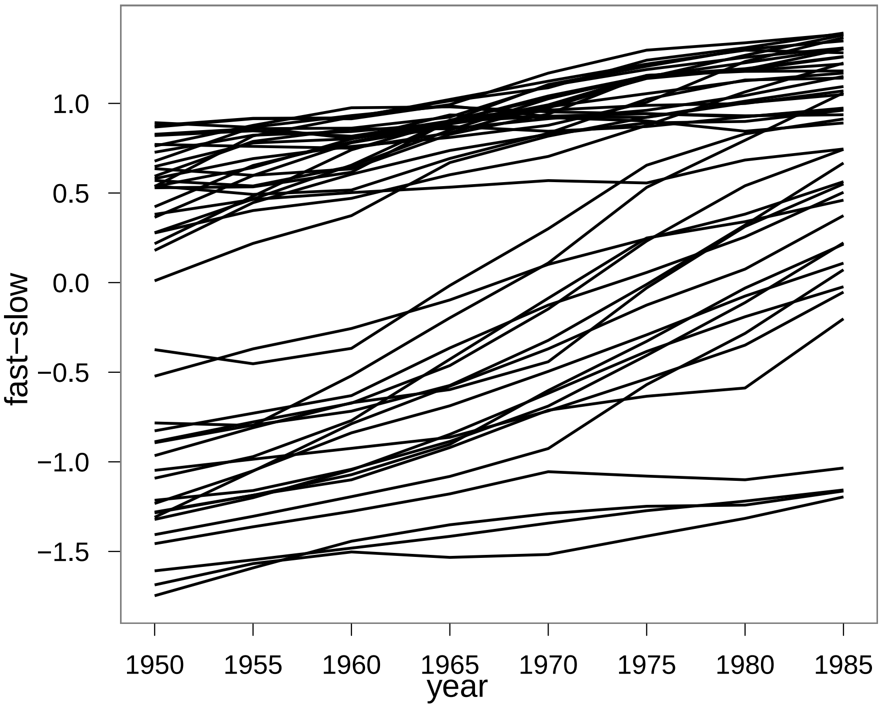

Figure 3.2: LH index for 49 countries, 1950–1985.

## 3.3 Spatial dependency

Countries that are close together are likely to resemble each other in ecological, cultural, and climactic factors that could influence both personality and LH strategies. I assessed spatial autocorrelation using Moran's I (Moran, 1950) which captures the correlation among measurements weighted by spatial proximity. Values of Moran's I that are significantly greater than 0 indicate neighbouring units are more similar than expected by chance. Because countries are neither equally sized nor randomly distributed, I used areal rather than continuous spatial methods. I used the spdep package (version 0.5-31, Bivand, 2011) to join countries with their three nearest neighbours and correlate their aggregate personality scores (Figs. 3.3, 3.4). The distance between neighboring countries was determined using the great-circle distance between the center coordinates of each country.

Except for neuroticism, all aggregate personality scores showed significant spatial autocorrelation (Table 3.1) although, in general, neighboring countries were less similar in aggre-

| | Moran's I | $p$ |
|---|---|---|
| Personality | | |
| Neuroticism | -.02 | .50 |
| Extraversion | .14 | .05 |
| Openness | .35 | $< .001$ |
| Agreeableness | .19 | .02 |
| Conscientiousness | .18 | .02 |
| Life history | | |
| Total fertility | .63 | $< .001$ |
| Life expectancy | .44 | $< .001$ |
| LH index | .55 | $< .001$ |

Table 3.1: Spatial autocorrelation of aggregate personality scores and life history variables. Each culture (personality traits) or country (life history traits) was clustered with its three nearest neighbors using great-circle distance between center coordinates of each region.

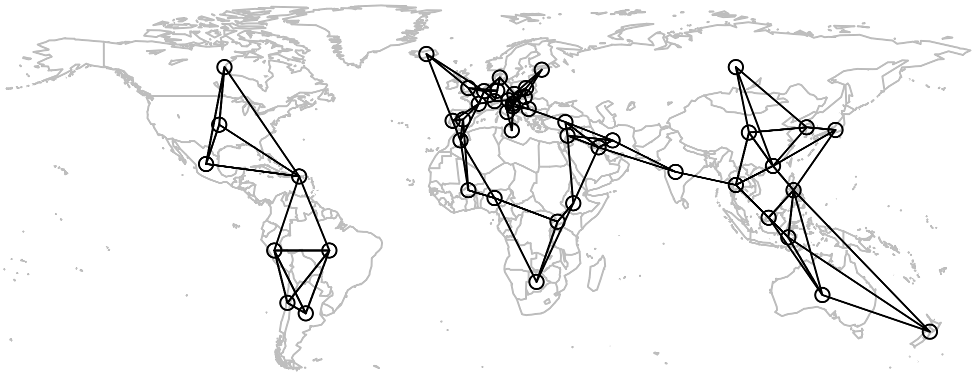

Figure 3.3: Sampled countries joined with their 3-nearest neighbors.

gate personality profile than in life history parameters.

I used semiparametric filtering (Tiefelsdorf & Griffith, 2007) to remove non-independence among data points from spatial autocorrelation as implemented in spdep. This technique generates an optimal set of eigenvectors that reduces the Moran's I of the residuals of a linear regression model. These spatial eigenvectors were then used in subsequent analyses. I ran the semiparametric filtering using culture-level personality as the outcomes and country-level LH and socioeconomic (SED) indices as the predictors.

Figure 3.4: Sampled countries joined with their 3-nearest nieghbors, detail of Europe.

## 3.4 Aggregate personality along the fast–slow continuum

Because there were multiple personality measures for young and old men and women in each culture, I used multilevel models to explore the effect of LH on the personality profiles within and between cultures. Multilevel modelling is useful for capturing the structure of the data to understand the effect of the variable of interest. I built four models for each personality domain. I started with baseline models that predicted aggregate personality from cohort, sex, and country (Model 0). I then characterized how aggregate personality scores differed under fast and slow life-history regimes (Model 1). I repeated this procedure for a similar index of socioeconomic development (Model 2). Significant predictors from Models 1 and 2 were then combined (Model 3).

The full model I fit for relating LH to the aggregate personality score of age/sex group *i* in culture *j* was

$$\begin{aligned} y_{ij} &= u_0 + \mathrm{cohort}_{ij} + \mathrm{sex}_{ij} + \mathrm{cohort}_{ij} \times \mathrm{sex}_{ij} + \textstyle\sum_k \mathrm{vec}_{kj} + \\ &\quad \mathrm{LH}^W_{ij} + \mathrm{LH}^B_j + \mathrm{sex}_{ij} \times \mathrm{LH}^W_{ij} + \mathrm{sex}_{ij} \times \mathrm{LH}^B_j + u_{0j} + e_{ij} \end{aligned}$$

where $\mathrm{vec}_{kj}$ is the $k$th spatial eigenvector for culture $j$, $u_{0j}$ is an intercept for the country of culture $j$, and $e_{ij}$ is the residual. Sex (female = 1, male = -1) and cohort (old = 1, young = -1) variables were contrast coded so that the LH and SED parameter estimates could be interpreted as averaging across cohorts. The change within cultures ($\mathrm{LH}_W$) is modeled as $\mathrm{LH}^W_{ij} = \mathrm{LH}_{ij} - \mathrm{L\bar{H}}_j$ where $\mathrm{LH}_{ij}$ is the life-history index at time of birth for cohort $i$ in culture $j$ and $\mathrm{L\bar{H}}_j$ is the average LH index of culture $j$. $\mathrm{LH}^W_{ij}$ is therefore the centered LH index within each culture that removes the effect of between-culture variation (Pol & Wright, 2009). The fitted estimate represents the change in aggregate personality attributable to within-culture changes in LH. $\mathrm{LH}_j^B = \mathrm{L}\bar{\mathrm{H}}_j$ fits the between-culture effect ($\mathrm{LH}_B$) that estimates the difference in aggregate personality scores between cultures in different positions on the LH spectrum.

### Socioeconomic development index

To control for broad economic and lifestyle differences between countries that may account for differences in aggregate personality profiles of cultures, I produced a single socioeconomic index (SED) using Gross Domestic Product (log transformed current US dollars per capita), the percentage of the population living in urbanized areas, and calorie supply (Kilocalories per person per day). I did not use the Human Development Index[2] because it incorporates life-expectancy, which I wanted to treat separately as part of LH. For the specified time periods, data on GDP were not available for Czech Republic (i.e., Czechoslovakia); Lebanon, Estonia and Russia (Union Republics of USSR); or Croatia, Serbia, and Slovenia (SFR Yugoslavia). Data on urbanization was also missing for Serbia and on calorie supply for Hong Kong, Puerto Rico, and Serbia. All countries but Serbia had at least one economic indicator that could be used to construct the index. I obtained these data from the World Resource Institute.

I repeated the model building procedure using SED index in place of LH index (Model 2). In the final stage, I combined the predictors from models 1 and 2 together to see if the estimates of the effect of LH changed after conditioning on SED (Model 3). I fit varying-intercept models with country as the group. I fit the models by REML estimation using lme4 (D. Bates & Maechler, 2010) and specified country as a random effect and the other predictors as fixed effects.

### Model averaging

Among all countries (not just those with personality data) where longevity, fertility, and (at least one) economic variables were available, LH and SED were highly correlated, $r$ = .83, 95% confidence interval .78–.87, N = 192. One of the consequences of entering two highly correlated predictors into a regression model is that the standard errors tend to increase which

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[2] `http://hdr.undp.org/en/statistics/hdi/`

leads to less certainty about the exact parameter estimates, an issue referred to as variance inflation (O'Brien, 2007; Freckleton, 2011). The variance inflation factor (VIF) indicates the amount that regression coefficients are inflated because of collinearity with other variables in the regression, defined as

$$\mathrm{VIF}_i = \frac{1}{1 - R_i^2}$$

where $R_i^2$ is from a regression of variable $i$ on the other variables in the model. One standard rule-of-thumb is that a VIF $> 4$ indicates some degree of collinearity while $> 10$ indicates exceedingly problematic collinearity that needs to be corrected (O'Brien, 2007). I calculated VIFs using the DAAG package in R (Maindonald & Braun, 2011). The VIF of the between country LH and SED indices was 4.9.

Because there was some variance inflation from collinearity, I used multimodel inference (Burnham & Anderson, 2002) to check that the contribution of LH and SED to aggregate personality variation could be distinguished. One way to do this is to average parameter estimates across models that include, exclude, and combine each of the predictors in turn as models 0–3 do with regard to the LH and SED predictors. I averaged the parameter estimates from the models using AIC weights (Burnham & Anderson, 2002; Freckleton, 2011). For each parameter $b_j$ I created an average coefficient estimate across all models as

$$\bar{b}_j = \sum_{i=1}^{R} w_i \hat{b}_{j,i}^{+}$$

where $\hat{b}_{j,i}^{+}$ is the fitted parameter estimate of $b_j$ from model $i$ or 0 if model $i$ does not include the predictor, $w_i$ is the AIC-weight,

$$w_i = \frac{e^{-0.5\Delta\mathrm{AIC}_i}}{\sum_{r=1}^{R} e^{-0.5\Delta\mathrm{AIC}_r}},$$

and $\Delta\mathrm{AIC}_i$ is the difference between the AIC of the best model and the AIC of model $i$ for $R$ models. R code for this procedure is listed in Appendix A.1.

### Contributions from individual life-history and economic variables

The multilevel models using LH index as the predictor of interest test the speficic hypothesis that the trade-off between fertility and longevity, as a core part of human life-history strategies, will influence personality at the level of cultures. The relative contributions of each of the components of the LH and SED indices can be explored but models containing all these predictors would suffer from the same issue solved by averaging the multilevel models (Sec. 3.4). That is, entering many highly correlated predictors into a regression tends to give estimates that are unstable because a large positive estimate on one predictor could be balanced out by an estimate on a correlated predictor of equal but opposite magnitude (Hastie, Tibshirani, & Friedman, 2009).

One way to handle a number of correlated predictors is to employ shrinkage methods such as ridge regression (Hoerl & Kennard, 1970). Ridge regression uses a tuning parameter ($\lambda > 0$) that penalizes the total sum-of-squares of the parameters. This has the effect of shrinking parameter estimates toward 0 and toward each other. The best value for the tuning parameter can be chosen by cross-validation where parameter estimates are fit using a subset of the data and then assessed against the remaining data (Hastie et al., 2009). Because the number of countries sampled was small, I simply explored the rank ordering of the ridge regression coefficients over a range of $\lambda$ values. I used the `lm.ridge` function (Venables & Ripley, 2002) in R to fit a ridge regression of average personality scores for each country on $z$-transformed fertility, life expectancy, log(GDP), urbanization, daily calorie intake, and spatial vectors constructed as in Sec. 3.3. I used multiple imputation with Amelia (Honaker, King, & Blackwell, 2010) to replace missing values for the SED indicators as the input to the spatial filtering function. Input to the ridge regression procedure used the raw data with missing values.

### Model inferences

Population-level life history strategies were related to several aggregate personality dimensions after controlling for spatial resemblance among neighboring nations, broad social and economic factors, and mean differences between cohorts within and between countries, as well as other unmeasured factors (i.e., country as a random effect). Country as a random effect explained 21-46% of the variation in country-level aggregate personality scores relative to the total variance among average scores of cohort/sex groups in all countries (Table 3.2). Model 3, which included both LH and SED predictors, had the best fit for all personality domains (Table 3.3). Parameter estimates for LH and SED predictors for all models are listed in in Table 3.4 and all parameter estimates from the best fitting models are visualized in Figure 3.5. Figure 3.6 is a plot of inferred within- and between-country effects of LH on

| | Country | Residual | Country/Total |
|---|---|---|---|
| Neuroticism | 2.03 | 2.75 | 0.42 |
| Extraversion | 2.82 | 3.28 | 0.46 |
| Openness | 1.33 | 4.92 | 0.21 |
| Agreeableness | 2.22 | 3.38 | 0.40 |
| Conscientiousness | 1.99 | 5.37 | 0.27 |

Table 3.2: Variance components and proportion of variance attributable to country intercepts for the best fitting models for each personality domain.

| | Model AIC (weight) | | | |
|---|---|---|---|---|
| | 0 | 1 | 2 | 3 |
| Neuroticism | 894.5 (.00) | 858.7 (.00) | 856.6 (.01) | **847.0** (.99) |
| Extraversion | 913.6 (.00) | 897.1 (.00) | 879.4 (.31) | **877.8** (.69) |
| Openness | 946.0 (.00) | 939.5 (.00) | 927.6 (.08) | **922.6** (.92) |
| Agreeableness | 920.3 (.00) | 891.4 (.00) | 885.6 (.01) | **877.0** (.99) |
| Conscientiousness | 970.1 (.00) | 957.2 (.00) | 949.8 (.05) | **943.7** (.95) |

Table 3.3: Model set 0 includes only sex, cohort, and country effects. Model set 1 adds life-history index while model set 2 uses socioeconomic index. Models in set 3 fit both indices. AIC from the best fitting models are given in bold. Relative AIC weights for calculating model-average parameter estimates are given in parentheses. Variance components are for the random effects of country (varying intercept) from the best-fitting models.

personality for men and women. Rather than focus on $p$-values, I interpreted effects that had robust magnitudes across models when averaged. This helps protect against Type II errors, as an effect could be statistically significant in model 1 but not in model 3 even though the two estimates might not be significantly different from each other. Model averaging protects against Type I errors as the averaged estimates are pulled toward zero. Countries on the slow end of the LH continuum had higher aggregate openness (b = 1.7; CI = .40, 3.0; model average $\bar{b} = 1.6$) and agreeableness (b = 1.2; CI = -.19, 2.5; $\bar{b}$ = 1.1). Within countries, a shift to slower LH also led to higher aggregate agreeableness ($b = 1.8$; CI = .30, 3.2; $\bar{b} = 1.7$) and lower extraversion ($b = -1.6$; CI = -3.0, -.16; $\bar{b} = -1.1$). SED also had effects on aggregate personality independent of LH. Between countries, economic development was related to higher extraversion ($b = 1.5$; CI = .02, 2.9; $\bar{b} = 1.5$).

### Sex differences

To infer the effects of between-country LH and SED for men and women separately, I simulated model-implied regression coefficients using the `sim()` function from the arm package

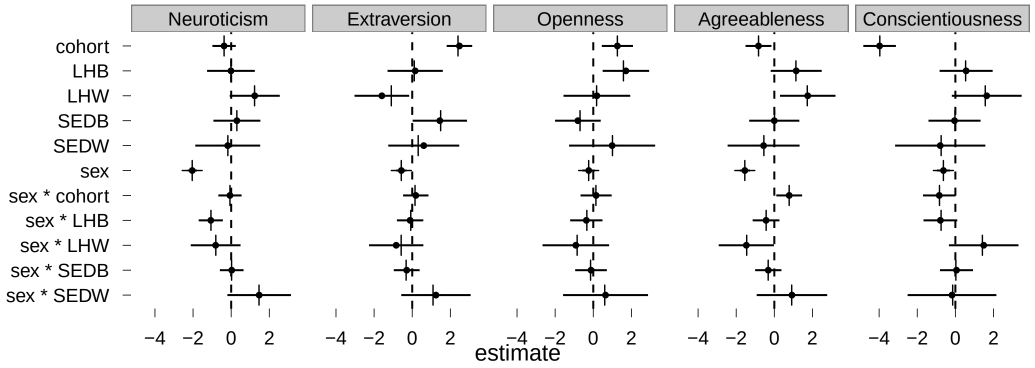


Figure 3.5: Fitted parameter estimates for demographic and life-history variables from best fitting models. Parameter estimates plotted as circles with 95AIC-model averaged coefficients plotted as vertical lines. Sex was contrast coded as male (+1) versus female (-1). Cohort was contrast coded as birth year 1960 (+1) versus 1980 (-1). LHB and LHW = life-history between and within countries; SEDB and SEDW = socioeconomic development between and within countries.

Figure 3.6: Scatterplot of Life History (fast-slow) index against aggregate personality scores for the 18-21 and 40+ cohorts for each country after removing spatial, age, and main sex effects. Positive LH scores corresponds to slow life history characteristics. Regression lines for the between-country (black) and within-country (dark gray) effects are from the final models. Between-country regression line shows personality profile predicted from position of the LH spectrum. Within-country lines show change predicted in countries as they move toward the slow end of the continuum, plotted at LH index = -1, 0, and +1. The two cohorts for each country are plotted using ISO 3166-1 alpha-3 codes and connected by gray lines.

(Gelman et al., 2011). This allows coefficients to be added together but also expresses uncertainty in the estimate. Slower between-country LH also predicted higher aggregate neuroticism for women (simulated coefficient $b_{sim}$= 1.0, CI = -.45, 2.4, Fig. 3.6) but lower aggregate neuroticism for men ($b_{sim}$= -1.1, CI = -2.5, .32). Womens conscientiousness was higher in slower LH countries ($b_{sim}$= 1.4, CI = -.32, 3.0), whereas there was no effect for men ($b_{sim}$= -.18, CI = -1.9, 1.5). Within countries, a shift to higher LH led to higher average neuroticism for women ($b_{sim}$= 2.0; CI = .31, 3.9).

### Model averaging

Because of the multicollinearity between the LH and SED predictors and because in some cases the best models had only marginally better fit, I averaged the coefficients across models.

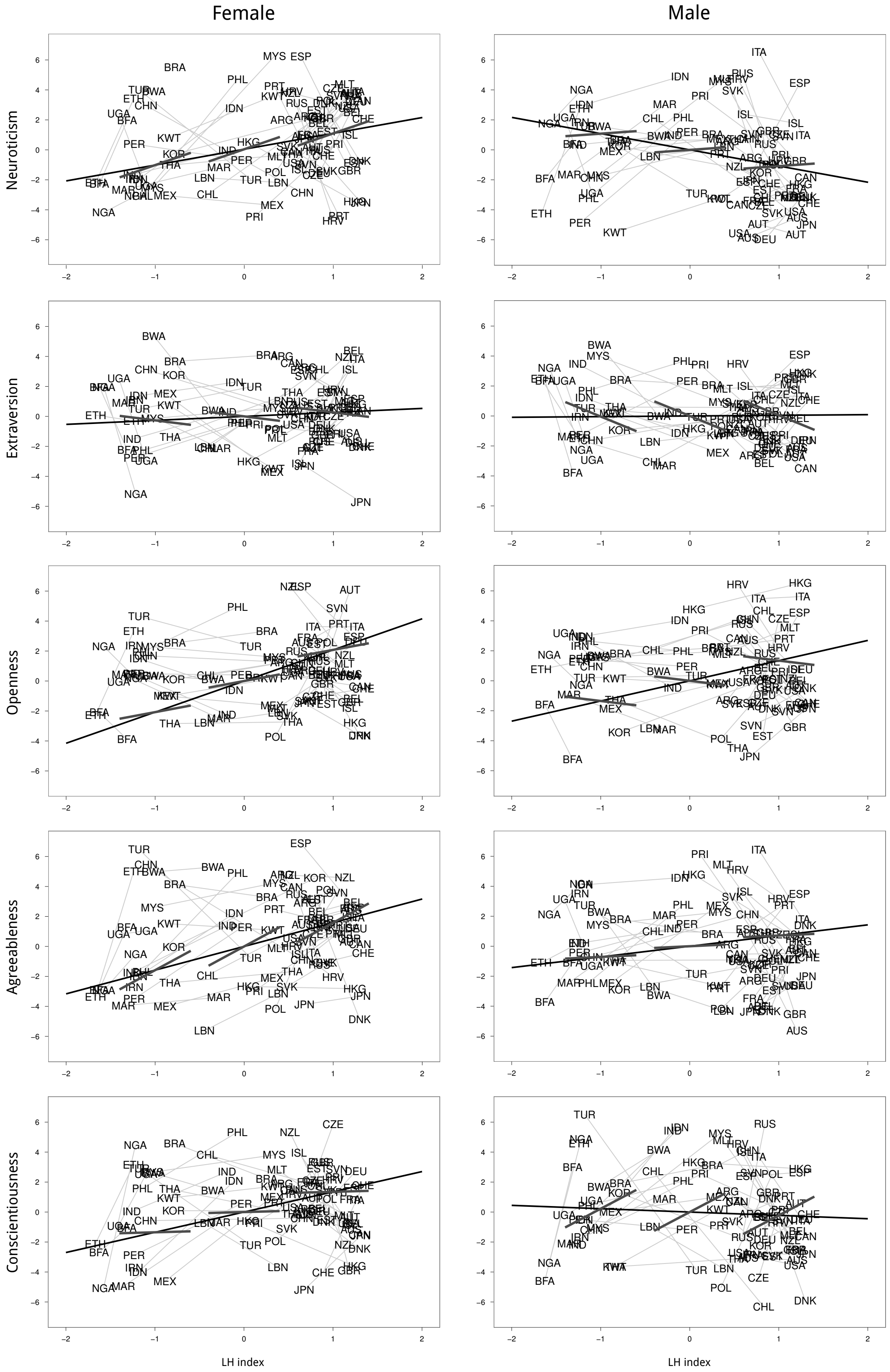

Female
Male
Neuroticism
Extraversion
Openness
Agreeableness
Conscientiousness
6
4
2
0
−2
−4
−6
−2
−1
0
1
2
LH index
LH index

Table 3.4: Coefficients with 95% confidence intervals. For each personality dimension, models estimating the effects of aggregate life-history patterns (1) or socioeconomic development (2) are contrasted with models that include both sets of predictors (3). Subscript W specifies within-country effect (e.g., the predictor ) and B specifies between-country effect (e.g., ). A dashed line indicates the predictor was not included in the model. Sex was contrast coded as male (+1) versus female (-1). Cohort was contrast coded as older (+1) versus younger group (-1). Model average gives the AIC-weighted averages for each estimate from models 0-3 (contributed estimate = 0 if a parameter not included in a model).

The AIC-weighted averaged estimates that combined information from all models, weighted by model fit (Table 3.4), supported the influence of LH within and between countries on personality. Although several estimated coefficients were not nominally significant (P > .05) in the best-fitting models, several additional averaged coefficients were in the same direction and of the same magnitude across the models. Thus there may be additional effects that, while small, are not zero.

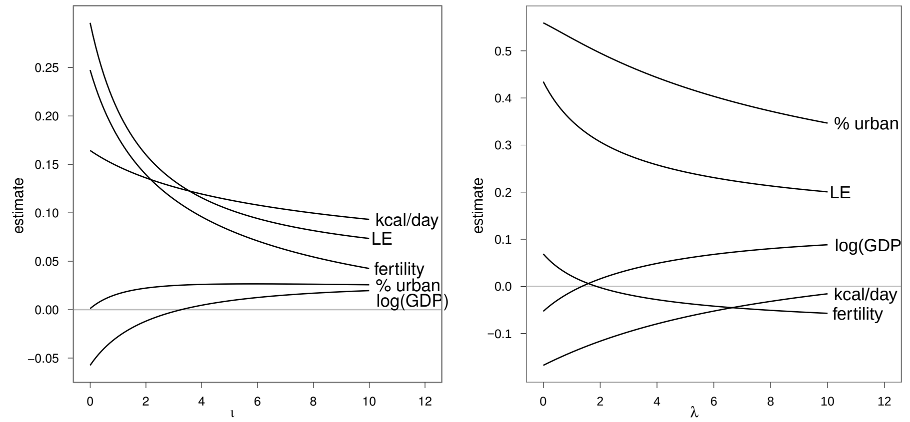
### Life-history and economic variables

Parameter estimates from ridge regressions of average personality scores for each country across a range of values for the tuning parameter ($\lambda$) are shown in Fig. 3.7. There was evidence for a trade-off between longevity and fertility, where each variable had large but opposing effects on aggregate personality scores, for openness and agreeableness. For neuroticism, extraversion, and conscientiousness, increasing the tuning parameter caused the estimate for fertility to shrink rapidly towards zero. The effect of fertility on neuroticism and conscientiousness was in the same direction as longevity (that is, countries that had both long lifespan and high fertility were higher in conscientiousness and higher in neuroticism). Ridge regression also showed that, among the components of the SED index, log(GDP) and urbanization had a larger positive effect on agreeableness and on extraversion, respectively, than did life expectancy.

### Sensitivity analysis

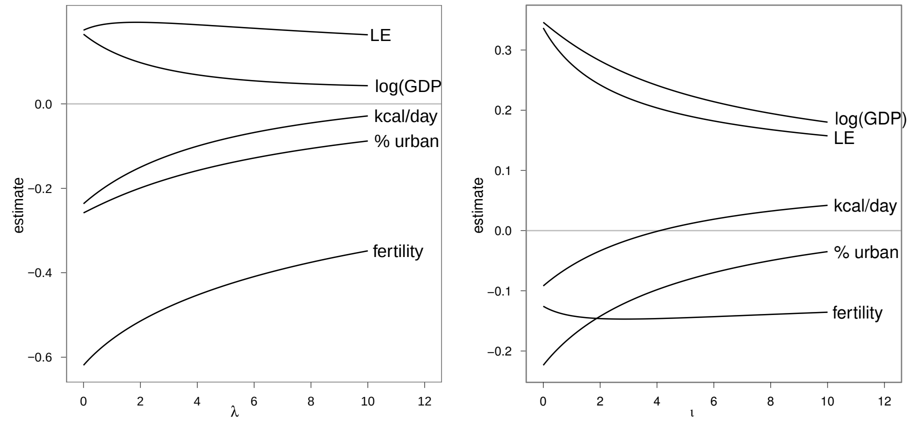
A country's values of LH and SED indices are strongly autocorrelated from year to year, i.e., their values in one year will correlate highly with values in subsequent years (mean $\rho = .74$). Because of this I used LH and SED calculated in approximate birth year of each cohort as

| Model | (1) LH | (2) SED | (3) LH and SED | Model average |
|---|---|---|---|---|
| Dimension | | | | |
| (a) Neuroticism | | | | |
| LH$_W$ | 1.17 [0.11, 2.33] | — | 1.24 [-0.08, 2.55] | 1.23 |
| LH$_B$ | 0.25 [-0.32, 0.82] | — | -0.01 [-1.26, 1.24] | -0.01 |
| LH$_W$ × sex | -0.30 [-1.46, .086] | — | -0.81 [-2.12, 0.49] | -0.81 |
| LH$_B$ × sex | -1.04 [-1.32, -0.75] | — | -1.07 [-1.70, -0.44] | -1.06 |
| SED$_W$ | — | 0.56 [-1.02, 2.13] | -0.18 [-1.88, 1.52] | -0.17 |
| SED$_B$ | — | 0.28 [-0.28, 0.85] | 0.30 [-1.93, 1.53] | 0.30 |
| SED$_W$ × sex | — | 0.90 [-0.66, 2.45] | 1.47 [-0.20, 3.14] | 1.46 |
| SED$_B$ × sex | — | -0.90 [-1.20, -0.60] | 0.03 [-0.59, 0.65] | 0.02 |
| (b) Extraversion | | | | |
| LH$_W$ | -1.42 [-2.68, -0.15] | — | -1.59 [-3.03, -0.16] | -1.1 |
| LH$_B$ | 1.44 [0.75, 2.14] | — | 0.16 [-1.30, 1.61] | 0.11 |
| LH$_W$ × sex | -0.42 [-1.69, 0.85] | — | -0.84 [-2.27, 0.58] | -0.58 |
| LH$_B$ × sex | -0.37 [-0.69, -0.05] | — | -0.11 [-0.80, 0.58] | -0.08 |
| SED$_W$ | — | -0.33 [-2.01, 1.34] | 0.60 [-1.26, 2.47] | 0.31 |
| SED$_B$ | — | 1.59 [0.93, 2.25] | 1.45 [0.02, 2.87] | 1.49 |
| SED$_W$ × sex | — | 0.75 [-0.89, 2.40] | 1.24 [-0.58, 3.06] | 1.09 |
| SED$_B$ × sex | — | -0.39 [-0.70, -0.07] | -0.29 [-0.97, 0.39] | -0.14 |
| (c) Openness | | | | |
| LH$_W$ | 0.55 [-0.99, 2.09] | — | 0.19 [-1.56, 1.94] | 0.17 |
| LH$_B$ | 1.02 [0.44, 1.59] | — | 1.71 [0.49, 2.93] | 1.58 |
| LH$_W$ × sex | -0.68 [-2.21, 0.86] | — | -0.92 [-2.66, 0.83] | -0.85 |
| LH$_B$ × sex | -0.46 [-0.80, -0.13] | — | -0.37 [-1.21, 0.48] | -0.34 |
| SED$_W$ | — | 1.23 [-0.77, 3.24] | 0.99 [-1.27, 3.35] | 1.01 |
| SED$_B$ | — | 0.68 [0.08, 1.28] | -0.81 [-2.01, 0.39] | -0.69 |
| SED$_W$ × sex | — | 0.09 [-1.90, 2.07] | 0.64 [-1.59, 2.87] | 0.6 |
| SED$_B$ × sex | — | -0.44 [-0.81, -0.06] | -0.12 [-0.95, 0.71] | -0.14 |
| (d) Agreeableness | | | | |
| LH$_W$ | 1.56 [0.27, 2.84] | — | 1.75 [0.30, 3.21] | 1.73 |
| LH$_B$ | 1.12 [0.52, 1.73] | — | 1.15 [-0.19, 2.49] | 1.13 |
| LH$_W$ × sex | -1.13 [-2.42, 0.14] | — | -1.47 [-2.92, -0.02] | -1.45 |
| LH$_B$ × sex | -0.70 [-1.02, -0.39] | — | -0.43 [-1.14, 0.27] | -0.43 |
| SED$_W$ | — | 0.52 [-1.20, 2.25] | -0.56 [-2.45, 1.32] | -0.55 |
| SED$_B$ | — | 0.99 [0.37, 1.61] | 0.01 [-1.32, 1.31] | 0.01 |
| SED$_W$ × sex | — | 0.04 [-1.66, 1.74] | 0.92 [-0.93, 2.77] | 0.91 |
| SED$_B$ × sex | — | -0.69 [-1.02, -0.37] | -0.32 [-1.01, 2.77] | -0.32 |
| (e) Conscientiousness | | | | |
| LH$_W$ | 1.37 [-0.24, 2.97] | — | 1.65 [-0.19, 3.48] | 1.57 |
| LH$_B$ | 0.52 [-0.11, 1.15] | — | 0.56 [-0.83, 1.96] | 0.54 |
| LH$_W$ × sex | 1.43 [-0.17, 3.03] | — | 1.49 [-0.34, 3.31] | 1.42 |
| LH$_B$ × sex | -0.73 [-1.13, -0.33] | — | -0.79 [-1.67, 0.10] | -0.75 |
| SED$_W$ | — | 0.22 [-1.93, 2.37] | -0.79 [-3.16, 1.57] | -0.75 |
| SED$_B$ | — | 0.44 [-0.19, 1.07] | -0.04 [-1.41, 1.32] | -0.02 |
| SED$_W$ × sex | — | 0.59 [-1.54, -2.72] | 0.06 [-0.81, 0.93] | -0.14 |
| SED$_B$ × sex | — | -0.63 [-1.04, -0.22] | 0.06 [-0.81, 0.93] | 0.03 |



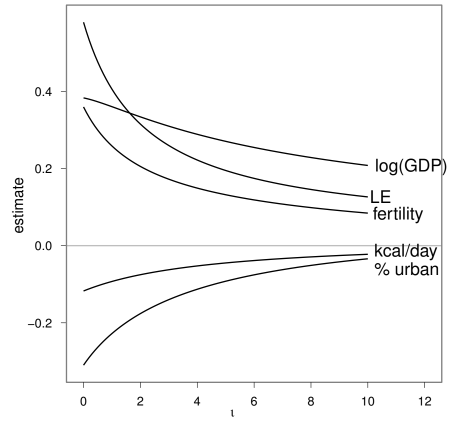
(a) Neuroticism

(b) Extraversion



(c) Openness

(d) Agreeableness



(e) Conscientiousness

Figure 3.7: Parameter estimates from ridge regressions with varying penalization parameter ($\lambda$) for country-level aggregate personality scores on each component of the life-history or socioeconomic development indices. LE = life expectancy.

a proxy for conditions experienced during ontogeny even though personality also changes during late adolescence and adulthood (Soto, et al., 2011). Thus, it is possible that model inferences will be sensitive to the range of years used to summarize LH and SED experienced during development. I therefore conducted a sensitivity analysis to test whether using averages of the LH and SED variables experienced during the first 15 years of life (instead of 5 and 10 for the young and old cohort) made any difference to the model inferences. I reran each of the models using the recalculated indicators. The sensitivity analysis showed that averaging LH and SED inputs over approximately the first 15 years of life for the two cohorts did not change the results (Fig. 3.8).

### Personality and life-history shifts

Population-level life history strategies were related to the population averages of personality dimensions after controlling for spatial resemblance among neighboring nations, broad social and economic factors, and mean differences between cohorts within and between countries. In particular, I found that (i) although LH and SED variables tended to be highly correlated, the effects of LH on personality were more detectable, (ii) personality traits differed in their flexibility with regard to adaptive plasticity to LH conditions, and (iii) for personality traits that were related to shifts in LH, the effects were often sex specific, being either in opposite directions or present in women only.

As I predicted, openness, agreeableness, and (although in women only) conscientiousness were higher in countries experiencing slow LH regimes. However, average neuroticism of women in different countries was positively related to slower between-country LH. For men in different countries, mean conscientiousness was stable across the LH spectrum while neuroticism was lower in slower LH countries. Cohorts within countries that experienced a slower LH regime during ontogeny had higher average agreeableness and neuroticism. Within-country changes in agreeableness as LH slowed down were in the same direction as the global trend whereas the between-country trend for neuroticism in men was opposite that in women. Thus, between- and within-country differences in fast-slow LH strategy account for some of the cross-cultural differences in personality.

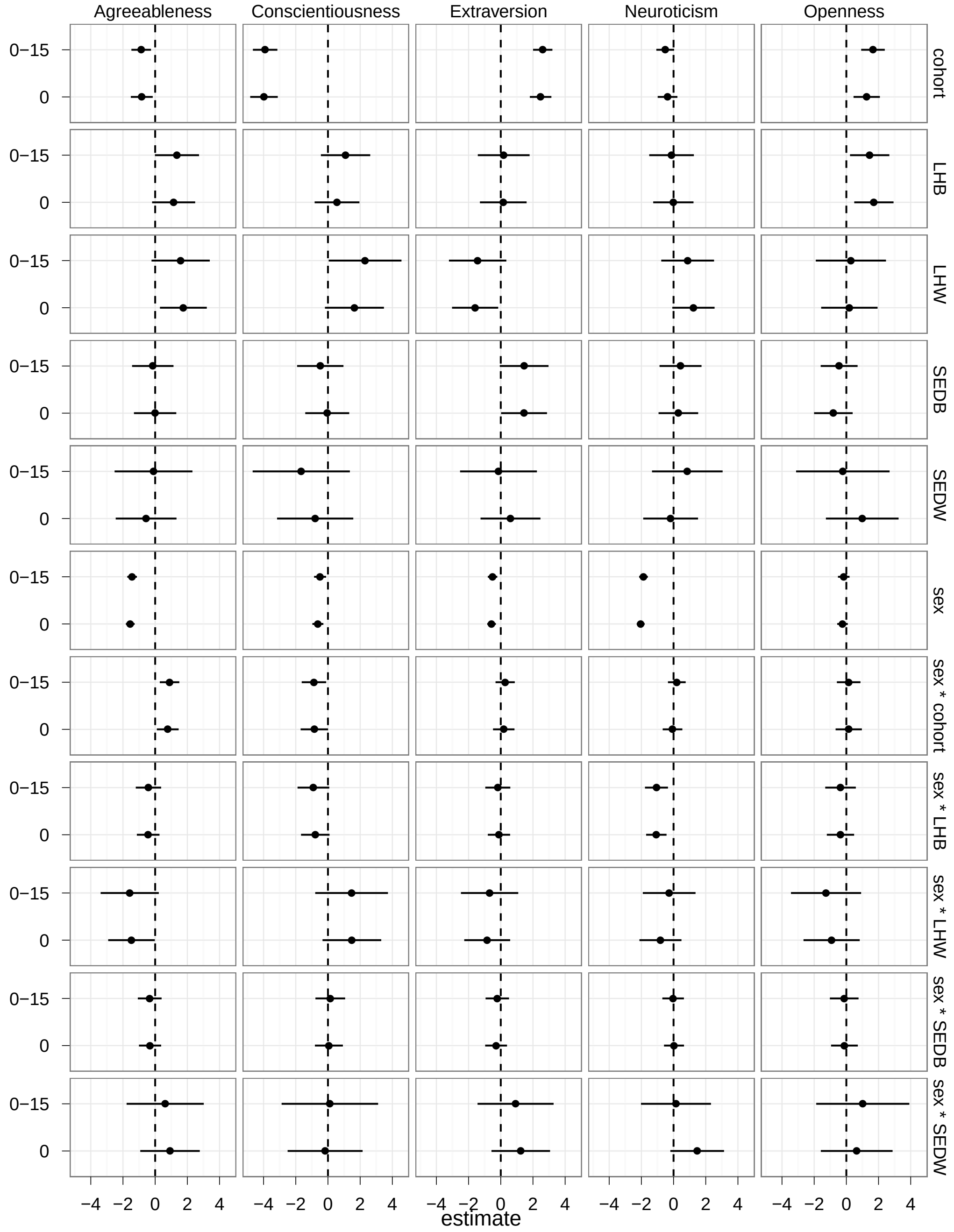

Agreeableness
Conscientiousness
Extraversion
Neuroticism
Openness
cohort
LHB
LHW
SEDB
SEDW
sex
sex * cohort
sex * LHB
sex * LHW
sex * SEDB
sex * SEDW
0–15
0
−4
−2
0
2
4
estimate

Figure 3.8: Comparison of parameter estimates from models that summarize life-history and socioeconomic development variables using only data from year-of-birth (0) or the average value of variables experienced during childhood and adolescence (0-15). The model inferences do not change substantially between the two sets of inputs. Childhood/adolescence was approximately 1960-1975 for the older cohort and 1980-1995 for the younger cohort. Sex was contrast coded as male (+1) versus female (-1). Cohort was contrast coded as birth year 1960 (+1) versus 1980 (-1). LHB and LHW = life-history between and within countries; SEDB and SEDW = socioeconomic development between and within countries.

## 3.5 Adaptive developmental plasticity

Because the LH regime of the population an individual is born into is a significant predictor of the population average adult personality, both within and between countries, I propose that early-life conditions simultaneously affect the development of LH trajectories and personality. Adaptive developmental plasticity, by which developing individuals adopt different phenotypic characteristics in response to the prevailing environment to increase fitness, has been documented in many species (West-Eberhard, 2003), including humans (Gluckman & Hanson, 2006; Nettle, 2011b). If several components of a life-history course can be adjusted in a coordinated manner, as life-history theory suggests (Stearns, 1992), then it is reasonable to expect that changes in personality are part of the adaptive reaction norm (Réale et al., 2010; Stamps & Groothuis, 2010b). For example, as an extension of Draper and Harpending (1982), Belsky, Steinberg, and Draper (1991) theorized that humans evolved sensitivity and responsiveness to the environmental context of early-rearing (e.g., availability and predictability of resources, trustworthiness of others), and as a consequence developed behavioral patterns that guide (or are guided by) how they allocate their reproductive effort (see also Bjorklund & Pellegrini, 2000; Del Giudice, 2009).

In understanding how population variation in LH leads to personality differences, it is essential to know at what stages of development personality and individual LH strategy are affected (Stamps & Groothuis, 2010b). Similar to the sensitive periods of imprinting (Bateson, 1979), animal personalities are also shaped by early experiential and environmental conditions. For example, early exposure to predators leads threespined sticklebacks to become less aggressive (Bell & Sih, 2007) but also prompts an increase in rates of growth (Bell, Dingemanse, Hankison, Langenhof, & Rollins, 2011) and thereby also influence trade-offs between growth and reproduction. In humans, data on multiple cultures shows a consistent pattern where personality stabilizes around age 30 with slight increases in agreeableness and conscientiousness and decreases in neuroticism, extraversion, and openness as individuals continue to age (McCrae et al., 1999). Human personality could have the greatest sensitivity to prevailing LH conditions during childhood and adolescence before the core facets of personality stabilize. Human LH traits such as age at primiparity and lifespan are likewise responsive to stress and other aspects of early life experiences such as parental involvement (Chisholm, Quinlivan, Petersen, & Coall, 2005; Nettle, 2011b; Nettle, Coall, & Dickens, 2011).

The aggregate personality data consisted of two cohorts within each country who would have grown up under more or less different LH regimes depending on the occurrence and timing of the demographic transition of their country. This structure in the data allowed a test of the hypothesis of adaptive developmental plasticity of personality to LH conditions by comparing departures from predicted age differences in aggregate personality profiles depending on within-country, cohort differences in position on the fast-slow continuum.

I found the greatest support for adaptive developmental plasticity for the two personality domains, agreeableness and neuroticism, that also showed detectable within-country effects. The high resource stability and somatic investment of members of a population could prompt an individual to be more prosocial (higher agreeableness) and to seek novelty and explore the environment (higher openness). In contrast, environments where overall somatic investment is low, individuals would adopt slightly more conservative and less cooperative strategies (lower agreeableness and openness). High agreeableness is related to the quality of interpersonal relationships (Asendorpf & Wilpers, 1998) and is preferred in long-term mating partners (Penke, Todd, Lenton, & Fasolo, 2007), so it would be advantageous to become more agreeable in environments where slow strategies are favored. An increase in neuroticism might be related to status striving (Nettle, 2006) as a resource control strategy (Hawley, 2011) necessary for the increased investment costs of individual offspring. Conscientiousness would also play a role in fostering the long-term strategies needed to sustain slow LH (Figueredo et al., 2005; Nettle, 2006). However, the between-country effect of LH on neuroticism and conscientiousness was positive for women but negative or absent for men. The larger difference in neuroticism between those men and women living in developed cultures (which I identify as having slow LH) (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007; Schmitt, Realo, Voracek, & Allik, 2008) has been interpreted as arising from a return to more egalitarian conditions under which sexually dimorphic personality traits first evolved (Schmitt et al., 2008). In contrast, I interpret the divergence as a sex difference in an adaptive developmental response to prevailing LH conditions.

Here I examined the effect of only one LH trade-off on personality: that between fertility and longevity. A ridge regression on country-level personality scores showed that fertility and longevity were only having strong opposing effects on openness and agreeableness. Because the scores were aggregated for countries rather than for age/sex groups, the differential effects of sex could not be seen in this analysis. Sex effects from the multilevel model that showed the effects for women's and men's neuroticism and conscientiousness scores being affected in opposite directions by the LH trade-off explains why the separate effects for life expectancy and fertility appeared to go in the same direction. However, it may also mean that the effects of the trade-off are not as strong on these two personality dimensions or that other LH trade-offs are involved. Because humans vary in maturation and reproductive timing (K. Hill & Kaplan, 1999) and personality is related to the onset of childbearing (Jokela et al., 2009, 2010), personality may also be responsive to differences in these conditions that are expressed in cross-cultural personality profiles. Unfortunately the exploration of these effects is limited by data availability. While relevant international data, such as on teenage pregnancy,[3] are being collected that could act as proxies for reproductive onset, such data only extend back 1 or 2 decades and therefore do not cover the period of ontogeny of the two cohorts.

The within- and between- country estimates of the relationship between LH and aggregate personality will reflect the effect of the demographic transition over two different time scales. Changes within countries were detected using departures from the cross-cultural (i.e., likely species-typical) differences in personality during maturation (McCrae et al., 1999; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005) of one cohort born circa 1960 compared to another born circa 1980 and therefore captures the outcome of recent demographic changes. Developmental response of personality to LH would be a function of the rate of fertility and longevity changes during this period. In contrast, between-

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[3] Teenage mothers (% of women ages 15–19 who have had children or are currently pregnant), `http://data.worldbank.org/indicator/SP.MTR.1519.ZS`; adolescent fertility rate (births per 1,000 women ages 15–19), `http://data.worldbank.org/indicator/SP.ADO.TFRT/`

country variation in personality and LH would be the result of longer term trends, such as historical differences among countries in the onset of the decline in fertility and mortality (Chesnais, 1992). The confluence of LH patterns and aggregate personality also suggests that population-level personality profiles have varied throughout the demographic transition. Although life expectancy has been rising steadily, fertility has not decreased monotonically (Chesnais, 1992) and the very latest data show a reversal of the fertility decline among the most economically developed nations (Myrskylä, Kohler, & Billari, 2009). If changes in LH influence aggregate personality profiles, this also has implications for cross-cultural studies of longitudinal changes in personality as same-aged cohorts from different countries may have experienced different LH conditions during ontogeny. Future longitudinal studies on personality should therefore explore changes between adolescence and adulthood with an eye on the LH regime experienced by the population being studied. Furthermore, cross-sectional studies should consider LH as a key birth cohort effect that may have a strong influence on personality differences between cohorts.

If neuroticism and agreeableness are plastic to LH conditions experienced during ontogeny, I would expect them to show the least stability during childhood and adolescence but the most stability in adulthood. Personality shows some of these expected developmental characteristics. Personality tends to change most during childhood and adolescence and becomes more stable as individuals reach reproductive age (Roberts & DelVecchio, 2000; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Soto et al., 2011). Personality traits that cluster as negative emotionality, which is similar to neuroticism and includes aspects such as stress reaction and aggression, show an increase in environmental relative to genetic influence during the transition to adulthood (McGue, Bacon, & Lykken, 1993) and thus could be an indicator of increased plasticity. Change in neuroticism during adolescence exhibits a pronounced sex difference with a sharp upward trend in females and a shallow downward trend in males which then decrease slightly and converge during adulthood (Soto et al., 2011). Agreeableness shows a sharp decrease in late childhood before increasing during adolescence (Soto et al., 2011). Agreeableness, conscientiousness, and, to a lesser extent, neuroticism all show change across adulthood, in contrast with flat trends in extraversion and openness. Detailed longitudinal studies that include individuals of the same age when their personalities are measured but who were born under different

LH conditions are needed to distinguish change attributable to environmental responsiveness from age-related developmental trends. In contrast to within-country change attributable to plasticity, between-country variation in personality and LH would be the result of longer term trends, such as historical differences among countries in the onset of the decline in fertility and mortality (Chesnais, 1992) as well as genetic differences among populations along the fast-slow LH continuum.

Group-level personality correlates do not automatically extend to the individual level (Rentfrow, Gosling, & Potter, 2008; Robinson, 1950). The results presented are ecological correlates only and thus do not necessarily entail that people who live longer lives and bear fewer children are more open and agreeable, only that, on average, people in slower nations are higher in these traits, irrespective of their individual LH strategies. However, it is interesting to note that the trade-off between life expectancy and fertility registers at both the individual (Pettay et al., 2005; Westendorp & Kirkwood, 1998) and the country level (Thomas et al., 2007) and that the same five dimensions that describe individual differences in personality also differentiate countries (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005). Furthermore, the results show that the relationship of agreeableness to LH on the individual level (Figueredo et al., 2005; Gladden et al., 2009) also extends to differences between populations and change within populations. This indicates that the same processes maintaining variation in personality and LH within populations may be influencing differences between populations.

Several of my findings did not match individual-level effects. On the individual level, high neuroticism is associated with a fast LH strategy while high extraversion is associated with slower LH (Gladden et al., 2009). In contrast I found that as a population shifted to slower LH conditions, average neuroticism increased while average extraversion decreased. I also did not detect any strong within-country trends for openness. These differences in ecological correlates of personality on the population level may be outcomes of the parts of personality that are flexible to the environment while individual level relationships are caused by common genetic influences on personality and LH (Figueredo & Rushton, 2009) that would not change substantially between generations. Differences in findings about the association between personality and LH may also be a measurement issue. For example, Alvergne et al. (2010) found that high extraversion was related to a greater number of sexual partners and more offspring (a 'fast' strategy). The personality instrument used in that study, the International English Mini-Markers (Thompson, 2008), measures extraversion with items related to the gregarious, activity, and excitement-seeking facets of the broad extraversion domain (Costa & McCrae, 1992c) and thus may miss 'slow LH' facets of warmth and positive emotion. Future studies of the relationship between personality and LH may therefore be fruitfully conducted at the level of lower-order facets.

Estimating the exact effect that LH conditions have on personality is limited by collinear predictors, particularly those related to social and economic development. While this was partially addressed by model averaging and penalization, conditioning on SED may be overly conservative as economic development is the cause of at least some of the variation in LH between populations, or at least differences in longevity if not fertility rates (Bongaarts & Watkins, 1996). Similarly, plastic changes in both LH and personality during development may be sensitive to some of the variables incorporated into the SED index, such as calorie supply. Finally, indices of social and economic development are predictable from personality at the individual and cultural level, too (Roberts et al., 2007; Allik & McCrae, 2004).

Although the results suggest that the average LH regime of a population influences the developmental calibration of personality, the complete story is likely to be bidirectional and self-reinforcing (Réale et al., 2010). While country-level LH strategy influences average personality profiles, the personalities of the next generation will also guide their reproductive choices and the probability of both having children and living longer. Such a scenario may lead to correlational selection where LH and personality traits are under simultaneous selection and the direction of selection on personality varies consistently according to LH traits. When applied over sufficient generations, correlational selection would lead to genetic correlations between LH and personality traits, as expected from the pace-of-life syndrome hypothesis which predicts that behavioral, life-history, and physiological traits will coevolve (Réale et al., 2010). The interplay between an individual's personality versus its LH strategy likely explains some of the persistence of personality in humans (Biro & Stamps, 2008). Future studies should aim at identifying whether personality and LH traits are subjected to correlated selection, genetically correlated, and/or fine-tuned to each other via adaptive developmental plasticity mechanisms at play during early-development.

# Chapter 4

# Quantitative genetics of orang-utan personality and subjective well-being

## 4.1 Genetic architecture and evolution

Most behavior genetic studies focus on the 'narrow-sense' heritability, $h^2 = V_A/V_P$ or the ratio between additive genetic variance and phenotyptic variance, to the exclusion of nonadditive sources of genetic variance. I believe this is a likely historical artifact of two trends: the basis of early quantitative genetics in animal breeding and that twins are the primary sample used in behavior genetics. If our goal is to estimate effects of genes or environments on a phenotype, we start by partitioning an indivdual's phenotypic value into a genotypic value and an environmental deviation (Falconer & Mackay, 1996). The variation in these values is informative of the relative contributions of genes and environments to the phenotypic variance.

The genotypic and environmental variances can themselves be broken into different kinds of effects. Additive genetic variance, $V_{\mathrm{A}}$, is produced by the effects of genes that are independent of the rest of the genotype and thus their combined effect can be thought of as the simple 'addition' of each allele's effect. Nonadditive genetic effects also exist. They come from the interaction between alleles at the same locus or between genes at different loci. Interactions between alleles at the same locus produce dominance deviations, the variance of which is dominance genetic variance $V_{\mathrm{D}}$, a quantitative parallel to the classic Mendelian effects of dominant and resessive alleles. Interactions between alleles at different loci produce epistatic variance $V_{\mathrm{I}}$. These different kinds of genetic effects are additive or nonadditive in the statistical rather than biological sense (Rice, 2004). The proportion of total genotypic variance from additive, dominance, and epistatic effects yields the 'broad-sense' heritability $H^2$.

For historical reasons the values that $V_{\mathrm{A}}$ is the variance of are called breeding values. Heritability gives information about the effects of genes, *not* genotypes. Because genotypes get broken up during meiosis, each parent in most species with separate sexes contributes only a set of their genes to their offspring, not their whole genotype (Falconer & Mackay, 1996). Thus, if you are an animal breeder looking to improve your stock then you care only about the ability to predict an offspring's phenotype given the parents from the independent, that is, additive, effects of individual genes. Assuming the average breeding value is zero, an individual's breeding value is defined as twice the difference in the expected mean of its offsprings' phenotypes from the population mean if it were to mate with random individuals from the population (whose expected breeding values are zero). If you want to know how much genetic material you have to play with for selecting animals to breed, you are interested in calculating the proportion of additive genetic variance, namely, the narrow-sense heritability. Quantitative genetics, born out of agricultural concerns, was thus primarily concerned with methods to estimate narrow-sense heritability (Falconer & Mackay, 1996; Lynch & Walsh, 1998).

The foundational studies in behavior genetics are based on analyzing twins and most behavior genetics research continues in this vein. In addition to their aptitude for riding tandem bicycles and chewing gum at the same time, twins have several useful properties for disentangling genetic from environmental effects. First, twins are born at the same time and are thus the same age while sharing many aspects of their environment, from the uterus to their household to their neighborhood. Second, twins differ in the proportion of their genes that are identical by descent, which is $2\Theta_{xy} = 1$ for monozygotic (MZ) twins and $2\Theta_{xy} = \frac{1}{2}$ for dizygotic (DZ) twins, where $\Theta_{xy}$ is the cofficient of coancestry, or the probability that if you select one allele from each twin you will get the 'same' allele (Wright, 1922; Lynch & Walsh, 1998). In other words, MZ twins share all of their genome while DZ twin share on average half. Monozygotic twins reared together differ only in the unique environments they experience while dizygotic twins differ also from each other in their exact genetic makeup. The difference in phenotypic correlations between MZ and DZ twins is the basis for separating estimates of genetic and environmental causes of similarity using either ANOVA (Kempthorne & Osborne, 1961; Christian, Kang, & Norton, 1976; Eaves et al., 1978; Lynch & Walsh, 1998) or structural equation model approaches (Loehlin, 2004). However, because the comparison is being made based on a contrast between only two types of relatives (MZ or DZ twins), there is limited power to detect certain genetic effects. In particular, classic twin designs have low power to detect nonadditive sources of genetic variance (Martin, Eaves, Kearsey, & Davies, 1978; Posthuma & Boomsma, 2000). In practice, researchers using SEM methods are forced to choose between estimating nonadditive genetic or common environment effects. As a result, nonadditive genetic components of variance are usually found to be nonsigificant or never estimated in the first place (Keller et al., 2005).

Quantitative genetic studies of human personality traits such as those described by the Five-Factor Model (Digman, 1990) consistently show that the additive effects of genes, as summarized by heritability, have an influence on personality variation (Bouchard & Loehlin, 2001) and that the additive genetic structure of personality (the **G** matrix) is a human universal (McCrae et al., 2001; Yamagata et al., 2006). Happiness, also known as subjective well-being, is similarly underpinned by genetic variation (Bartels & Boomsma, 2009; Caprara et al., 2009; Lykken & Tellegen, 1996; Nes et al., 2006, 2010) that is shared with the Five-Factor Model domains of neuroticism (reversed), extraversion, and conscientiousness (Weiss et al., 2008). In addition, extended family designs, that incorporate information from non-twin family members, have also uncovered non-additive genetic effects on personality. These dominance and interaction effects of genes account for more than twice the amount of personality variance attributed to additive genetic effects (Eaves et al., 1998; Keller et al., 2005; Pilia et al., 2006; Rettew et al., 2008). While extended designs still make it difficult to distinguish between dominance and epistatic effects, Eaves et al. (1998) found that models with epistatic effects fit better than those with dominance effects. The correlations between parent and offspring phenotypes were close to those of DZ twins and siblings, and this fits with additive and epistatic effects because the coefficients for the components of covariance ($\sigma^2_A$ = additive, $\sigma^2_D$ = dominance, $\sigma^2_A$ = additive × additive [epistatic] genetic variance) for parent-offspring

$$\frac{1}{2}\sigma_A^2 + 0\sigma_D^2 + \frac{1}{4}\sigma_{AA}^2$$

is the same as that for siblings

$$\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \frac{1}{4}\sigma_{AA}^2$$

if there is no dominance genetic variance ($\sigma_D^2 = 0$) (Lynch & Walsh, 1998). This can be compared with the components of genetic covariance between MZ twins

$$\sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2$$

Dominance and epistatic effects are caused by several molecular mechanisms (Wilkie, 1994; Lehner, 2011). Epistasis at the molecular level occurs through mechanisms such as protein–protein interfaces, feedback in regulatory networks (Hartman, Garvik, & Hartwell, 2001), and basic physical constraints (Lehner, 2011). Redundancy also influences epistasis (Kafri, Springer, & Pilpel, 2009). For example, gene duplication creates two functional copies of a gene (Musso et al., 2008). A mutation in one copy still leaves the other functioning, so both copies might have to be mutated before an effect is seen. Redundancy also occurs in pathways. If two pathways are involved in a trait, a change in one can be buffered by the other. Interactions also occur within a pathway, where a mutation that blocks a pathway will not be further modified by other mutations influencing different points on the same pathway (Papp, Pal, & Hurst, 2004). Molecular mechanisms for dominance include alternations of expression level and gain/loss of function (Wilkie, 1994).

The proportion of additive to nonadditive genetic variance can also be informative of the evolution of a trait (Merilä & Sheldon, 1999). The fitness of an additively-acting allele will always be the same in every individual whereas alleles with nonadditive effects will differ depending on the state of other genes. Additive genetic variance comes from such independent effects of genes and is thereby eroded more efficiently by selection than nonadditive effects which arise from combinations of genes (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999). High nonadditive genetic variance is therefore one sign of long-term directional or stabilizing selection because the alleles with additive effects will reach fixation first. While the presence of non-additive genetic effects on personality is consistent with balancing selection (Penke, Denissen, & Miller, 2007) or with joint directional selection for personality and life-history traits (Figueredo & Rushton, 2009), the ratio of additive to non-additive genetic variance is not a strong test of particular evolutionary mechanisms (Keller, 2007).

## 4.2 Personality and subjective well-being in great apes

A complementary approach to understanding the evolutionary history of a trait is to see whether it is present in closely related species. This is because the most parsimonious explanation for species similarity is that the trait is ancestral, i.e., existed in the species common ancestor, while traits that differ between species are most parsimoniously explained as being derived, i.e., the product of evolutionary divergence (Harvey & Pagel, 1991; Gosling & Graybeal, 2007). Humans and nonhuman primates share the basic biological bases of behavior (Fleagle, 1999) and comparing species that are more or less closely related indicates when in time a particular trait originated (Gosling & Graybeal, 2007). Studies of nonhuman primate personality reveal dimensions akin to some or all of the Five-Factor Model domains and one or two dimensions not typically identified in humans, the most prominent being labeled "dominance" or "confidence", which describe individual differences in competitive prowess (Freeman & Gosling, 2010). Like humans, chimpanzees, one of our closest living relatives and a highly social species (Goodall, 1986b), also exhibit genetic variance in personality (Weiss et al., 2000). The similar phenotypic and genetic correlations between personality and subjective well-being suggests that this link existed in our common ancestors approximately 6 million years ago (King & Figueredo, 1997; King & Landau, 2003; Weiss et al., 2002, 2009). Humans and chimpanzees shared a more distant ancestor approximately 15 million years ago with orang-utans, a semi-solitary species of great ape (Galdikas, 1985) with similar personality and subjective well-being traits (Weiss et al., 2006).

Humans, chimpanzees, and orang-utans all share the personality domains of neuroticism, extraversion, and agreeableness (Digman, 1990; King & Figueredo, 1997; Weiss et al., 2006). Chimpanzees (King & Figueredo, 1997) and orang-utans (Weiss et al., 2006) differ from humans in having a domain called dominance related to social competitiveness and assertiveness, although in chimpanzees it is a broader domain capturing facets of timidity and fearfulness that in humans and orang-utans make up neuroticism. Chimpanzees and humans are distinguished by the presence of openness and conscientiousness domains. Orang-utans instead have a domain called intellect that appears to be a blend of openness and conscientiousness (King & Figueredo, 1997; King & Weiss, 2011).

Subjective well-being encompasses long-term pleasant and unpleasant affect (as opposed to momentary mood) as well as global satisfaction with one's life and is related to positive outcomes such as health (Diener et al., 1999). People who are lower in neuroticism and higher in extraversion and agreeableness are generally happier (DeNeve, 1999). Chimpanzees (King & Landau, 2003; Weiss et al., 2009) and orang-utans (Weiss et al., 2006) can also be distinguished in terms of subjective well-being that captures both affect and positive functioning in social relationships. Although nonhuman primate subjective well-being is assessed by observers and therefore not "subjective" in the sense that humans report their own happiness and life satisfaction from their perspective (Diener et al., 1999), the term "subjective well-being" is appropriate to studying other primates. The trait is subjective in so far as attempting to capture normal variation in overall mood as opposed to physical health or well-being that is not an individual difference, such as through enrichment in captivity.

These personality and subjective well-being dimensions were defined using items derived from human inventories that were modified so as to be appropriate for rating nonhuman primates (King & Figueredo, 1997; King & Landau, 2003). The ratings are made on each individual primate by knowledgeable judges. There is convergent evidence for the reliability and validity of these and similar ratings of nonhuman primate personality. For one, there is moderate to high agreement among raters assessing the same individual (King & Figueredo, 1997; King & Landau, 2003; Uher & Asendorpf, 2008; Weiss et al., 2006) and ratings are stable over time in apes (King et al., 2008; Uher & Asendorpf, 2008) and Old World monkeys (Capitanio, 1999; Stevenson-Hinde et al., 1980; Weiss, Adams, Widdig, & Gerald, 2011). For example, the correlations of rhesus macaque personality scores over a one-year follow-up ranged from .63 to .78 (Weiss, Adams, Widdig, & Gerald, 2011) and of chimpanzee scores over a $\approx$ 7-year follow up ranged from .39 to .74. In addition, the structure derived from ratings of chimpanzees has been replicated in three independent samples (King et al., 2005; Weiss et al., 2007, 2009). Evidence of the validity of ratings such as these, includes the fact that they correlate with behavior measures (Pederson et al., 2005; Uher & Asendorpf, 2008). For example, chimpanzees rated as high in extraversion engaged in more play and frequently approached other chimpanzees for friendly interactions (Pederson et al., 2005).

The validity of subjective well-being ratings has also been demonstrated. For one, the phenotypic correlations between personality and subjective well-being are consistent across chimpanzees, humans, and orang-utans. Human subjective well-being is related to higher extraversion, agreeableness, and conscientiousness and lower neuroticism (DeNeve & Cooper, 1998) while chimpanzee subjective well-being is related to higher dominance, extraversion, and conscientiousness (King & Landau, 2003). Orang-utan subjective well-being is related to lower neuroticism and both higher extraversion and agreeableness (Weiss et al., 2006).

The subjective well-being of nonhuman primate species resembles their human counterpart in other ways, too. For one, as is in humans (Diener & Chan, 2011), orang-utans higher in subjective well-being live longer (Weiss, Adams, & King, 2011). Also, like human subjective well-being (Weiss et al., 2008), approximately 40% of the variance in chimpanzee subjective well-being is heritable with all of the heritable variance being shared in common with personality variance (Weiss et al., 2002).

Here I explore the quantitative genetic structure of personality and subjective well-being in orang-utans to test whether non-additive genetic variance is present in other primates and whether the genetic basis of subjective well-being is a unique feature of chimpanzees and humans. If a large proportion of the genetic variance in orang-utan personality can be attributed to non-additive effects, it would support the idea that similar evolutionary processes are maintaining variation in personality across primate species. Alternatively, if non-additive effects are absent or small relative to additive genetic variance, then this would support the idea that the genetic structure in humans is the result of more recent evolutionary processes unique to the hominid lineage. Existing findings do not rule out the possibility that the personality-subjective well-being nexus arose independently in humans and chimpanzees as, for example, an adaptation to their particular social environments where encounters with other individuals are frequent. Using chimpanzees and humans alone, it is therefore not possible to distinguish which aspects of the relationship between personality and subjective well-being are shared or derived. Orang-utans are a good species to address these questions. Unlike chimpanzees and humans, orang-utans are semi-social and because of their phylogenetic relationship with humans, the presence or absence of a similar genetic structure can be used to distinguish ancestral features. In this study I relied on rater assessments of personality because of the large sample sizes required to get accurate heritability estimates.

| Relationship | Informative | Full pedigree |
|---|---|---|
| maternities | 175 | 1711 |
| paternities | 163 | 1688 |
| full sibs | 79 | 1881 |
| maternal sibs | 149 | 3389 |
| maternal half sibs | 70 | 1508 |
| paternal sibs | 210 | 5775 |
| paternal half sibs | 131 | 3894 |
| maternal grandmothers | 50 | 722 |
| maternal grandfathers | 41 | 710 |
| paternal grandmothers | 45 | 564 |
| paternal grandfathers | 39 | 556 |

Table 4.1: Number of records for parental, sibling, and grandparental relationships calculated for only individuals informative for a quantitative genetic analysis because both members of the relationship pair have been measured and for the full pedigree, including unmeasured ancestors. Although it contains unmeasured individuals, the full pedigree is still used in calculating the additive genetic relationship matrix ($\mathbf{A}$) because it yields estimates of relatedness between potentially measured aunts, uncles, and cousins, etc.

## 4.3 Orang-utans

Orang-utans are a genus of apes descended from species that evolved in Asia (Steiper, 2006) and presently inhabit the islands of Sumatra and Borneo (Singleton et al., 2004; Husson et al., 2008).

Subjects were 54 Bornean (*Pongo pygmaeus*), 100 Sumatran (*Pongo abelii*), and 30 hybrid orang-utans housed across 42 zoological parks in the United States, Canada, Australia, and Singapore. Each zoo held between 1 and 22 orang-utans (mean = 4.3, mode = 3). There were 109 females and 75 males (mean age = 21.6, SD = 12.1). One hundred fifty-two of the orang-utans participated in a previous study of personality (Weiss et al. 2006) while ratings on the additional 32 orang-utans, from zoos in Australia and Singapore, were new to this study.

Across zoos, subjects were connected through an extended pedigree containing 358 individuals and encompassing up to 4 generations. (see table 4.1). Both the mother and father were known for 158 subjects. Only the mother was known for 27 subjects and only the father for one. Among the genetically informative individuals contributing to estimates of quantitative genetic parameters there were 50 full sibships and 134 half sibships. The pedigree also contained two inbred individuals ($2\Theta_{xy} = 1.25$ for both).

## 4.4 Orang-utan personality and subjective well-being

Orang-utan personality consists of five dimensions: extraversion, dominance, neuroticism, agreeableness, and intellect (Weiss et al., 2006) defined by the intercorrelations among items describing orang-utan personality. Extraversion captures differences in interpersonal traits and is defined by items such as *playful*, (not) *solitary*, and *social* but differs from human and chimpanzee extraversion by also including aspects of openness, such as *inquisitive*. Dominance, as in chimpanzees, is defined by traits related to dominance and submissive behaviours and traits similar to the negative pole of human agreeableness, such as *manipulative* and *aggressive*. Neuroticism is made up of traits similar to human neuroticism such as *anxious*, (not) *stable*, and *impulsive*. Agreeableness was similar to the identically named dimension in chimpanzees and is defined by items related only to the positive pole of human agreeableness, such as *sympathetic* and *protective*. Finally, intellect was made up of items similar to both human conscientiousness (*decisive*, [not] *disorganized*) and openness (*intelligent*).

Personality was measured by ratings of each individual provided by 113 zoo employees who worked regularly with the orang-utans and who did not specifically receive training on measuring personality apart from the instructions included in the questionnaire. Each orang-utan was rated by between 1 and 7 raters (mean = 2.6). Personality was assessed in 137 subjects using the 48-item orang-utan Personality Questionnaire (OPQ, Weiss et al., 2006) and in 37 subjects using the expanded 54-item Hominoid Personality Questionnaire (HPQ, Weiss et al., 2009) and 10 subjects were also rated on an earlier, 43-item version of the OPQ that was based on the Chimpanzee Personality Questionnaire (King & Figueredo, 1997). Each item consisted of an adjectival descriptor and one to three clarifying sentences describing the adjective in terms of orang-utan behaviour. For example, the item *active* was defined as “Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behaviour.” Ratings were made on a 7 point scale. Across all raters and subjects the data contained 20446 personality item scores.

Subjective well-being (SWB) was assessed in 164 orang-utans by ratings of their balance of positive and negative moods, their enjoyment of social interaction, and their ability to achieve goals, as well as an evaluation by the human raters as to how happy they would be if they were the target orang-utan for a week (Box 6.1). This instrument was based on a previous assessment of chimpanzee well-being (King & Landau, 2003). In total there were 1578 subjective well-being item scores included in the analysis.

**Box 4.1 Items from the orang-utan subjective well-being questionnaire**

- *Moods* Estimate the amount of time the orang-utan is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the orang-utan is unhappy, bored, frightened, or otherwise in a negative mood.
- *Social* Estimate the extent to which social interactions with other orang-utans are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the orang-utan. Use as many social interactions that you can recall as a basis for your judgment.
- *Goals* Estimate, for this orang-utan, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each orang-utan will presumably have its own set of goals that may be different from other orang-utans.
- *Be orang-utan* Imagine how happy you would be if you were that orang-utan for a week. You would be exactly like that orang-utan. You would behave the same way as that orang-utan, would perceive the world the same way as that orang-utan, and would feel things the same way as that orang-utan.

## 4.5 Quantitative genetic analysis

Heritability estimates are based on correlations among the phenotypes of individuals who differ in their amount of genetic relatedness. Behavior genetic studies of humans typically derive heritability estimates using the difference in correlations between monozygotic and dizygotic twins (Bouchard & Loehlin, 2001). I used two methods to estimate heritability in the sample of orang-utans: a parent–offspring regression and an "animal model". The regression of breeding values on phenotypic values is an alternative definition of heritability and can be estimated most directly using parent and offspring phenotypes (Falconer & Mackay, 1996). Because I had a full pedigree for the orang-utans in the sample, and thus could calculate relatedness among all the individuals in the sample, I also used the animal model. The animal model is a biometrical genetic model increasingly used in human studies (Pilia et al., 2006) and is commonly used in agriculture and evolutionary genetics (Lynch & Walsh, 1998; Kruuk, 2004; A. J. Wilson & Nussey, 2009).

### Parent–offspring regression

Heritability can be estimated from data on parents and offspring (Falconer & Mackay, 1996; Lynch & Walsh, 1998) as twice the slope coefficient (*b*) from a regression of offspring on parent phenotype

$$h^2 = 2b$$

There were 80 orang-utans in the sample whose mother's personality and subjective well-being had also been assessed but only 28 whose father's had. Because it offered the larger sample size and thus greater power, I calculated heritability by regressing the offsprings phenotypes on those of their mothers, e.g.

$$\text{extraversion}_{\text{offspring}} = a + b \cdot \text{extraversion}_{\text{mother}} + e$$

Because the variances in offspring and maternal personality were not equal (Table 4.2), I adjusted the regression coefficients as

$$b' = b\frac{\sigma_P}{\sigma_O}$$

where $\sigma_P$ and $\sigma_O$ are the parent and offspring standard deviations (Falconer & Mackay, 1996). Each mother in the sample was paired with between 1 and 4 offspring (mean = 1.8, mode = 1) as input into the regression. The sampling variance of the regression coefficient as an estimate of heritability needs to take into account the correlations among the siblings and is approximately (Falconer & Mackay, 1996)

$$\sigma_b^2 = \frac{k(1+(n-1)t)}{nN}$$

| | Offspring | | | Mother | | |
|---|---|---|---|---|---|---|
| | mean | sd | N | mean | sd | N |
| Extraversion | .46 | .95 | 80 | -.80 | .89 | 80 |
| Dominance | -.06 | .98 | 80 | -.06 | 1.1 | 80 |
| Neuroticism | .30 | .89 | 80 | -.38 | .87 | 80 |
| Agreeableness | .12 | 95 | 80 | -.19 | 1.1 | 79 |
| Intellect | -.38 | 1.0 | 80 | .22 | .82 | 80 |
| Subjective well-being | .09 | .96 | 80 | -.31 | .93 | 69 |

Table 4.2: Summary statistics for offspring and mothers used in regression analysis of heritability

| | $b$ | SE | $h^2$ | s.e.$(h^2)$ | CI |
|---|---|---|---|---|---|
| Extraversion | .23 | .12 | .43 | .19 | .04, .81 |
| Dominance | -.19 | .10 | -.40 | .20 | -.78, .00 |
| Neuroticism | .07 | .12 | .13 | .22 | -.34, .56 |
| Agreeableness | -.10 | .10 | -.22 | .20 | -.59, .18 |
| Intellect | .14 | .14 | .23 | .20 | -.13, .65 |
| Subjective well-being | .10 | .12 | .20 | .22 | -.23, .61 |

Table 4.3: Heritability estimates from mother–offspring regression; $b$ and SE are the regression coefficient and standard error; $h^2$ = heritability; CI = 95% confidence interval of the heritability estimate.

where $k$ = number of parents per family (since only mothers were used, $k = 1$), $n$ = mean number of offspring in each family, $t$ = intraclass correlation of siblings, $N$ = total sample size. I calculated the intraclass correlation from an ANOVA of a regression of offspring phenotype on mother's ID as

$$t = \frac{\sigma^2_{\text{dam}}}{\sigma^2_{\text{dam}} + \sigma^2_{\text{error}}}$$

which gives the expected correlation of personality between two siblings. The standard error of the heritability estimate is then

$$\text{s.e.}(h^2) = 2\sigma_b$$

I calculated 95% confidence intervals for each heritability estimate from the predictive distribution taken from simulating 1000 samples from a normal distribution $\sim N(2b', 2\sigma_b)$.

Using parent–offspring regression, only extraversion had a signficantly positive heritability (Table 4.3, Figures 4.1, 4.2). Contrary to expectation, the heritability estimate for dominance and agreeableness were negative and, more surprisingly still, significantly so for dominance. The negative relationships may be attributable to an environmental effect contributing to the divergence in mother and offspring dominance. The sample size of mother–offspring

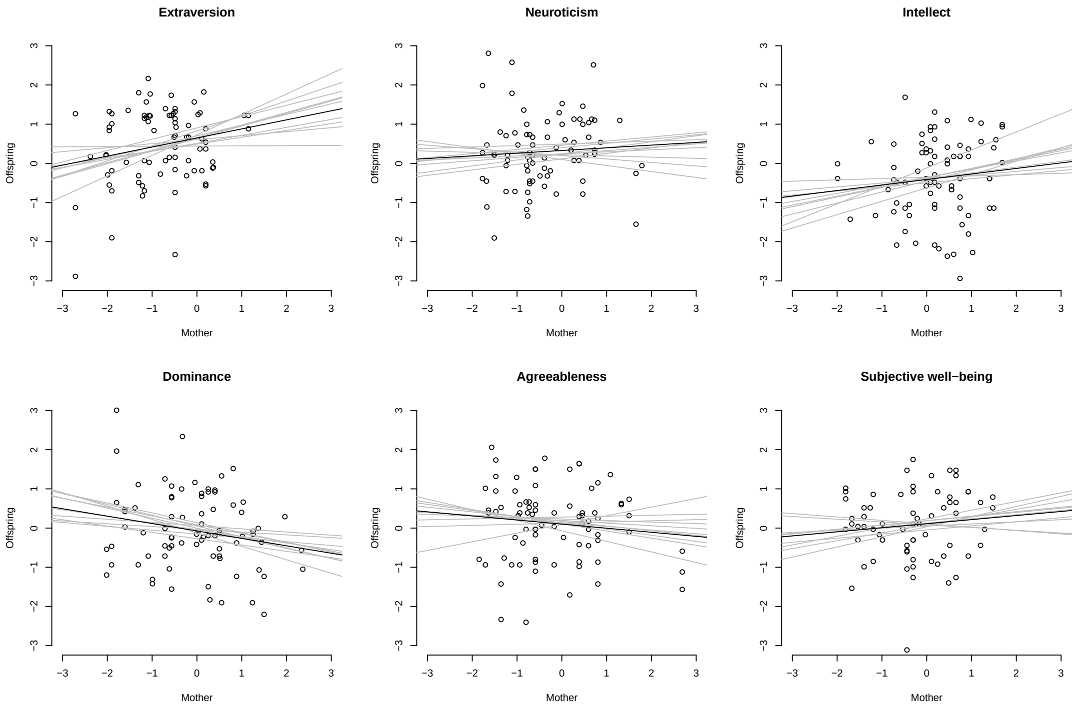

Figure 4.1: Resemblance between mothers and offspring calculated using a linear regression model. Dark lines indicate best fit, gray lines are simulations of the regression coefficients to visualize uncertainty.

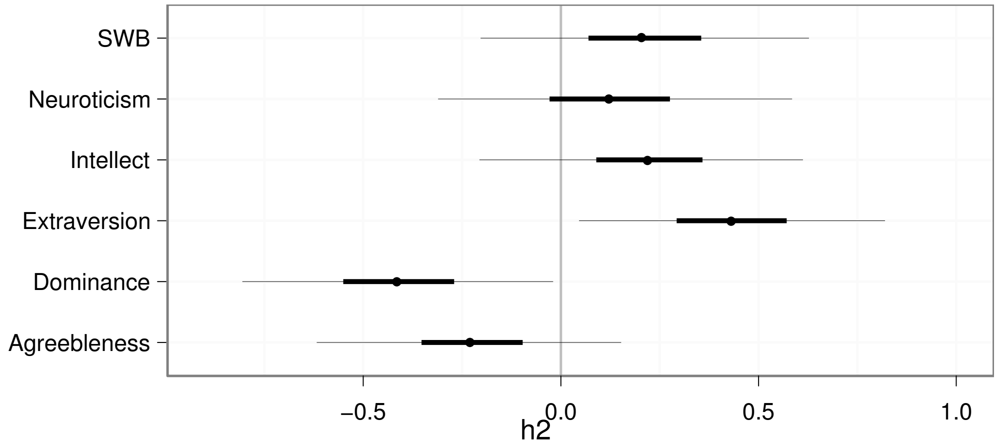

Figure 4.2: Heritability of personality and subjective well-being. Fitted coefficients plotted as points with 50% and 95% uncertainty intervals.

pairs was too small to yield precise estimates of heritability. The accuracy of the regression method also rests on assumptions of random mating, no correlation in environmental effects between relatives, and genetic effects that are only additive. Because in many cases the parents and offspring are housed in the same zoo, both the shared zoo environment and assessment by the same set of raters could contribute to environmental similarity between relatives. Such complications can be addressed by using a multilevel model that relies on relatedness between all individuals in the sample and also allows environmental sources of resemblance to be modeled, i.e., by an animal model.

### Animal model

Just as twin models can be viewed as a particular instance of structural equation models, the animal model is a type of multilevel or mixed-effects model. If a trait is influenced by genetic differences, two genetically related individuals should deviate from the mean in the same direction and by a similar amount; both corresponding to how closely related these individuals are. For example, full siblings should be more similar in their deviation from the mean than full cousins. The additive genetic relationships among animals are used as the basis for a random effect estimating an individual's deviation from the mean phenotype attributable to additive genetic effects (Lynch & Walsh, 1998; Kruuk, 2004).[1] The proportion of variance attributable to these genetic deviations is an estimate of heritability. Similarly, information about the extent to which individuals share genotypes (for example, full siblings will on average share half their genes but will have only a quarter of their genotypes in common) can be used to estimate nonadditive sources of genetic variance such as dominance genetic variance. While in most twin models dominance genetic variance is confounded with shared family effects, these can be separated using extended twin family designs (Eaves et al. 1978) or pedigree data containing a large number of full- and half-siblings (A. J. Wilson & Nussey, 2009), as was the case with the orang-utan pedigree. I also explored whether heritability estimates were consistent between Bornean and Sumatran orang-utans. Significant differences in genetic structure between these species could be a potential signal of evolutionary divergence in their personality or subjective well-being.

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[1] The model is referred to as an "animal" model because each individual animal gets its own row of data inputs. This is in contrast to methods such as parent–offspring regression where each row of data consists of information on two or more relatives.

Individuals who share environments may also resemble each other in terms of their personality or subjective well-being. I therefore considered whether individuals with the same mother or who lived in the same zoo environment when rated were more similar than those living in different zoo environments. The maternal environment captures effects that make offspring of the same mother resemble each other (independent of transmitted genes) such as natal effects or rearing style and may be caused by either environmental effects or indirect genetic effects. A zoo environment effect would account for any features of the captive environment that make individuals living together more similar to each other such as the level of enrichment, the social environment and group size, or observer effects. Because siblings did not always live in the same zoo when assessed, maternal and zoo effects were not perfectly confounded. I explored the amount of variance in each personality trait and subjective well-being these effects accounted for by fitting a series of univariate models. I then estimated genetic and environmental covariances among traits using a multivariate model.

The model had measurement and variance decomposition components. The measurement component was used to capture the structure and distribution of the raw data by treating each item on a personality scale as repeated observations of animals and raters. The variance decomposition component attributes phenotypic variances in personality item scores among various genetic (additive and nonadditive), environmental (unique, maternal, shared zoo), and assessment (rater, residual) effects. The models consisted of a vector of latent variable $\mathbf{l}$

$$\mathbf{l} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e} \tag{4.1}$$

where $\mathbf{X}$ is a design matrix indexing fixed effects, $\mathbf{Z}$ is the design matrix indexing random effects, $\boldsymbol{\beta}$ is a vector of fixed effect parameters, $\mathbf{u}$ is a vector of random effect parameters, and $\mathbf{e}$ is the residuals. On the latent scale the parameters $\boldsymbol{\beta}$ and $\mathbf{u}$ and residual vectors $\mathbf{e}$ are distributed multivariate normal as:

$$\begin{bmatrix} \boldsymbol{\beta}_0 \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} \sim N \left( \begin{bmatrix} \boldsymbol{\beta} \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{B} & 0 & 0 \\ 0 & \mathbf{G} & 0 \\ 0 & 0 & \mathbf{R} \end{bmatrix} \right) \tag{4.2}$$

$\boldsymbol{\beta}_0$ is a vector of means for each outcome (personality or subjective well-being trait), $\mathbf{B}$ is the covariance matrix of fixed effects, $\mathbf{G}$ is the covariance matrix of random effects, and $\mathbf{R}$ is the covariance matrix of residuals (Hadfield, 2010).

### Measurement component

Rather than analyzing factor scores for each personality trait, I built the models up from each raters assessments of each orang-utan on every item and thus modeled personality and subjective well-being as latent variables. Each rating on the 7-point scale was treated as ordinal and connected to an underlying latent scale with a probit link parameterized using cut-points (Hadfield & Nakagawa, 2010). The probability of the item rating $y$ equalling $k$ is

$$Pr(y = k) = F_N(\gamma_k|l, 1) - F_N(\gamma_{k-1}|l, 1)$$

where $F_N$ is the normal density function, $\gamma_k$ is the $k$th cutpoint with $\gamma_1 = 0$ (Hadfield, 2010). Each item contributed to the latent score of the personality domain it had a salient loading on as described previously (Weiss et al., 2006). I reverse coded items with negative loadings. This approach handled heterogeneity in the number of items for each personality domain that was a consequence of the different versions of the questionnaires used to rate the orang-utans. Using the raw observations allowed uncertainty about individual orang-utans personality scores to propagate through the model and thus allowed us to control for relationships among personality and subjective well-being introduced by raters. All models used residual variances fixed to 1 while residual covariances in the multivariate model were fixed to 0 because each item only gave information on one personality or subjective well-being domain, that is the residual matrix from Eqn. 4.2 was $\mathbf{R} = \mathbf{I}$.

### Variance partition component

One advantage of using the animal model for heritability estimates is that it can be extended to include fixed effects that are known to affect the phenotype as well as additional group-level random effects to partition the variance (Kruuk 2004). A mixed effects model is composed of both fixed and random explanatory variables that contribute to phenotypic similarity between individuals. A fixed effect is an estimate of mean differences in phenotypes where each factor level of the variable is known. In contrast, each level of a random effect is taken to be sampled from a larger population of values where the goal is to estimate the population variance of the variable. An individual's personality can deviate from the the grand mean for several reasons. In all models I controlled for potential differences attributable to age and sex by fitting them as fixed effects. Secondarily, I considered the effect of different genetic groups (in this case species) using species ancestry (1 for Sumatran and 0 for Bornean with an intermediate percentage calculated for hybrids depending on the mixture of their parentage) as a fixed effect (Quaas, 1988).

I built the following models to explore the partitioning of variance among combinations of genetic and environmental factors:

1. The first model estimated individual orang-utan ($V_{\mathrm{ID}}$) and rater ($V_{\mathrm{J}}$) variances (model 1) using orang-utan and rater IDs as predictors;

2. The second model added parameters to estimate additive genetic variance ($V_{\mathrm{A}}$) for all species together using a design matrix derived from the additive genetic relationship matrix calculated from the pedigree.

3. The next model added nonadditive genetic variance ($V_{\mathrm{D}}$) using the dominance genetic relationship matrix (Lynch & Walsh, 1998, p 768; Appendix A.2).

4. The fourth model included individual, rater, and additive genetic effects and added an estimate for maternal environment variance ($V_{\mathrm{M}}$).

5. The fifth model was the same as the previous model except it fit shared zoo environment variance ($V_{\mathrm{Z}}$) instead of maternal variance.

6. The final model included all the effects to give more conservative estimates of effects that are difficult to separate when families share a common environment (A. J. Wilson & Nussey, 2009).

In the models that estimate additive and nonadditive genetic or maternal and zoo environment variances, the orang-utan identity matrix fits an effect comparable to the unique environment variance ($V_{\mathrm{E}}$) in twin models, that is, effects that cause an orang-utan to differ from other individuals who share genes or environments.

The full model of fixed and random effects was

$$y_{ijk} = \mu_{0k} + \mathrm{age}_i + \mathrm{age}_i^2 + \mathrm{sex}_i + \mathrm{species}_i + a_{ik} + d_{ik} + m_{ik} + z_{ik} + j_{jk} + e_{ijk}$$

where $y_{ijk}$ is orang-utan's latent score on personality or subjective well-being trait $k$ as assessed by rater $j$; $\mu_{0k}$ is the mean of trait $k$; $\mathrm{age}_i$, $\mathrm{sex}_i$, and $\mathrm{species}_i$ are the age, sex, and species of orang-utan $i$; $a_{ik}$ and $d_{ik}$ are the breeding value (additive genetic effect) and dominance deviation (nonadditive genetic effect) of individual $i$; $m_{ik}$ and $z_{ik}$ are the environmental deviations for individual $i$'s mother and zoo; $j_{jk}$ is the rater deviation; and $e_{ijk}$ is the residual.

I additionally tested models that fit unique environment effects separately for each species group (Bornean, Sumatran, and hybrid) and additive and dominance genetic effects for Bornean and Sumatran orang-utans (model 7). I did this by creating separate genetic relationship matrices for each species.

### Model fitting

I estimated fixed effects and components of variance using a Bayesian animal model (Sorensen & Gianola, 2002) as implemented in MCMCglmm (Hadfield, 2010). I used Bayesian methods because they better handle confounded variables (Ovaskainen et al. 2008) such as parents and offspring who shared genes and a zoo environment. Bayesian inferences can be made by summarizing random draws from the joint posterior distribution of the parameter estimates. MCMCglmm uses an inverse-Wishart distribution as the prior for variance components. I specified priors with variances of 1 and covariances of 0 and degrees of freedom parameter of 1 for the univariate models and 6 for the multivariate models. I ran the models for $10^6$ iterations, discarded the first half of the samples, and thinned the samples from the posterior distribution to 1000. The autocorrelations among the successive samples from the posterior distributions were less than .1. I compared model fit using the deviance information criterion or DIC (Hadfield 2010). Because there is error in calculating DIC from Monte Carlo simulations, I ran each model twice. Because of the variance in the DIC between the two runs of each of the univariate models (Table 1), it was not possible to definitively choose the best model for each personality domain. I therefore interpreted the modes and credible intervals for each parameter estimate for all models.

### Heritability and variance proportion coefficients

To exclude measurement error from the heritability estimates, I calculated narrow-sense heritability as the ratio between the additive genetic variance and the repeatable variance ($V_{\mathrm{RPT}} = V_{\mathrm{A}} + V_{\mathrm{D}} + V_{\mathrm{M}} + V_{\mathrm{Z}}$) on the latent variable scale as $h^2 = V_{\mathrm{A}}/V_{\mathrm{RPT}}$. The heritability estimate thus only reflects variance from effects assigned to individual orang-utans and not measurement variance from rater effects and the probit distribution used to model item scores. I calculated the broad-sense heritability as $H^2 = (V_\mathrm{A} + V_\mathrm{D})/V_\mathrm{RPT}$ and the proportion of nonadditive genetic variance to total genetic variance (Crnokrak & Roff, 1995) as $D_\alpha = V_\mathrm{D}/(V_\mathrm{A} + V_\mathrm{D})$. I estimated correlations among traits attributable to additive genetic ($r_\mathrm{A}$), nonadditive genetic ($r_\mathrm{D}$), and unique environment ($r_\mathrm{E}$) effects as well as rater effects ($r_\mathrm{J}$) using a multivariate animal model. Covariances, like variances, can also be added together, so I also examined the total genetic correlations ($r_\mathrm{G}$) from adding the additive and nonadditive genetic covariance matrices ($\mathrm{cov}_\mathrm{G} = \mathrm{cov}_\mathrm{A} + \mathrm{cov}_\mathrm{D}$) and the phenotypic correlations among personality and subjective well-being statistically controlling for rater effects ($\mathrm{cov}_\mathrm{P} = \mathrm{cov}_\mathrm{A} + \mathrm{cov}_\mathrm{D} + \mathrm{cov}_\mathrm{E}$).

Variance components, heritability, and the other variance proportion coefficients of models 1-6 are given in Tables 4.4 and 4.5. The narrow-sense heritabilities of personality traits and subjective well-being in orang-utans were moderate and across the models and traits ranged from about 20-30% of the repeatable variance (Table 4.5, Fig. 4.3). The nonadditive genetic effects explained on average more of the variance (30-50%) than additive genetic effects. The total genetic effects (broad-sense heritability or $H^2$) thus accounted for upwards of three quarters of the repeatable variance (Table 4.6, Fig. 4.3). The proportion of nonadditive genetic variance ($D_\alpha$) was greater than half for all traits (Table 4.5). The estimates for maternal environment and zoo effects were low but the variance accounted for by nonadditive genetic effects was generally reduced when a maternal environment effect was included in the model. The separate heritability estimates for Bornean and Sumatran orang-utans (Table 4.6) were consistent with the estimates from the whole sample.

In these models I used the dominance genetic relationship matrix, defined as the probability that two individuals share the same genotype at a locus (Lynch & Walsh, 1998), to estimate nonadditive genetic variance. Dominance genetic variance comes from interactions between alleles at the same locus but additive × additive and other epistatic interactions could also contribute to nonadditive genetic variance. However, as only small fractions of variance from epistatic effects contributes to correlations among related individuals, the design matrix needed to estimate them will be very close to that used to estimate dominance genetic relationships. Therefore the estimate of nonadditive genetic variance would include some variance from any epistatic effects.

| Model | DIC | $V_{\mathrm{E}}$ ($V_{\mathrm{ID}}$) | $V_{\mathrm{A}}$ | $V_{\mathrm{D}}$ | $V_{\mathrm{M}}$ | $V_{\mathrm{Z}}$ | $V_{\mathrm{J}}$ |
|---|---|---|---|---|---|---|---|
| Extraversion | | | | | | | |
| 1 | 16046; 16046 | .53 (.41, .68) | | | | | .14 (.10, .24) |
| 2 | 16036; 16046 | .38 (.25, .55) | .17 (.06, .32) | | | | .17 (.10, .23) |
| 3 | 16028; 16036 | .18 (.09, .38) | .15 (.07, .29) | .22 (.10, .40) | | | .14 (.10, .24) |
| 4 | 16031; 16002 | .33 (.22, .53) | .16 (.07, .32) | | .09 (.06, .20) | | .14 (.10, .23) |
| 5 | 16042; 16026 | .36 (.24, .57) | .13 (.08, .36) | | | .11 (.06, .24) | .13 (.10, .24) |
| 6 | 15978; 16018 | .20 (.07, .36) | .14 (.06, .30) | .17 (.08, .35) | .09 (.06, .22) | .11 (.06, .26) | .15 (.09, .23) |
| Dominance | | | | | | | |
| 1 | 17788; 17792 | 1.0 (.77, 1.2) | | | | | .17 (.10, .25) |
| 2 | 17781; 17790 | .82 (.47, 1.0) | .25 (.09, .57) | | | | .16 (.10, .25) |
| 3 | 17778; 17787 | .21 (.08, .60) | .18 (.07, .44) | .58 (.24, .92) | | | .16 (.11, .26) |
| 4 | 17791; 17785 | .57 (.34, .88) | .19 (.08, .51) | | .21 (.08, .46) | | .18 (.11, .25) |
| 5 | 17779; 17781 | .84 (.5, 1.05) | .24 (.09, .56) | | | .11 (.05, .27) | .16 (.11, .25) |
| 6 | 17777; 17776 | .27 (.10, .61) | .18 (.07, .45) | .22 (.12, .66) | .18 (.07, .45) | .13 (.06, .29) | .16 (.11, .26) |
| Neuroticism | | | | | | | |
| 1 | 13543; 13540 | .42 (.32, .55) | | | | | .11 (.07, .19) |
| 2 | 13524; 13536 | .33 (.20, .45) | .14 (.06, .25) | | | | .11 (.07, .18) |
| 3 | 13532; 13535 | .14 (.07, .29) | .10 (.06, .23) | .20 (.10, .36) | | | .10 (.07, .18) |
| 4 | 13524; 13523 | .29 (.16, .41) | .12 (.06, .25) | | .13 (.06, .23) | | .12 (.07, .18) |
| 5 | 13531; 13529 | .31 (.2, .43) | .12 (.06, .25) | | | .15 (.05, .28) | .11 (.07, .17) |
| 6 | 13524; 13510 | .14 (.08, .26) | .10 (.05, .21) | .13 (.07, .27) | .10 (.06, .22) | .13 (.06, .30) | .11 (.07, .17) |
| Agreeableness | | | | | | | |
| 1 | 10129; 10098 | .95 (.72, 1.2) | | | | | .36 (.24, .55) |
| 2 | 10134; 10088 | .73 (.47, 1.1) | .19 (.09, .49) | | | | .40 (.25, .56) |
| 3 | 10124; 10126 | .23 (.08, .65) | .15 (.08, .40) | .56 (.23, .87) | | | .38 (.24, .57) |
| 4 | 10123; 10125 | .67 (.37, .95) | .16 (.08, .49) | | .19 (.08, .40) | | .38 (.24, .58) |
| 5 | 10091; 10115 | .70 (.46, 1.0) | .20 (.08, .51) | | | .15 (.08, .46) | .34 (.23, .52) |
| 6 | 10122; 10121 | .26 (.13, .68) | .19 (.09, .42) | .36 (.09, .65) | .17 (.07, .36) | .18 (.06, .44) | .34 (.24, .54) |
| Intellect | | | | | | | |
| 1 | 8149; 8149 | .48 (.35, .64) | | | | | .24 (.15, .37) |
| 2 | 8149; 8149 | .31 (.17, .49) | .21 (.09, .39) | | | | .28 (.15, .37) |
| 3 | 8087; 8136 | .15 (.08, .35) | .19 (.07, .33) | .23 (.09, .38) | | | .21 (.15, .35) |
| 4 | 8144; 8148 | .29 (.13, .45) | .18 (.08, .42) | | .12 (.05, .23) | | .27 (.13, .37) |
| 5 | 8131; 8123 | .33 (.16, .48) | .23 (.07, .39) | | | .15 (.06, .34) | .18 (.13, .34) |
| 6 | 8144; 8143 | .17 (.08, .33) | .16 (.06, .32) | .14 (.06, .30) | .12 (.05, .23) | .14 (.07, 33) | .22 (.13, .35) |
| Subjective well-being | | | | | | | |
| 1 | 4222; 4195 | .92 (.65, 1.3) | | | | | .69 (.43, .96) |
| 2 | 4174; 4234 | .64 (.31, 1.0) | .29 (.08, .76) | | | | .65 (.43, .98) |
| 3 | 4212; 4234 | .21 (.09, .68) | .19 (.07, .53) | .49 (.17, .90) | | | .62 (.44, 1.0) |
| 4 | 4230; 4247 | .56 (.17, .83) | .28 (.08, .63) | | .19 (.08, .55) | | .67 (.44, 1.0) |
| 5 | 4249; 4228 | .72 (.31, 1.1) | .21 (.07, .69) | | | .20 (.06, .58) | .53 (.40, .95) |
| 6 | 4242; 4217 | .32 (.10, .58) | .23 (.06, .50) | .20 (.10, .62) | .23 (.07, .50) | .25 (.09, .57) | .67 (.43, 1.0) |

Table 4.4: Variance components and model fit criteria. DIC = deviance information criterion, with values from 2 runs of each model. $V_{\mathrm{E}}$ = unique environment variance, $V_{\mathrm{ID}}$ = individual variance, $V_{\mathrm{A}}$ = additive genetic variance, $V_{\mathrm{D}}$ = nonadditive (dominance) genetic variance, $V_{\mathrm{M}}$ = maternal environment variance, $V_{\mathrm{Z}}$ = zoo environment variance, $V_{\mathrm{J}}$ = rater variance. Residual variance, $V_{\mathrm{R}}$, fixed at 1 in all models. The first variance component column gives $V_{\mathrm{ID}}$ for model 1 and $V_{\mathrm{E}}$ for all other models. Posterior modes of each estimate are given with 95% credible intervals in parentheses.

| Model | $h^2 = V_A/V_{RPT}$ | $d^2 = V_D/V_{RPT}$ | $m^2 = V_M/V_{RPT}$ | $z^2 = V_Z/V_{RPT}$ | $e^2 = V_E/V_{RPT}$ | $D_\alpha = \frac{V_D}{V_A+V_D}$ |
|---|---|---|---|---|---|---|
| Extraversion | | | | | | |
| 2 | .30 (.13, .53) | | | | .70 (.47, .87) | |
| 3 | .23 (.13, .45) | .32 (.17, .55) | | | .38 (.18, .60) | .63 (.34, .80) |
| 4 | .25 (.11, .46) | | .19 (.09, .29) | | .51 (.37, .75) | |
| 5 | .22 (.11, .46) | | | .17 (.08, .30) | .54 (.34, .73) | |
| 6 | .16 (.08, .33) | .20 (.09, .40) | .13 (.07, .24) | .13 (.07, .28) | .29 (.09, .41) | .51 (.28, .77) |
| Dominance | | | | | | |
| 2 | .21 (.07, .49) | | | | .79 (.51, .93) | |
| 3 | .22 (.08, 42) | .35 (.18, .70) | | | .27 (.11, .60) | .73 (.45, .91) |
| 4 | .19 (.07, .42) | | .17 (.09, .38) | | .60 (.31, .74) | |
| 5 | .18 (.08, .44) | | | .09 (.05, .22) | .71 (.43, .82) | |
| 6 | .15 (.06, .32) | .21 (.09, .48) | .20 (.06, .33) | .09 (.04, .20) | .19 (.08, .45) | .73 (.34, .87) |
| Neuroticism | | | | | | |
| 2 | .30 (.13, .50) | | | | .70 (.50, .87) | |
| 3 | .22 (.12, .42) | .36 (.19, .58) | | | .38 (.15, .55) | .69 (.43, .83) |
| 4 | .21 (.11, .42) | | .24 (.11, .39) | | .49 (.29, .66) | |
| 5 | .23 (.11, .40) | | | .25 (.12, .41) | .48 (.34, .68) | |
| 6 | .15 (.07, ) | .17 (.10, ) | .16 (.09, ) | .18 (.10, ) | .24 (.10, ) | .57 (.34, .77) |
| Agreeableness | | | | | | |
| 2 | .18 (.08, .43) | | | | .82 (.57, .92) | |
| 3 | .22 (.06, .38) | .52 (.17, .69) | | | .24 (.12, .60) | .78 (.45, .89) |
| 4 | .14 (.08, .41) | | .14 (.07, .33) | | .64 (.38, .8) | |
| 5 | .19 (.07, .40) | | | .20 (.07, .31) | .61 (.36, .77) | |
| 6 | .14 (.06, .30) | .19 (.07, .46) | .13 (.05, .24) | .15 (.06, .29) | .27 (.09, .47) | .61 (.30, .83) |
| Intellect | | | | | | |
| 2 | .35 (.21, .68) | | | | .65 (.32, .79) | |
| 3 | .29 (.14, .52) | .28 (.14, .53) | | | .29 (.13, .55) | .52 (.27, .78) |
| 4 | .28 (.13, .57) | | .20 (.09, .33) | | .43 (.21, .65) | |
| 5 | .23 (.14, .53) | | | .22 (.10, .40) | .41 (.21, .64) | |
| 6 | .16 (.08, .35) | .15 (.08, .34) | .14 (.06, .25) | .21 (.09, .35) | .18 (.09, .38) | .51 (.23, .72) |
| Subjective well-being | | | | | | |
| 2 | .18 (.09, .64) | | | | .82 (.36, .91) | |
| 3 | .24 (.07, .47) | .38 (.15, .65) | | | .24 (.11, .60) | .78 (.37, .89) |
| 4 | .19 (.08, .51) | | .26 (.08, .47) | | .47 (.20, .72) | |
| 5 | .18 (.05, .52) | | | .16 (.07, .38) | .54 (.25, .77) | |
| 6 | .15 (.04, .33) | .21 (.05, .39) | .19 (.06, .34) | .14 (.07, .34) | .17 (.07, .40) | .55 (.25, .84) |

Table 4.5: Heritability ($h^2$) and variance partition coefficients for nonadditive (dominance) genetic ($d^2$) and maternal ($m^2$), zoo ($z^2$) and unique ($e^2$) environments calculated relative to the repeatable variance, $V_{RPT} = V_A + V_D + V_M + V_Z + V_E$. $D_\alpha$ = proportion of nonadditive genetic variance.

| | $h^2$ | | | $H^2$ | | |
|---|---|---|---|---|---|---|
| | Combined | Bornean | Sumatran | Combined | Bornean | Sumatran |
| Extraversion | .23 (.13, .45) | .29 (.10, .55) | .22 (.09, .45) | .66 (.41, .86) | .67 (.43, .89) | .73 (.40, .87) |
| Dominance | .22 (.08, 42) | .26 (.08, .54) | .19 (.06, .46) | .78 (.49, .93) | .72 (.36, .91) | .78 (.43, .93) |
| Neuroticism | .22 (.12, .42) | .25 (.13, .53) | .29 (.14, .52) | .69 (.48, .85) | .68 (.40, .85) | .70 (.50, .87) |
| Agreeableness | .22 (.06, .38) | .25 (.09, .55) | .16 (.07, .43) | .82 (.41, .91) | .69 (.43, .90) | .71 (.40, .92) |
| Intellect | .29 (.14, .52) | .27 (.10, .53) | .28 (.15, .58) | .69 (47, .86) | .64 (.38, .88) | .73 (.46, .89) |
| SWB | .24 (.07, .47) | .19 (.06, .60) | .23 (.06, .48) | .77 (.44, .92) | .72 (.32, .90) | .78 (.40, .92) |

Table 4.6: Heritability estimates for the combined sample and each species. Posterior modes of narrow-sense, $h^2 = V_A/(V_A + V_D + V_E)$, and broad sense, $H^2 = (V_A + V_D)/(V_A + V_D + V_E)$, heritability with 95% credible intervals in parentheses.

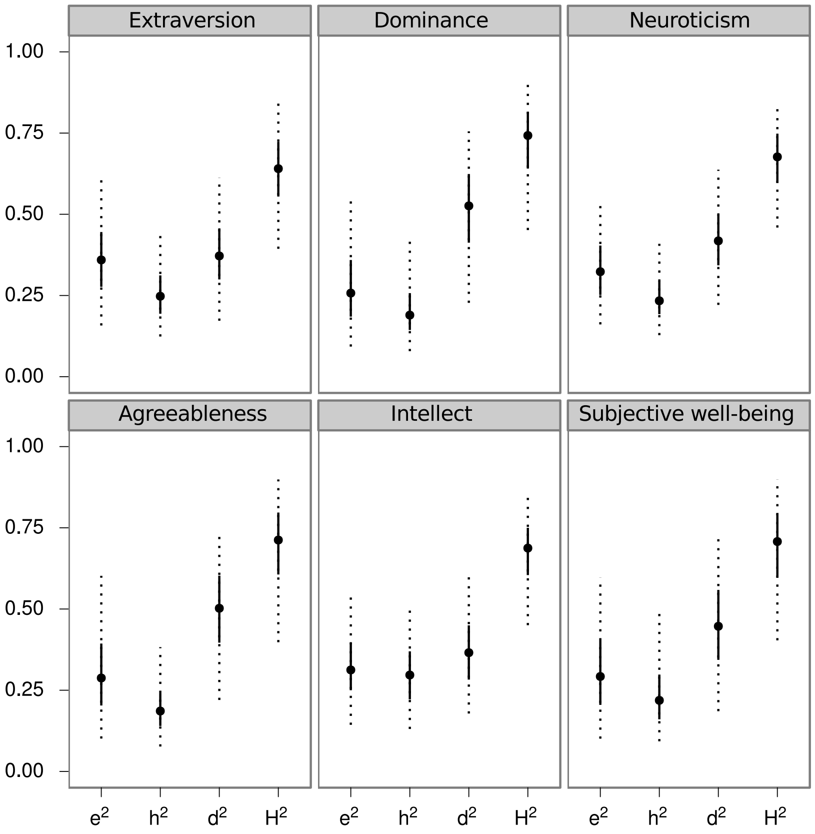

Figure 4.3: Variance proportion coefficients for repeatable variance. Points indicate posterior modes of each estimate with 50% credible intervals in solid and 95% credible intervals in dotted lines. $h^2$ = (narrow-sense) heritability, $d^2$ = dominance, $H^2$ = broad-sense heritability, $e^2$ = unique environment.

I also detected maternal environment effects. In addition to behaviors of mothers such as rearing-style, the maternal environment could include the effects of prenatal factors and maternal genes that influence offspring phenotype apart from inherited genes that the offspring expresses directly (Lynch & Walsh, 1998; A. J. Wilson & Nussey, 2009). Variance from the zoo environment could likewise arise from any effect that makes the orang-utans in the same zoo more similar to each other in personality including differences in social dynamics, group composition, zoo enrichment, or shared biases of raters within each zoo.

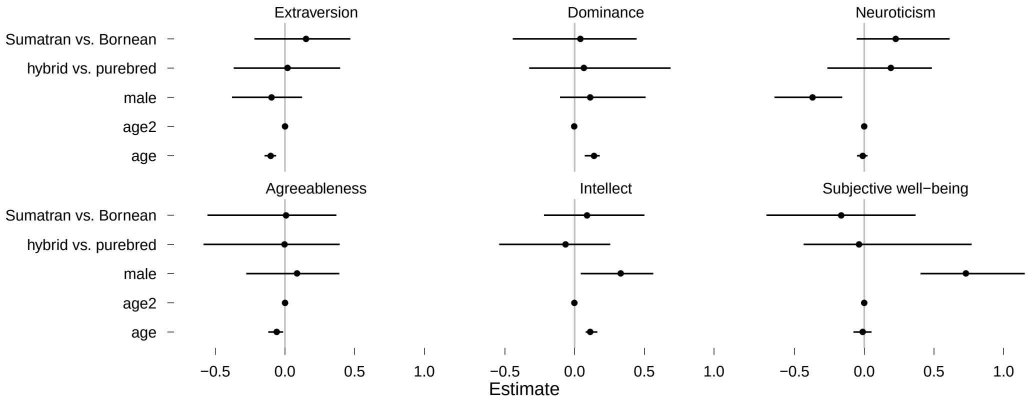

Figure 4.4: Fixed effects from Bayesian animal model (posterior mode and 95% uncertainty intervals).

### Age, sex, and species differences

There was some evidence that, compared to Bornean orang-utans, Sumatran orang-utans in this sample were higher in neuroticism ($b$ = .22, CI = -.05, .61; see Figure 4.4). Male orang-utans were lower in neuroticism and higher in intellect and subjective well-being. Age was also associated with lower extraversion and agreeableness and higher dominance and intellect.

### Genetic structure

While there was uncertainty in the additive genetic ($r_A$), nonadditive genetic ($r_D$), and unique environment ($r_E$) correlations between personality and subjective well-being (Table 4.7, Figure 4.5), the effects all went in the same direction (negative for neuroticism and positive for extraversion, dominance, agreeableness, and intellect). From these models I was also able to derive estimates of the phenotypic correlations among personality and subjective well-being that controlled for covariances among traits attributable to rater effects: extraversion $r_P$ = .24 (95% CI = .05, .37), dominance .13 (95% CI = -.09, .28), neuroticism -.22 (95% CI = -.38, -.05), agreeableness .20 (95% CI = .05, .40), and intellect .18 (95% CI = .02, .36). There was also some evidence for a positive dominance genetic and unique environment correlation between agreeableness and extraversion (Table 4.7, Figure 4.6).

Because studies of humans and chimpanzees found that all or most of the genetic variance

Additive genetic $r_A$

| | Extraversion | Dominance | Neuroticism | Agreeableness | Intellect |
|---|---|---|---|---|---|
| Dominance | .14 (-.24, 37) | | | | |
| Neuroticism | -.01 (-.24, .37) | -.04 (-.30, .33) | | | |
| Agreeableness | .17 (-.12, .52) | -.20 (-.49, .19) | -.03 (-.38, .28) | | |
| Intellect | .08 (-.22, .39) | .17 (-.11, .50) | -.10 (-.42, .16) | .01 (-.38, .28) | |
| SWB | .23 (-.15, .45) | .13 (-.21, 43) | -.16 (-.47, .13) | .12 (-.19, .47) | .10 (-.18, 46) |

Nonadditive (dominance) genetic $r_D$

| | Extraversion | Dominance | Neuroticism | Agreeableness | Intellect |
|---|---|---|---|---|---|
| Dominance | .13 (-.20, .45) | | | | |
| Neuroticism | -.03 (-.29, .30) | .03 (-.29, .31) | | | |
| Agreeableness | .29 (-.02, .55) | -.22 (-.55, .12) | -.13 (-.48, .13) | | |
| Intellect | .15 (-.17, .40) | .20 (-.15, .47) | -.16 (-.47, .10) | .06 (-.23, .39) | |
| SWB | .22 (-.09, .51) | .14 (-.24, .44) | -.17 (-.48, .07) | .20 (-.07, .56) | .25 (-.11, .47) |

Unique environment $r_E$

| | Extraversion | Dominance | Neuroticism | Agreeableness | Intellect |
|---|---|---|---|---|---|
| Dominance | .16 (-.21, .44) | | | | |
| Neuroticism | -.03 (-.30, .31) | -.02 (-.31, 30) | | | |
| Agreeableness | .31 (.02, .59) | -.21 (-.52, .14) | -.16 (-.48, .13) | | |
| Intellect | .12 (-.12, .47) | .13 (-.18, .44) | -.15 (-.45, .11) | .16 (-.19, .46) | |
| SWB | .26 (-.07, .51) | .02 (-.30, .40) | -.25 (-.50, .04) | .30 (-.06, .54) | .20 (-.10, .50) |

Rater $r_J$

| | Extraversion | Dominance | Neuroticism | Agreeableness | Intellect |
|---|---|---|---|---|---|
| Dominance | .11 (-.15, .30) | | | | |
| Neuroticism | -.10 (-.30, .19) | .36 (.12, 55) | | | |
| Agreeableness | .41 (.16, 57) | -.10 (-.40, 10) | -.21 (-.38, .10) | | |
| Intellect | .20 (.06, .51) | -.17 (-.35, .13) | -.44 (-.54, -.09) | .30 (.04, .50) | |
| SWB | .24 (.00, .46) | -.17 (-.39, .13) | -.36 (-.55, -.09) | .30 (.06, .55) | .41 (.16, 61) |

Table 4.7: Genetic, environmental, and rater correlations. Parameter estimates from Model 2 with 95% credible intervals in parentheses. SWB = subjective well-being.

underlying subjective well-being was shared with personality, I calculated the conditional genetic variance of subjective well-being. The conditional genetic variance (Hansen & Houle, 2008) is genetic variance that is unique to subjective well-being, excluding variance from genetic factors that also influence the personality domains defined as

$$c(y|\mathbf{x}) = G_y - \mathbf{G}_{y\mathbf{x}}\mathbf{G}_{\mathbf{x}}^{-1}\mathbf{G}_{\mathbf{x}y},$$

where $c(y|\mathbf{x})$ is the conditional genetic variance of trait $y$ given traits $\mathbf{x}$, $\mathbf{G}_{y\mathbf{x}}$ and $\mathbf{G}_{\mathbf{x}y}$ are vectors of the genetic covariance between $y$ and the other traits, and $G_{\mathrm{x}}$ is the genetic covariance matrix of the other traits. Fifteen percent (95% credible interval [CI] = .03, .38) of the additive genetic and 19% (95% CI = .05, .44) of the nonadditive genetic variance in subjective well-being was shared with personality.

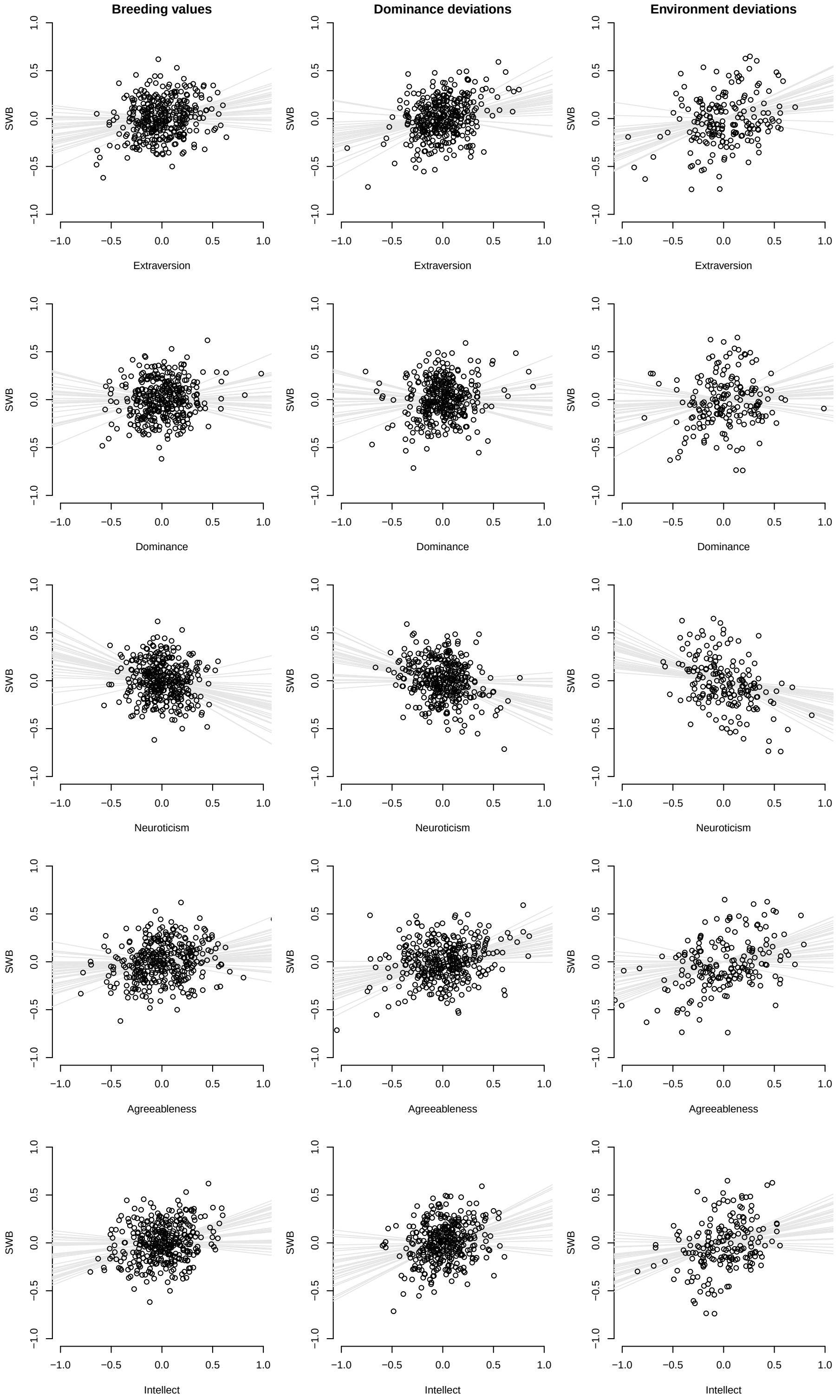

Figure 4.5: Random effects for personality vs subjective well-being for breeding values (left column), dominance deviations (center column), environment deviations (right column). Points are posterior modes of each random effect. Regression lines plotted using draws sampled from the posterior distribution of the variance-covariance matrices.

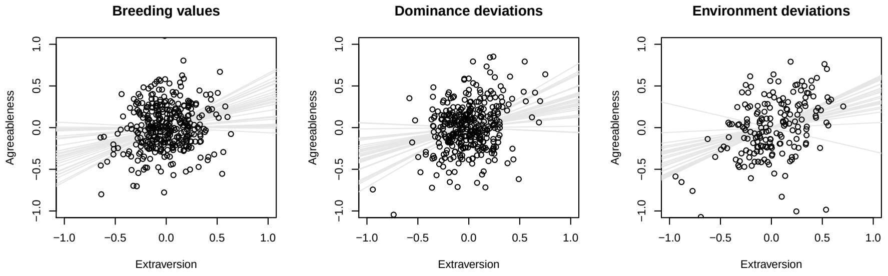

Figure 4.6: Random effects for extraversion vs agreeableness.

## 4.6 Psychometrics and reliability analysis

Because the animal model analysis incorporated a measurement component and rater effects that accounted for both the variances of and covariances among the personality traits, it was possible to conduct psychometric inferences from the genetic model. I calculated the reliability of the personality and subjective well-being assessments as intraclass correlation coefficients (ICCs) in two ways using estimates from the genetic models. First, to estimate the consistency of the items making up each personality domain or subjective well-being, I calculated the ratio of the animal variance (that is, the repeatable variance from genetic or environmental effects that are assigned to individual animals) plus the rater variance over the residual and link function variances

$$\mathrm{IC}_{\mathrm{scale}} = \frac{V_{\mathrm{RPT}} + V_{\mathrm{J}}}{V_{\mathrm{RPT}} + V_{\mathrm{J}} + V_{\mathrm{R}} + 1}$$

where $V_{\mathrm{RPT}}$ is the repeatable variance, $V_{\mathrm{J}}$ is the rater variance, $V_{\mathrm{R}}$ is the error variance (including animal × rater interaction), and the final 1 is from the variance of the probit distribution used to model the ordered categorical scores. This ICC is on the scale of the raw data and represents the expected correlation between an individual's scores on two items made by the same rater. Although it is not the same as Cronbach's $\alpha$, it specifies the degree to which the rating of an individual on one item generalized to other items on that scale and is therefore a type of model-derived estimate of internal consistency. Second, I calculated reliability on the latent scale as $\mathrm{IC}_{\mathrm{subject}} = V_{\mathrm{RPT}}/(V_{\mathrm{RPT}} + VJ)$ to represent the expected correlation between two assessments of the same individual's personality domain by different raters. This ICC estimates interrater agreement and is similar to ICC(2,1) (Shrout & Fleiss, 1979).

| | Consistency | Reliability |
|---|---|---|
| Extraversion | .28 (.24, .33) | .81 (.71, .87) |
| Dominance | .38 (.34, .44) | .87 (.81, .91) |
| Neuroticism | .23 (.20, .28) | .86 (.73, .90) |
| Agreeableness | .41 (.38, .48) | .77 (.64, .82) |
| Intellect | .31 (.25, .35) | .73 (.60, .83) |
| SWB | .49 (.42, .54) | .60 (.50, .74) |

Table 4.8: Scale consistency and reliability of assessments by multiple raters. Parameter estimates with 95% confidence intervals in parentheses. SWB = subjective well-being. Domain-scale consistency calculated as $(V_{RPT} + V_J)/(V_{RPT} + V_J + V_R + 1)$; latent reliability calculated as $V_{RPT}/(V_{RPT} + V_J)$ where $V_{RPT} = V_A + V_D + V_E$.

The intraclass correlation coefficient from the animal and rater variances on the scale of the raw data ranged from .31 for intellect to .41 for agreeableness and was .49 for subjective well-being (Table 4.8). These coefficients represents the expected correlation between two items assessed on the same animal by the same rater and can act as a form internal consistency of items making up each scale, Combining information from multiple raters produced highly reliable assessments of latent personality values which ranged from .73 for intellect to .87 for dominance. Reliability of subjective well-being on the latent scale was .60, and thus acceptable. Rater effects contributed to the observed correlations among personality and subjective well-being scores (Table 4.7). After decomposing the covariance among personality and subjective well-being into animal components (genetic and environment) and a rater component, raters who rated an orang-utan as higher on extraversion agreeableness, and intellect and lower on dominance and neuroticism also tended to rate that orang-utan as higher on subjective well-being. Notably, the estimate of rater effects for the correlation between dominance and subjective well-being correlation tended to go in the opposite direction from genetic and unique environmental estimates. There were also detectable rater effects on the extraversion–agreeableness, extraversion–intellect, neuroticism–intellect, and agreeableness–intellect correlations.

These results show the importance of conditioning on rater effects and other sources of measurement error when analyzing questionnaire-based assessments of animal personality. To wit, while raters were consistent in the scores they assigned to individual subjective well-being items, the interrater reliability of subjective well-being was lower than for the personality traits, which is consistent with the subjective well-being factor scores having a lower interrater agreement than those of personality (Weiss et al., 2006). Also, while rater variance was small compared to genetic and environmental variance, as shown by the high interrater reliability estimates, raters contributed to some of the covariance among personality traits and between personality traits and subjective well-being. Rater covariance effects that go in the same direction as the animal effects would tend to inflate the magnitude of the observed correlations. Thus, I found that the phenotypic correlations as estimated by the genetic and environmental covariances between subjective well-being and extraversion, neuroticism, and agreeableness were smaller than the observed correlations previously reported (Weiss et al., 2006), which were inflated by covariance introduced by the raters. The opposite was true for dominance; the animal and rater covariances went in opposite directions and cancelled out, explaining why no correlation was found between dominance and subjective well-being at the phenotypic level (Weiss et al., 2006).

While my analysis modeled rater effects or perceptions that introduce correlations among the personality and subjective well-being dimensions, it does not address to what extent the five personality dimensions and one SWB dimension themselves are products of rater beliefs and perceptions. The generalizability of chimpanzee personality dimensions across samples living in different environments (King et al., 2005; Weiss et al., 2007) and raters with different cultural backgrounds (Weiss et al., 2009), their relationship with observed behaviors (Pederson et al., 2005), and the recoverability when rater effects on chimpanzee and orang-utan personality structure have been removed (Weiss et al., 2012) indicate that the structure of these nonhuman primate personality dimensions is inconsistent with them being solely an artifact of human perception. Orang-utan SWB has also shown external validity through its relationship with mortality (Weiss, Adams, & King, 2011). Furthermore, although similar, the personality structure of orang-utans is not identical to that of humans and the personality structure of humans, chimpanzees, and orang-utans differ in ways consistent with phylogeny (e.g., humans and chimpanzees share a personality domain, conscientiousness, that is absent in orang-utans) and social structure (e.g., the primacy of the chimpanzee dominance domain) (Weiss & Adams, 2008). However, even factor models of human personality can be understood in terms of our faculties for social perception (Srivastava, 2010) and thus rater-based assessments of nonhuman primate personality may miss individual differences that are entirely absent in humans (Uher, 2008b). Understanding the full genetic structure of orang-utan personality may very well require multiple methods for measuring personality variation.

## 4.7 Genetics of personality and subjective well-being

I found that the most genetic variation in orang-utan personality and subjective well-being could be assigned to nonadditive genetic effects. This is consistent with the results from human personality research (Eaves et al., 1998; Keller et al., 2005; Pilia et al., 2006; Rettew et al., 2008). The narrow-sense heritability estimates of about 20% were likewise consistent with human findings that used a similarly specified, pedigree-based animal model (Pilia et al., 2006). This suggests that a high proportion of nonadditive genetic variance may be a common feature of personality in primates under long-term directional or stabilizing selection and not exclusively the result of evolutionary processes unique to the human lineage. The low estimates of shared zoo environment effects on personality match results from chimpanzees (Weiss et al. 2000) and are consistent with findings from human personality research on the effect of the shared (family) environment (Bouchard & Loehlin, 2001).

While this study lacked sufficient power to get precise estimates of genetic correlations between personality and subjective well-being, the direction of the correlations matched results from chimpanzees (Weiss et al., 2002) and humans (Weiss et al., 2008). Human and great ape subjective well-being may therefore have a common genetic basis in personality traits related to emotional stability and social assertiveness. However, unlike chimpanzees and humans, less than half of the genetic variance in orang-utan subjective well-being could be explained by genetic effects shared with personality. Thus, while the personality–subjective well-being link is likely ancestral in great apes, the greater genetic overlap in humans and chimpanzees may be a derived characteristic. Alternatively, personality and subjective well-being may have become more genetically uncoupled as orang-utans diverged from these species.

### Evolutionary context

The quantitative genetic structure of personality within one species cannot act as strong evidence for past and current evolutionary scenarios (Keller, 2007; Gangestad, 2011). However, finding similar patterns of additive versus nonadditive genetic variation in human and orang-utan personality suggests that similar processes of mutation and selection maintain variation in both species. A high proportion of nonadditive genetic variance is consistent with long-term selection on a trait (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999) and while it may be a sign of strong selection reducing the additive genetic variance (Stirling et al., 2002) it is not indicative of recent selection (*pace* Rushton et al., 2008; Figueredo & Rushton, 2009; Penke, Denissen, & Miller, 2007).[2] The recentness of novel selective pressures operating on human psychological characteristics since the agricultural revolution ($\approx$ 10 kya), which we interpret as the meaning of 'recent' in this context (see Figueredo et al., 2011), is a matter of perspective, as they are long-term compared to contemporary selection (Dingemanse & Réale, 2005; Stearns et al., 2010) but recent relative to evolution before the split between human and chimpanzee lineages. Whether the large nonadditive genetic variance in orang-utan and human personality evolved independently or is the result of long-term selection common in both species ancestor could be investigated by estimating dominance or epistatic genetic sources of variation in chimpanzees. While we did not have the power to explore species differences in genetic structure between Bornean and Sumatran orang-utans, future studies of orang-utans or other closely related species (such as in macaques) or subspecies (such as in chimpanzees) may be informative. Such studies may also lead to an understanding of the genetic underpinnings of species divergence in personality dimensions, such as whether the genetic correlation we found between extraversion and agreeableness is related to the blend, at the phenotypic level, of these two domains in rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). Furthermore, the presence of nonadditive genetic variance in bird personality (van Oers, Drent, Jong, & Noordwijk, 2004) suggests that this phenomenon may be a more general part of how personality evolves.

### Happiness

The genetic correlation between neuroticism and subjective well-being reveals that happiness is not just an outcome of an animal's situation but shares a common genetic cause with personality (Weiss et al., 2002). There are several evolutionary explanations for the connection

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[2] My best guess as to the inversion of the logic to arrive at "$V_A < V_{NA}$ implies recent selection" may be attributed to Penke, Denissen, and Miller (2007, p 556), who write "Traits with a recent history of selection, by contrast, should show a significant absolute and proportional amount of $V_{\mathrm{NA}}$." This may be a misreading of Stirling et al. (2002, p 279): "we expect the [full-sib breeding design] heritability estimates should be higher on average than the [half-sib, maximum likelihood, and regression estimates] and interpret the difference between them as an index of the **strength of recent selection**" (emphasis added). It seems that the 'strength of' modifier was dropped in the transmission of this idea from evolutionary genetics into evolutionary psychology.

between personality and subjective well-being, but the phenotypic and genetic correlations among positive affect and boldness-like personality domains across great apes suggest that the personality–well-being nexus (or mental quality) is an ancestral feature. Subjective well-being and personality have evolved as a set in great apes. Any explanation of the relationship between personality and subjective well-being must be consistent with species differences in personality and with the maintenance of within-species genetic variation.

Weiss et al. (2002) suggested that happiness may be a fitness indicator in chimpanzees and humans, a cue that individuals use to assess and choose mates. Happiness in this case would be an honest signal of underlying fitness that is hard to fake. Female orang-utans prefer males who can acquire more resources (Schürmann & Hooff, 1986; Fox, 2002), so if male dominance relates to resource acquisition, happiness may act as a similar sexual signal through its correlation with dominance. This requires that orang-utans are able to detect each other's happiness (Weiss et al., 2002). However, because socially dominant males advertise their status through physical appearance (cheek flanges) and vocalisations (MacKinnon, 1974), they may not need a subtle behavioural signal such as happiness.

An alternative, though not mutually exclusive, explanation is that orangutan subjective well-being is, with neuroticism, related to social striving, where neuroticism captures reactivity to social stressors (Denissen & Penke, 2008b) and low subjective well-being would prompt an individual to improve their social standing (Nettle, 2006). In the wild, Sumatran orang-utans associate in larger social groups (van Schaik, 1999) and thus may need to be more sensitive to social cues of inclusion. Alternative ecological explanations concerning attentiveness to non-social cues, such as vigilance towards predators (which are absent on Borneo, though absence of predators does not necessarily remove antipredator vigilance, e.g., Byers, 1998) or risk-avoidance during seasonal food shortages (MacKinnon, 1974; Knott, 1998), would need to be evaluated in wild populations.

### Species differences

The lack of clear mean-level differences in other personality dimensions between species is not consistent with known variation in orang-utan social organisation. Orang-utans normally avoid each other to reduce feeding competition but they come together by necessity to mate and to forage in rich food patches (van Schaik, 1999). Access to fruit is resolved through contest competition (Utami, Wich, Sterck, & Hooff, 1997) so it may be beneficial to be slightly more stingy (higher in dominance and lower in agreeableness). Sumatran orang-utans also have larger behavioural repertoires and show more complex cultural innovations in the wild (Schaik et al., 2003), which might manifest as differences in intellect. Tool use and other behaviours are facilitated by the more extensive social learning that comes from associating with larger groups. Thus, apart from neuroticism, species differences in behavior and social organisation are not reflected in rater assessments of personality in captive settings.

Subjective well-being in orang-utans might be an aspect of coping that helps the individual make decisions in stressful situations and is tied in to personality as part of a suite of behavioral adaptations. Nesse (2000) and Nettle (2008) have suggested that for humans depression and, more generally, negative affect are adaptations to deal with unfavorable situations where the organism needs to avoid risky actions and not expend too much energy. Being an orang-utan is, energetically speaking, exceedingly expensive (Knott, 1998). Orang-utans also experience severe seasonality in fruit availability which requires them to adjust their diet and rely on fat reserves stored up during times of plenty (MacKinnon, 1974; Knott, 1998). During these shortages, orang-utans face starvation and an increase in disease susceptibility. In such cases, higher neuroticism might be beneficial if the associated low mood leads individuals to take fewer risks during fruit shortages. Additionally, personality domains, such as dominance, may relate to the ability to obtain sufficient fat reserves during times of high fruiting.

Although a fitness trade-off with neuroticism and subjective well-being between the moderation of risk-taking in poor situations versus stress consequences in other situations could maintain variation within species (Nettle, 2006), the risk-avoidance hypothesis is largely inconsistent with higher mean neuroticism among Sumatran orang-utans. The reason is that, while both species experience fruit shortages in the wild, shortages are less severe and less frequent on Sumatra (Marshall et al., 2008). If being slightly more prone to a low mood state is an adaptation to deal with resource deficits during fruit shortages, we would expect that Bornean rather than Sumatran orang-utans would be higher in neuroticism and lower in subjective well-being. One way to resolve this would be if Bornean orang-utans have lower neuroticism to avoid becoming overexcited during periods of extremely poor food availability. Theory suggests that an organism should switch to a risk-averse strategy under poor conditions but should be willing to take more risks when the situation is extremely grim (Nettle, 2006). The problem with this explanation is that it would require the personality measure to be sensitive to this sort of difference even when orang-utans live in a resource rich and stable captive environment. This does not rule out fluctuating selection from year-by-year heterogeneity in resource availability as a process maintaining variation within each species (Dingemanse et al., 2004) when risk aversion would be favored only during particularly severe food shortages.

### Into the wilds of personality

Orang-utans offer an important case for weighing social and ecological explanations of personality and variation in subjective well-being because differences between Sumatran and Bornean orang-utans in morphology, behaviour, and social organisation follow clear geographical and ecological gradations (van Schaik, Marshall, & Wich, 2008). Individual behavioural variation can be related to socioecological variables that differ in quantity rather than kind. While proclivities toward social striving and competitiveness are apparent in captivity, other species-level differences may be salient in the wild. If species differences in orang-utan personality and subjective well-being also manifest in non-captive populations, then I hypothesise that personality differences will occur among the Bornean subspecies that vary along the same geographical gradient in group size, diet, and cultural repertoire that explains most between-species differences (van Schaik et al., 2008). Yet despite differences between species, within species variation in personality and subjective well-being is still apparent. Such differences have also been noted in the wild where, for example, orang-utan females with infants vary in social tolerance (van Schaik, 1999). The results here show that some of this individual variation is genetic. Comparing orang-utans on the species and subspecies levels will be particularly useful for exploring how individual behavioural variation persists as great apes migrate, speciate, and adapt to local conditions and for understanding the ecological and social parameters that shape primate personality variation.

Quantitative genetic models were originally devised for the purposes of animal breeding (Falconer & Mackay, 1996; Lynch & Walsh, 1998) but are now increasingly adapted for use in evolutionary studies (Kruuk, 2004). Multilevel models, such as the animal model, are particularly useful for making genetic inferences on personality in nonhuman primates, whether in captivity or the wild, because they can tease apart genetic, environment, and measurement effects. Nonhuman primates tend to share an environment (enclosure or troop) with their close relatives so appropriate modelling is also needed to avoid subtle instances of pseudoreplication, as observations of different individuals may not be completely independent. For example, if a trait is heritable then two siblings will tend to deviate from the mean in the same direction, and their residual values in a linear regression would be correlated. Genetic modeling accounts for this nonindependence and thus help make better inferences about phenotypic correlations among traits in the population. I have shown here how the measurement process can also be incorporated into an animal model to handle some of the effects that raters will have. Finally, the results reveal that the total genetic variance in primate personality dimensions may be considerably higher than heritabilities would suggest because of the presence of nonadditive genetic variance. Because nonhuman primates tend to have multiple mates throughout their lives, genetically-informed samples will contain a proportion of half siblings. As half siblings resemble their relatives through additive and interaction but not dominance genetic variance (Lynch & Walsh, 1998), their inclusion can help tease apart additive, dominance, and epistatic effects. Nonhuman primates thus make an excellent study group for the evolution of the genetic structure of personality.

# Chapter 5

# The genotypic countergambit to contemporary selection on personality

## 5.1 Adaptationist programs and selectionist approaches

Evolutionary studies of psychological traits typically focus on discerning the processes that have led to our current set of behavioral adaptations (Tooby & Cosmides, 1990b). This adaptationist (or optimality) approach attempts to determine the adaptive function of a particular phenotype; that is, what features of the environment have, through natural selection over thousands of generations, shaped the current composition and function of the phenotype and how it leads to maximizing fitness. Both the standard Evolutionary Psychology approach (Tooby & Cosmides, 1990b) and more recent incorprations of evolutionary genetics into psychological research (Penke, Denissen, & Miller, 2007) have been criticized for placing too much emphasis on 'steady states' of evolutionary processes (T. C. Bates, 2007; Miller, 2011). These approaches focus on neutrality, balancing selection, and mutation-selection balance as alternative explanations for the maintenance of variation in personliaty and assume that the environment or sets of environments to which a psychological trait is adapted are roughly fixed. Neutrality assumes that the psychological trait is independent of fitness while mutation-selection balance carries the unstated assumption that the fitness optimum that mutation pulls individuals away from and that selection pushes the population back toward does not need to vary. Even balancing selection, where fitness might differ across space and time, only requires an established collection of states that the environment transitions between with the population, or rather the distributions of underlying genetic factors, in hot pursuit. These explanations for the diversity of psychological traits, however, do not take into account genomic evidence that adaptive evolution in humans has been accelerating over the last 40,000 years (Hawks et al., 2007). In contrast to the *adaptationist program*, a *selectionist approach* to evolutionary psychology predicates that current selection is still shaping behaviour (Krebs & Davies, 1978; Réale & Dingemanse, 2011; Stearns et al., 2010). The goal of this approach is to characterize the direction and shape of selection pressures acting on extant populations. Under this view, evolution is not an end state but a continuously occurring process and it is therefore likely that our psychological makeup is still undergoing natural selection.

Tooby and Cosmides (1990b, p 376) chastize the selectionist approach as merely studying the "*correspondence* between present conditions and present fitness-maximizing behaviors" (emphasis in original). A correspondence approach runs into trouble if it takes whatever the current relationship between a trait and fitness happens to be and uses that to make inferences about past selection pressures that led to the adaptive design of the trait. How the trait maximized fitness in the past might not be reflected in the present if environmental conditions have changed sufficiently. While studying adaption as opposed to selection can effectively be carried out using a combination of observation and experimentation (Grafen, 1988), humans are typically not so cooperative when it comes to controlled studies of their reproductive biology.[1] The adaptationist program in Evolutionary Psychology takes it as given that there is a lag between environmental (read 'cultural') change and the population's ability to adapt. The selectionist approach, however, is actually relying on a different assumption entirely. The assumption is that a species is *never* perfectly adapted to its environment. By studying the correspondence between a trait and fitness in current populations, it is possible to measure selection on the smallest scale as the change in mean phenotype between generations. Rather than being informative of adaptive design, the selectionist approach can indicate maladaptation to the current environment and be used to predict how the population will respond to current selective pressures. This approach is necessary to understand the maintenance of genetic variation in personality traits in current environments (Réale &

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[1] Perhaps there is something here for the enterprising reality televison producer.

Dingemanse, 2011).

### Personality and fitness

The relationship between a trait and fitness is the core element in any evolutionary analysis. A basic measure of fitness is simply the number of children that one has who survive to adulthood, or lifetime reproductive success (LRS). In both developed and developing countries, personality differences are linked to differences in childbearing decisions and reproductive success, though the number of studies taking a selectionist approach to human personality is limited (Réale & Dingemanse, 2011). Australian women who were high in neuroticism and low in extraversion (or vice-versa) had more children while women who were either high or low in both dimensions had lower fitness (Eaves et al., 1990). This characterizes a fitness surface with stabilizing selection along the +E, +N axis (where the intermediate phenotype has greatest fitness) and disruptive selection along the +E, -N axis (fitness is highest at the extremes). Eaves et al. (1990) note that if you rotate extraversion and neuroticism 45° (per Gray, 1982) to yield impulsivity (+E, +N) and anxiety (-E, +N), then the fitness surface describes stabilizing selection on impulsivity and disruptive selection on anxiety. Among Sengalese women reproductive success was highest at an intermediate level of neuroticism while for men higher extraversion was associated with higher fitness (Alvergne et al., 2010). In two American samples, high extraversion and low openness to experience and neuroticism were related to increased reproductive success in both sexes while for women high agreeableness and low conscientiousness were additional predictors of high fitness (Jokela et al., 2011). Thus, all populations where a selection analysis on personality was undertaken show some signals of directional and of stabilizing selection.

### Selection gradients

Directional, stabilizing, and disruptive selection on a trait $z_i$ can be expressed as the linear combination (Lande & Arnold, 1983; Stinchcombe, Agrawal, Hohenlohe, Arnold, & Blows, 2008):

$$w = \alpha + \beta z + \frac{1}{2}\gamma z^2 + \epsilon$$

where $w$ is relative fitness, $\beta$ is the linear selection gradient (indicating directional selection), and $\gamma$ is the nonlinear selection gradient ($\gamma < 0$ indicates stabilizing selection, $\gamma > 0$ leads to

| Term | Regression estimate | Selection gradient |
|---|---|---|
| Extraversion | $b_E = .0475$ | $\beta_E = .0475$ |
| Neuroticism | $b_N = .0477$ | $\beta_N = .0477$ |
| Extraversion$^2$ | $q_{EE} = -.00072$ | $\gamma_{EE} = -.00144$ |
| Neuroticism$^2$ | $q_{NN} = -.00058$ | $\gamma_{NN} = -.00116$ |
| Extra. × Neuro. | $q_{EN} = -.00403$ | $\gamma_{EN} = -.00403$ |

Table 5.1: Coefficients from a quadratic regression of extraversion and neuroticism on fitness (Eaves et al. 1990) and the associated directional ($\beta$) and stabilizing/disruptive ($\gamma$) selection gradients.

disruptive selection). When selection gradients are estimated using a quadratic regression of the form

$$w = a + bz + qz^2$$

it is necessary to double the coefficients estimated for the quadratic term $q$ to express the proper selection gradient because the gradient represents the second derivative of fitness with respect to the phenotype (Stinchcombe et al., 2008). Thus, the quadratic regression coefficients presented by Eaves et al. (1990) do not describe the curvature of fitness surface in terms of selection gradients, even if they do properly capture the best-fit surface through extraversion and neuroticism on lifetime breeding success. When there are two traits, $z_1$ and $z_2$, the selection gradients are

$$w = \alpha + \beta_1 z_1 + \beta_2 z_2 + \frac{1}{2}\gamma_{11} z_1^2 + \frac{1}{2}\gamma_{22} z_2^2 + \gamma_{12} z_1 z_2 + \epsilon$$

and the coefficients from a quadratic regression map on to the fitness surface as $\gamma_{ii} = 2q_{ii}$ and $\gamma_{ij} = q_{ij}$. Failing to double the appropriate regression coefficients can lead to incorrect inferences about the selection surface (Stinchcombe et al., 2008). To see if this was the case with the analysis by Eaves et al. (1990), I recalculated the correct selection gradients from the published regression coefficients (Table 5.1) and compared the selection surface with the surface of best-fit of extraversion and neuroticism on reproductive success (Fig. 5.1). While the selection surface does differ from that presented by Eaves et al. (1990, Fig 2 p 567), the qualitative inference of stabilizing and disruptive selection does not change. This highlights the need to carefully consider how statistical models map on to evolutionary inferences (Stinchcombe et al., 2008).

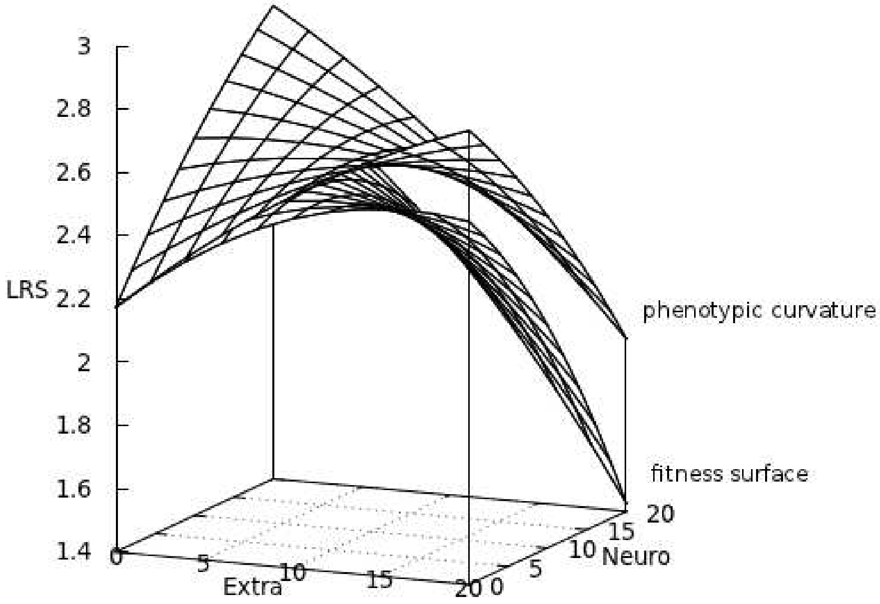


Figure 5.1: Selection surface of extraversion (Extra) and neuroticism (Neuroc) compared with best-fit surface from a quadratic regression of personality on lifetime reproductive success (LRS). After Eaves et al. (1990).

### Selection on nonhuman animal personality

Studies of the microevolution of animal personality in the wild have primarily focused on, and found, variation in selection pressures across space and time (Dingemanse & Réale, 2005; Réale & Dingemanse, 2011). For example, temporal variation in selection pressures on personality have been observed for great tits (Dingemanse et al., 2004) where the optimal level of exploration is a function of the level of intra-sexual competition for food, which fluctuates from year-to-year. Likewise, the fitness consequences of activity and boldness in red squirrels varies between seasons depending on food availability (Boon, Réale, & Boutin, 2007). Selection pressures have also been found to vary across habitats, such as when great tits that are high on exploration have the highest fitness only when population density is low (Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). Similar patterns of fluctuating or balancing selection driven by ecological variability have been found in crickets (Cade & Cade, 1992), lizards (Cote, Dreiss, & Clobert, 2008), bluebirds (Duckworth, 2006), owls (Kontiainen et al., 2009), and bighorn sheep (Réale & Festa-Bianchet, 2003). Reviewing the evidence, Réale and Dingemanse (2011) conclude that heterogeneous selection is the rule when it comes to animal personality.

### A genotypic gambit

Prior studies of personality and reproductive success in humans have estimated selection based on the covariances between phenotypes and fitness (Eaves et al., 1990; Jokela et al., 2011). However, the capacity of selection to change the population mean of personality traits rests on the so-far untested assumptions that fitness itself is heritable and that the covariance between personality and fitness is at least partly genetically based (M. B. Morrissey et al., 2011). A non-random association between genotypes and fitness can be directly tested by estimating the genetic covariance of a trait with fitness. This is known as the Robertson-Price identity, $\Delta z = \mathrm{cov}_A(z, w)$, where $\Delta z$ is the predicted change in mean phenotype and $\mathrm{cov}_A(z, w)$ is the genetic covariance between trait $z$ and relative fitness $w$ (Robertson, 1966; G. Price, 1970; M. B. Morrissey et al., 2011). The logic behind this relationship is that it is the genes that are causing differences in both the trait and fitness that are more represented (that is, selected) in the next generation.

In studies of selection in wild populations there is often an uncoupling of the observed direction of selection from that predicted by the relationship between phenotype and fitness (Merilä, Sheldon, & Kruuk, 2001). Among other reasons, these include instances where selection is fluctuating or where selection is pulling in opposite directions on two correlated traits. Another possibility is that the relationship between a trait and fitness only occurs through a non-heritable environmental factor (T. Price, Kirkpatrick, & Arnold, 1988) or when the fitness effects of the environmental factor mask or apparently enhance the effects of genes (M. B. Morrissey et al., 2011). For example, if there is a positive correlation between a trait and fitness and individuals who have a higher environmental deviation are more fit but the genes that increase the trait value decrease fitness, the mean value of the trait in the next generation will decrease rather than increase. Likewise, even if both the environmental and genetic covariances between a trait and fitness are both positive, examining the phenotypic relationships only would lead to an overestimate of the trait mean in the next generation.

While a change in the mean of a trait depends on the additive genetic variance, traits closely linked to fitness are also predicted to have a high proportion of nonadditive genetic variance (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999). This is because the additive effect of a gene is indepenent of the genetic background and thus is 'exposed' more easily to the selection. Nonadditive genetic effects, such as dominance and epistatis, depend on the state of the allele at the same locus or on genes at different loci and are thus found in different combinations of each individual. Because personality in both humans (Eaves et al., 1998; Keller et al., 2005; Pilia et al., 2006; Rettew et al., 2008) and orang-utans (Chap. 4) is characterized by nonadditive genetic variance, some of this variance may be shared with fitness.

To test whether natural selection on personality has a genetic basis, I estimated the genetic covariance between personality and fitness in genetically-informative samples from the US and Scotland. Differences between the samples, particularly with regard to the type of kin relationships between participants and in information on measures of fitness, necessitated different approaches to analysis. The US sample included explicit information on lifetime breeding success, so I used this sample to directly predict the expected change in personality over the next (overlapping) generation. In the second sample, reproductive success had to be inferred from the data set in such a way that individuals with no offspring could not be included in the analysis. Because this might effect the predicted change from the genetic covariance, I took an alternative approach of testing for the genetic covariance between personality and fitness and then estimating whether mean genetic values were undergoing change in the population.

## 5.2 Population samples and measures

I drew samples from two large studies that included data on family members whose personalities had been assessed.

### Participants

For the first sample, I used data drawn from the MacArthur Foundation Survey of Midlife Development in the United States (MIDUS; Brim, Ryff, & Kessler, 2004) on 3474 non-twin singletons and 449 twin pairs (Kessler, Gilman, Thornton, & Kendler, 2004). The MIDUS is a nationally-representative sample of adults at midlife with a twin and sibling subsample. This was the same data set used by Jokela et al. (2011) although that study was restricted

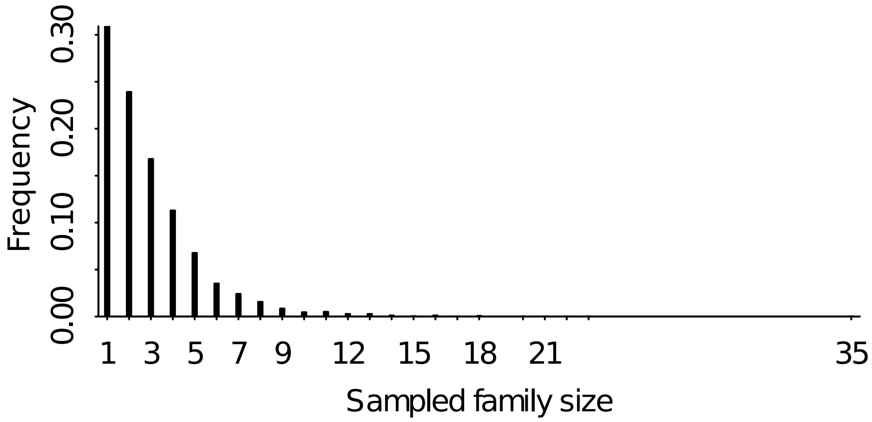


Figure 5.2: Distribution of sampled family sizes from the Generation Scotland Scottish Family Health Study.

to the main representative sample and did not undertake a genetic analysis with the twin subsample. I restricted the sample to individuals aged 34–65. There were 118 female and 127 male monozyotic twin pairs and 132 female and 72 male same-sex dizygotic twin pairs. The mean age of female twins was 47 (SD=8.4) and of male twins was 46 (SD=8.4). I used 1759 female and 1715 male singletons from the MIDUS as part of the fitness analysis.

The second sample was drawn from the Generation Scotland Scottish Family Health Study (GS:SFHS or GS; B. Smith et al., 2006), a family-based genetic epidemiological study in Scotland that includes siblings and parents of the proband. The sample included data on 4357 families comprising 7511 women and 5200 men. The mean sampled family size was 2.9 (median = 2) and ranged from 1–35 (Fig 5.2). The number of kinship types included in the whole pedigree is summarized in Table 5.2. The mean age of women was 48.3 years (SD = 15.5, range = 18–100) and of men was 48.1 years (SD = 15.6, range = 18–94).

### Personality measures

The US twins were assessed on the big five personality dimensions (neuroticism, extraversion, openness to experience, conscientiousness, and agreeableness) personality scales from the Midlife Development Inventory (MIDI: Lachman & Weaver, 1997). The questionnaire

| | | Informative | |
|---|---|---|---|
| Kin type | Total | LRS | Personality |
| Maternities | 24253 | 1488 | 6947 |
| Paternities | 24253 | 1352 | 6455 |
| Full siblings | 16948 | 839 | 4117 |
| Maternal siblings | 17197 | 840 | 4167 |
| Paternal siblings | 17045 | 839 | 4128 |
| Maternal grandmothers | 5846 | 29 | 1321 |
| Maternal grandfathers | 5846 | 29 | 1273 |
| Paternal grandmothers | 3166 | 20 | 636 |
| Paternal grandfathers | 3166 | 20 | 623 |

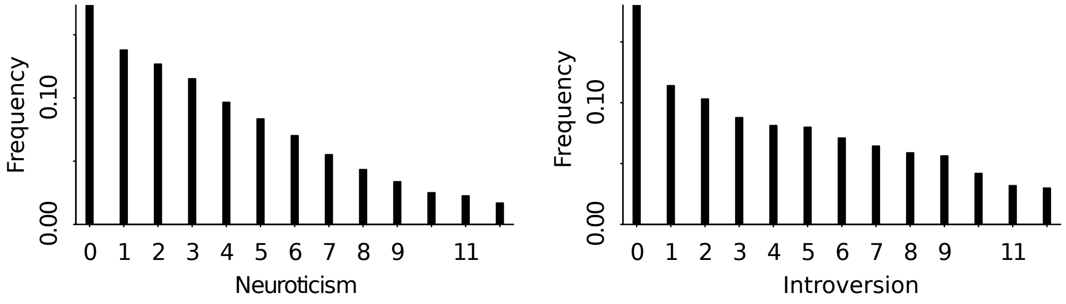
Table 5.2: Count of kinship types in the full pedigree from Generation Scotland. Types of relationships that are informative with regard to the genetic structure of LRS and personality are also listed.

consisted of 4-8 adjectives for each personality domain. Participants rated themselves on a scale from 1 (a lot) to 4 (not at all). The domains showed specific genetic and environmental factors suggesting they were not unified traits, with the exception of extraversion and neuroticism (W. Johnson & Krueger, 2004). I adjusted the personality domain scores for age and sex using a linear regression model (McGue & Bouchard, 1984).

The Scottish family sample was assessed on neuroticism and extraversion using the Eysenck Personality Questionnaire Revised Short Form (EPQ-R: S. Eysenck, Eysenck, & Barrett, 1985; B. Smith et al., 2006). Each scale consisted of 12 questions with yes/no responses that were tallied to yield scores between 0 and 12. 11030 of the participants had been assessed on neuroticism and 11034 had been assessed on extraversion. Because of the skewness in the personality scores (Fig. 5.3), I treated them as count data and reverse coded extraversion as introversion because this looked likely to be a better fit to the Poisson distribution (Fig. 5.3b), and the skewness indicating nonnormality could therefore be incorporated into the Bayesian animal model (Sec. 5.6).

### Fitness measures

There is no single best working definition of fitness (Charlesworth, 1994) though the most general definition of fitness is relative contribution to long-term population growth (Coulson et al., 2006). Fitness is a function of both survival and fecundity and in practice components such as reproductive lifespan, fecundity, and offspring recruitment can be used as proxies for



(a) Neuroticism scores

(b) Extraversion scores reverse coded

Figure 5.3: Distribution of neuroticism and introversion scores from Generation Scotland

fitness (D. Brown, 1988). Two fitness measures that are commonly used are: annual (ABS) or lifetime breeding success (LBS), which capture the number of offspring an individual has; and lifetime reproductive success (LRS), the number of offspring that survive to breeding age. Because survival to adulthood is so high in developed countries, LBS and LRS are generally equivalent and LRS is a good measure of fitness (Byars, Ewbank, Govindaraju, & Stearns, 2010; Stearns et al., 2010).

In the MIDUS participants were directly asked how many biological children they had although the coded responses were censored at 5. Participants were also asked to list the birthdate and sex for up to 10 children. Only 20 out of the 898 monozygotic and dizygotic twins used in the analysis listed more than 5 children, and for all twins who stated they had 5 or fewer children, the two ways of inferring reproductive success gave the same answer. I thus used the number of listed children (censored at 10) as a proxy for fitness. Mean LRS in the whole sample was 2.0 (median = 2, SD = 1.6, range = 0–10). In the twin subsample, mean LRS was 2.1 (median = 2, SD = 1.5, range = 0–10).

The Generation Scotland sample did not include direct information on biological child count. However, this information could be inferred in two ways. The first was by counting each individual's number of children included in the pedigree. Second, participants were asked how many brothers and sisters they had as part of the process to recruit family members as participants. If a participant had at least one child in the sample, I used this information to assign a number of children to each parent. The measure is imperfect for

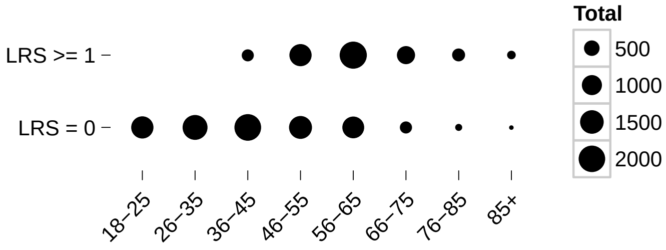


Figure 5.4: Total count of Generation Scotland participants who had at least one offspring in the cohort (LRS >= 1) versus no offspring sampled (LRS = 0).

two reasons: (1) the wording of the question is ambiguous as to whether the sibling count included full-, half-, or stepsiblings and (2) to obtain information on the number of children it was necessary for the participant to have at least one 18-year-old-or-older child in the sample. If an individual's offspring gave conflicting answers as to their number of siblings, I used the lowest reported number to exclude half-siblings that were not the biological child of the target individual. This second point raises the issue of missing data, because zeros in the offspring count are a mix of true zeros (no biological offspring) and missing zeros (participant has offspring but none were included in the sample). There were 2948 women and 1823 men who had at least one child included in the sample (Fig. 5.4). Among participants with at least one reported child and assigning offspring count using the children's reported numbers of brothers and sisters, the mean LRS for women was 2.5 (median = 2, SD = 1.2, range = 1–9) and for men was 2.4 (median = 2, SD = 1.0, range = 1–8). The GS data set did not include information on year of birth but only age at time of assessment. Data collection for the Scottish Family Health Study occured between 2006 and 2011 (*Generation Scotland: timeline*, 2011) so I calculated approximate year of birth using age relative to 2009.

## 5.3 Phenotypic selection on personality

Before studying the genetic basis of selection on personality, I tested whether there was any detectable phenotypic association. A previous study that incorporated data from the MIDUS found that LRS was positively correlated with extraversion and agreeableness and negatively correlated with neuroticism and openness (Jokela et al., 2011). I used the twin subsample from the US and the Scottish families sample to obtain bivariate correlations between personality and reproductive success. I did not make age and sex adjustments because these would be incorporated into the genetic models, which would also handle the potential non-independence in the data from observations of individuals from the same family. I used both twins from each pair from the MIDUS, restricted to individuals age 35+, and all individuals with at least one observed offspring from Generation Scotland. Among the US twin sample and among the Scottish family sample, there were no sigificant raw phenotypic correlations between personality and reproductive success (Table 5.3). Although not significant, the negative correlation between neuroticism and LRS trended in the same direction in both samples.

## 5.4 Heritability of fitness

For there to be a genetic correlation between a trait and fitness, it is first necessary to establish whether fitness itself is heritable. This is because if there is no genetic variation in fitness then there could be no genes under selection that could also be having pleiotropic effects on the trait of interest. I used different types of quantitative genetic models to analyze the MIDUS and GS data because of the different types of relatives included in each sample. In the twin sample I calculated a version of relative fitness that could be used to compare individuals across the age cohorts in the sample. In the family sample I used the observed offspring counts so that the model could account for missing data.

|  | *r* | CI | *p* |
|---|---|---|---|
| MIDUS |  |  |  |
| Extraversion | .07 | -.00, .13 | .06 |
| Neuroticism | -.06 | -13, .01 | .10 |
| Openness | .02 | -.05, .08 | .66 |
| Agreeableness | .02 | -.05, .09 | .53 |
| Conscientiousness | -.02 | -.08, .05 | .56 |
| Generation Scotland |  |  |  |
| Neuroticism | -.02 | -.05, .01 | .14 |
| Introversion | .02 | -.01, .05 | .25 |

Table 5.3: Phenotypic correlations between personality and lifetime reproductive success. CI = 95% confidence interval. MIDUS: N = 820, GS: N = 4209.

### Relative fitness (MIDUS)

Because the twin sample reported lifetime reproductive success (as number of biological children), I used this as the measure of fitness (Fig. 5.5a). To account for changes in fertility rates over the lifespan of the participants, I calculated a cohort-adjusted measure of relative fitness. First, I used a generalized additive model (Hastie, 2011) with 4 degrees of freedom to regress LRS on year of birth for the non-twin participants. This model captured fluctuations in fertility trends between the years of birth (1930–1960) and created a "moving" or locally-weighted average LRS for each year. I then used this fitted model to predict LRS for each birth year $j$, $\widehat{\mathrm{LRS}}_j$. I calculated individual $i$'s fitness relative to their cohort $j$ as

$$\mathrm{rLRS}_i = \frac{\mathrm{LRS}_i \times \overline{\mathrm{LRS}}}{\widehat{\mathrm{LRS}}_j}$$

where $\overline{\mathrm{LRS}}$ is the mean LRS for the whole sample. I did this rather than use residuals from the model so that the mean cohort-relative fitness is constant across cohorts and so that a value of 0 is the minimum. From the cohort-relative fitness scores I calculated total relative fitness $w_i$ for each twin and non-twin as

$$w_i = \frac{\mathrm{rLRS}_i}{\max(\mathrm{LRS}_i)}.$$

The transformed fitness values are plotted against cohort in Figure 5.5b.

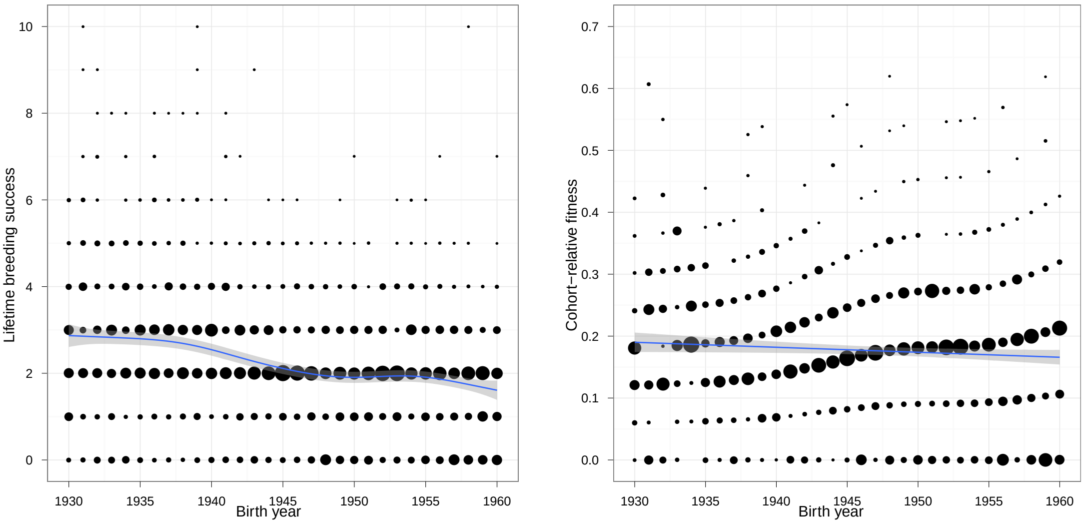
### Classical twin model

The basis of the twin model is in comparing the covariances in phenotypes among two types of twins: monozygotic (MZ) twins who share all of their genome and dizygotic (DZ) twins who share on average half of their genome. The assumption is that the phenotypic covariance between twins can be decomposed into contributions from additive genetic ($\sigma^2_A$), common environment (that is, aspects of the environment shared by siblings growing up in the same household, or $\sigma^2_C$), and unique environment (aspects of the environment that affect each individual uniquely including measurement error, or $\sigma^2_E$) effects. The phenotypic covariance between MZ twins is

$$\sigma^2_{\mathrm{MZ,MZ}} = \sigma^2_A + \sigma^2_C + 0 \cdot \sigma^2_E$$

and DZ twins is

$$\sigma^2_{\mathrm{DZ,DZ}} = \frac{1}{2}\sigma^2_A + \sigma^2_C + 0 \cdot \sigma^2_E$$



(a) Lifetime reproductive success

(b) Relative fitness

Figure 5.5: (a) Lifetime reproductive success (LRS) by year of birth for the non-twin MIDUS sample. A fitted line from a generalized additive model is plotted over the data. (b) Relative fitness versus cohort for the non-twin MIDUS sample. The fitted line shows that average relative fitness is constant across cohorts.

Because the common environment variance contributes equally to both types of twins and the unique environment variance not at all, the difference between the MZ and DZ covariances is

$$\sigma^2_{\mathrm{MZ,MZ}} - \sigma^2_{\mathrm{DZ,DZ}} = \sigma^2_A - \frac{1}{2}\sigma^2_A = \frac{1}{2}\sigma^2_A$$

so the additive genetic variance can be estimated as

$$\sigma^2_A = 2(\sigma^2_{\mathrm{MZ,MZ}} - \sigma^2_{\mathrm{DZ,DZ}})$$

and if the phenotypic variance is the same for both types of twins the heritability is approximately

$$h^2 = 2(r_{\mathrm{MZ}} - r_{\mathrm{DZ}})$$

where $r_{\mathrm{MZ}}$ and $r_{\mathrm{DZ}}$ are the correlations among MZ and DZ twin pairs. For the MIDUS sample, the heritability for cohort relative fitness was $h^2 = .12$ for females and $h^2 = .18$ for males (Table 5.4).

Because the twin–twin covariances indicated that fitness was heritable, I estimated the additive genetic, common environment, and unique environment variances using an ACE twin

| | $r_{\mathrm{MZ}}$ | $r_{\mathrm{DZ}}$ | $h^2$ |
|---|---|---|---|
| Female | 0.32 [.15, .47] | 0.26 [.09, .41] | .12 |
| Male | 0.31 [.14, .47] | 0.22 [-.02, .43] | .18 |

Table 5.4: Monozygotic (MZ) and dizygotic (DZ) correlations for cohort-relative fitness, $w_i$, with 95% CIs in brackets. $h^2$ = heritability.

model (Loehlin, 2004). The ACE model is a type of structural equation model that decomposes the phenotypic covariance into its genetic and environmental components (Fig. 5.6). Each effect is modelled as a latent variable and the model is identified because the correlation of additive genetic effects is fixed at 1 for MZ twins and at 0.5 for DZ twins, the correlation for common environment effects is 1 for both types of twins, and the unique environment effects are uncorrelated.

Because the twin-pair correlations for men and women were within each other's confidence intervals (Table 5.4) and the variance in relative fitness did not differ between the sexes (women: $s^2 = .013$; men: $s^2 = .014$; Levene's Test $F_{1,447} = .024$, $p = .88$), I analyzed both sexes together in a single model using OpenMx (Boker et al., 2011). I first fit a full ACE model and then compared it to models that excluded either the common environment (AE) or additive genetic (CE) components (Table 5.5). The fit of the full model was not significantly better than either of the two restricted models. The AIC also did not differ substantially between the models, indicating there was not sufficient power to differentiate between additive genetic and common environment variance. I therefore used the full ACE model to give a conservative estimate of both effects. To generate confidence intervals I ran the model on 1000 bootstrapped data sets that randomly sampled each twin pair with replacement. The mean variance proportion coefficients and 95% confidence intervals for relative fitness were: $h^2$ = .18 (CI = .06–.32), $c^2$ = .15 (.04–.27), $e^2$ = .67 (.57–.76). Heritability of relative fitness in the US sample was low and more than half of the variance could be attributed to unique environment effects. Because fitness is heritable, any trait that is genetically correlated with fitness in this population would be selected.

### Distribution of reproductive success (GS)

The distribution of lifetime reproductive success in the Generation Scotland sample showed considerable zero inflation (Fig. 5.7). This is because, given that the sample only included

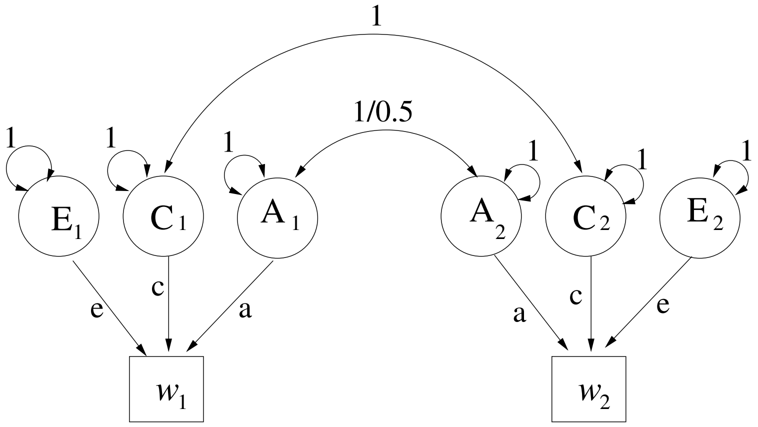


Figure 5.6: Schematic of the ACE twin model. Boxes represent observed variables ($w_1$ and $w_2$ are fitness of twins 1 and 2). Circles represent latent variables ($A$ = additive genetic, $C$ = common environment, $E$ = unique environment). Path between latent $A_1$ and $A_2$ variables fixed at 1 for MZ twins and 0.5 for DZ twins. Paths for the loadings ($a$, $c$, and $e$) of the latent variables on the observed variables are estimated from the data.

| Model | $h^2$ | $c^2$ | $e^2$ | AIC | $\Delta\chi^2$ | $\Delta$ df | $p$ |
|---|---|---|---|---|---|---|---|
| ACE | .14 | .17 | .69 | -3171 | — | — | — |
| AE | .33 | 0 | .67 | -3172 | 1.38 | 1 | .24 |
| CE | 0 | .28 | .72 | -3173 | 0.70 | 1 | .40 |

Table 5.5: Variance proportion coefficients and model fit statistics for ACE models on twin relative fitness. AE and CE models that drop the common environment or additive genetic paths are compared to the full model. $h^2$ = heritabiliy, $c^2$ and $e^2$ = proportion of common and unique environment variances. AIC = Akaike Information Criterion. $\Delta\chi^2$, $\Delta$ df gives the difference in log-likelihoods and degrees of freedom between each model and the full model.

adult children, many of the zeros in the data set are not *true zeros* (individual did not have any children) but are instead *missing zeros* where the individual had children that were not included in the dataset. Thus, there are more zeros than we would expect assuming that lifetime reproductive success follows a Poisson distribution (Kruuk, Clutton-Brock, Rose, & Guinness, 1999). The Poisson distribution is defined with one parameter, $\lambda$, which equals the mean. To get an idea of the amount of zero-inflation, we can compare the observed LRS = 0 frequency against the expectation $\mathrm{Prob}(x = 0|\lambda) = \frac{\lambda^0 e^{-0}}{0!}$. I used the `fitdistr` function from the MASS package in R (Venables & Ripley, 2002) to get maximum likelihood estimates for the $\lambda$ parameters describing for men and women the distribution of LRS $\sim$ Pois($\lambda$). I then used these scale parameters to calculate the expected frequency of an LRS equal to zero. Table 5.6 lists the observed and expected frequencies of LRS = 0 for men and women. The observed

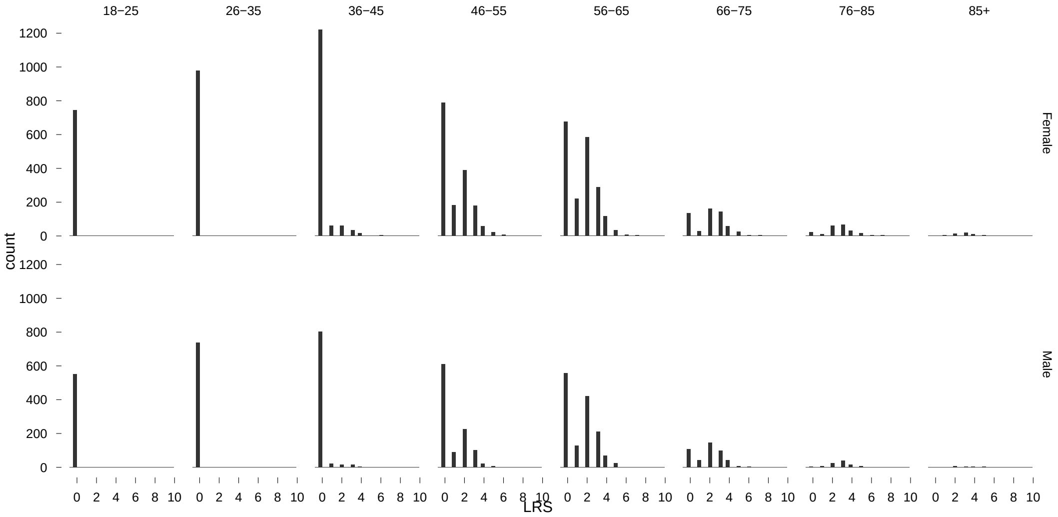


Figure 5.7: Distribution of lifetime reproductive success for the Generation Scotland sample.

| Sex | $\lambda$ (SE) | Freq(LRS $= 0$)<br>(observed) | Prob(LRS $= 0\|\lambda$)<br>(expected) |
|---|---|---|---|
| Female | .96 (.01) | .61 | .38 |
| Male | .84 (.01) | .65 | .43 |

Table 5.6: Observed versus expected frequency of lifetime reproductive success = 0 for men and women in the Generation Scotland sample assuming that LRS $\sim$ Pois($\lambda$).

| Number of mates | Females | Males |
|---|---|---|
| 1 | 11730 | 11912 |
| 2 | 136 | 44 |
| 3 | 2 | 4 |
| 4 | 1 | 0 |

Table 5.7: Counts of number of mates appearing in the Generation Scotland pedigree for women and men.

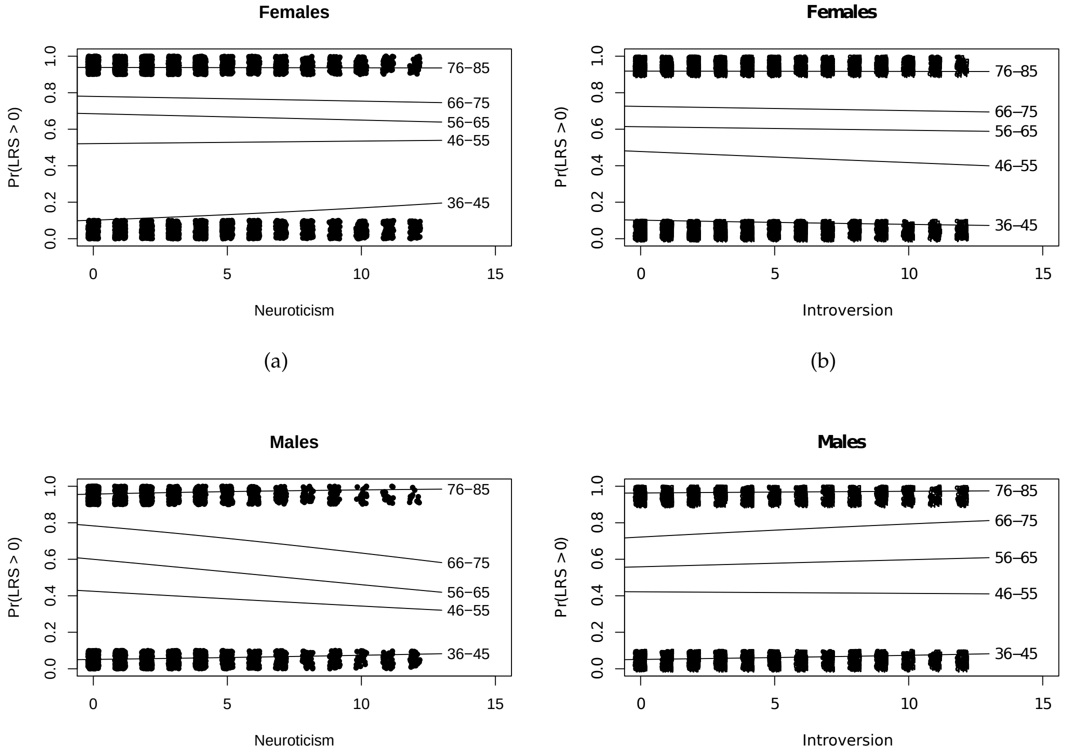
frequencies are considerably greater, indicating that the distribution is zero-inflated.

To determine whether the missing observations would influence inferences about the genetic covariance between personality and fitness, I estimated the effect of neuroticism and extraversion on nulliparity (that is, having zero observed offspring). I analyzed females and males separately because the data set included information on both mates, in contrast to the MIDUS twin data where mates were not included. The vast majority of subjects had children in the pedigree with only one other individual (Mean = 1.0, SD = .09; see Table 5.7).

I used multilevel logistic regression to explore the effect of neuroticism and extraversion on having at least one offspring appear in the sample. Individuals were binned into 10-year cohorts based on age. I used the subsample of cohorts that showed a mix of nulliparity and parity, which included individuals between 36 and 85 years old. I fit the models with lme4 (D. Bates & Maechler, 2010) with neuroticism, introversion, and cohort as predictors and varying intercepts for each family (capturing heterogeneity from the environment common to extended families) and used simulation to estimate uncertainty in predictive inferences from the model (Gelman & Hill, 2007; Gelman et al., 2011).

There was heterogeneity in the effect that neuroticism had on the probability of having at least one child in the Generation Scotland sample (LRS $>=$ 1). The predicted probabilities for each cohort are plotted in Figure 5.8. For women aged 36–45, one point increase in neuroticism score increased the probability of having a child in the sample by 2.3% (CI = 0.1–3.7%). For men aged 56–75, a one point increase in neuroticism score reduced the probability of having a child in the sample by 2.6% (CI = -5.1–0.0%). The fitted coefficients for all effects are plotted in Figure 5.9. The extended family environment explained very little of the variance in observed nulliparity (.09 for women and .02 for men).

The logistic regression model also revealed information about the sample with regard to LRS. Almost no participants in the 36–45 age category had a child in the sample while almost all of the 76–85 year-old participants do (Fig. 5.8). This makes sense given the sample criteria. To be included in the study, participants had to be at least 18 years old. Thus, at least one adult child of a participant needs to have been sampled for the participant to have an LRS > 0. Participants in the 26–45 cohort would have been between the ages of 18 and 27 when having their first offspring, so LRS as measured would also be conflated with the age when the individual started having children. Personality may be partly informative of age at primiparity rather than reproductive success *per se*. Conversely, the oldest participants included in the sample are likely the parents of the proband and are thus being included precisely because they have at least one child. Estimating the heritability of LRS in this sample as well as any possible phenotypic or genetic covariance with personality thus requires models that account as much as possible for the data collection procedure or that take a different approach entirely to inferring a genetic basis to selection.



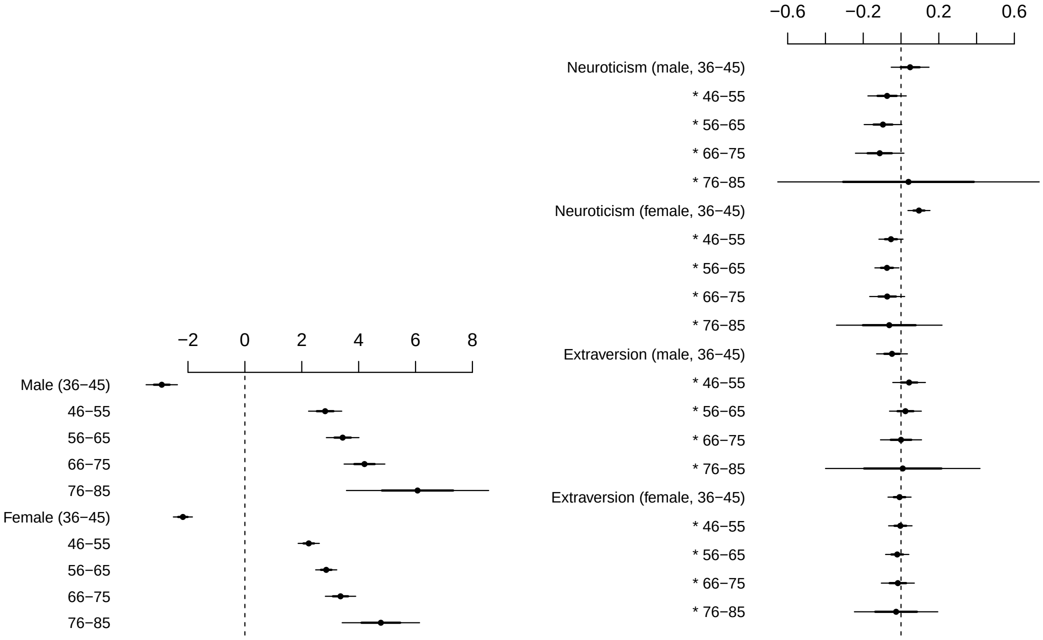
(a) (b)

(c) (d)

Figure 5.8: Effect of neuroticism and introversion on nulliparity in Generation Scotland. Model-fitted lines are shown for each age cohort indicating the probability of having at least one child included in the sample.

### Animal model

Despite the caveats about how offspring count was derived in the Generation Scotland sample, I wanted to see whether there was any evidence for family resemblance in LRS in the Scottish population. To estimate the heritability of LRS I used the subset of participants with at least one offspring and modeled the LRS as following a truncated Poisson distribution (i.e., count data with no observed zeros; Fig. 5.10). Because the Scottish sample included multiple types of family relationships, I analyzed them using an animal model (see also Sec. 4.5). An animal model is a multilevel, mixed effects model that uses pairwise relatedness of all individuals in the sample to estimate the additive genetic variance of each trait (Lynch & Walsh, 1998; Kruuk, 2004; A. J. Wilson et al., 2010). The animal model is flexible in also allowing



(a) Cohort effects

(b) Personality effects

Figure 5.9: Plot of coefficents from a logistic regression on nulliparity in Generation Scotland. Bars around point estimates show 50% and 95% uncertainty intervals.

known sources of mean-level differences, such as age cohort, to be incorporated into the model as fixed effects. In addition to additive genetic variance ($V_{\mathrm{A}}$), I also fit nonadditive genetic variance ($V_{\mathrm{D}}$) and common/extended family environment variance ($V_{\mathrm{K}}$). The residual variance from the model captured a unique environment effect ($V_{\mathrm{E}}$) for each individual. To model nonadditive genetic variance I used the dominance genetic relationship matrix (Lynch & Walsh, 1998, p 768; Appendix A.2). While the additive genetic relationship matrix captures the probability of having each allele in common, the dominance matrix is based on the probability of each individual having the same genotype at a locus. The sample included 100 maternal but no paternal half-siblings that were informative with regards to LRS; inclusion of half-siblings in the pedigree is particularly helpful in getting good estimates of nonadditive genetic variances (A. J. Wilson et al., 2010).

I fit the models using Bayesian estimators in MCMCglmm (Hadfield, 2010) run for $2 \times 10^5$ iterations and summarized the model inferences using 1000 draws from the posterior distribution. I used a Bayesian animal model because it could incorporate outcomes variables with nonnormal distributions (Sorensen & Gianola, 2002; Hadfield & Nakagawa, 2010) without the muss and fuss involved with REML estimators (A. J. Wilson et al., 2011). I calculated the variance proportion coefficients as ratios with the estimated phenotypic variance ($V_{\mathrm{P}}$ = $V_{\mathrm{A}}$ + $V_{\mathrm{D}}$ + $V_{\mathrm{K}}$ + $V_{\mathrm{E}}$), conditioned over the fixed effects for each model, including narrow-sense heritability ($h^2 = V_{\mathrm{A}}/V_{\mathrm{P}}$) and the coefficients for nonadditive (dominance) genetic ($d^2 = V_{\mathrm{D}}/V_{\mathrm{P}}$) and extended family ($k^2 = V_{\mathrm{K}}/V_{\mathrm{P}}$) and unique environment ($e^2 = V_{\mathrm{E}}/V_{\mathrm{P}}$) variances. To understand the amount of variation explained by the genetic and environmental effects relative to the demographic factors of age and sex, I estimated the standard deviations of each of the model coefficients (Gelman, 2005). This method can be used on hierarchical models to yield information similar to a classic ANOVA. For the variance components I simply took the square root of each parameter estimate drawn from the posterior distribution (i.e., $\mathrm{sd} = \sqrt{\mathrm{var}}$). For each fixed effect, I created a vector that repeated the fitted coefficient for each level in the estimator the number of times that that level appeared in the data set, then took the standard deviation of the resulting vector. I did this for each of the 1000 draws from the joint posterior distribution to estimate uncertainty in the standard deviation estimates.

The models suggested that LRS was moderately heritable ($h^2 \approx .26$–$.39$, Table 5.8) and underlain by an equal amount of nonadditive genetic variance ($d^2 \approx .15$–$.26$). Most of the environmental variance on LRS was from effects shared between members of the same family ($k^2 = .43$) as opposed to environmental effects unique to each individual ($e^2 \approx .16$–$.26$). Most of the variance in LRS was explained by differences among the cohorts (Fig. 5.11). However, to what extent these estimates describe the actual reproductive success in the population is difficult to infer because of the extent of missing LRS data in the sample. Doing so requires making the assumption that having no children (i.e., LRS = 0) is part of the same continuous process of reproductive output as having one or more children. Getting around this issue required finding a way to estimate the effects of selection on a genetic level without recourse to direct estimates of fitness.

## 5.5 Mean population change in the US

As stated above, the predicted change in a phenotype from the process of directional selection is equal to the genetic covariance between the phenotype and fitness. I estimated the genetic covariance between personality and relative fitness in the US twin sample using the Cholesky

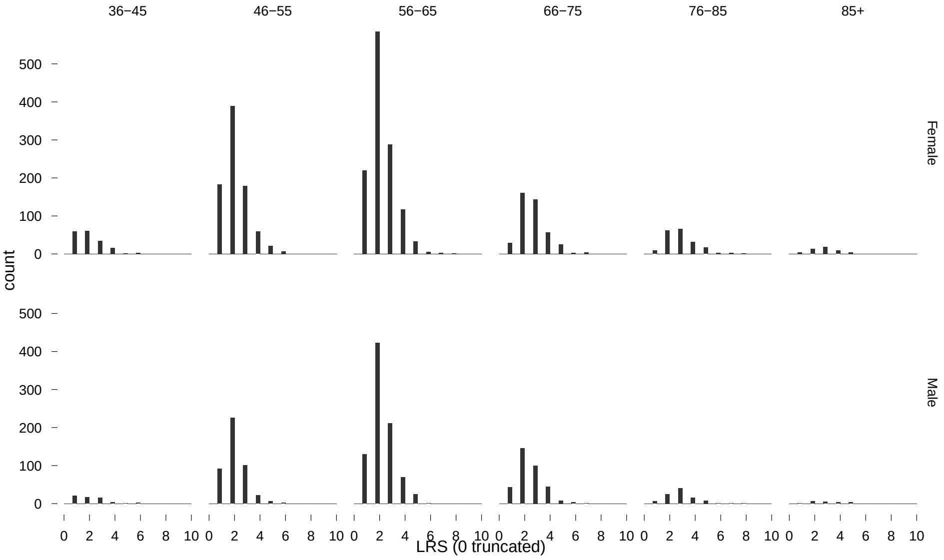


Figure 5.10: Distribution of zero-truncated lifetime reproductive success for the Generation Scotland sample.

| Model | $h^2$ | $d^2$ | $k^2$ | $e^2$ |
|---|---|---|---|---|
| AE | .39 (.17, .64) | | | .61 (.36, .82) |
| ADE | .35 (.12, .63) | .26 (.09, .56) | | .39 (.16, .64) |
| AKE | .32 (.10, .60) | | .43 (.10, .75) | .26 (.08, .54) |
| ADKE | .26 (.02, .54) | .15 (.06, .44) | .43 (.12, .81) | .16 (.04, .32) |

Table 5.8: Variance proportion coefficients for LRS from Generation Scotland treating observed reproductive success as a truncated Poisson variable. Models: A = additive genetic effect, D = nonadditive (dominance) genetic effect, K = extended-family environment effect, E = unique environment effect.

decomposition of the multivariate ACE model where fitness was entered as the last variable in the decomposition. The model parameters were estimated using maximum likelihood with OpenMx (Boker et al., 2011) and I used bootstrapping to sample twin pairs with replacement (1000 replicates) to calculate confidence intervals for each parameter.

There was a detectable genetic correlation of relative fitness with extraversion and agreeableness indicating that mean levels of both personality domains would increase in the next generation (Table 5.9). At the level of the unique environment, agreeableness was negatively environmentally correlated with fitness. The other personality domains were not associated with fitness.

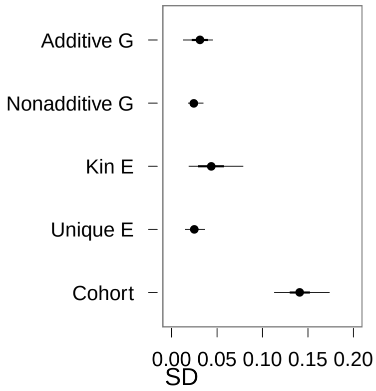


Figure 5.11: Estimated standard deviation of fixed and random effects from the full animal model on lifetime reproductive success in the Generation Scotland sample. The plot illustrates the relative amount of variance explained by each effect. Point estimates surrounded by 50% and 95% uncertainty intervals. G = genetic, E = environmental, SD = standard deviation.

| Domain | $\Delta z = \text{cov}_A(z, w)$ | $r_A$ | $r_C$ | $r_E$ |
|---|---|---|---|---|
| Neuroticism | .005 (-.003, .012) | .29 (-.19, .72) | -.33 (-.90, .43) | -.06 (-.16, .05) |
| Extraversion | .007 (.002, .013) | .45 (.12, .77) | -.19 (-.87, .62) | -.07 (-.18, .05) |
| Openness | .001 (-.004, .006) | .09 (-.30, .46) | -.06 (-.56, .47) | -.01 (-.11, .09) |
| Agreeableness | .006 (.002, .010) | .55 (.19, .85) | .09 (-.46, .76) | -.15 (-.26, -.04) |
| Conscientiousness | -.001 (-.005, .003) | -.09 (-.46, .24) | -.01 (-.68, .66) | .03 (-.09, .15) |

Table 5.9: Genetic covariance ($\text{cov}_A$) between personality and relative fitness in the US sample that equals the predicted change in the mean phenotype between generations, $\Delta z$. $r_A$, $r_C$, and $r_E$ give additive genetic, common environment, and unique environment correlations between the trait and fitness. 95% confidence intervals are given in brackets.

## 5.6 Evolution of breeding values in Scotland

Because of the missing data issue in information about reproductive success in Generation Scotland, I took an alternative approach to estimating evolutionary change by examining changes in breeding values over the years of birth. A breeding value is the additive genetic effect assigned to each individual. An individual's breeding value is an estimatable quantity of its genetic merit and equal to twice the expected difference between its offsprings' phenotype and the population mean when the individual is mated randomly (Falconer & Mackay, 1996; Lynch & Walsh, 1998). The variance in breeding values is the additive genetic variance. Similarly, the dominance genetic variances is the variance of dominance deviations and the unique environment variance is the variance of environment deviations.

A breeding value is, as its name suggests, a quantity that an animal breeder can estimate and then use to decide which animals to select and breed for the purpose of, for example, increasing milk yield (Mrode, 1996). Breeding values can therefore be used to detect selection if the pedigree includes individuals whose years of birth cover a sufficient amount of time (Postma, 2006). Rather than regressing breeding values on fitness (Kruuk, Merilä, & Sheldon, 2003; Postma, 2006), mean breeding values for each cohort can be estimated directly and the change in breeding values over time can be compared to the expectation under drift (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010). This therefore gets around the problem of incomplete data on reproductive success because the breeding values of the traits of interest, such as personality, are examined without reference to individual fitness. Examining breeding values directly also gets around the problem of misestimating lifetime reproductive success based on assumed paternity.

I used a bivariate animal model on neuroticism and introversion using all individuals in the sample with personality assessments. The model included additive ($V_\mathrm{A}$) and nonadditive genetic effects ($V_\mathrm{D}$), both with unstructured covariance matrices. This meant that the model estimated genetic and environmental covariances between neuroticism and introversion or, put another way, that the breeding values for both personality traits were allowed to correlate. I excluded common/extended family environment effects because they contribute only very little, if at all, to variance in personality (Bouchard & Loehlin, 2001). However, I did include nonadditive genetic variance so as not to overestimate the additive genetic variance. There were 50 maternal and 110 paternal half siblings that were informative with regards to personality for getting better estimates of the nonadditive or dominance genetic variance. Both personality variables were modelled as following a Poisson distribution. While there was evidence of some assortative mating for extraverison (correlation between female and male partners $\rho_z$ = .14; 95% CI = .08, .20) though not for neuroticism ($\rho_z$ = .04; CI = -.02, .11), the animal model estimates are not biased by such effects (Sorensen & Kennedy, 1984). I used Bayesian estimation methods because they could straightforwardly incorporate the nonnormal distribution of the outcome variables and propagate uncertainty about the estimates for each predicted breeding value when analyzing the models (Sorensen & Gianola, 2002; Hadfield, 2010; Hadfield et al., 2010). For the purpose of evolutionary analysis, Bayesian techniques also give more conservative estimates of evolutionary change compared with REML methods (Hadfield et al., 2010). I fit the models using MCMCglmm (Hadfield, 2010) and saved the posterior distributions of predicted breeding values (PBV) for the additive genetic effects. I ran the model for $6 \times 10^5$ iterations. From the model I calculated narrow-sense heritability, $h^2 = V_{\mathrm{A}} \ / \ (V_{\mathrm{A}} + V_{\mathrm{D}} + V_{\mathrm{E}})$, and the variance proportion for nonadditive genetic variance, $d^2 = V_{\mathrm{D}} \ / \ (V_{\mathrm{A}} + V_{\mathrm{D}} + V_{\mathrm{E}})$. I also calculated the

- additive genetic correlation: $r_A = \mathrm{cov}_A(N, I) / \sqrt{V_A(N)V_A(I)}$;
- nonadditive genetic correlation, $r_D = \mathrm{cov}_D(N, I) / \sqrt{V_D(N)V_D(I)}$; and
- unique environment correlation ($r_E = \mathrm{cov}_E(N, I) / \sqrt{V_E(N)V_E(I)}$;

where $\mathrm{cov}_A(N, I)$ is the additive genetic covariance between neuroticism and introversion, $V_A(N)$ is the additive genetic variance of neuroticism, and so on.

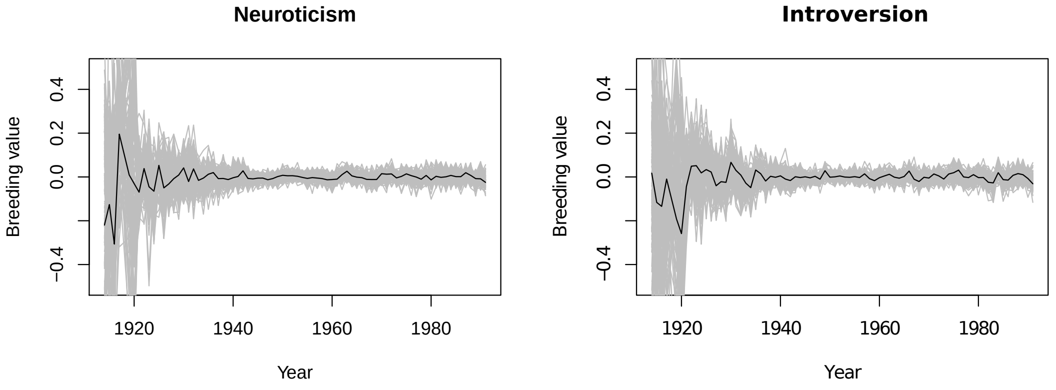
Both neuroticism ($h^2$ = .26, CI = .12, .38; $d^2$ = .32, CI = .16, .57) and introversion (i.e., *reversed* extraversion) ($h^2$ = .19, CI = .10, .32; $d^2$ = .28, CI = .16, .46) showed moderate additive and nonadditive genetic variance. Neuroticism and introversion had positive but nonsignificant genetic correlations ($r_A$ = .19, CI = -.19, .54; $r_D$ = .39, CI = -.05, .67) and a positive environmental correlation ($r_E$ = .58, CI = .28, .75) with each other. A positive genetic correlation between the two personality domains would allow for correlational selection, where selection on one trait would also change the mean of the other trait (Lande & Arnold, 1983; Falconer & Mackay, 1996).

For each draw from the posterior distribution of the PBVs, I matched each individual to their approxmiate year of birth and calculated a mean breeding value for each year, spanning 1914-1991. The posterior distribution of breeding values are plotted in Figure 5.12a, b. There was little certainty in the mean breeding values for the earlier years covered by the study because there were few individuals sampled from these years. I therefore restricted the analysis to the years 1939–1991 where each year had at least 100 participants with that year of birth. I then regressed mean breeding value on year of birth for each sample from the posterior distribution.

I also compared the change in breeding values to what would be expected under random drift. To do this, I took each posterior draw of the additive genetic covariance matrix and simulated change in breeding values from random sampling (that is, genetic drift) using the pedantics package (M. M. Morrissey, 2010). For each member of the founder generation (that is, individuals who do not have any ancestors included in the pedigree) a replicated breeding value for neuroticism and introversion is drawn from a multivariate normal distribution with mean zero and variance equal to the additive genetic matrix. The actual pedigree is then used to simulate the transmission of breeding values from one generation to the next. This models the amount of change in breeding values that could occur just by chance (Hadfield et al., 2010). Because the model does not include selection, the expected change in breeding values is 0. As with the predicted breeding values, I regressed mean replicated breeding value on year.

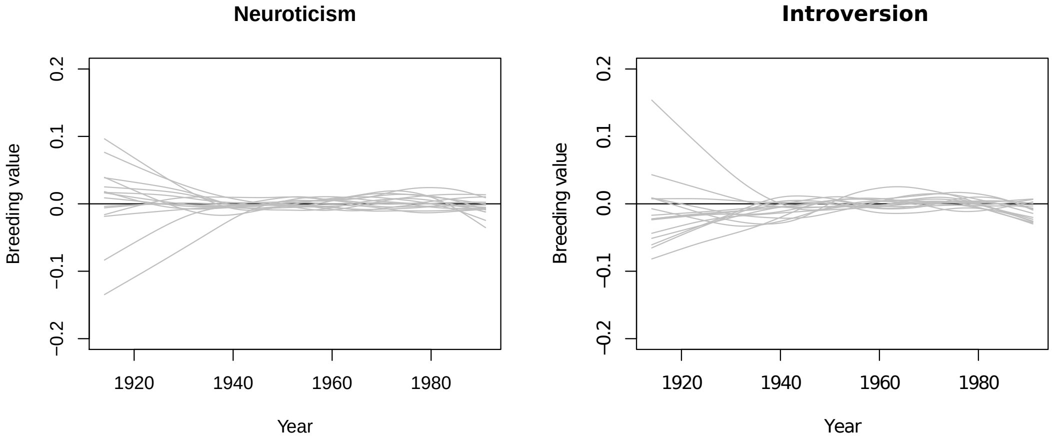
There was no evidence that mean breeding values changed between 1939 and 1991. The estimated change in neuroticism scores from changes in breeding value was .01 (CI = -.10, .08) and in introversion scores was -.02 (CI = -.13, .10). These changes are $\approx$ 1-3% of a standard deviation in personality scores. Uncertainty in regression slopes of mean predicted breeding value versus year are plotted in Figure 5.13.

If the change in breeding values were significant, the simulated replicates of breeding values modelling drift could be used to determine whether the change in breeding values was deterministic (i.e., from selection) or consistent with what would be expected from chance. However, because I did not detect any change in mean breeding values, I used the simulations to determine whether the mean breeding values changed *less* than would be expected by chance. Less change than expected by chance would be consistent with stabilizing selection acting counter to genetic drift. To test this, I calculated the proportion of samples where the absolute values of the slope from the predicted breeding values was less than the absolute value of the slope from the replicated breeding values. This gives the probability that the change is less than expected by chance. For neuroticism and introversion 47% and 48% of the slopes on predicted breeding values were less than the slope from the simulated replicates. Thus, the change in breeding values from directional selection or constraint from stabilizing selection was not signifantly different from expectation under random drift. The amount of variability in change in mean breeding value under genetic drift, as determined from simulated replicates, is compared to estimates of the actual change in breeding values in Figure 5.13. I used a generalized additive model (Hastie et al., 2009) to explore nonlinear trends in breeding values. I fit a smoothed spline using the gam package (Hastie, 2011) of



(a) Cohort mean PBV

(b) Cohort mean PBV



(c) PBV, smoothed splines

(d) PBV, smoothed splines

Figure 5.12: Predicted breeding values (PBV) in personality from Generation Scotland. (a, b) In black, posterior mode of mean cohort breeding values. In gray, 100 draws from the full posterior distribution. (c, d) Smoothed splines fit to predicted breeding values from a generalized additive model with 4 degrees of freedom, using 15 draws from the posterior distribution.

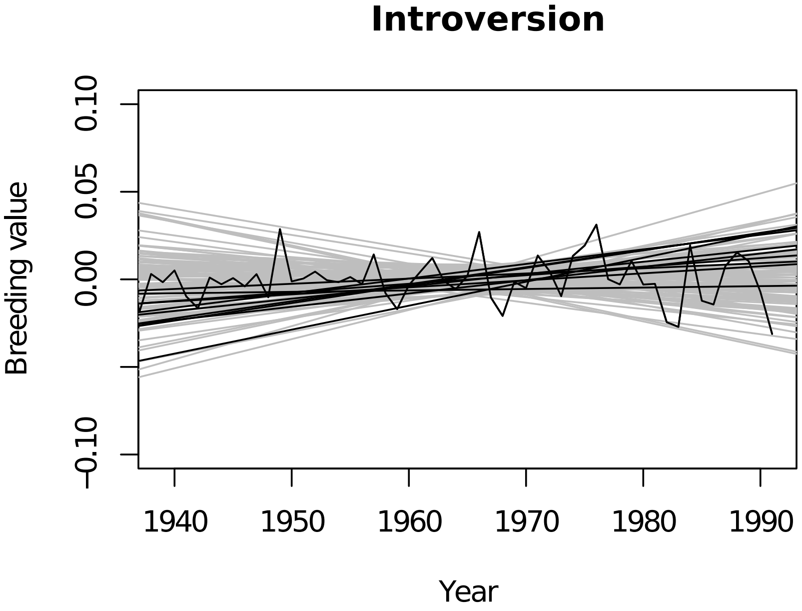
predicted breeding value on year using values on all individuals (rather than mean breeding values) for each draw from the posterior distribution of random effects. Plots of the smoothed splines did not reveal any fluctuations in breeding values (Figure 5.12c, d).

## 5.7 Contemporary selection on personality

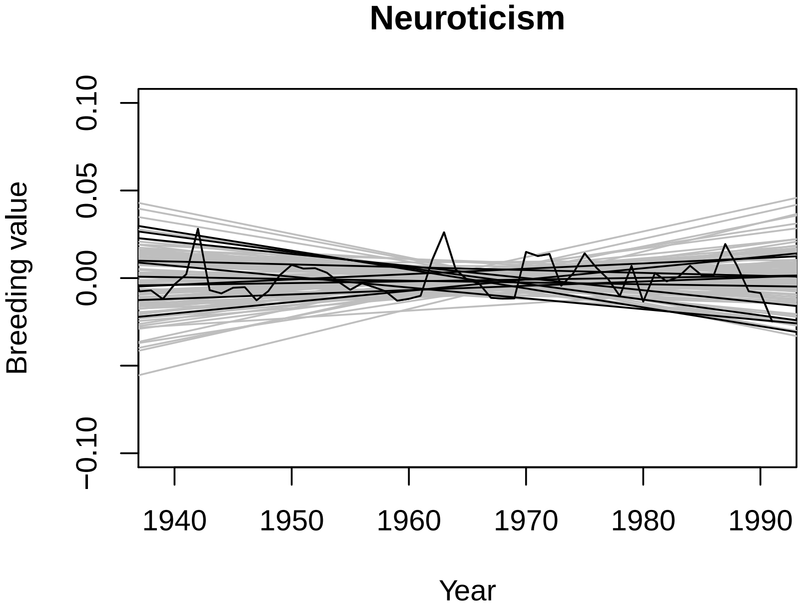
Estimating selection gradients in contemporary populations starts from the idea that species are never perfectly adapted to their environment so that some phenotypic difference or another will always lead to differences in fitness outcomes. Although the study of current selection pressures cannot for certain indicate anything about adaptation in the past, particularly if one starts from the assumption that the environment has and is changing, estimating selection gradients is necessary to understanding personality evolution because of its potential to reveal how genetic variation in personality traits is being maintained (Réale & Dingemanse, 2011). While long term selection will govern the emergence of new phenotypes, a selectionist approach can be used to determine how selection will shape the standing genetic variation in a trait.

I explored the genetic basis of personality in the US and Scotland. Both samples were genetically informative but differed in the kind of family relationships included. The US sample included twins and the Scottish sample included extended families. Neither sample showed detectable phenotypic correlations between personality and LRS. However, a twin model revealed that fitness had a positive genetic covariance with extraversion and agreeableness in a US sample. A pedigree-based model did not show any evidence for changes in mean genetic values over a 53-year period in the Scotland sample.

Extraversion has been found to relate to the timing of childbearing whereby more extraverted individuals have their first child at a younger age (Jokela et al., 2009, 2011). The effect is particularly strong in individuals who are not married when they have their first child (Schmitt & Shackelford, 2008; Jokela et al., 2011). Individuals who start breeding earlier have the opportunity for a longer reproductive lifespan in which to maximize fitness. Like extraversion, agreeableness is also related to birth of the first child but, unlike extraversion, was not as strongly tied to reproductive timing (Jokela et al., 2011). Although the effects of agreeableness on childbearing was only found in women previously (Jokela et al., 2011), a positive genetic correlation with fitness will increase the trait mean regardless of which



(a)



(b)

Figure 5.13: Estimated change in predicted breeding values in personality from Generation Scotland compared with expectation from drift. In black, posterior mode of mean cohort breeding values and 10 samples from the regression of mean breeding values on year-of-birth. In gray, 25 draws from simulated replicate under random drift.

sex the association is found in. In other words, more agreeable women also pass on their alleles that increase agreeableness additively to their sons. There was also a negative environmental correlation between agreeableness and fitness in the US sample (Table 5.9). This means that individuals who become more agreeable as an effect of the unique environment they experience, that makes them differ from their twin, tend to have fewer children. High agreeableness is preferred in long-term mates (Penke, Todd, et al., 2007) and thus environmental effects may lead to increased parental investment (MacDonald, 1995, 1998) that could come at the cost of overall fecundity (Bielby et al., 2007; Pettay et al., 2005). The negative environmental correlation could equally be the effect that having children has on personality. Having children influences emotionality and sociality (Jokela et al., 2009) and may also effect personality facets related to agreeableness.

If the inferences from the genetic models are accurate, then directional selection is predicted to change the mean phenotypic values in the US, namely by increasing mean extraversion and agreeableness, but not to change mean personality levels in Scotland over several generations. There was also no evidence of stabilizing selection on personality in Scotland. This implies that the fitness surface for extraversion and neuroticism in the Scottish population is flat while the US population is still moving toward a fitness optimum. The fitness consequences of personality differ between the US and Scottish environments. This may be either because the distribution of underlying genetic factors differ between the two populations (Rice, 2004) or because the fitness landscape differs because of differences in distribution of the recurrent problems that personality is an adaptation to (D. M. Buss & Greiling, 1999; D. M. Buss, 2009b).

There are many gene frequency differences between human populations (Cavalli-Sforza et al., 1994; Romero, Manica, Goudet, Handley, & Balloux, n.d.; Coop et al., 2009), including between the UK and the US. While some of this differentiation is from selection pressures unique to each population (Sabeti et al., 2007; Barreiro, Laval, Quach, Patin, & Quintana-Murci, 2008; Pickrell et al., 2009), because the overall strength of selection is weak, other evolutionary processes such as migration and genetic drift also contribute to population variation in gene frequencies (Coop et al., 2009). Even if selection is present but not detectable given the power of both samples, it can at least be said that the selection gradient in both populations is very shallow. The effects of migration, drift, and mutation are inversely related to the strength of selection (Kimura, 1957; Crow & Kimura, 1970; Rice, 2004; Hartl & Clark, 2007) and thus are more likely to have an effect over the timespan of several generations.

An alternative but not mutually exclusive explanation is that the environment or distribution of environments to which personality is an adaptation (D. M. Buss, 1996; D. M. Buss & Greiling, 1999; Nettle, 2006; Denissen & Penke, 2008b) also differ between the US and Scotland. Countries as a whole may thus capture a level at which fitness optima vary in space. Variation in the direction and magnitude of selection on personality may also fluctuate over time because of cyclical or secular changes in environmental characteristics (Penke, Denissen, & Miller, 2007; Réale & Dingemanse, 2011). If human personality is primarily an adaptation to the social environment (Penke, Denissen, & Miller, 2007; D. M. Buss, 2009b), then that social environment will be composed of the distribution other people's personalities. The US and UK differ in mean personality at the population level (McCrae, Terracciano, & 79 Members of the Personality Profiles of Cultures Project, 2005; Schmitt et al., 2007). While the Scottish were not sampled, McCrae, Terracciano, and 79 Members of the Personality Profiles of Cultures Project (2005) found that the English and Northern Irish were on average higher on neuroticism, extraversion, agreeableness and lower on conscientiousness than Americans. Schmitt et al. (2007), who sampled the whole UK, found that people in the UK were higher on neuroticism but lower on agreeableness, conscientiousness, and openness than the US. If personality is under frequency dependent selection (Penke, Denissen, & Miller, 2007), then this distribution of personality within a population will determine some of the features of the fitness landscape. While balancing selection on individual personality genes can probably be ruled out because otherwise the resulting frequencies and effect sizes would have turned up in genome-wide association studies (Miller, 2011), balancing selection may still be occuring on the level of the phenotype as the changing environment, including the frequency of other phenotypes, slowly changes the fitness landscape. Heterogeniety in fitness effects of personality also entail that the direction of selection, as well as its magnitude or even presence, will differ between populations that are studied. If selection is maintaining variation in personality then every population will present its own case. This also means that, with data on only a few populations, it is impossible to come to general conclusions about which demographic, cultural, ecological, or behavioral characteristics are determining the relationship between personality and fitness (Nettle, 2009).

If selection is weak there is also more chance for mutation to increase and maintain the genetic variance in personality. Selection may also be weak because mutations that affect both personality and fitness are sufficiently buffered (Hartman et al., 2001; Hermisson & Wagner, 2004) by the action of other genes. This is consistent with the large proportion of nonadditive genetic variance in personality (Eaves et al., 1998; Keller et al., 2005; Pilia et al., 2006; Rettew et al., 2008) because gene-by-gene interaction or epistasis contributes to nonadditive genetic variance (Falconer & Mackay, 1996; Lynch & Walsh, 1998).

Besides these substantial explanations, methodological differences might also influence the observed relationships between fitness and personality. First, the two samples used different personality instruments. The assumption is often made in evolutionary studies of human personality that personality traits measured with different scales are interchangable. For example, Jokela et al. (2011) combined two different samples together in their study of personality and reproductive outcomes. While both samples were measured on scales in the mold of the Five-Factor Model, one sample was assessed using the Big Five Inventory (BFI, John, Donahue, & Kentle, 1991) while the other used the MIDI (Lachman & Weaver, 1997). I drew the twins from this same sample that was assessed using the MIDI, so the measurement was also different from the Generation Scotland participants who were assessed using the EPQ-R (S. Eysenck et al., 1985). The MIDI neuroticism scale is composed of the items *moody*, *worrying*, *nervous* and (not) *calm* while the EPQ scale also contains, in addition to items pertaining to fluctuating moods and worry, questions such as *Do you often feel lonely?* and *Are you often troubled by feelings of guilt?*. Thus, while related, each instrument might be tapping slightly different aspects (or facets) of personality.

On top of item content, several pieces of evidence are important to keep in mind when studying personality phenotypes using a selectionist approach. Although Jokela et al. (2011) reported strong negative associations between openness and reproductive success, my preliminary analysis of the phenotypic correlation between openness and LRS was not only not statistically significant but the effect went in the opposite direction. W. Johnson and Krueger (2004) found that the items making up the agreeableness, openness, and conscientious domains in the MIDI did not show genetic and environmental coherence. Models that specified either independent pathways where the items shared genetic and environmental effects or models that specified a single, common latent structure showed poor fit to the data for these three domains, which implies that the genetic effects leading to the score on each item differed between the items (W. Johnson & Krueger, 2004). This lack of coherence would impede the estimation of genetic effects common between a personality domain and fitness because each item could vary in its relationship to fitness. I also found a significant negative environmental correlation between the neuroticism and extraversion domains in the Generation Scotland sample. While not significant, the additive and nonadditive genetic correlations were also negative, suggesting a shared genetic basis for the two domains as well. In this sample, at least, they do not describe separate phenotypes. Selectionist studies of personality must therefore be wary of falling prey to the "jingle–jangle" fallacy (Block, 1995) of assuming that because two personality constructs have the same name they are the same phenotype and, conversely, that differently named constructs describe independent phenotypes.

The samples also differed in the types of relatives used to make the genetic inferences. The analysis of the MIDUS sample was based on monozygotic and dizygotic twins while the Generation Scotland sample used extended families. Twin designs rest on more stringent assumptions (Eaves et al., 1978; Keller, Medland, & Duncan, 2010) than designs that incorporate multiple types of relatives. Twin models are underidentfied when estimating additive genetic ($V_{\mathrm{A}}$), nonadditive genetic ($V_{\mathrm{NA}}$ or $V_{\mathrm{D}}$), and common environment ($V_{\mathrm{C}}$) variances so one of the variance components has to be set to zero. The animal model on the other hand, like other extended family designs, can address these and other limitations of twin models (Lynch & Walsh, 1998; Keller et al., 2010). Because the estimate for $h^2$ from a twin model includes effects from both $V_{\mathrm{A}}$ and $V_{\mathrm{D}}$ , it is better seen as an estimate of the broad-sense rather than the narrow-sense heritability (Bouchard & Loehlin, 2001; Keller et al., 2010). This can be seen in genetic studies of personality using pedigree models (Pilia et al., 2006) or that otherwise incorporate non-twin relatives along with twins (Eaves et al., 1998; Keller et al., 2005; Rettew et al., 2008) that model nonadditive genetic effects. These family studies report $h^2 \approx .2$ rather than the $\approx .4$–$.5$ typically yielded by twin studies (Bouchard, 1994; Bouchard & Loehlin, 2001). If only the total amount of genetic influence is of interest, this is a minor point. However, the mean change in a phenotype from directional selection is only a function of the addtive genetic variance. When making evolutionary inferences using a genetically-informed selectionist approach, separating out additive and nonadditive genetic variance is critical. Thus, the estimates of the additive genetic covariance between personality and relative fitness may not accurately predict evolutionary change from selection if some of the covariance is coming from nonadditive genetic effects on both personality and fitness.

Multivariate selection analysis should also not be confused with causal inference. Predicting the relevance of a trait for fitness by examining only one trait at a time assumes that differences in the trait are the sole cause of the related differences in fitness (Pigliucci, 2006; Hadfield, 2008; M. B. Morrissey et al., 2011). While a genetic covariance between a trait and fitness means that the mean phenotype will deterministically change in the direction and amount predicted (the actual change will also be determined by joint effects of other aspects of the fitness surface combined with nondeterminstic processes of mutation and genetic drift; Rice, 2004), this does not speak to how variation in the phenotype *caused* differences in fitness. The analysis also does not speak to what exactly it is that is being passed on from one generation to the next and being selected, only that whatever it is it is heritable and works additively on both fitness and the phenotype. Animal breeders, who gave birth to these techniques, had traditionally made the assumption that the environment each individual experiences is unique and that it is only genes that are being passed from parent to offspring. Studies of the relationship between fitness and personality usually condition on non-personality traits that also relate to reproductive success, such as educational attainment and socioeconomic status (Jokela et al., 2011). Rather than seeing these as variables to control for, a multivariate analysis could be used that treats these sociological factors as potentially genetically correlated outcomes. Here I have only looked at personality variables, but future analysis should incorporate additional psychological and sociological variables.

If selection on personality is weak, it may require data on a greater number of generations to detect than was available in the Scottish pedigree sample. The maximum pedigree depth for the personality data was only three generations. In contrast, studies of nonhuman animals may incorporate up to 10 generations or more (Réale & Dingemanse, 2011) which is more feasible with organisms with shorter lifespans. The power of breeding-value based estimates of selection in reasonable human samples should be explored.

Barring all of these assumptions, however, we can conclude that directional selection for personality will be either absent or, at most, weak in at least some contemporary populations. While the span of time over which this microevolutionary change occurs can be experienced within a single human lifetime, the amount of change, even where detectable, amounts to only a few percents of a standard deviation, and is therefore most likely imperceptible to any observer without a genetic model in their toolkit. Cohort effects such as the adjustment of personality through adaptive developmental plasticity to life-history conditions (Chap. 3) or migration would have a larger and more noticeable effect to the casual observer. However, only a genetically-based selectionist approach can help us infer how we humans continue to psychologically adapt to our environment.

# Chapter 6

# Orchid hypotheses: developmental evolution of reactivity and resilience to environmental stress

## 6.1 Sensitivity to context

When an organism encounters a stressor in its environment, a cascade of interconnected systems activate to generate the appropriate biological and behavioral response to effectively handle the stress (McEwen, 1998; Karatsoreos & McEwen, 2011). An organism's reactivity describes the extent to which various physiological systems, such as mediation of central nervous sytem activity by systemic hormones, respond to stress of a given level (Matthew, 1986). The stress response system describes the suite of functions that allow the organism to maintain this stability in the face of environmental challenges and opportunities. The stress response system functions in a coordinated manner on different timescales and includes components of the neuroendocrine system such as the hypothalamic-pituitary-andrenal (HPA) axis and the sympathetic and parasympathetic nervous systems (Porges, 1995; Habib, Gold, & Chrousos, 2001; Schlotz et al., 2008; Boyce & Ellis, 2005; Del Giudice et al., 2011). The stress response system coordinates behavioral and physiological responses to both harmful and beneficial situations and in doing so acts as both a filter and an amplifier of information about the environment (Del Giudice et al., 2011). These responses come as reactions to immediate situational changes as well as to long-term sources of stress in the environment and the stress response system exhibits variation both in specific reactivity and baseline activity (Bauer, Quas, & Boyce, 2002; El-Sheikh, Erath, Buckhalt, Granger, & Mize, 2008).

While the goal of the system as a whole is to keep the organism in equilibrium, dysregulation can result in psychological, psychiatric, and somatic disorders. Both humans and animals show individual differences in basic stress reactivity and sensory processing sensitivity (Cacioppo et al., 1998; Koolhaas et al., 1999; Boyce & Ellis, 2005; Ellis et al., 2005; Aron, Aron, & Jagiellowicz, 2012) and this variation is the result of genetic and environmental effects (Caspi & Moffitt, 2006; Belsky & Beaver, 2011). The environment experienced early in life has a complex relationship during development with the sensitivity of the stress response system. One early study found that in children who had relatively unreactive immune systems, the incidence of respiratory illness was independent of the degree of adversity in their environment (Boyce et al., 1995). However, for children who had high psychobiological reactivity, high adversity led to the worst health outcomes but low stress environments led to the best health outcomes (Boyce & Ellis, 2005). Reactivity of the sympathetic nervous system was also found to follow the same curvilinear shape in two samples of children experiencing different levels of stressful life events, family discord, and social support (Ellis et al., 2005). Similar findings have been found in mice where both very low and very high doses of corticosterone during infant development produced high reactivity in adulthood (Macrì et al., 2009).

Boyce and Ellis (2005) synthesized this theory and evidence as the Biological Sensitivity to Context (BSC) model (Ellis et al., 2005; Ellis & Boyce, 2008). They suggested a U-shaped relationship between stress experienced during ontogeny and biological reactivity to the environment later in life (Fig. 6.1). Individuals growing under moderate stress and psychosocial support develop a low biological sensitivity. Those born under conditions of either low or high stress should develop reactivity as either sensitivity or vigilance (Del Giudice et al., 2011). However, while individuals with low sensitivity are buffered against moderate and even high stress, they are less receptive to the beneficial effects of good environments. The stress response system is thus seen as conditionally adaptive: during development the system is 'tuned' by the environment experienced during ontogeny to be optimally receptive or resistant later in life (this is similar in principal to the adaptive phenotypic plasticity of

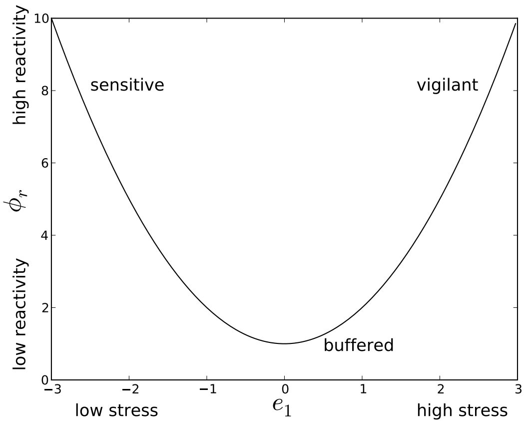


Figure 6.1: U-shaped relationship between early stress and biological reactivity. Adapted from Boyce and Ellis (2005) and Del Giudice et al. (2011).

personality to life history conditions, see Chap. 3). The U-shaped curve is a norm of reaction (Pigliucci, 2001; Dingemanse, Kazem, Réale, & Wright, 2010) which specifies how the phenotype (in this case, stress reactivity) will develop under different environmental values.

Individuals also show differential susceptibility to environmental stressors (Belsky, 1997; Belsky & Pluess, 2009) and there is some evidence that variation in reaction norms to early stress is partly genetic. Genetic studies in humans originally focused on variants that acted as risk factors for negative behavioral and health outcomes, following the diathesis-stress model that the risk of psychopathology or other negative outcomes of stress exists on a continuum of vulnerability (Monroe & Simons, 1991; Belsky & Pluess, 2009). For example, genetic variants underlying the serotonergic system increase the risk of anxiety-related disorders (Lesch et al., 1996). While some genotypes buffer against environmental stressors, there is some cross-species evidence that variants conferring risk in moderately and highly stressful environments may also be beneficial in environments of low stress (Caspi & Moffitt, 2006; Suomi, 2006; Caspi et al., 2010; Belsky & Beaver, 2011).

There is thus a reconceptualization underway that sees certain alleles as conferring plasticity rather than risk since whether their effects are harmful or beneficial depend on the environment (Belsky, Bakermans-Kranenburg, & IJzendoorn, 2007; Belsky, 1997; Ellis et al., 2011). However, the evidence for single genes influencing the reaction norm is inconsistent (Caspi & Moffitt, 2006; Risch et al., 2009; Caspi et al., 2010; Belsky & Beaver, 2011). One possible reason for the inconsistency is that multiple genes contribute to plasticity so that the effects of any one gene can be masked by the effects of other genes (Belsky & Beaver, 2011). An alternative explanation is that because the reaction norm is curviliner the relationship between gene, environment, and phenotype will depend on which part of the reaction norm is being sampled (Boyce & Ellis, 2005). For example, a cross-over interaction might not be detected if the sample consisted primarily of individuals from moderate and high-stress environments. If such relationships are difficult to determine empirically (Eaves, 2006), it is pertinent to ask whether a U-shaped reaction norm is likely to exist in theory, based on an evolutionary analysis. Boyce and Ellis (2005) argue that variation in stress reactivity is maintained because the optimal reactivity varies across environments. Yet the phenotypic variation observed could be an outcome of variability in stress experienced early in life, even if there is no genetic variability underlying the reaction norm. However, if we model genetic influences on different aspects of the reaction norm specified by the BSC theory, then it is possible to see how the gene × environment interaction for the development of reactivity will be shaped by evolutionary processes and under what conditions genetic variation could be maintained. This has the potential to support the idea that individuals differ in terms of plasticity (Belsky et al., 2009).

The BSC (Boyce & Ellis, 2005) model and its extension, the adaptive calibration model (ACM) (Del Giudice et al., 2011), were conceived in terms of evolutionary development but have yet to be explored formally. Mathematical analysis can help clarify how the distribution of underlying genetic factors affects the evolutionary dynamics of phenotypes like the stress response system. By formalizing the descriptions of the system, we can come to understand the ways that the evolutionary development of risk and resilience will change in ways that are not necessarily intuitively obvious. The models, then, help guide our theories and our thinking. This work extends the BSC/ACM models by calling more directly on rigorous evolutionary theory via mathematical prototyping. The application of this theory relies on building a mathematical model that connects genetic architecture influencing the trait to fitness outcomes and deriving expressions showing how natural selection will shape the distribution of the underlying factors in the population. While the model makes many simplifying assumptions, the key idea is to express the essential developmental aspects of the stress response system proposed by the theory. The results of the models can then guide further theoretical and empirical work.

Here I describe a simple model encoding the essential features of the U-shaped reaction norm for the stress response system proposed by Boyce and Ellis (2005). The model will assume that the shape of the reaction norm (its position and width) is controlled by a set of genetic factors. The analysis will show how the distribution of these variants will change under selection. In particularly, I am interested in what aspects of the distribution of the underlying factors will combine with the fitness landscape to maintain genetic variation in the BSC/ACM system.

## 6.2 Phenotypic landscape models

The evolution of development can be explored using a general mathematical framework that ties together the joint distribution of underlying genetic and environmental factors, the contribution of each factor to the phenotype, and the relationship between the phenotype and fitness (Rice, 2002, 2004). The focus of such mathematical models is twofold: (1) to explore how selection changes the distribution of underlying factors and (2) how the structure of the phenotype influences the evolution of its development.

Phenotypic development can be formalized and modeled by means of tensor analysis (Rice, 2002). A tensor is a multidimensional extension of a matrix, where the rank of the tensor indicates its dimensionality. A vector is a tensor of rank 1 while a matrix is a tensor of rank 2.

The models are composed of several parts

- an equation specifying how the phenotype ($\phi$) is related to the genetic and environmental factors. This is the phenotypic landscape. The equation can be based on knowledge of the system being studied or on a theory of the phenotype's ontogeny. The phenotype is represented as a function of genetic ($g$) and environmental ($e$) factors

  $$\phi = f(g_1, g_2, \ldots g_k, e_1, e_2, \ldots e_n)$$

  that can take any form. Modeling involves identifying the essential relationships between the underlying factors and the development of the phenotype that one would like to explore.

- The distribution of the underlying factors. The different moments of the distribution are stored in tensors: $P^1$ = means, $P^2$= (co)variances, $P^3$ = multivariate skewnesses, $P^4$ = multivariate kurtoses. $P^n$ is represented as a tensor of rank $n$. The first central moments

  $$P^1 = \begin{bmatrix} \mathrm{E}[g_1] \\ \vdots \\ \mathrm{E}[g_k] \\ \mathrm{E}[e_1] \\ \vdots \\ \mathrm{E}[e_n] \end{bmatrix}$$

  is a rank 1 tensor (vector) that holds the means of each underlying factor. Subscripts can be used to index the elements: $P^1_1 = \mathrm{E}[g_1]$, $P^1_{k+1} = \mathrm{E}[e_1]$. The parameters of the distribution are more technically defined as central moments although they do appear as terms in the empirical calculations of skewness and kurtosis. Skewness is represented by the 3rd central moment and is contained in a three dimensional tensor $P^3$. The element of this tensor for a factor $x$ is

  $$P_{xxx} = \frac{1}{n}\sum_{i=1}^{n}(x_i - \bar{x})^3.$$

  Like the relationship between variance and covariance, higher order moments also have elements that are mixed moments of two or more variables. For example, the 'co-skew' between three factors would be

  $$P_{xyz} = \frac{1}{n}\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})(z_i - \bar{z})$$

- $D$ tensors specifying how the phenotype changes with changes in the underlying factors. This captures different aspects of the shape of the phenotypic landscape; for example, how steep or curved it is for various combinations of the genetic and environmental factors. They are constructed as derivatives of the phenotypic function. For example, the first derivatives of the phenotype with respect to each underlying factor yields the slope of the landscape at each point and would look like

$$D^1 = \nabla_\phi \begin{bmatrix} \frac{\partial \phi}{\partial g_1} \\ \vdots \\ \frac{\partial \phi}{\partial g_k} \\ \frac{\partial \phi}{\partial e_1} \\ \vdots \\ \frac{\partial \phi}{\partial e_n} \end{bmatrix}$$

where $\partial\phi/\partial g_1$ is the first derivitative of the phenotype $\phi$ with respect to the genetic factor $g_1$.

- an equation specifying the relationship between phenotype and fitness ($w$).

  $$w = g(\phi, e_m, \ldots, e_z)$$

  The inclusion of additional environmental factors into the fitness function allows the specification of situations where the optimal phenotype varies across environments.

- $Q$ vectors indicating how selection changes the distribution of the genetic factors. $Q^1$ gives the change in means and is encoded as a vector. $Q^2$, a matrix, specifies the change in variances and covariances, and so on. The general equation for a $Q$ vector is

  $$Q_a^k = \frac{\gamma}{\bar{w}} \frac{\partial^B w}{\partial \phi^B} \langle P^{A+k}, \otimes^i D^{a_i} \rangle \tag{6.1}$$

  where $B = \sum_i b_i$ enumerates the number of order $i$ derivatives; $A = \sum_i a_i$ are the degrees of differentiation; $\otimes$ is the outer product operator and $\otimes^i D^{a_i} = D^{a_1} \otimes D^{a_2} \otimes \cdots$ and represents the joint effect of different aspects of the phenotypic landscape; $\gamma$ is a scaling factor; and $\bar{w}$ is the mean fitness. $\langle P, D \rangle$ is an inner product that maps the distribution of variation in the underlying factors $D$ onto the phenotypic landscape $P$.

### Tensor algebra

Analyzing phenotypic landscape models proceeds by multiplying tensors to determine how the distribution of underlying factors maps on to the phenotypic landscape. An inner product projects one tensor onto another tensor of smaller dimension, resulting in a tensor of rank equal to the difference in ranks of the two original tensors. For example, the 4th moments (kurtoses) of the underlying factors, $P^4$, maps onto the 2nd derivatives of fitness, $D^2$ as

$$\langle P^4, D^2 \rangle_{i,j} = \sum_k \sum_l P^4_{i,j,k,l} D^2_{k,l}$$

resulting in a new tensor of rank 2 that is part of a Q vector influencing the 2nd moments (variances). This formula would therefore indicate how selection would increase or decrease the variance of a trait as a function of the curvature of the fitness landscape and the thickness of the tails of the distribution of underlying factors.

## 6.3 Model specification

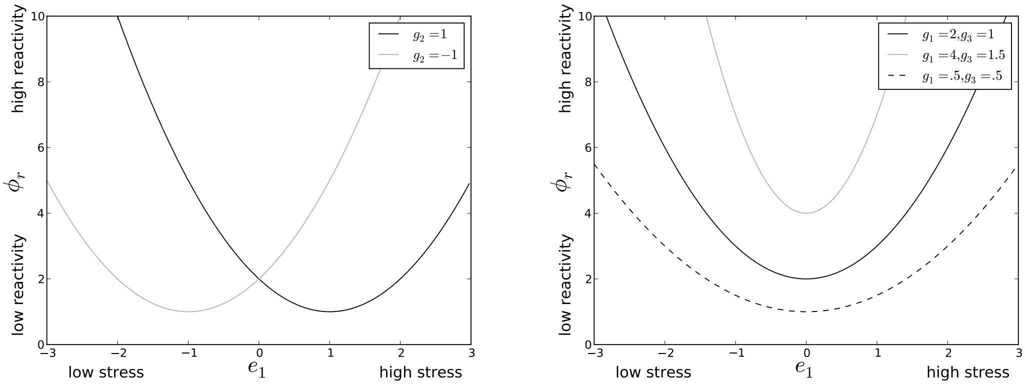
Boyce and Ellis (2005) conceptualized a U-shaped function to represent the relationship between early-life stress or psychosocial support and biological reactivity ($\phi_r$, see Fig. 6.1). The BSC model posits that sensitivity is the product of gene × environment interaction, so the model needs to specify that the phenotype is a product of both genetic and environmental factors. I paramaterized the U-shaped reaction norm as a quadratic function with 3 genetic and 1 environmental factor:

$$\phi_r(g_1, g_2, g_3, e_1) = g_1 + g_3(e_1 - g_2)^2 \tag{6.2}$$

where

- $g_1$: genetic factor controlling the minimum possible reactivity.
- $g_2$: genetic factor controlling under what value of the environmental factor ($e_1$) minimum reactivity occurs.
- $g_3$: genetic factor influencing the rate of increase in reactivity under progressively more and less stress.
- $e_1$: environmental factor representing stress early in life (higher value equals more stress).

The model is very general as to what the genetic factors are: they could represent functional variants of a protein or different transcription levels of one or more genes. As a first step, the model is meant to capture the phenomenology of the BSC theory. The reaction norm



(a) Environment of minimum reactivity.

(b) Minimum reactivity and curvature.

Figure 6.2: Reaction norm for for a biological sensitivity to context phenotype as a function of three genetic and one environmental factors, $\phi_r(g_1, g_2, g_3, e_1) = g_1 + g_3(e_1 - g_2)^2$. **(a)** Variation in genetic factor $g_2$ controls the environment ($e_1$) under which minimum reactivity develops. **(b)** Genetic factor $g_1$ controls the height and $g_3$ the curvature of the reaction norm.

$\phi_r$ under different parameters for the genetic factors is plotted in Figure 6.2. The genetic factors control the position, height, and curvature of the reaction norm. The system thus displays phenotypic plasticity because the same genotype will produce a different phenotype depending on the environmental factor encoding early childhood stress. The ability of the genetic factors to change the position and shape of the curve also means that children with different genotypes who develop in the same environment will have different phenotypes. The equation's specification of a single phenotype also encodes the property of "equifinality" (Waddington, 1957; Bertalanffy, 1968; Cicchetti & Tucker, 1994) that Boyce and Ellis (2005) note is consistent with the final BSC phenotype has the same health and fitness consequences regardless of the exact combination of environmental and genetic values that result in a particular phenotypic value.

### Fitness function

The key aspect of the fitness function is that buffered phenotypes should have fairly constant fitness across environments but achieve a lower maximum fitness under good environments. Reactive phenotypes, whether sensitive or vigilant, should have higher fitness in good environments and much lower fitness in poor environments. A logistic function, $\text{logit}(x) = \frac{1}{1+e^{-x}}$, can be used to capture some of these characteristics. Fitness is therefore a function of the re-

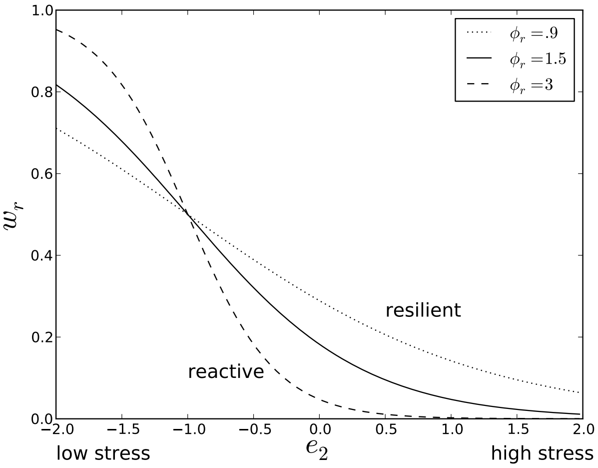


Figure 6.3: Fitness function for the biological sensitivity to context model. Fitness $w_r$ is a function of the reactivity phenotype $\phi_r$ and the level of stress in the environment experienced as an adult $e_2$. $w_r(\phi_r, e_2) = \text{logit}(-\phi_r(e_2 + 1))$. Under low stress the more reactive phenotype has the highest fitness while under high stress the resilient phenotype is buffered and achieves highest fitness. The model assumes a crossover point of intermediate stress where all phenotypes achieve equal fitness.

activity ($\phi_r$) and stress during the reproductive lifespan ($e_2$)

$$w_r(\phi_r, e_2) = \text{logit}(-\phi_r(e_2 + 1)) \tag{6.3}$$

The fitness curve for different levels of reactivity is plotted in Figure 6.3. As theorized, this fitness function shows a crossover in maximum fitness between reactive and resilient individuals depending on the level of stress experienced. The resilient phenotype shows less of a difference in fitness between high and low stress environments so it is more robust. The reactive phenotype shows more of a fitness differential between environments. The fitness functions also flatten out at the extremes so that there is less of a difference in fitness between reactive and resilient types in very good and very poor environments. While the fitness function captures the main features of the BSC theory, it does not model the requirement that highly reactive phenotypes have the best fitness in extremely poor environments (Boyce & Ellis, 2005).

## 6.4 Evolutionary dynamics

The model can be used to study the developmental evolution of reactivity as defined by BSC theory. The goal of the analysis is to derive expressions for the $Q$ tensors, which describe the changes in the distribution of the underlying genetic factors, from the phenotypic function and the $P$ and $D$ tensors and the application of Eq. 6.1. I will explore the effect that selection has on the means and variances of the underlying traits. Therefore, the focus will be on $Q$ vectors that change the $P^1$ and $P^2$ tensors.

### Change in means

The change in the means of the genetic factors is determined by the first derivative of fitness, the 2nd moments of the distribution, and the first derivatives of phenotype

$$Q_1^1 = \frac{1}{\bar{w}} \frac{\partial w_r}{\partial \phi_r} \langle P^2, D^1 \rangle \tag{6.4}$$

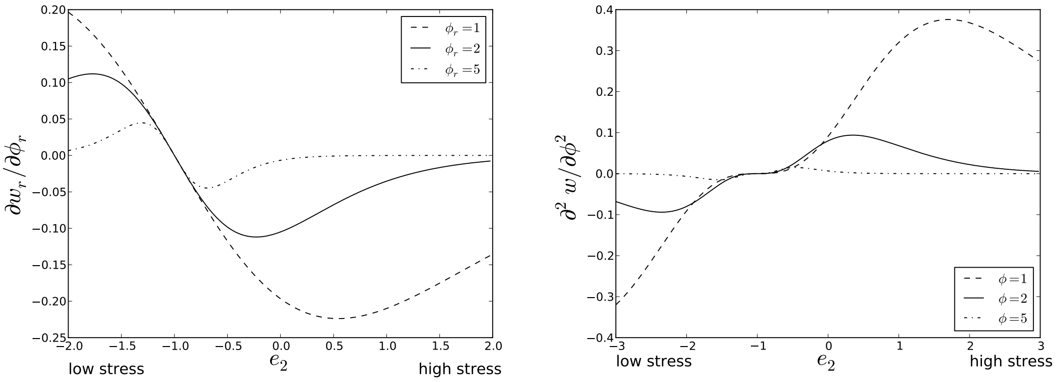
The model specification of the fitness function (Eqn. 6.3) includes a 'good', low-stress environment (arbitrarily $e_2 = -1$) where fitness is constant across phenotypes. The direction of change is influenced primarily by the derivative of fitness

$$\frac{\partial w_r}{\partial \phi_r} = -\frac{(e_2+1)e^{(e^2+1)\phi_r}}{(e^{(e_2+1)\phi_r}+1)^2}, \tag{6.5}$$

plotted in Figure 6.4a. The first derivative is positive when the average environment ($e_2$) is unstressful and negative when more stressful environments are common. The means of the genetic factors, $g_1$–$g_3$, change in proportion to their variances ($P^2$) but the direction of change is a function of the average quality of the environments early ($e_1$) or late ($e_2$) in life.

The magnitude and direction of change for each genetic factor is also determined by the shape of the phenotypic landscape with respect to each factor. Here the relevant shape parameter when we want to know the mean change in each factor given the genetic variances, as seen in Equation 6.5, is the first derivative of the phenotype with respect to each factor

$$D^1 = \begin{bmatrix} \frac{\partial \phi_r}{\partial g_1} \\ \frac{\partial \phi_r}{\partial g_2} \\ \frac{\partial \phi_r}{\partial g_3} \\ \frac{\partial \phi_r}{\partial e_1} \end{bmatrix} = \begin{bmatrix} 1 \\ -2(e_1 - g_2)g_3 \\ (e_1 - g_2)^2 \\ 2(e_1 - g_2)g_3 \end{bmatrix} \tag{6.6}$$



(a) First derivative of fitness.

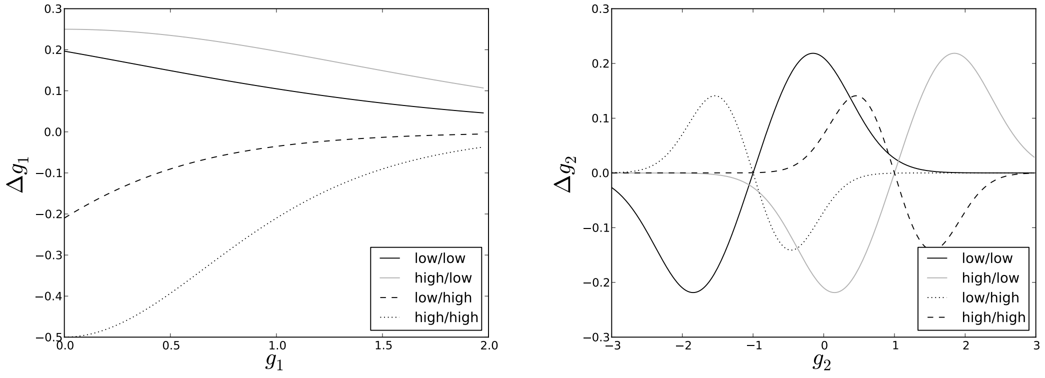
(b) Second derivative of fitness.

Figure 6.4: Derivative of fitness with respect to phenotype for different values for mean stress later in life ($e_2$). **(a)** $\partial w/\partial \phi_r$ = first derivative of fitness. The function is always positive when average stress experienced during adulthood is low and negative when it is high. **(b)** $\partial w/\partial \phi_r$ = second derivative of fitness.

showing that the change in sensitivity as the first genetic factor ($g_1$) changes is constant, or $\partial \phi_r/\partial g_1 = 1$, while the change from factors $g_2$ and $g_3$ depend on the average values of the genetic and environmental factors.

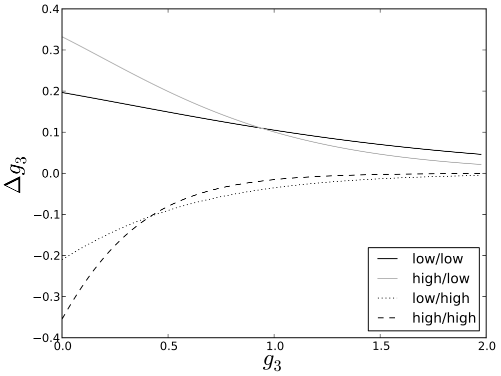
The change in the genetic factors from selection are visualized in Figure 6.5. When the average environment experienced during adulthood is one of low stress, selection will increase the genetic factor controlling minimum reactivity ($g_1$), that is, the reaction norm moves up (Fig. 6.2b). This is because it is beneficial to be more receptive to the good environment. If the average adult environment is stressful, however, $\Delta g_1$ is negative, so the population will move to positions on the reaction norm surface that minimize reactivity (Fig. 6.5a).

The genetic factor $g_2$ determines under what value of $e_1$ (early stress) minimum reactivity is achieved. When the average environment in adulthood is good, selection will move the reaction norm right or left depending on its position relative to the average environment experienced during development ($e_1$). For example, if $e_1 = 0$ and $g_2 = 1$ (black line, Fig. 6.2a), the reaction norm will move to the right, increasing mean reactivity. If the reaction norm is on the other side ($g_2 = -1$, for example), reactivity is increased by moving the curve to the left. If the curve is poised so that minimum reactivity is achieved under the mean value of $e_1$ then $\Delta g_2 = 0$. This is an unstable equilibrium so if mutation or drift pushes mean $g_2$ either above or below this point, the reaction norm will move away from it. If the later environment



(a) Minimum reactivity.

(b) Offset of reaction norm.



(c) Reaction norm curvature.

Figure 6.5: Mean in genetic factors from selection under stressful and unstressful environments. Lines show combinations of low and high early/late stress environments. Black: $e_1$ = *low* = -1, $e_2$ = *low* = -2. Gray: $e_1$ = high = 1, $e_2$ = low = -2. Dotted: $e_1$ = *low* = -1, $e_2$ = *high* = 1. Dashed: $e_1$ = *high* = 1, $e_2$ = *high* = 1. **(a)** Change in minimum reactivity ($\Delta g_1$). $g_1$ increases when later stress ($e_2$) is low (top two lines) and decreases when high (bottom two lines). The magnitude of change depends on the average stress during development, $e_1$. **(b)** Change in the offset of the reaction norm from average early stress ($\Delta g_2$). When later stress is low ($e_2 < -1$, solid lines), the reactivity curve will move away from its current value in the direction that maximizes reactivity at the average value of the early stress factor, $e_1$. When later stress is moderate or high ($e_2 > -1$, dotted and dashed lines) $g_2$ will move to match $e_1$ such that reactivity is minimized under the average amount of early stress. **(c)** Change in reaction norm curvature ($\Delta g_3$). High average late-life stress causes the reaction norm to flatten out, making low reactivity more robust across a wider range of stress levels early in life.

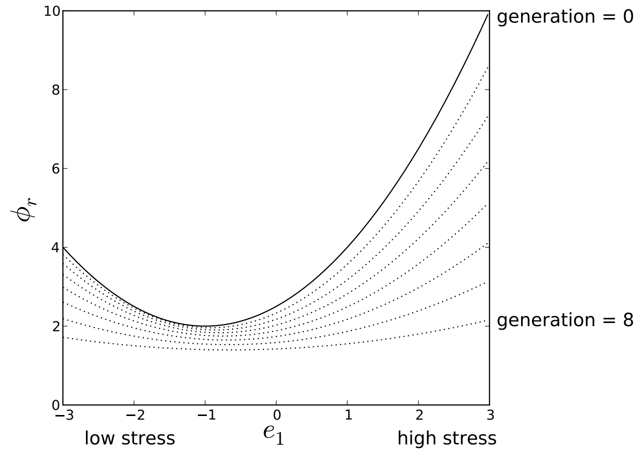


Figure 6.6: Evolution of the reactivity phenotype under directional selection when the average environments are moderately stressful. Selection has the effect of lowering and flattening the reaction norm. At generation 0: $g_1$ = 2, $g_2$ = -1, $g_3$ = 0.5. By generation 8: $g_1$ = 1.4, $g_2$ = -0.6, $g_3$ = 0.06. Environment factors $e_1 = e_2 = 0$.

is more stressful on average, however, selection will move the reaction norm toward the point where $g_2 = e_1$. The biological reactivity curve in this case will thus track the value of stress in the early environment to minimize reactivity later in life.

Change in reaction norm curvature ($g_3$) follows a similar dynamic to $g_1$ (Fig. 6.5c). When the good environments are more common later in life, the curvature of the reaction norm will increase to maximize the biological reactivity that develops independent of the early environment. If most environments in which fitness is expressed are poor and stressful, the reaction norm will flatten out to create a phenotype that is more robust across early environments in order to minimize sensitivity to the environment later in life.

The BSC model specifies that moderately stressful environments (here $e_1 = e_2 = 0$) are most common. Thus the evolutionary dynamics will be described by the curves in Figures 6.5a–c that are labelled as *high/high*. Selection will therefore generally tend to move the reactivity curve downward and toward the mean of $e_1$ while making the curve flatter. The evolution of the reaction norm over eight generations is visualized in Figure 6.6.

## 6.5 Change in variance

If we are interested in how genetic variance in reactivity is maintained, then we need to calculate the effect of selection on the variance of and covariances between the underlying genetic factors. The $Q$ tensors relevant to the change in the (co)variance matrix are

$$Q_1^2 = \frac{1}{\bar{w}_r}\frac{\partial w_r}{\partial \phi_r}\langle P^3, D^1\rangle \tag{6.7}$$

$$Q_2^2 = \frac{1}{\bar{w}_r}\frac{\partial w_r}{\partial \phi_r}\langle P^4, D^2\rangle \tag{6.8}$$

$$Q_{1,1}^2 = \frac{1}{2\bar{w}_r}\frac{\partial^2 w_r}{\partial \phi_r^2}\langle P^4, D^1 \otimes D^1\rangle \tag{6.9}$$

where the amount that the phenotype curves as a function of the underlying genetic factors are the second derivatives of the phenotype

$$D^2 = \begin{bmatrix} \frac{\partial^2\phi_r}{\partial g_1^2} & \frac{\partial^2\phi_r}{\partial g_1 g_2} & \frac{\partial^2\phi_r}{\partial g_1 g_3} \\ \frac{\partial^2\phi_r}{\partial g_2 g_1} & \frac{\partial^2\phi_r}{\partial g_2^2} & \frac{\partial^2\phi_r}{\partial g_2 g_3} \\ \frac{\partial^2\phi_r}{\partial g_3 g_1} & \frac{\partial^2\phi_r}{\partial g_3 g_2} & \frac{\partial^2\phi_r}{\partial g_3^2} \end{bmatrix} \tag{6.10}$$

$$= \begin{bmatrix} 0 & 0 & 0 \\ 0 & 2g_3 & -2(e_1 - g_2) \\ 0 & -2(e_1 - g_2) & 0 \end{bmatrix}, \tag{6.11}$$

and the outer product of the first derivatives

$$D^1 \otimes D^1 = \begin{bmatrix} \frac{\partial\phi_r}{\partial g_1}\frac{\partial\phi_r}{\partial g_1} & \frac{\partial\phi_r}{\partial g_1}\frac{\partial\phi_r}{\partial g_2} & \frac{\partial\phi_r}{\partial g_1}\frac{\partial\phi_r}{\partial g_3} \\ \frac{\partial\phi_r}{\partial g_2}\frac{\partial\phi_r}{\partial g_1} & \frac{\partial\phi_r}{\partial g_2}\frac{\partial\phi_r}{\partial g_2} & \frac{\partial\phi_r}{\partial g_2}\frac{\partial\phi_r}{\partial g_3} \\ \frac{\partial\phi_r}{\partial g_3}\frac{\partial\phi_r}{\partial g_1} & \frac{\partial\phi_r}{\partial g_3}\frac{\partial\phi_r}{\partial g_2} & \frac{\partial\phi_r}{\partial g_3}\frac{\partial\phi_r}{\partial g_3} \end{bmatrix} \tag{6.12}$$

$$= \begin{bmatrix} 1 & -2(e_1 - g_2)g_3 & (e_1 - g_2)^2 \\ -2(e_1 - g_2)g_3 & 4(e_1 - g_2)^2 g_3^2 & -2(e_1 - g_2)^3 g_3 \\ (e_1 - g_2)^2 & -2(e_1 - g_2)^3 g_3 & (e_1 - g_2)^4 \end{bmatrix}, \tag{6.13}$$

$P^3$ is the tensor of skews, and $P^4$ is the tensor of kurtoses. The total change in the variance/covariance matrix $P^2$ is the addition of these $Q$ vectors

$$\Delta P_{\text{sel}}^2 = Q_1^2 + Q_2^2 + Q_{1,1}^2 \tag{6.14}$$

The $Q_1^2$ tensor is determined by how the skew of the genetic factors ($P^3$) maps onto the slope of the phenotype ($D^1$, Eqn 6.6). This mapping is given by the inner product $\langle P^3, D^1\rangle$

which takes a 3-dimensional tensor of skews and a 1-dimensional vector of derivatives, producing a 2-dimensional matrix of terms related to the change of the covariance matrix. The diagonals of this matrix indicate the relevant change in variances while the off diagonals give changes to covariances among the genetic factors. The mapping relevant to the variance of factor $g_1$ is

$$\begin{aligned}\langle P^3, D^1\rangle_{11} &= P_{111}D_1 + P_{211}D_2 + P_{311}D_3 \\ &= P_{111} - 2(e_1 - g_2)g_3P_{211} + (e_1 - g_2)^2 P_{311},\end{aligned}$$

to $g_2$ is

$$\begin{aligned}\langle P^3, D^1\rangle_{22} &= P_{122}D_1 + P_{222}D_2 + P_{322}D_3 \\ &= P_{122} - 2(e_1 - g_2)g_3P_{222} + (e_1 - g_2)^2 P_{322},\end{aligned}$$

to $g_3$ is

$$\begin{aligned}\langle P^3, D^1\rangle_{33} &= P_{133}D_1 + P_{233}D_2 + P_{333}D_3 \\ &= P_{133} - 2(e_1 - g_2)g_3P_{233} + (e_1 - g_2)^2 P_{333},\end{aligned}$$

Most of the components of this tensor contain the term $e_1 - g_2$ so much of the skew between underlying factors will only influence the variance and covariance when early-environmental stress fluctuates away from the fitness optimum where $g_2 = e_1$. When $g_2 = e_1$ then the diagonals of the tensor reduce to

$$\begin{aligned}\langle P^3, D^1\rangle_{11} &= P_{111} \\ \langle P^3, D^1\rangle_{22} &= P_{122} \\ \langle P^3, D^1\rangle_{33} &= P_{133}\end{aligned}$$

Thus only the skew between the minimum reactivity factor, $g_1$, and the other genetic factors, namely $P_{111}$, $P_{122}$, and $P_{133}$, will have an influence on the change in variances.

Kurtosis of the factors ($P^4$) describes whether the tails of the distribution of each factor are thinner (positive kurtosis) or thicker (negative kurtosis) and the peakedness of the distribution. When $g_2 = e_1$ the only nonzero element of the second derivatives of the phenotype ($D^2$, Eq. 6.11) is $D_{22} = 2g_3$, involving the factor controlling how robust reactivity is over different amounts of stress in the early environment. The elements of $\langle P^4, D^2\rangle$ that contain $D_{22}$ and relate to change in variances are

$$\begin{aligned}\langle P^4, D^2\rangle_{11} &= 2g_3P_{2211} \\ \langle P^4, D^2\rangle_{22} &= 2g_3P_{2222} \\ \langle P^4, D^2\rangle_{33} &= 2g_3P_{2233}\end{aligned}$$

Kurtosis is also involved in the $Q^2_{1,1}$ tensor. This $Q$ tensor involves the second derivative of fitness

$$\frac{\partial^2 w_r}{\partial \phi_r^2} = \frac{2(e_2+1)^2 e^{2(e_2+1)\phi_r}}{(e^{(e_2+1)\phi}+1)^3} - \frac{(e_2+1)^2 e^{(e_2+1)\phi_r}}{(e^{(e_2+1)\phi}+1)^2}, \tag{6.15}$$

which is plotted in Figure 6.4b, and the outer product of the first derivatives of phenotype $D^1 \otimes D^1$ (Eq. 6.13). At the equilibrium point the only nonzero term of this matrix is $[D^1 \otimes D^1]_{11} = 1$. The elements of the mapping of $P^4$ onto $D^1 \otimes D^1$ related to changes in variances are

$$\begin{aligned}
\langle P^4, D^1 \otimes D^1 \rangle_{11} &= P_{1111} \\
\langle P^4, D^1 \otimes D^1 \rangle_{22} &= P_{1122} \\
\langle P^4, D^1 \otimes D^1 \rangle_{33} &= P_{1133}
\end{aligned}$$

If the population is at the equilibrium point $g_2 = e_1$ then the changes in the variance of $g_1$, $g_2$, and $g_3$, combining the elements of the $Q$ vectors derived above, are

$$\begin{aligned}
\Delta P_{11} &= \tfrac{1}{\bar{w}_r}\left(\tfrac{\partial w_r}{\partial \phi_r} P_{111} + \tfrac{\partial w_r}{\partial \phi_r} 2 g_3 P_{2211} + \tfrac{1}{2}\tfrac{\partial^2 w_r}{\partial \phi_r^2} P_{1111}\right) \\
\Delta P_{22} &= \tfrac{1}{\bar{w}_r}\left(\tfrac{\partial w_r}{\partial \phi_r} P_{122} + \tfrac{\partial w_r}{\partial \phi_r} 2 g_3 P_{2222} + \tfrac{1}{2}\tfrac{\partial^2 w_r}{\partial \phi_r^2} P_{1122}\right) \\
\Delta P_{33} &= \tfrac{1}{\bar{w}_r}\left(\tfrac{\partial w_r}{\partial \phi_r} P_{133} + \tfrac{\partial w_r}{\partial \phi_r} 2 g_3 P_{2233} + \tfrac{1}{2}\tfrac{\partial^2 w_r}{\partial \phi_r^2} P_{1133}\right)
\end{aligned}$$

When environments experienced during reproduction are adverse, the first derivative of fitness is negative while the second derivative is positive (Fig. 6.4)

$$\begin{aligned}
\Delta P_{11} &= \tfrac{1}{\bar{w}_r}(-P_{111} - 2 g_3 P_{2211} + \tfrac{1}{2} P_{1111}) \\
\Delta P_{22} &= \tfrac{1}{\bar{w}_r}(-P_{122} - 2 g_3 P_{2222} + \tfrac{1}{2} P_{1122}) \\
\Delta P_{33} &= \tfrac{1}{\bar{w}_r}(-P_{133} - 2 g_3 P_{2233} + \tfrac{1}{2} P_{1133})
\end{aligned}$$

Variance in the genetic factors will increase when these terms are positive and decrease when they are negative. The 4th central moments of a single factor are raised to the 4th power, so the terms $P_{1111}$ and $P_{2222}$ will always be positive. The other terms can be either positive or negative and the mixed terms ($P_{122}$, $P_{133}$, $P_{1122}$, $P_{1122}$, $P_{2233}$) will be zero if there is no association between the underlying factors. If the genetic factors are uncorrelated then the change in variances will be

$$\begin{aligned}
\Delta P_{11} &= \tfrac{1}{\bar{w}_r}(-P_{111} + \tfrac{1}{2} P_{1111}) \\
\Delta P_{22} &= \tfrac{1}{\bar{w}_r}(-2 g_3 P_{2222}) \\
\Delta P_{33} &= 0
\end{aligned}$$

Thus variance in the minimum reactivity of genotypes could be maintained either when there is negative skew in the distribution of $g_1$ (i.e., $P_{111} < 0$) or when $-P_{111} < \frac{1}{2} P_{1111}$. Selection will always work to decrease the variance of the offset parameter $g_2$ but would not shape the curvature parameter $g_3$.

If environmental fluctuation in $e_1$ or mutation or migration shift the mean value of $g_2$ then terms in the $Q^2$ vectors involving $(e_1 - g_2)$ will come into play. If the genetic factors are uncorrelated, this will have the biggest effect on the variance of $g_3$ from the term in the $Q^2_{1,1}$ tensor $[D^1 \otimes D^1]_{33} = (e_1 - g_2)^4$ (Eqn. 6.13). This term maps the kurtosis of $g_3$ so its change in variance would be

$$\Delta P_{33} = \frac{1}{\bar{w}_r}\frac{1}{2}(e_1 - g_2)^4 P_{3333}. \tag{6.16}$$

As this term will always be positive, fluctuations causing $g_2$ and $e_1$ to depart from each other will increase the variance in the genetic parameter underlying the curvature of the reaction norm for biological sensitivity.

## 6.6 Evolution of orchids and dandelions

With equal parts seriousness and whimsy Boyce and Ellis (2005) talk about robust and sensitive children as *dandelions* and *orchids*, respectively.[1] Dandelion children thrive and do well in pretty much any environment. Their more delicate peers, the orchids, collapse in poor environments but flourish in exceptionally good ones. Although the reaction norms defined in the models are simple and do not capture all of the developmental complexities of dandelion and orchid children, the models allow us to formalize our intuitions about how biological sensitivity to context will evolve.

First, specifying the phenotypic and fitness functions separately shows that robustness enters the system in two places. The buffered/sensitive distinction in the BSC theory refers to the shape of the fitness function (Eq. 6.3), where buffered individuals have relatively constant fitness across the environment gradient of stress in adulthood whereas the fitness of sensitive individuals shows more considerable differences (Fig. 6.4). Robustness also describes the norm of reaction for the sensitivity phenotype (Eq. 6.3, Fig. 6.2b). The genetic factor ($g_3$) determining how the sensitivity phenotype changes with the square of early stress determines how plastic or robust the phenotype is to early life stress. When the development of sensitivity is very robust to early stress ($g_3 \to 0^+$), the individual will have the same level

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[1] After the Swedish idioms *maskrosbarn* (dandelion child) and *orkidebarn* (orchid child).

of sensitivity to stress as an adult independent of stress experienced early in life. Whether this leads to high or low reactivity will depend on the height of the reaction norm (specified by the $g_1$ genetic factor).

Lowest achievable reactivity is important because the evolutionary analysis showed that when the average stress in adulthood is moderate selection will tend to flatten out sensitivity reaction norm. Selection will also act to make the reaction norm 'track' the mean value of the childhood environment so that minimum reactivity is achieved under the most prevalant amount of stress. When the reaction norm is very curved it will more quickly shift to match the average level of stress while a shallower reaction norm would not be as sensitive to environmental fluctuations. The evolutionary–development theory of BSC specifies that variation in (phenotypic) reactivity is maintained by variability in stress early in life. A curved reaction norm can produce differential susceptibility to stress even if there is no underlying genetic variation. However, according to the mathematical model, this alone is not sufficient to maintain variation in reactivity because selection will prefer a robust phenotype that results in the same reactivity level in all individuals. The driver of this flattening of the sensitivity reaction norm is that environments of moderate stress, where high reactivity achieves higher fitness, are most prevalent. Thus, it was necessary to see if any features of the developmental system could promote the maintenance of genetic variation in the reaction norm.

Analysis of the effects of selection on quantitative traits (Lande & Arnold, 1983; Falconer & Mackay, 1996, see Chap. 5) typically only relies on the mean of the trait (to determine where on the fitness surface the population is) and the amount of genetic variance in and covariance among the traits (which determines the evolvability of the trait, i.e., the extent to which a given strength of selection will translate into a change in the mean phenotype). Selection, however, both works on and is determined by all the aspects of the distribution of the underlying genetic and environmental factors (Rice, 2002, 2004). Not only mean and variance but higher order moments of the distribution such as skew and kurtosis can also play a role in developmental evolution. The analysis showed that variation can be maintained if certain kinds of asymmetries exist in the distribution of the genetic factors. Such asymmetries could arise if the genetic factors follow nonnormal joint distributions which would lead to skew within and among the genetic factors. If there is no association between the genetic factors, then variation in the reaction norm curvature can still be maintained if fluctuations in the quality of the average childhood environment depart from the point at which minimum reactivity is achieved ($e_1 \neq g_2$, Eq. 6.16). This could occur, for example, through year-to-year variation in resource availability that contributes to childhood adversity or other unpredictable events such as natural disasters and wars. The evolvability of variance in the reaction norm's width is limited by the 4th moment of the genetic factor's distribution. Mutations have more of an influence on higher-order moments than they do on the variance (Rice, 2004), so it would take less mutational input when the environment fluctuates to maintain a given amount of genetic variance. Thus, under this simple model, temporal fluctuations in the average quality of the environment experienced during childhood are necessary to maintain variation in adult sensitivity. Variation between individuals in their childhood environment is not sufficient.

The results from the theoretical model thus raise several important empirical questions that should be addressed to understand the developmental evolution of behavioral sensitivity to context and stress responsivity. The amount of variation in sensitivity is a function of the curvature of the reaction norm. A flatter curve will produce less phenotypic variation. Studying individuals whose genotypes are at the extremes of the reaction norm (either very flat or very curved) would be useful for understanding the range of biologically plausible shapes that could be achieved in the population through selection on variance for curvature. Once the systems underlying the curvature are better understood, the extent to which mutations influence the extremes of the distribution could also be studied to estimate the evolvability of the reaction norm. Finally, the model predicts that the minimum reactivity achievable should occur at or near the mean value of stress expressed. Testing this in the real world will require clarifying exactly what is meant by the *average* level of early stress and designing ways to measure and assess it.

More complex models can be developed if the results of the theoretical analysis do not match what we actually find to be the case. While the model is as generic as possible with regard to the biological details, the flexibility of the modeling language is such that more specific systems can be described. For example, a model could be specified that includes multiple phenotypes for the separate aspects of the stress response system, such as the division between inhibitory and activating subsystems. Following empirical results (Belsky & Beaver, 2011) the model could also be expanded to include multiple genetic factors contributing to the plasticity of the reaction norm.

An additional feature of the BSC theory is that in extremely poor environments, the more reactive phenotypes achieve higher fitness compared to the robust phenotypes. This might be incorporated into the model using a generalized logistic function so that the asymptote differs depending on the reactivity. The phenotypic function also allows biologically implausible values. For example, if $g_3 < 0$ the phenotypic curve flips over so that reactivity is minimized in the least and the most stressful environments. Also, any combination of factors that make the phenotype $\phi_r < 0$ would cause the fitness function to invert such that highest fitness is achieved in the most stressful environment. Such minor annoyances could be overcome by amending the phenotypic landscape function so that neither the contribution of $g_3$ not the whole function can take on negative values.

A further extension of the BSC theory that I did not explore is the idea of adaptive calibration (Del Giudice et al., 2011). The encoding of the information about adversity by the stress response system allows the organism to tune its reactivity to achieve maximum fitness. This assumes that the environment experienced during development is predictive of the environment experienced during reproduction. However, the mathematical model did not make any assumptions about or explore the effects of the amount of covariance between the two environmental parameters ($e_1$ and $e_2$). Expanding the model to study adaptive plasticity would require treating the two environmental factors as phenotypes of the individual[2] and study the joint developmental evolution of the reactivity phenotype and the environments (Rice, 2004). This analysis would reveal how the distribution of the environments (including their higher moments) would shape the slope and curvature of the reaction norm.

Here I have shown how mathematical modeling can clarify evolutionary–development theories of stress responsivity. Formalizing a theory and carrying out a rigorous analysis can provide strong confirmation or refutation of the plausibility of evolutionary scenarios for the origins and maintenance of genetic variation in complex phenotypic traits. The modelling framework (Rice, 2004) allows for a very general understanding of the evolution of development and is thus highly suited to advancing theories about biological sensitivity to context, differential susceptibility, and plasticity of psychological traits. The orchid hypothesis is a viable one, evolutionarily speaking, but the maintenance of genetic variation in the reaction

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[2] Although the environmental-factor-as-phenotype has zero heritability.

norm for sensitivity requires temporal fluctuations in average levels of early-life stress and positive kurtosis in genetic factors determining the amount of curvature.

## Chapter 7

# Individuality and diversity in evolutionary time

> I assumed, like many evolutionary psychologists, that vague memories of outdated undergraduate biology classes, plus some acquintence with genetic correlations, life-history trade-offs, and frequency dependent selection, would suffice to understand individual differences. Now I think we need to do better.
>
> Geoffrey Miller (2011, p. 376)

## 7.1 Summary of findings

Personality is part of our evolutionary heritage shared with other primates. In a series of studies I explored approximately 30 million years of personality evolution (a phylogenetic tree for the species I studied is presented again in Fig. 7.1). Basic evolutionary theory indicates that closely related species should be similar in terms of personality structure (Weiss & Adams, 2008). Comparing closely related species indicates over what orders of evolutionary time, from millions to tens of millions of years, personality structure is conserved or can diverge. Comparisons with nonhuman primates can also reveal if phenomenological aspects of personality quantitative genetics, such as the relative proportions of additive to nonadditive genetic variance, are unique to humans or also found in other species. Comparing human populations that differ in average personality or estimating changes of personality between generations can also show how personality evolves and diversifies on much shorter timescales, ranging from decades to tens of thousands of years. Apart from data, the strong

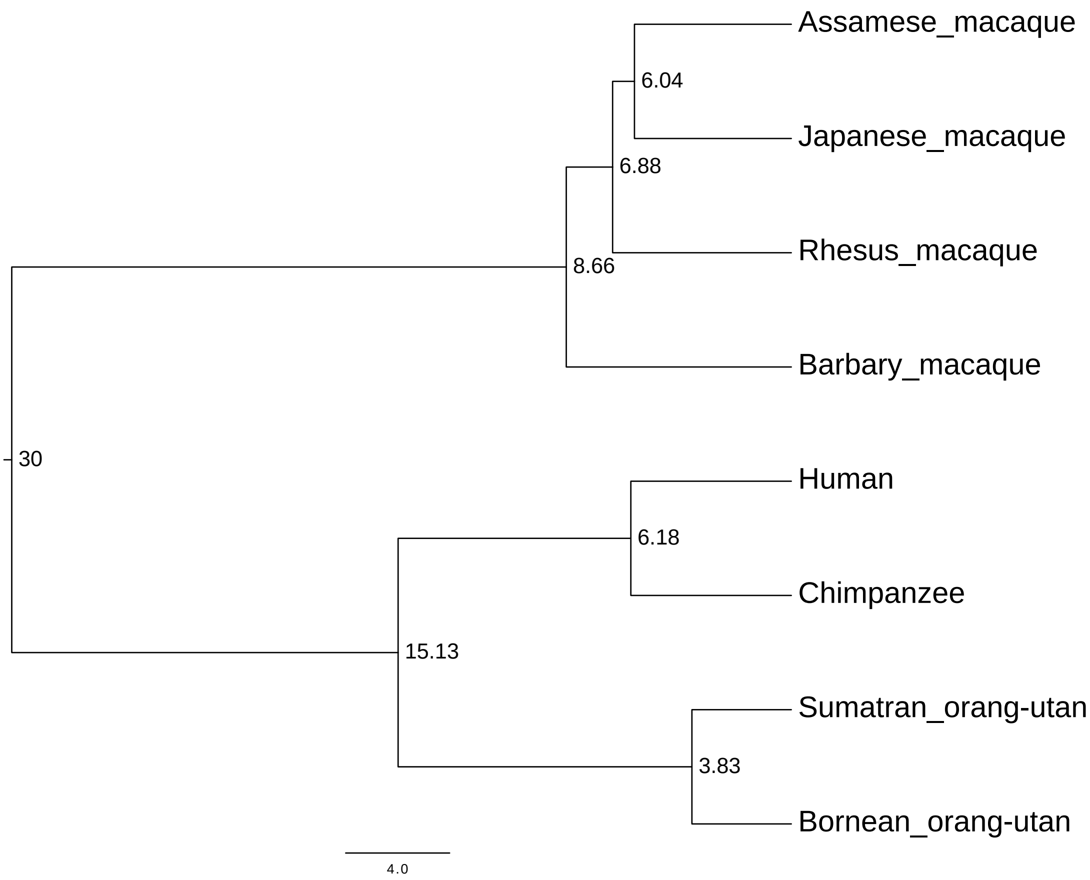

Figure 7.1: Phylogeny of species considered in the studies. I determined the personality structure of the Assamese, Japanese, and Barbary macaques and compared the phylogenetic patterning with rhesus macaques and chimpanzees. I used the two species of orang-utans to determine the heritability of their personality. I used human data for a life-history and selection analysis. Node labels give time to common ancestor in millions of years. Tree and branch lengths from consensus tree inferred using 10kTrees `http://10ktrees.fas.harvard.edu/` (C. Arnold et al., 2010).

mathematical basis of much evolutionary theory can also be used to test the plausibility of theories about personality development.

### Macaque species have similar personality structures

I analyzed personality ratings on three species of macaques (Japanese, Barbary, and Assamese) and compared their personality structures to that of rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011) assessed using the same instrument. A principal components analysis revealed that the species could be characterized by the personality dimensions

- Japanese macaque: dominance, openness, friendliness, and anxiety;
- Barbary macaque: confidence, opportunism, friendliness, openness;
- Assamese macaque: confidence, activity, openness, friendliness, and opportunism;

that were comparable to the rhesus macaque dimensions of confidence, openness, dominance, friendliness, anxiety, and activity.

To quantify the equivalence of personality dimensions from different species that had similar names and similar but not identical item content, I analyzed the personality domains as fuzzy sets where the inclusion of an item in a particular domain was continuous rather than discrete (King & Weiss, 2011). After encoding each personality domain as a fuzzy set by treating the absolute value of each item loading as a membership value, I used fuzzy set theory (Zedeh, 1965; Smithson & Verkuilen, 2006) to define core sets of items that consistently described different personality facets across species. Using this method, I found that all macaque species were consistently defined by a friendliness domain that captured sociability and affiliativeness. I compared this with chimpanzee personality domains and found that friendliness did indeed describe a blend of extraversion and agreeableness. The four species of macaques also had very similar openness dimensions.

The aspect of personality structure that differentiated the species the most was whether aggression-related items formed a separate personality domain or were part of the dominance dimension. Rhesus and Japanese macaques, species that both have strict hierarchies (Thierry, 2000), had a single dimension called dominance that captured both social competence and aggression. In contrast, Barbary and Assamese macaques, that are both characterized by more egalitarian societies, had an independent dimension made of up items related to aggression, stinginess, and irritability that I labelled opportunism. The presence or absence of covariation between the basic dominance and opportunism dimensions may be an adaptation to social structure.

If dominance and opportunism are a single domain this allows two types of individuals to exist at the extremes of the personality dimension. Individuals high in dominance would be independent while individuals at the other extreme would be pliant. Those high on opportunism would be aggressive while individuals low on this facet would be peaceful. Rhesus and Japanese macaque societies would therefore have aggressive–independent individuals and peaceful–pliant individuals. When the basic dominance and opportunism dimensions are independent, as in Barbary and Assamese macaques, four different personality styles would emerge: aggressive–independent, aggressive–pliant, peaceful–independent, and peaceful–pliant. This suggests that macaque societies differ in allowing more or fewer social niches to evolve.

Two of the macaque species (Japanese and Barbary) had also been assessed on four subjective well-being items that measured an individual's balance of positive and negative moods, pleasure from social interaction, ability to achieve goals, and a global assessment of how happy the rater would be to be the target individual. In both species the subjective well-being items composed a single dimension. Individuals in both species who were rated as higher on subjective well-being were also rated higher on friendliness. In Japanese macaques, subjective well-being also correlated positively with dominance and negatively with anxiety. In Barbary macaques, individuals higher on subjective well-being were also higher on confidence. This was consistent with results of the relationship between subjective well-being and high extraversion and low neuroticism in humans (Steel et al., 2008); high dominance, extraversion, and agreeableness and low neuroticism in chimpanzees (King & Landau, 2003; Weiss et al., 2009); and high extraversion and agreeableness and low neuroticism in orang-utans (Weiss et al., 2006).

### Population-level personality is sensitive to LH conditions

Theory and data suggest that an individual's personality should be consistent with their life history (LH) strategy for the timing of growth, reproduction, and survival (Wolf et al., 2007; Biro & Stamps, 2008; Careau et al., 2010). Countries differ both in terms of average personality levels (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005) and their position on the fast–slow continuum of LH (Borgerhoff Mulder, 1998; Westendorp & Kirkwood, 1998). Average personality of a country correlates with a variety of economic variables (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005) though what drives these patterns has yet to be explained (Allik & McCrae, 2004). I theorized that because human personality and LH go together at the individual level (Figueredo et al., 2005, 2007), LH differences between countries might explain some of the differences in personality.

I compared personality and LH data on 49 countries using average personality ratings for men and women from two cohorts, one born circa 1960 and one born circa 1980. Countries on the slow end of the LH continuum (low fertility, long life expectancy) were higher in openness and agreeableness. In these slow LH countries women also tended to be higher in conscientiousness while men were on average lower in neuroticism. These patterns held even while controlling for socioeconomic factors and resemblance between neighboring countries. While this is suggestive, I also took the additional step of seeing whether shifts in LH led to shifts in personality *within* countries. I found that as a country moved to a slower average LH strategy, both agreeableness and neuroticism increased. This indicates that there is some adaptive developmental plasticity in personality that is sensitive to LH conditions experienced during ontogeny.

### Majority of genetic variation in orang-utan personality and subjective well-being is nonadditive

Traditional behavior genetic studies of personality using twins found an even split between genetic and unique environment effects but little room for the shared environment (Bouchard & Loehlin, 2001). Studies that used other types of relatives, such as parents and non-twin siblings, in addition to twins found that the genetic variance in personality was made up of both additive and nonadditive effects (Keller et al., 2005; Pilia et al., 2006). While additive effects come from the main effects of genes, nonadditive genetic variance comes from interactions between genes at the same locus (dominance variance) or between genes at different loci (epistatic variance). The general factor of personality is also characterized by nonadditive genetic variance and Rushton et al. (2008) and Figueredo and Rushton (2009) have argued that this is consistent with 'recent' selection on human personality. I tested whether personality of a great ape was also explained by nonadditive genetic variance by estimating the genetic structure of of orang-utan personality and subjective well-being. This sample was particularly well suited for estimating nonadditive genetic because it contained a mix of full and half siblings (Lynch & Walsh, 1998; A. J. Wilson & Nussey, 2009).

I found that orang-utan personality and subjective well-being dimensions had heritabilities (that is, from additive genetic variance) of about 20%. Around 40% of the phenotypic variance, however, was explained by nonadditive genetic variance. Only around 15% of the variance of personality was explained by maternal or shared environmental effects, though slightly more of the variance in subjective well-being ($\approx$ 20%) could be explained by common environment effects, similar to findings in chimpanzees (Weiss et al., 2002). There were no statistically significant genetic correlations between personality and subjective well-being, though in total 15% of the additive genetic and 19% of the nonadditive genetic variance in subjective well-being was shared with personality. Thus, a high proportion of nonadditive genetic variance underlying personality is not unique to humans.

The biometrical model also controlled for the effects of raters on personality scores and revealed rater effects on the intercorrelations among personality and well-being dimensions. Specifically, while rater effects enhanced the correlations between subjective well-being and extraversion, neuroticism, agreeableness, and intellect, they masked a positive phenotypic correlation between subjective well-being and dominance.

### Natural selection on personality has a genetic basis

Several studies (Eaves et al., 1990; Alvergne et al., 2010; Jokela et al., 2011) found that differences in personality are related to differences in reproductive success suggesting that personality is under selection in contemporary populations. Because these studies looked only at phenotypic correlations between personality and fitness, they rely on an untested assumption, known as the phenotypic gambit, that the phenotypic and genetic relationships are the same. Because selection can only have an effect on the population by differential transmission of genes, testing this assumption is an important step in evolutionary analysis (M. B. Morrissey et al., 2011).

I estimated the genetic relationship between personality and fitness using a twin sample from the US and a pedigree sample from Scotland. In the US sample, I found that reproductive success positively genetically covaried with extraversion and agreeableness. However, the covariances, while significant, were very small compared to the phenotypic variance. Because of missing and incomplete data on reproductive success in the Scottish sample, I tested whether there were any changes to mean breeding values over time. I found that the breeding values did not change more than by chance, indicating that personality in Scotland is either neutral with respect to fitness or under very weak selection.

### Environmental fluctuations maintain plasticity to context

The Biological Sensitivity to Context (BSC) model (Ellis et al., 2005; Ellis & Boyce, 2008) proposes that differential vulnerability to detrimental effects and responsiveness to beneficial effects of the environment is based in a U-shaped relationship between early-life stress and reactivity of the stress response system. Individuals in very low and high stress environments develop high reactivity while individuals in moderately stressful but common environments develop low reactivity. The fitness benefits of high and low reactivity also depend on the environment, where individuals with low reactivity, compared with high reactivity individuals, achieve higher fitness under moderate stress but have lower fitness in very good environments. This model has been described in terms of developmental evolution (Ellis & Boyce, 2008; Del Giudice et al., 2011) and I sought to formalize the model mathematically for the purpose of understanding its evolutionary dynamics.

Using the tensor analysis framework of developmental evolution advanced by Rice (2002, 2004), I constructed a mathematical model of the BSC system where the U-shaped curve was influenced by genetic factors controlling its position and curvature. I found that when moderately stressful environments (under which low reactive or buffered individuals have highest fitness) are most prevalent, selection will produce a flattening to the U-shaped reactivity curve. The evolutionary dynamics also have the property that the curve minimum where the lowest reactivity is achieved will track the average stress level in the early environment. Temporal fluctuations in this average level of stress will maintain genetic variability in the shape of the curve.

## 7.2 Primate personality evolves, but slowly

Synthesizing the results from the empirical studies on contemporary selection, quantitative genetics, and LH, it appears that personality in primates evolves slowly. By slow I mean relative to physiological and dietary adaptations (Fleagle, 1999). I was able to detect a genetic link between personality and fitness in one large population (the US) but not another (Scotland). However, while the results from the US indicate that the coming generations will be more extraverted and agreeable because of natural selection on genes underlying these domains, the change from selection only amounts to about .01 SD per generation. Assuming the selection gradient remains constant, it would take several dozen generations and several hundred years for selection to have a noticeable effect. I did not detect selection on personality in the Scottish population, but even if the change in breeding values had been statistically significant, it too would only add up to a $\approx$ .02 SD change in personality over a 50-year period.

Does this mean personality evolution is 'over' (Jones, 2009)? No. The results from the US sample show that, while gradual from the point of view of a longitudinal study in psychology, the psychological makeup of at least some populations is continuing to adapt to the environment. Given the heritability of personality (Bouchard & Loehlin, 2001) and fecundity (Pettay et al., 2005) in humans, it is likely that natural selection in other populations where it has been detected (Eaves et al., 1990; Alvergne et al., 2010) also has a genetic basis. This slow rate of evolution is consistent with personality structure being a human universal (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005) and explains why the genetic structure of personality is also largely consistent between populations in North America, Europe, and Asia (Yamagata et al., 2006). The dimensional structure of personality is part of "the common heritage of the human species" (McCrae, 2004, p 7) because selection may not have resulted in much divergence between populations. When populations are on the order of $10^4$ or larger, as humans are, processes of random genetic drift can usually be ignored because they can be overcome by even weak selection (Hartl & Clark, 2007). Differences in personality in human populations could therefore have small contributions from drift and selection, and may be more attributable to gene flow via selective migration (Camperio Ciani & Capiluppi, 2010) and adaptive plasticity to local LH conditions, as was seen in the between generation changes in agreeableness and neuroticism across cultures.

The genetic correlation between personality and fitness in the US refutes personality being selectively neutral (Tooby & Cosmides, 1990a). The difference in results between the US and Scottish populations may mean that the two populations are at different positions on the fitness landscape, with the US farther from the optimum. While recent evolution has changed a lot about us (Hawks et al., 2007) and may have resulted in lots of behavioral changes (Hrdy, 2009; Figueredo et al., 2011), evolution has left the overall structure of our personality largely untouched. That is, while personality is adaptive, the social environment to which it is adapted has not changed enough to radically alter personality structure. This also explains why personality structure is largely consistent between closely related species of primates. These species share with us the same basic problems of social living that personality functions as an adaptation to. Both chimpanzee–human and Japanese–Assamese macaque lineages are separated by about the same amount of evolutionary time (i.e., $\approx 6$ millions years to the most recent common ancestor, Fig. 7.1). Each species resembles its evolutionary cousin in terms of personality traits related to social affiliation and altruism (extraversion and agreeableness for chimpanzees and humans, friendliness for the macaques) but differ in terms of the presence and composition of a dominance dimension. This common heritage, both in term of genetic variation and the environment we primates are adapting to, also explains other similarities between human and nonhuman primate personality, such as correlates with happiness and subjective well-being (Steel et al., 2008; King & Landau, 2003; Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011) and age-related differences (McCrae et al., 2000; King et al., 2008).

### Personality structure and social epigenesis

The socioecological hypothesis (Jarman, 1974; Clutton-Brock & Harvey, 1977; Sterck, Watts, & van Schaik, 1997; Kappeler & van Schaik, 2002) proposes that patterns of social organization should adapt readily to changes in ecological conditions. However, ecology does not explain all aspects of macaque social organization (Ménard, 2004) and primate societies seem to show phylogenetic signals (Thierry et al., 2000; Shultz et al., 2011) that defy unrestricted transitions between types of social organizations.

If personality is an adaptation to the social environment, then because Barbary macaques are thought to be closest to the ancestral social organization of macaques (Thierry et al., 2000) their personality structure may also be the true "living fossil" (per Weiss, Adams, Widdig, & Gerald, 2011). That the two most socially similar but not most phylogenetically related species, rhesus and Japanese macaques, differed from the ancestral condition by not having a separate opportunism dimension may well be a case of convergent evolution. Under strict hierarchies, the opportunistic use of aggressive and defiant behavior is not an adaptive niche to occupy, so these behaviors were instead selected to covary with social competence. This story is also consistent with rhesus and Japanese macaque personality being similar but not identical. The result may be similar functionally (the lack of an independent opportunism domain) but the 'solution' (a single dominance/confidence dimension in Japanese macaques and separate dominance and confidence dimensions in rhesus macaques) differs because they are evolutionarily independent. The opportunism dimension may also explain a unique feature of human personality: the lack of a clear dominance dimension (King & Figueredo, 1997; Gosling, 2001). Opportunism resembles the negative pole of agreeableness and in chimpanzees is a facet of dominance. Chimpanzee agreeableness is made up of items related to the positive pole of human agreeableness. Our more egalitarian social structure (Hrdy, 2009) may have resulted in a reversion to the ancestral personality structure, where opportunism separates from dominance, resulting in a uniquely human agreeableness dimension. Personality therefore ties into the social space that individuals within a species are able to occupy (Butovskaya, 2004; Thierry, 2004) and social structure emerges out of the behavioral dispositions and interactions among individuals.

While these results are certainly suggestive, the independence of opportunism and dominance domains should be investigated behaviorally. Given species differences in aggressiveness and arousal (Clarke & Boinski, 1995; Thierry, 2000), methods that can compare personality between and within species on the same dimension would be particularly fruitful (Uher, 2011b, 2011a). These results also show how, by 'imposing' a personality structure on a species using a common inventory, useful hypotheses can be generated that are then amenable to confirmation or rejection by more focused behavioral observation. Before proceeding, it would also be worthwhile to see whether the macaque personality structures I describe replicate in new samples, as has been done with chimpanzees (King et al., 2005; Weiss et al., 2007, 2009).

### Facet level structure of personality

That personality domains may be described as evolutionary blends or divisions of more basic dimensions (Weiss, Adams, Widdig, & Gerald, 2011, see Fig. 1.1) also suggests that evolutionary studies of human personality should also start exploring lower-level facets. If facets relate to the different fitness trade-offs for each personality domain, then we also might expect the facets to covary more strongly with reproductive success and perhaps even have fitness effects cancel each other out when examined only on the domain level. Because the facets of human personality dimensions hang together genetically (Yamagata et al., 2006), correlational selection on the lower order facets could pull in different directions, causing overall directional selection to appear very small. In proposing fitness trade-offs for personality, Nettle (2011a) also asked why these facets should vary together. Nettle suggested that sociable, sexually motivated individuals would also need a level of activity needed to seek out such activities. However, the risk of accident from higher activity levels would keep these facets from covarying perfectly. A higher predation risk for diseased individuals is offered as reason for vigilance and disease avoidance to covary as facets of neuroticism. However, group living largely solves the problem of predation risk for primates (van Schaik & van Hooff, 1983; Strier, 2003; Silk, 2007), making it less likely that individuals within a species would need to vary on this trait. A more likely scenario is the interplay between predation pressure and group size. When predation risk is high, larger groups form (R. A. Hill & Lee, 1998). More anxious individuals might then prefer to join larger groups when possible. Yet larger groups would also entail more stress from social challenges. In macaques this trade-off can be handled by making confidence (social fearfulness) and anxiety ("free-floating" fearfulness, that seems more suited to antipredator vigilance) separate dimensions. In macaques another potential fitness tradeoff involved could be time spent allogrooming and vigilance over infants (Maestripieri, 1993). In humans the confidence and anxiety facets have been marshalled handle threats of social rejection (Denissen & Penke, 2008a). Nettle also proposed that two facets of human agreeableness, altruism and compliance, covary together because both are needed to enter into cooperative agreements while monitoring the intentions of the other party. In macaques, social norms, such as they are, are established through dominance hierarchies so the altruism facet works through the affiliative network that would vary as a function of friendliness.

## 7.3 Behavior genetics and natural selection

One approach to understanding the evolutionary history of a trait is to see whether it is present in closely related species. Finding that two traits, such as neuroticism and SWB, are genetically correlated can be informative of their origins because a shared genetic basis is the first test of whether two traits have evolved together as a set (van Oers et al., 2005) and can thus act as further evidence that the personality-SWB nexus is ancestral in great apes. The common genetic basis among a set of traits can be approximated as a matrix (**G**) whose elements are the genetic variances of and genetic covariances between traits (S. J. Arnold, Bürger, Hohenlohe, Ajie, & Jones, 2008). Although in general the **G** matrix can not be used to detect specific processes of evolution, as divergence in structure can be a result of both selection and genetic drift (Pigliucci, 2006), consistency in the pattern of genetic correlations between traits among two or more species is an indication of long-term evolutionary stability, where the traits originated together in the common ancestor and continue to evolve as a set in each species, even as the species diverge in other ways (S. J. Arnold et al., 2008). The general stability of the genetic covariances among personality facets is therefore, again, an indication that they have been coevolving together. The same applies to the common genetic basis of subjective well-being in personality in humans (Weiss et al., 2008), chimpanzees (Weiss et al., 2002), and orang-utans. Humans and chimpanzees were more similar in that more of the genetic variance in subjective well-being could be accounted for by genetic factors shared with personality, consistent with the closer phylogenetic relationship between the two species. Similarly, the genetic covariance of extraversion and agreeableness in orang-utans could be a remnant of incomplete separation of an ancestral friendliness dimension. An examination of the **G** matrix alone, however, does not reveal the causal relationship between two variables. For example, the genetic correlation between personality and SWB might be a consequnces of personality differences leading to differences in SWB. Data on the development of personality and SWB could be used to test alternative causal explanations.

The lack of divergence in personality structure across cultures is not to say that there will not be between-population variation in the frequencies of genes underlying personality. For example, frequency of variants in the dopamine D4 receptor differs between human populations (Chang et al., 1996). Even when selection pressures are the same (or at least varying within the same general parameter space), new mutations only arise in one place. Thus, even if the genetic structure of personality is the same across populations, the actual alleles contributing to genetic variances may differ. Such variation makes it difficult to replicate genome-wide association results because these different variants will be tagged by different sets of SNPs (Miller, 2011).

### Nonadditive genetic variance indicates long-term, not recent, selection

Rushton et al. (2008) and Figueredo and Rushton (2009) state repeatedly, though without spelling out the logic, that the large proportion of nonadditive genetic variance for the general factor of personality is consistent with "recent" selection. It is not. Because the additive effects of a gene will influence a trait and fitness independent of genetic background, an allele that acts additively is more directly exposed to selection because it does not have any interactions to hide behind. For example, in a dominance interaction, a recessive allele at frequency $p$ will only be exposed to selection in the $p^2$ fraction of individuals who are homozygous recessive. Selection will thus erode nonadditive genetic more slowly than additive genetic variance (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999; Stirling et al., 2002). Most genetic variance is additive (W. G. Hill, Goddard, & Visscher, 2008). If a selection pressure is recent, then, the expectation is that additive genetic variance will still be higher than nonadditive variance because there would not have been sufficient time to reduce the genetic variance at all. If the selection pressure persists for a long time, the proportion of additive genetic variance will drop below that of the nonadditive genetic variance. A high proportion of nonadditive genetic variance in both human and orang-utan personality is therefore consistent with long-term selection in both species. A study of exploration and boldness in great tits also found an effect of nonadditive genetic variance (van Oers et al., 2004) and some behaviors in fruit flies are also characterized by large proportions of epistasis (Sambandan, Yamamoto, Fanara, Mackay, & Anholt, November 2006). One possible scenario is that fluctuating selection pressure erodes additive genetic variance but changes before there is sufficient time to reduce the nonadditive genetic variance. Evolution thus appears to shape personality traits be affected by epistatic and dominance interactions.

The high proportion of nonadditive genetic variance in personality may also be informative of the fitness effects of the underlying genes. W. G. Hill et al. (2008) found that both data and theory point to additive genetic effects explaining most of the genetic variance in complex traits. The main reason is that, as most alleles are extremely rare, their combinations with other alleles to create dominance or epistatic interactions will be rarer still. Summarizing data on MZ/DZ correlations for 86 phenotypes, W. G. Hill et al. (2008) found that the MZ correlations were on average less than twice the DZ correlations indicating mostly additive genetic variance underlying these traits. However, the summarized data included morphological traits as well, so the $V_{\mathrm{A}} > V_{\mathrm{NA}}$ rule might not apply to every category of trait. A theoretical model indicated that high $V_{\mathrm{NA}}$ should be expected under selection when the allele with highest fitness is dominant or when only one genotype combination has low fitness and the rest have equal fitness (W. G. Hill et al., 2008). Estimating the frequencies of alleles influencing personality can be used to determine their likely fitness effects (Eyre-Walker, 2010; Keightley & Eyre-Walker, 2010). The strength of selection against an allele determines its frequency with more deleterious alleles found at lower frequencies. The amount of variance contributed by an allele also scales with its effect on both the phenotype and fitness, as alleles with stronger effects entail higher selection coefficients. Only alleles under very weak selection can get to frequencies over the minor allele threshold used in association studies but the entire frequency spectrum of the alleles influencing the trait and fitness can be used to infer the mean strength of selection (Eyre-Walker, 2010). Evolutionary-minded behavior geneticists should therefore pay attention to minor alleles rather than discarding them.

### Plausible genetic mechanism underlying phylogenetic patterning

The phylogenetic patterns of blending basic personality dimensions into higher-level dimensions suggests that the basic dimensions can be shaped by evolution to start and stop covarying. How might this work? Developmental genetics has recently uncovered genetic loci that function to affect the covariation among different traits (Cheverud, 2001; Pavlicev et al., 2008). These relationship quantitative trait loci (rQTL) modify the correlations between traits by regulating the expression of epistatic interactions between genes affecting each trait. When the rQTL is ‘off’, the expression levels of the two traits would be able to vary independently. When the rQTL is ‘on’, the gene expression levels are linked. A hypothetical example of such covariance regulation are limb lengths in quadrapedal versus bipedal animals (Pavlicev, Cheverud, & Wagner, 2011). In quadrapeds, the lengths of the forelimbs and hindlimbs correlate more highly whereas in many primates or other species with specialized forelimbs, such as bats, the correlation is lower. Personality facets, dimensions, and higher order factors could presumably operate the same way if individuals in a species share the rQTL but vary on the underlying genes that are being co-regulated. A population genetic model exploring the evolution of rQTL revealed that when directional selection acted to make traits correlate together via rQTL, new genetic variance in the trait was generated (Pavlicev et al., 2011). Thus, the coordination of multiple behavioral dispositions as behavioral syndromes or personality dimensions could help maintain genetic variation in the whole trait.

## 7.4 Retooling evolutionary and comparative approaches to personality

I agree with Miller's (2011, p. 377) call to begin "re-tooling" evolutionary psychology by making greater use of specific analytic techniques from evolutionary biology to understand the ultimate origins of personality. I have attempted to show how the integration of comparative psychology and evolutionary behavior genetics can answer some of these questions. While evolutionary genetics and theoretical biology offer methods such as making genetically-informed assessments of selection gradients (M. B. Morrissey et al., 2011) or rigorous frameworks for building models of developmental evolution (Rice, 2004), comparing our personality to that of nonhuman animals gives us an idea of what sorts of evolutionary time frames are needed to understand where and when psychological diversity arose and how quickly it changes (Gosling & Graybeal, 2007). Timing is everything. The number of generations of evolutionary change under consideration determines the relative magnitude of effects that selection, mutation, random drift, and migration can have on a trait (Hartl & Clark, 2007, and see Chap. 1).

One way to reconcile contemporary selection on personality with species-level stability (for even the small changes detected would add up to a lot over thousands of generations) is that personality may be an adaptation to an environment that is unstable on a generation-by-generation basis but that is relatively consistent over the longer term. That is, the overall adaptive problems remain the same even if the fitness optimum is constantly changing. Personality is both the adaptation and the environment to which it is adapted. The ways that behaviors vary due to selection appears to be largely conserved even as species-typical behavior changes signifcanty.

My research has relied primarily on trait psychology. McCrae (2009) described this approach as analogous to physics. The goal is to seek the high-level regularities in personality dimensions. Cross species comparisons are therefore very valuable to this enterprise because they show how principles of human personality structure might generalize and where, ultimately, they came from. A chemistry based approach, which places behavior in its context, is complementary and will be useful for understanding how personality dispositions lead to fitness differences and how the adaptive environment for personality is constructed out of interactions between individuals. This context-sensitive approach is already represented in animal personality research by behavioral repertoire (Uher, 2008a) and behavioral syndrome (Sih, Bell, Johnson, & Ziemba, 2004) methods. A combined approach is the best way forward (Weiss & Adams, in press). Everything I have written here and the analytical approaches I have used can be applied equally to study the evolution of other individual differences such as intelligence and psychopathology. Nonhuman primates also show individual differences in general intelligence (Banerjee et al., 2009; Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2010) and psychopathology (Lilienfeld et al., 1999; Brüne et al., 2006).

A recent collected volume on the evolution of individual differences (D. M. Buss & Hawley, 2011) devoted considerable attention to evolutionary quantitative genetics and to demonstrating the untenability of neutral models when applied to the evolution of psychological traits, concluding that evolutionary processes will have shaped our psychological makeup considerably since the Holocene (Gangestad, 2011; Keller et al., 2011; Miller, 2011; Penke, 2011). These essays, however, make little mention of our shared evolutionary heritage with nonhuman primates.[1] We must keep in mind that psychological evolution happened *before* the Holocene as well (Gosling & Graybeal, 2007). The similarity in human and nonhuman primate personality and our phylogenetically shared genetic bases of behavior and social organization means that other primate species will serve as good models for the evolution of human personality. Convergent evolution in distantly related taxa with complex social life such as cetaceans and corvids will be equally informative. We may therefore be able to discover general principles about the evolution of personality structure in big-brained, long-lived, gregarious species by taking a comparative approach and asking *How else could our personalities have ended up?*

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[1] The words *primate*, *monkey*, *chimpanzee*, and *rhesus macaque* do not appear in the index. Within the text, these terms appear sporadically in reference to the serotonin transporter, comparative genomics, and dominance hierarchies. This is not to knock these studies, just point out an area where primatologists can make contributions to evolutionary psychology.

# Appendices

# Appendix A

# Codes

The following are a list of custom R functions developed during the course of this research.

## A.1 AIC-weighted average

The following function takes as its input a list of lmer models and returns AIC-weighted averages of each fixed-effect parameter estimate. This function is used in model averaging in Chapter 3.

```
weight.by.aic <- function(...) {
# Given lmer models as the argument
# return a table of fixed coefficient
# estimates that are the AIC weighted
# average of each model

  args <- list(...)

  # gather AICs and parameter names
  parameters <- c()
  AICs <- c()
  for(model in args) {
    parameters <- c(parameters, names(model@fixef))
```

```
  AICs <- c(AICs, summary(model)@AICtab$AIC)
}

parameters <- unique(parameters)

# calculate Akaike weights

# delta AIC = diff between best model
min.AIC <- min(AICs)
delta.AICs <- AICs - min.AIC

# relative likelihood = e^(-0.5 * dAIC)
relative.lik <- exp(-0.5 * delta.AICs)
AICweights <- relative.lik / sum(relative.lik)

the.coefficients <- c()
# gather the coefficients together
for(model in args) {
  # coefs are 0 if they are not included in this model
  unweighted.coefs <- matrix(0, nrow=length(parameters))
  # name a row for each parameter
  rownames(unweighted.coefs) <- parameters
  # stuff the parameters the model did include
  # into the right rows
  unweighted.coefs[names(model@fixef),] <- model@fixef

  the.coefficients <- cbind(the.coefficients, unweighted.coefs)

}

# matrix * vector performs column-wise
```

```
  weighted.coefs <- rowSums(t(t(the.coefficients) * AICweights))

  return(weighted.coefs)

}
```

## A.2 Dominance relationship matrix

These functions calculate the dominance relationship matrix $\mathbf{D}$ and its inverse $\mathrm{D}^{-1}$ given a standard pedigree data frame. The D matrix contains pairwise coefficients of fraternity between all individuals. An individual's coefficient of fraternity with themselves is 1, so the diagonal elements are $\mathbf{D}_{ii} = 1$. Given the additive genetic relationship matrix $\mathbf{A}$, the off-diagonal elements are (Lynch & Walsh, 1998, p 768)

$$\mathbf{D}_{ij} = \frac{\mathbf{A}_{gk}\mathbf{A}_{hl} + \mathbf{A}_{gl}\mathbf{A}_{hk}}{4} \tag{A.1}$$

where $g$ and $h$ are $i$'s parents and $k$ and $l$ are $j$'s parents.

The function `dominanceRelationship` calculates the $\mathbf{D}$. The convenience function `inverseD` will return the inverse matrix as this is what is fed into `MCMCglmm` as the design matrix.

```
library(pedantics)
library(MCMCglmm)

dominanceRelationship <- function(ped) {

  ped <- fixPedigree(ped)

  # coefficients of relatedness
  # check that pedigree has dams and sires
  if (all(is.na(ped[, 2])) & all(is.na(ped[, 3]))) {
    # if not, A matrix is an identity matrix
    A <- diag(dim(ped)[1])
    dimnames(A) <- list(ped$id, ped$id)
```

```
} else {
  # otherwise make it quickly from the A^-1 matrix
  Ainv <- inverseA(ped)$Ainv
  A <- round(solve(Ainv), 4)
  dimnames(A)[[1]] <- dimnames(Ainv)[[1]]
  dimnames(A)[[2]] <- dimnames(Ainv)[[1]]
}

Dij <- diag(1, length(diag(A)))
dimnames(Dij) <- dimnames(A)

ids <- dimnames(Dij)[[1]]
n <- length(ids)

# make pedigree easy to index
ped <- transform(ped, id = as.character(id),
                      dam=as.character(dam),
                      sire=as.character(sire))
rownames(ped) <- ped$id

if(n > 1) { # only need off diagonal elements
            # if there are >= 2 individuals
  for(i_ in 2:n) {
    for(j_ in 1:(i_ - 1)) {

        i = ids[i_]
        j = ids[j_]

        # parents of i
        g = ped[i,'dam']
        h = ped[i,'sire']
```

```
        # parents of j
        k = ped[j,'dam']
        l = ped[j,'sire']

        if(is.na(g) || is.na(k)) { Agk = 0} else { Agk = A[g,k] }
        if(is.na(h) || is.na(l)) { Ahl = 0} else { Ahl = A[h,l] }
        if(is.na(g) || is.na(l)) { Agl = 0} else { Agl = A[g,l] }
        if(is.na(h) || is.na(k)) { Ahk = 0} else { Ahk = A[h,k] }

        Dij[i,j] = Dij[j,i] = (Agk * Ahl + Agl * Ahk) / 4
      }
    }
  }

  return(Matrix(Dij, sparse=TRUE))

}

inverseD <- function(ped) {

  Dij <- dominanceRelationship(ped)

  Dinv <- Matrix(solve(Dij), sparse=TRUE)

  return(Dinv)

}
```

## A.3 Intraclass correlation coefficients

Calculates ICC(3, 1) and ICC(3, *k*) (Shrout & Fleiss, 1979). See Chapter 2. The function item reliabilities takes a *data.frame* of scores indexed by named `subject` and `judge` columns. ICCs are calculated for each column named in `item.names`.

```
# calculated per Shrout & Fleiss Psychol. Bul. 1979
icc31 <- function(BMS, EMS, k) {
  (BMS - EMS)/(BMS + (k - 1) * EMS)
}

icc3k <- function(BMS, EMS) {
  (BMS - EMS)/BMS
}

# Input a data.frame of individually judged, personality scores
# with a list of quoted item column names for each monkey, including
# monkey and rater name as columns
icc3.reliability <- function(.data, item.names, subject, judge) {

  icc.31s <- c();
  icc.3ks <- c();

  for(item in item.names) {
    anova.Factor <- anova(lm(as.formula(paste(item,
                                          paste(subject, judge, sep='+'),
                                          sep='~')),
                             data=.data))

    monkeys <- as.character(.data[,subject]);

    k <- mean(tapply(rep(1, length(monkeys)), monkeys, sum));

    BMS <- anova.Factor[1,3]
    EMS <- anova.Factor[3,3]
```

```
    icc.31s <- c(icc.31s, icc31(BMS, EMS, k=k));
    icc.3ks <- c(icc.3ks, icc3k(BMS, EMS));
  }

  return(data.frame(item=item.names, icc31=icc.31s, icc3k=icc.3ks));
}
```

## A.4 Procrustes rotation

Targeted Procrustes rotation takes a matrix of loadings from a factor analysis and rotates it to a target with the same number of loadings (McCrae, Zonderman, Costa, Bond, & Paunonen, 1996). The returned output shows the rotated loadings. The last row and last column of the output give the component and item congruence coefficients.

This code was modified from SAS code by McCrae et al. (1996) and developed for the analysis conducted by Weiss et al. (2012). It was used during an exploratory analysis of data presented in Chapter 2.

```
unit.weight <- function(Loadings) {
  rows <- length(Loadings[,1])

  # unweigted loadings of +1, 0, -1
  for (i in 1:rows) {
    # replace the max of each row with 1
    len <- length(Loadings[1,])
    row <- Loadings[i,][1:len]

    where.maximum <- abs(row) >= max(abs(row));
    salient.loading <- row[where.maximum][1];
```

```
    if(salient.loading > 0) {
      fill <- 1;
    } else if(salient.loading < 0) {
      fill <- -1;
    } else {
      fill <- 0;
    }
    Loadings[i,][1:len][ where.maximum] <- fill;
    Loadings[i,][1:len][!where.maximum] <- 0
  }
  Loadings
}

ssq <- function(V) {
  sum(V^2);
}

# Based on SAS code from
# MCCRAE et al. Evaluating replicability of factors in the revised NEO
# Personality Inventory: Confirmatory factor analysis versus Procrustes
# rotation. J Pers Soc Psychol. (1996).  vol. 70. pp 552-566.

# loadings: factor loadings for a varimax matrix
# norm: loadings for the target matrix
# weight "unit" or "none". Unit weight the loadings before applying
# the rotation
#
# Last column and last row of the result gives variable and
# factor congruences.
procrustes <- function(loadings, norm, weight="none") {
```

```
if(weight == "unit") {
  loadings <- unit.weight(loadings);
  norm <- unit.weight(norm);
}

S <- t(loadings) %*% norm;
W <- eigen(S %*% t(S))$vectors;

V <- eigen(t(S) %*% S)$vectors;

O <- t(W) %*% S %*% V;
K <- diag(diag(sign(O)));

WW <- W %*% K;
T <- WW %*% t(V);

procrust <- loadings %*% T;

#congruence coeffcients

# A
norm.diag.root <- sqrt(diag(t(norm) %*% norm));
A <- matrix(norm.diag.root, ncol=1);

#B
procrust.diag.root <- sqrt(diag(t(procrust) %*% procrust));
B <- matrix(procrust.diag.root, ncol=1)

# C
norm.procrust.diag <- diag((t(norm) %*% procrust) / (A %*% t(B)));
C <- matrix(norm.procrust.diag, ncol=1)
```

```
  # D
  D <- matrix(sqrt(diag(norm %*% t(norm))), ncol=1)

  E <- matrix(sqrt(diag(procrust %*% t(procrust))), ncol=1)

  congruence = diag((norm %*% t(procrust))/(D %*% t(E)));

  factor.congruence = sum(norm * procrust)/sqrt((ssq(norm)) *
    (ssq(procrust)));

  procrustes.congruence <- rbind(cbind(procrust, congruence),
    cbind(t(C), factor.congruence));

  return(procrustes.congruence);

}
```

# Appendix B

# Instruments

Instructions and items for the Hominoid Personality Questionnaire and the Subjective Well-being Questionnaire.

## B.1 Monkey personality trait assessment

### Instructions

Monkey personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The monkey's own behaviors and interactions with other monkeys should be the basis for your numerical ratings. Use your own subjective judgment of typical monkey behavior to decide if the monkey you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait.
2. Displays small amounts of the trait on infrequent occasions.
3. Displays somewhat less than average amounts of the trait.
4. Displays about average amounts of the trait.
5. Displays somewhat greater than average amounts of the trait.

6. Displays considerable amounts of the trait on frequent occasions.
7. Displays extremely large amounts of the trait.

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the monkey and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number.

Finally, do not discuss your rating of any particular monkey with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

### Items

1. **FEARFUL** Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.
2. **DOMINANT** Subject is able to displace, threaten, or take food from other monkeys. Or subject may express high status by decisively intervening in social interactions.
3. **PERSISTENT** Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other monkeys.
4. **CAUTIOUS** Subject often seems attentive to possible harm or danger from its actions.
5. **STABLE** Subject reacts to its environment including the behavior of other monkeys in a calm, equable, way. Subject is not easily upset by the behaviors of other monkeys.
6. **AUTISTIC** Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self clasping.
7. **CURIOUS** Subject has a desire to see or know about objects, devices, or other monkeys. This includes a desire to know about the affairs of other monkeys that do not directly concern the subject.
8. **THOUGHTLESS** Subject often behaves in a way that seems imprudent or forgetful.
9. **STINGY/GREEDY** Subject is excessively desirous or covetous of food, favored locations, or other resources. Subject is unwilling to share these resources with others.

10. **JEALOUS** Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged monkeys.
11. **INDIVIDUALISTIC** Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.
12. **RECKLESS** Subject is rash or unconcerned about the consequences of its behaviors.
13. **SOCIABLE** Subject seeks and enjoys the company of other monkeys and engages in amicable, affable, interactions with them.
14. **DISTRACTIBLE** Subject is easily distracted and has a short attention span.
15. **TIMID** Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.
16. **SYMPATHETIC** Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.
17. **PLAYFUL** Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other monkeys.
18. **SOLITARY** Subject prefers to spend considerable time alone not seeking or avoiding contact with other monkeys.
19. **VULNERABLE** Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another monkey.
20. **INNOVATIVE** Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.
21. **ACTIVE** Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.
22. **HELPFUL** Subject is willing to assist, accommodate, or cooperate with other monkeys.
23. **BULLYING** Subject is overbearing and intimidating towards younger or lower ranking monkeys.

24. **AGGRESSIVE** Subject often initiates fights or other menacing and agonistic encounters with other monkeys.

25. **MANIPULATIVE** Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Monkey seems able and willing to use others.

26. **GENTLE** Subject responds to others in an easy-going, kind, and considerate manner.

27. **AFFECTIONATE** Subject seems to have a warm attachment or closeness with other monkeys. This may entail frequently grooming, touching, embracing, or lying next to others.

28. **EXCITABLE** Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most monkeys.

29. **IMPULSIVE** Subject often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior.

30. **INQUISITIVE** Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other monkeys, objects, or persons within its view.

31. **SUBMISSIVE** Subject often gives in or yields to another monkey. Subject acts as if it is subordinate or of lower rank than other monkeys.

32. **COOL** Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

33. **DEPENDENT/FOLLOWER** Subject often relies on other monkeys for leadership, reassurance, touching, embracing and other forms of social support.

34. **IRRITABLE** Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

35. **UNPERCEPTIVE** Subject is slow to respond or understand moods, dispositions, or behaviors of others.

36. **PREDICTABLE** Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

37. **DECISIVE** Subject is deliberate, determined, and purposeful in its activities.

38. **DEPRESSED** Subject does not seek out social interactions with others and often fails to respond to social interactions of other monkeys. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

39. **CONVENTIONAL** Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

40. **SENSITIVE** Subject is able to understand or read the mood, disposition, feelings, or intentions of other monkeys often on the basis of subtle, minimal cues.

41. **DEFIANT** Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

42. **INTELLIGENT** Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

43. **PROTECTIVE** Subject shows concern for other monkeys and often intervenes to prevent harm or annoyance from coming to them.

44. **QUITTING** Subject readily stops or gives up activities that have recently been started.

45. **INVENTIVE** Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using devices or materials.

46. **CLUMSY** Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

47. **ERRATIC** Subject is inconsistent, indefinite, and widely varying in its behavior and moods.

48. **FRIENDLY** Subject often seeks out contact with other monkeys for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other monkeys.
49. **ANXIOUS** Subject often seems distressed, troubled, or is in a state of uncertainty.
50. **LAZY** Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.
51. **DISORGANIZED** Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.
52. **UNEMOTIONAL** Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.
53. **IMITATIVE** Subject often mimics, or copies behaviors that it has observed in other monkeys.
54. **INDEPENDENT** Subject is individualistic and determines its own course of action without control or interference from other monkeys.

## B.2 Assessment of subjective well-being in monkeys

### Instructions

This questionnaire has four questions, all relating to the subjective well-being of the monkeys at your site. Each question asks about a different personality dimension or trait relating to subjective well-being. The following scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait or state.
2. Displays small amounts of the trait on infrequent occasions.
3. Displays somewhat less than average amounts of the trait.
4. Displays about average amounts of the trait.
5. Displays somewhat greater than average amounts of the trait.
6. Displays considerable amounts of the trait on frequent occasions.

7. Displays extremely large amounts of the trait.

Please give a rating for each item even if your judgment seems to be based on a purely subjective impression of the monkey and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number. Finally, do not discuss your rating of any particular monkey with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

### Items

1. **MOODS** Estimate the amount of time the monkey is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the monkey is unhappy, bored, frightened, or otherwise in a negative mood.
2. **SOCIAL** Estimate the extent to which social interactions with other monkeys is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the monkey. Use as many social interactions that you can recall as a basis for your judgment.
3. **GOALS** Estimate, for this monkey, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the environment. Keep in mind that each monkey will presumably have its own set of goals that may be different from other monkeys.
4. **BE** Imagine how happy you would be if you were that monkey for a week. You would be exactly like that monkey. You would behave the same way as that monkey, would perceive the world the same way as that monkey, and would feel things the same way as that monkey.

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Behav Genet
DOI 10.1007/s10519-012-9537-y

ORIGINAL RESEARCH

# The Majority of Genetic Variation in Orangutan Personality and Subjective Well-Being is Nonadditive

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Received: 3 February 2011 / Accepted: 12 March 2012

**Abstract** The heritability of human personality is well-established. Recent research indicates that nonadditive genetic effects, such as dominance and epistasis, play a large role in personality variation. One possible explanation for the latter finding is that there has been recent selection on human personality. To test this possibility, we estimated additive and nonadditive genetic variance in personality and subjective well-being of zoo-housed orangutans. More than half of the genetic variance in these traits could be attributed to nonadditive genetic effects, modeled as dominance. Subjective well-being had genetic overlap with personality, though less so than has been found in humans or chimpanzees. Since a large portion of nonadditive genetic variance in personality is not unique to humans, the nonadditivity of human personality is not sufficient evidence for recent selection of personality in humans. Nonadditive genetic variance may be a general feature of the genetic structure of personality in primates and other animals.

**Keywords** Heritability · Dominance genetic variance · Animal model · Nonhuman primate · Evolutionary psychology · Happiness

## Introduction

Quantitative genetic studies of human personality traits such as those described by the Five-Factor Model (Digman 1990) show that the additive effects of genes influence personality variation and structure (Bouchard and Loehlin 2001). In addition, extended family designs found that nonadditive genetic effects account for over twice as much personality variance as additive genetic effects (Eaves et al. 1998; Keller et al. 2005; Pilia et al. 2006). Additive genetic variance comes from the independent effects of genes and is thereby eroded more efficiently by selection than nonadditive effects which arise from combinations of genes (Crnokrak and Roff 1995; Merilä and Sheldon 1999). High nonadditive genetic variance is therefore one sign of long-term directional or stabilizing selection. While the presence of nonadditive genetic effects on personality is consistent with balancing selection on personality (Penke et al. 2007) or with joint directional selection for personality and life-history traits (Figueredo and Rushton 2009), the ratio of additive to nonadditive genetic variance alone is not a strong test of particular evolutionary mechanisms (Keller 2007).

A complementary approach to understanding a trait's evolutionary history is to see whether it exists in closely related species. This is because the most parsimonious explanation for species similarity is that the trait is ancestral, i.e., existed in a common ancestor, while the most parsimonious explanation for species differences is that they are the product of evolutionary divergence (Gosling and Graybeal 2007). Studies of nonhuman primate personality

Edited by Eric Turkheimer.

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reveal dimensions akin to some or all of the Five-Factor Model domains and one or two dimensions not typically identified in humans, the most prominent being labeled "Dominance" or "Confidence", which describe individual differences in competitive prowess (Freeman and Gosling 2010).

Chimpanzees are one of humans' closest living relatives, sharing a common ancestor as recently as 4 million years ago (Hobolth et al. 2007) and, like humans, are highly gregarious (Goodall 1986). Given these facts, it should not be surprising that, alongside a Dominance dimension, chimpanzees possess five personality dimensions resembling the human Five-Factor Model (King and Figueredo 1997). One study found that chimpanzee Dominance is substantially heritable in the narrow-sense (Weiss et al. 2000), suggesting that genetic influences may underlie the personalities of chimpanzees and possibly other great apes.

Humans and chimpanzees shared a more distant ancestor approximately 15 million years ago (Purvis 1995) with orangutans, a semi-solitary great ape species (Galdikas 1985). Orangutans' greater evolutionary distance from humans and chimpanzees and their lower levels of sociality would lead one to expect behavioral differences that are manifested in their personalities. This is, in fact, what is found. Orangutans possess five personality dimensions: three (Extraversion, Neuroticism, and Agreeableness) resemble like-named dimensions in humans and chimpanzees; one (Dominance) is a narrower version of its chimpanzee namesake; and one (Intellect) which resembles a combination of high Openness and high Conscientiousness, is a species-specific dimension (Weiss et al. 2006).

Another trait whose evolutionary history can be examined via cross-species comparisons is happiness or subjective well-being. In humans, subjective well-being refers to long-term pleasant and unpleasant affect as well as global satisfaction with one's life (Diener et al. 1999). Far from being the consequences of one's fortunes, subjective well-being is prospectively related to positive outcomes (Diener and Chan 2011; Lyubomirsky et al. 2005) and, like personality, is influenced by additive and nonadditive genetic variation (Bartels and Boomsma 2009; Caprara et al. 2009; Lykken and Tellegen 1996; Nes et al. 2006, 2010). One possible explanation for this is that subjective well-being is closely tied to personality; people lower in Neuroticism, higher in Extraversion, and higher in Agreeableness are generally happier (DeNeve and Cooper 1998). Moreover, these relationships appear to reflect genetic overlap as subjective well-being has a negative genetic correlation with Neuroticism and a positive genetic correlation with Extraversion, Conscientiousness, and Agreeableness (Weiss et al. 2008).

Chimpanzees (King and Landau 2003; Weiss et al. 2009) and orangutans (Weiss et al. 2006) also display individual differences in subjective well-being. As chimpanzee and orangutan subjective well-being is assessed by observers, it is not "subjective" in the human sense, i.e., individuals' reports of their own happiness and life satisfaction (Diener et al. 1999). However, the term is appropriate since the ratings capture normal variation in overall mood or affect as opposed to physical health or well-being that is not an individual difference, such as through environmental enrichment applied to an entire captive enclosure (King and Landau 2003; Weiss et al. 2006).

Beyond the face validity of the subjective well-being scale used in these studies, there is evidence that observer ratings of chimpanzee and orangutan subjective well-being tap the same underlying construct as human self-reports. For example, lower Neuroticism, higher Extraversion, and higher Agreeableness translate into higher chimpanzee and orangutan subjective well-being (King and Landau 2003; Weiss et al. 2006, 2009), a result similar to that in humans (DeNeve and Cooper 1998; Steel et al. 2008). In addition, orangutan subjective well-being is prospectively related to longevity (Weiss et al. 2011a). Finally, approximately 40 % of chimpanzee subjective well-being variance is heritable in the narrow-sense and these additive genetic effects overlap with those that contribute to individual differences in Dominance (Weiss et al. 2002).

Studying chimpanzees and humans alone does not allow one to determine how much of the common genetic components of the relationship between personality and subjective well-being are shared with a common ancestor. This is because the existing findings do not rule out the possibility that the genetic nexus underlying the personality-subjective well-being correlations arose independently in these species as, for example, an adaptation to social environments where encounters with other individuals are frequent. As a semi-solitary species closely related to humans and chimpanzees, the presence or absence of a similar genetic structure between personality and subjective well-being in orangutans can be used as evidence to differentiate between those features that are ancestral and those that are derived. Therefore, for the present study, we will explore the quantitative genetic structure of personality and subjective well-being in orangutans that have been rated on reliable and well-validated personality and subjective well-being questionnaires (Weiss et al. 2006). We relied on these questionnaires because they allowed us to obtain the large sample size required for accurate heritability estimates. The present study will enable us to determine whether nonadditive genetic variance underlies personality and subjective well-being variance in another primate species and whether the genetic basis of subjective well-being is a unique feature of chimpanzees and humans. If a large proportion of the genetic variance in orangutan personality can be attributed to nonadditive effects, it would support the idea that similar evolutionary processes maintain variation in personality across primate species. Alternatively, if nonadditive effects are absent or small in orangutans relative to additive genetic variance, then this would make selection or other evolutionary processes unique to the hominid lineage a more likely explanation for the genetic structure of human personality.

## Method

### Participants and pedigree

Subjects were 54 Bornean (*Pongo pygmaeus*), 100 Sumatran (*Pongo abelii*), and 30 hybrid orangutans housed across 42 zoological parks in the United States, Canada, Australia, and Singapore. Each zoo held between 1 and 22 orangutans (mean = 4.3, mode = 3). There were 109 females and 75 males (mean age = 21.6, SD = 12.1). Of these orangutans, 152 participated in a previous study of personality (Weiss et al. 2006) while ratings on the additional 32 orangutans, from zoos in Australia and Singapore, were new to this study.

The orangutans were connected across zoos through an extended pedigree containing 358 individuals and encompassing up to four generations. Both the mother and father were known for 158 of the subjects. Only the mother was known for 27 subjects and only the father for one subject. Among the genetically informative individuals contributing to estimates of quantitative genetic parameters there were 50 full sibships and 134 half sibships. The pedigree also contained two inbred individuals.

### Personality and subjective well-being

Orangutan personality consists of five dimensions: Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect (Weiss et al. 2006) defined by the intercorrelations among items describing orangutan personality. Extraversion captures differences in interpersonal traits and is defined by items such as *playful,* not *solitary,* and *social* but differs from human and chimpanzee Extraversion by also including aspects of Openness, such as *inquisitive.* Dominance, as in chimpanzees, is defined by traits related to dominance and submissive behaviours and traits similar to the negative pole of human Agreeableness, such as *manipulative* and *aggressive.* Neuroticism is made up of traits similar to human Neuroticism such as *anxious*, not *stable*, and *impulsive*. Agreeableness was similar to the identically named dimension in chimpanzees and is defined by items related only to the positive pole of human Agreeableness, such as *sympathetic* and *protective*. Finally, Intellect was made up of items similar to both human Conscientiousness (*decisive,* not *disorganized*) and Openness (*intelligent*).

Personality was measured by ratings of each individual provided by 113 zoo employees who worked regularly with the orangutans and who did not receive training on measuring personality. Each orangutan was rated by between 1 and 7 raters (mean = 2.6). Personality ratings were made on one of three versions of the same questionnaire: 137 subjects were rated on the 48-item Orangutan Personality Questionnaire (OPQ, Weiss et al. 2006), 37 subjects were rated on the expanded 54-item Hominoid Personality Questionnaire (HPQ, Weiss et al. 2009), and 10 subjects were rated on an earlier, 43-item version of the OPQ that was based on the Chimpanzee Personality Questionnaire (King and Figueredo 1997). Each item on these questionnaires consisted of an adjectival descriptor and one to three sentences clarifying the adjective in term of orangutan behavior. For example, *active* was defined as “Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.” Ratings were made on a 7 point scale. Across all raters and subjects the data contained 20,446 personality item scores.

Subjective well-being was assessed in 164 orangutans by ratings on four items: their balance of positive and negative moods, the degree to which they enjoyed social interactions, their ability to achieve goals, and by asking raters to indicate how happy they would be if they were the target orangutan for a week. The items were identical to those used to assess chimpanzee subjective well-being in prior studies (King and Landau 2003; Weiss et al. 2009). In total there were 1,578 subjective well-being item scores included in the analysis.[1]

Assessing personality in nonhuman primates using ratings such as these sometimes arouses skepticism (Uher 2008a, b). However, multiple studies in great apes and Old World monkeys support the reliability and validity of such ratings (see review by Freeman and Gosling 2010). For instance, there is moderate to high agreement among raters (King and Figueredo 1997; King and Landau 2003; Uher and Asendorpf 2008; Weiss et al. 2006) and ratings are stable over time (Capitanio 1999; King et al. 2008; Stevenson-Hinde et al. 1980; Uher and Asendorpf 2008; Weiss et al. 2011b). In addition, the personality structure derived from chimpanzee personality ratings replicated in three independent samples (King et al. 2005; Weiss et al. 2007, 2009). Finally, the pattern of correlations between ratings and specific behaviors supports the convergent and discriminant validity of ratings (Konečná et al. 2008;

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[1] Both personality and subjective well-being questionnaires can be obtained from http://www.sciencedirect.com/science/article/pii/S0006322311008572.

Pederson et al. 2005; Uher and Asendorpf 2008). Ratings of subjective well-being in nonhuman primates also show high reliability (King and Landau 2003; Weiss et al. 2006, Weiss et al. 2011b) and shows external validity by, for example, its associated with outcomes such as mortality in orangutans (Weiss et al. 2011a).

## Quantitative genetic analysis

Heritability estimates are based on correlations among the phenotypes of individuals who differ in their amount of genetic relatedness. Behavior genetic studies of humans typically use the difference in correlations between monozygotic and dizygotic twins as the basis for heritability estimates (Bouchard and Loehlin 2001). Because we had a pedigree and thus could calculate relatedness among all the individuals in the sample, we used an "animal model" to estimate heritability. The animal model is a biometrical genetic model increasingly used in human studies (Pilia et al. 2006) and is commonly used in agriculture and evolutionary genetics (Kruuk 2004; Lynch and Walsh 1998; Wilson et al. 2009).

Just as twin models can be viewed as a particular instance of a structural equation model, the animal model is a type of multilevel or mixed-effects model. If a trait is influenced by genetic differences, two genetically related individuals should deviate from the mean in the same direction and by a similar amount; both corresponding to how closely related these individuals are. For example, full siblings should be more similar in their deviation from the mean than full cousins. The additive genetic relationships among animals are used as the basis for a random effect estimating an individual's deviation from the mean phenotype attributable to additive genetic effects (Kruuk 2004; Lynch and Walsh 1998). The proportion of variance attributable to these genetic deviations is an estimate of the trait's heritability. Similarly, information about the extent to which individuals share genotypes (for example, full siblings will on average share half their genes but will have only a quarter of their genotypes in common) can be used to estimated nonadditive sources of genetic variance such as dominance genetic variance. While in most twin models dominance genetic variance is confounded with shared family effects, these can be separated using extended twin family designs (Eaves et al. 1978) or pedigree data containing a large number of full- and half-siblings (Wilson et al. 2009), as was the case with the orangutan pedigree. We also explored whether heritability estimates were consistent between the Bornean and Sumatran orangutans. Significant differences in genetic structure between these species could be a potential signal of evolutionary divergence in their personality or subjective well-being.

Individuals who share environments may also resemble each other in terms of their personality or subjective well-being. We therefore considered whether individuals with the same mother or who lived in the same zoo environment when rated were more similar than those living in different zoo environments. The maternal environment captures effects that make offspring of the same mother resemble each other (independent of transmitted genes) such as natal effects or rearing style and may be caused by either environmental effects or indirect genetic effects. A zoo environment effect would account for any features of the captive environment that make individuals living together more similar to each other. We explored the amount of variance in each personality trait and subjective well-being that these effects accounted for by fitting a series of univariate models. We then estimated genetic and environmental covariances among traits using a multivariate model.

### *Measurement component*

Rather than analyzing factor scores for each personality trait, we built the models up from each rater's assessments of each orangutan on every item and thus modeled personality and subjective well-being as latent variables. Each rating on the 7-point scale was treated as ordinal and connected to an underlying latent scale with a probit link parameterized using cut-points (Hadfield and Nakagawa 2010). Each item contributed to the latent score of the personality domain it had a salient loading on as described previously (Weiss et al. 2006). We reverse coded items with negative loadings. This approach handled heterogeneity in the number of items for each personality domain that was a consequence of the different versions of the questionnaires used to rate the orangutans. Using the raw observations allowed uncertainty about individual orangutans' personality scores to propagate through the model and thus allowed us to control for relationships among personality and subjective well-being domains introduced by raters. All models used residual variances fixed to 1 while residual covariances in the multivariate model were fixed to 0 because each item only gave information on one personality or subjective well-being domain.

### *Variance partition component*

One advantage of using the animal model for heritability estimates is that it can be extended to include fixed effects that are known to affect the phenotype as well as additional group-level random effects to partition the variance (Kruuk 2004). In all models we controlled for potential differences attributable to age and sex by fitting them as fixed effects. We started with models that estimated individual orangutan

($V_{\mathrm{ID}}$) and rater ($V_{\mathrm{J}}$) variances (model 1) using orangutan and rater IDs as predictors. We then added parameters to estimate additive genetic variance ($V_{\mathrm{A}}$) for all species together (model 2) using a design matrix derived from the additive genetic relationship matrix calculated from the pedigree. We created models that estimated nonadditive genetic variance ($V_{\mathrm{D}}$, model 3) using the dominance genetic relationship matrix (Lynch and Walsh 1998, p. 768).

We then created models that fit random effects using the mother and zoo IDs to estimate maternal environment variance ($V_{\mathrm{M}}$, model 4) and shared zoo environment variance ($V_{\mathrm{Z}}$, model 5). We also fit a model that included all the effects (model 6) to give more conservative estimates of effects that are difficult to separate when families share a common environment (Wilson et al. 2009). In the models that estimate additive and nonadditive genetic or maternal and zoo environment variances, the orangutan identity matrix fits an effect comparable to the unique environment variance ($V_{\mathrm{E}}$) in twin models, that is, effects that cause an orangutan to differ from other individuals who share genes or environments. We additionally tested models that fit unique environment effects separately for each species group (Bornean, Sumatran, and hybrid) and additive and dominance genetic effects for Bornean and Sumatran orangutans (model 7). We did this by creating separate genetic relationship matrices for each species.

### *Model fitting*

We estimated fixed effects and components of variance using a Bayesian animal model (Sorensen and Gianola 2002) as implemented in MCMCglmm (Hadfield 2010). We used Bayesian methods because they better handle confounded variables (Ovaskainen et al. 2008) such as parents and offspring who shared genes and a zoo environment. Bayesian inferences can be made by summarizing random draws from the joint posterior distribution of the parameter estimates. MCMCglmm uses an inverse-Wishart distribution as the prior for variance components. We specified priors with variances of 1 and covariances of 0 and degrees of freedom parameter of 1 for the univariate models and 6 for the multivariate models. We ran the models for $10^6$ iterations, discarded the first half of the samples, and thinned the samples from the posterior distribution to 1,000. The autocorrelations among the successive samples from the posterior distributions were less than .1. We compared model fit using the deviance information criterion or DIC (Hadfield 2010). Because there is error in calculating DIC from the Monte Carlo simulations, we ran each model twice.

### *Model inference*

To exclude measurement error from our heritability estimates, we calculated heritability as the ratio between the additive genetic variance and the repeatable variance ($V_{\mathrm{RPT}} = V_{\mathrm{A}} + V_{\mathrm{D}} + V_{\mathrm{M}} + V_{\mathrm{Z}}$) on the latent variable scale as $h^2 = V_{\mathrm{A}}/V_{\mathrm{RPT}}$. The heritability estimate thus only reflects variance from effects assigned to individual orangutans and not measurement variance from rater effects and the probit distribution used to model item scores. We calculated the broad-sense heritability as $H^2 = (V_{\mathrm{A}} + V_{\mathrm{D}})/V_{\mathrm{RPT}}$ and the proportion of nonadditive genetic variance (Crnokrak and Roff 1995) as $D_{\alpha} = V_{\mathrm{D}}/(V_{\mathrm{A}} + V_{\mathrm{D}})$. We estimated correlations among traits attributable to additive genetic ($r_{\mathrm{A}}$), nonadditive genetic ($r_{\mathrm{D}}$), and unique environment ($r_{\mathrm{E}}$) effects as well as rater effects ($r_{\mathrm{J}}$) using a multivariate animal model. Covariances, like variances, can also be added together, so we also examined the total genetic correlations ($r_{\mathrm{G}}$) from adding the additive and nonadditive genetic covariance matrices ($\mathrm{cov}_{\mathrm{G}} = \mathrm{cov}_{\mathrm{A}} + \mathrm{cov}_{\mathrm{D}}$) and the phenotypic correlations among personality and subjective well-being statistically controlling for rater effects ($\mathrm{cov}_{\mathrm{P}} = \mathrm{cov}_{\mathrm{A}} + \mathrm{cov}_{\mathrm{D}} + \mathrm{cov}_{\mathrm{E}}$).

Because studies of humans and chimpanzees found that all or most of the genetic variance underlying subjective well-being was shared with personality, we calculated the conditional genetic variance of subjective well-being. The conditional genetic variance is genetic variance that is unique to subjective well-being, excluding variance from genetic factors that also influence the personality domains (Hansen and Houle 2008), defined as

$$c(y|\mathbf{x}) = G_y - \mathbf{G}_{y\mathbf{x}}\mathbf{G}_{\mathbf{x}}^{-1}\mathbf{G}_{\mathbf{x}y}$$

where $\mathbf{G}_{\mathbf{yx}}$ and $\mathbf{G}_{\mathbf{xy}}$ are vectors of the genetic covariance between y and the other traits and $\mathbf{G}_{\mathbf{x}}$ is the genetic covariance matrix of the other traits.

## Reliability analysis

We calculated the reliabilities of the personality and subjective well-being assessments as intraclass correlation coefficients (ICCs) in two ways using estimates from the genetic models. First, to estimate the consistency of the items making up each personality domain or subjective well-being, we calculated the ratio of the animal variance (that is, the repeatable variance from genetic or environmental effects that are assigned to individual animals) plus the rater variance over the residual and link function variances $(V_{\mathrm{RPT}} + V_{\mathrm{J}})/(V_{\mathrm{RPT}} + V_{\mathrm{J}} + V_{\mathrm{R}} + 1)$ where the final 1 is from the variance of the probit distribution used to model the ordered categorical scores. This ICC is on the scale of the raw data and represents the expected correlation between an individual's scores on two items made by the same rater. Although it is not the same as Cronbach's $\alpha$, it specifies the degree to which the rating of an individual on one item generalized to other items on that scale and is therefore a type of model-derived estimate of internal consistency. Second, we calculated reliability on the latent scale as $V_{\mathrm{RPT}}/(V_{\mathrm{RPT}} + V_{\mathrm{J}})$ to represent the expected correlation between two assessments of the same individual by different raters. This ICC estimates interrater agreement and is similar to ICC(3,1) (Shrout and Fleiss 1979).

## Results

### Genetics

We built a series of models to estimate the variance in personality and subjective well-being attributable to the additive and nonadditive (dominance) effects of genes, the maternal environment, and the zoo environment that conditioned on effects from raters. Because of the variance in the DIC between the two runs of each of the univariate models (Table 1), it was not possible to definitively choose the best model for each personality domain. We therefore interpreted the modes and credible intervals for each parameter estimate for all models.

Variance components, heritability, and the other variance proportion coefficients of models 1–6 are given in Tables 1 and 2. The narrow-sense heritabilities of personality traits and subjective well-being in orangutans were moderate and across the models and traits ranged from about 20–30 % of the repeatable variance (Table 2; Fig. 1). The nonadditive genetic effects explained on average more of the variance (30–50 %) than additive genetic effects. The total genetic effects (broad-sense heritability or $H^2$) thus accounted for upwards of three quarters of the repeatable variance (Table 3; Fig. 1). The proportion of nonadditive genetic variance ($D_\alpha$) was greater than half for all traits (Table 2). The estimates for maternal environment and zoo effects were low but the variance accounted for by nonadditive genetic effects was generally reduced when a maternal environment effect was included in the model. The separate heritability estimates for Bornean and Sumatran orangutans (Table 3) were consistent with the estimates from the whole sample.

While there was uncertainty in the additive genetic ($r_{\mathrm{A}}$), nonadditive genetic ($r_{\mathrm{D}}$), and unique environment ($r_{\mathrm{E}}$) correlations between personality and subjective well-being (Table 4), the effects all went in the same direction (negative for Neuroticism and positive for Extraversion, Dominance, Agreeableness, and Intellect). Using the conditional genetic variances, we determined that 15 % (95% credible interval [CI] = .03, .38) of the additive genetic and 19 % (95% CI = .05, .44) of the nonadditive genetic variance in subjective well-being was shared with personality. From these models we were also able to derive estimates of the phenotypic correlations among personality and subjective well-being that controlled for covariances among traits attributable to rater effects which were Extraversion $r_{\mathrm{P}} = .24$ (95% CI = .05, .37), Dominance .13 (95% CI = −.09, .28), Neuroticism −.22 (95% CI = −.38, −.05), Agreeableness .20 (95% CI = .05, .40), and Intellect .18 (95% CI = .02, .36). There was also some evidence for a positive dominance genetic and unique environment correlation between Agreeableness and Extraversion (Table 4).

### Psychometrics

Using the fitted genetic models we estimated the reliability of the orangutan personality ratings. The intraclass correlation coefficient from the animal and rater variances on the scale of the raw data, which represents the expected correlation between two items assessed on the same animal by the same rater and can act as a form internal consistency of items making up each scale, ranged from .21 for Intellect to .41 for Agreeableness and was .49 for subjective well-being (Table 5). Combining information from multiple raters produced highly reliable assessments of latent personality values which ranged from .73 for Intellect to .87 for Dominance. Reliability of subjective well-being on the latent scale was .60, and thus acceptable.

Rater effects contributed to the observed correlations among personality and subjective well-being scores (Table 4). After decomposing the covariance among personality and subjective well-being into animal components (genetic and environment) and a rater component, raters who rated an orangutan as higher on Extraversion, Dominance, Agreeableness, and Intellect and lower on Neuroticism also tended to rate that orangutan as higher on subjective well-being. Notably, the estimate of rater effects for the correlation between Dominance and subjective well-being correlation tended to go in the opposite direction from genetic and unique environmental estimates. There were also detectable rater effects on the Extraversion–Agreeableness, Extraversion–Intellect, Neuroticism–Intellect, and Agreeableness–Intellect correlations.

## Discussion

We found that the most genetic variation in orangutan personality and subjective well-being could be assigned to nonadditive genetic effects. This is consistent with the results from human personality research (Eaves et al. 1998; Keller et al. 2005; Pilia et al. 2006). The narrow-sense heritability estimates of about 20 % were likewise

**Table 1** Variance components and model fit criteria

| Model | DIC | $V_{\mathrm{E}}$ ($V_{\mathrm{ID}}$) | $V_{\mathrm{A}}$ | $V_{\mathrm{D}}$ | $V_{\mathrm{M}}$ | $V_{\mathrm{Z}}$ | $V_{\mathrm{J}}$ |
|---|---|---|---|---|---|---|---|
| Extraversion | | | | | | | |
| 1 | 16,046; 16,046 | .53 (.41, .68) | | | | | .14 (.10, .24) |
| 2 | 16,036; 16,046 | .38 (.25, .55) | .17 (.06, .32) | | | | .17 (.10, .23) |
| 3 | 16,028; 16,036 | .18 (.09, .38) | .15 (.07, .29) | .22 (.10, .40) | | | .14 (.10, .24) |
| 4 | 16,031; 16,002 | .33 (.22, .53) | .16 (.07, .32) | | .09 (.06, .20) | | .14 (.10, .23) |
| 5 | 16,042; 16,026 | .36 (.24, .57) | .13 (.08, .36) | | | .11 (.06, .24) | .13 (.10, .24) |
| **6** | **15,978; 16,018** | **.20 (.07, .36)** | **.14 (.06, .30)** | **.17 (.08, .35)** | **.09 (.06, .22)** | **.11 (.06, .26)** | **.15 (.09, .23)** |
| Dominance | | | | | | | |
| 1 | 17,788; 17,792 | 1.0 (.77, 1.2) | | | | | .17 (.10, .25) |
| 2 | 17,781; 17,790 | .82 (.47, 1.0) | .25 (.09, .57) | | | | .16 (.10, .25) |
| 3 | 17,778; 17,787 | .21 (.08, .60) | .18 (.07, .44) | .58 (.24, .92) | | | .16 (.11, .26) |
| 4 | 17,791; 17,785 | .57 (.34, .88) | .19 (.08, .51) | | .21 (.08, .46) | | .18 (.11, .25) |
| 5 | 17,779; 17,781 | .84 (.5, 1.05) | .24 (.09, .56) | | | .11 (.05, .27) | .16 (.11, .25) |
| **6** | **17,777; 17,776** | **.27 (.10, .61)** | **.18 (.07, .45)** | **.22 (.12, .66)** | **.18 (.07, .45)** | **.13 (.06, .29)** | **.16 (.11, .26)** |
| Neuroticism | | | | | | | |
| 1 | 13,543; 13,540 | .42 (.32, .55) | | | | | .11 (.07, .19) |
| 2 | 13,524; 13,536 | .33 (.20, .45) | .14 (.06, .25) | | | | .11 (.07, .18) |
| 3 | 13,532; 13,535 | .14 (.07, .29) | .10 (.06, .23) | .20 (.10, .36) | | | .10 (.07, .18) |
| **4** | **13,524; 13,523** | **.29 (.16, .41)** | **.12 (.06, .25)** | | **.13 (.06, .23)** | | **.12 (.07, .18)** |
| 5 | 13,531; 13,529 | .31 (.2, .43) | .12 (.06, .25) | | | .15 (.05, .28) | .11 (.07, .17) |
| 6 | 13,524; 13,510 | .14 (.08, .26) | .10 (.05, .21) | .13 (.07, .27) | .10 (.06, .22) | .13 (.06, .30) | .11 (.07, .17) |
| Agreeableness | | | | | | | |
| 1 | 10,129; 10,098 | .95 (.72, 1.2) | | | | | .36 (.24, .55) |
| 2 | 10,134; 10,088 | .73 (.47, 1.1) | .19 (.09, .49) | | | | .40 (.25, .56) |
| 3 | 10,124; 10,126 | .23 (.08, .65) | .15 (.08, .40) | .56 (.23, .87) | | | .38 (.24, .57) |
| 4 | 10,123; 10,125 | .67 (.37, .95) | .16 (.08, .49) | | .19 (.08, .40) | | .38 (.24, .58) |
| **5** | **10,091; 10,115** | **.70 (.46, 1.0)** | **.20 (.08, .51)** | | | **.15 (.08, .46)** | **.34 (.23, .52)** |
| 6 | 10,122; 10,121 | .26 (.13, .68) | .19 (.09, .42) | .36 (.09, .65) | .17 (.07, .36) | .18 (.06, .44) | .34 (.24, .54) |
| Intellect | | | | | | | |
| 1 | 8,149; 8,149 | .48 (.35, .64) | | | | | .24 (.15, .37) |
| 2 | 8,149; 8,149 | .31 (.17, .49) | .21 (.09, .39) | | | | .28 (.15, .37) |
| 3 | 8,087; 8,136 | .15 (.08, .35) | .19 (.07, .33) | .23 (.09, .38) | | | .21 (.15, .35) |
| 4 | 8,144; 8,148 | .29 (.13, .45) | .18 (.08, .42) | | .12 (.05, .23) | | .27 (.13, .37) |
| **5** | **8,131; 8,123** | **.33 (.16, .48)** | **.23 (.07, .39)** | | | **.15 (.06, .34)** | **.18 (.13, .34)** |
| 6 | 8,144; 8,143 | .17 (.08, .33) | .16 (.06, .32) | .14 (.06, .30) | .12 (.05, .23) | .14 (.07, 33) | .22 (.13, .35) |
| Subjective well-being | | | | | | | |
| 1 | 4,222; 4,195 | .92 (.65, 1.3) | | | | | .69 (.43, .96) |
| **2** | **4,174; 4,234** | **.64 (.31, 1.0)** | **.29 (.08, .76)** | | | | **.65 (.43, .98)** |
| 3 | 4,212; 4,234 | .21 (.09, .68) | .19 (.07, .53) | .49 (.17, .90) | | | .62 (.44, 1.0) |
| 4 | 4,230; 4,247 | .56 (.17, .83) | .28 (.08, .63) | | .19 (.08, .55) | | .67 (.44, 1.0) |
| 5 | 4,249; 4,228 | .72 (.31, 1.1) | .21 (.07, .69) | | | .20 (.06, .58) | .53 (.40, .95) |
| 6 | 4,242; 4,217 | .32 (.10, .58) | .23 (.06, .50) | .20 (.10, .62) | .23 (.07, .50) | .25 (.09, .57) | .67 (.43, 1.0) |

*DIC* Deviance information criterion, with values from two runs of each model. Model for each personality dimension with the lowest average DIC is highlighted in bold although the variance in DIC meant it was not possible to choose overall best models based on parsimony criteria. $V_E$ unique environment variance, $V_I$ individual variance, $V_A$ additive genetic variance, $V_D$ nonadditive (dominance) genetic variance, $V_M$ maternal environment variance, $V_Z$ zoo environment variance, $V_J$ rater variance. $V_R$ Residual variance, fixed at 1 in all models. The first variance component column gives $V_{\mathrm{ID}}$ for model 1 and $V_{\mathrm{E}}$ for all other models. Posterior modes of each estimate are given with 95% credible intervals in parentheses

**Table 2** Variance partition coefficients

| Model | $h^2 = V_A/V_{RPT}$ | $d^2 = V_D/V_{RPT}$ | $m^2 = V_M/V_{RPT}$ | $z^2 = V_Z/V_{RPT}$ | $e^2 = V_E/V_{RPT}$ | $D_\alpha = V_D/(V_A + V_D)$ |
|---|---|---|---|---|---|---|
| Extraversion | | | | | | |
| 2 | .30 (.13, .53) | | | | .70 (.47, .87) | |
| 3 | .23 (.13, .45) | .32 (.17, .55) | | | .38 (.18, .60) | .63 (.34, .80) |
| 4 | .25 (.11, .46) | | .19 (.09, .29) | | .51 (.37, .75) | |
| 5 | .22 (.11, .46) | | | .17 (.08, .30) | .54 (.34, .73) | |
| 6 | .16 (.08, .33) | .20 (.09, .40) | .13 (.07, .24) | .13 (.07, .28) | .29 (.09, .41) | .51 (.28, .77) |
| Dominance | | | | | | |
| 2 | .21 (.07, .49) | | | | .79 (.51, .93) | |
| 3 | .22 (.08, 42) | .35 (.18, .70) | | | .27 (.11, .60) | .73 (.45, .91) |
| 4 | .19 (.07, .42) | | .17 (.09, .38) | | .60 (.31, .74) | |
| 5 | .18 (.08, .44) | | | .09 (.05, .22) | .71 (.43, .82) | |
| 6 | .15 (.06, .32) | .21 (.09, .48) | .20 (.06, .33) | .09 (.04, .20) | .19 (.08, .45) | .73 (.34, .87) |
| Neuroticism | | | | | | |
| 2 | .30 (.13, .50) | | | | .70 (.50, .87) | |
| 3 | .22 (.12, .42) | .36 (.19, .58) | | | .38 (.15, .55) | .69 (.43, .83) |
| 4 | .21 (.11, .42) | | .24 (.11, .39) | | .49 (.29, .66) | |
| 5 | .23 (.11, .40) | | | .25 (.12, .41) | .48 (.34, .68) | |
| 6 | .15 (.07,) | .17 (.10,) | .16 (.09,) | .18 (.10,) | .24 (.10,) | .57 (.34, .77) |
| Agreeableness | | | | | | |
| 2 | .18 (.08, .43) | | | | .82 (.57, .92) | |
| 3 | .22 (.06, .38) | .52 (.17, .69) | | | .24 (.12, .60) | .78 (.45, .89) |
| 4 | .14 (.08, .41) | | .14 (.07, .33) | | .64 (.38, .8) | |
| 5 | .19 (.07, .40) | | | .20 (.07, .31) | .61 (.36, .77) | |
| 6 | .14 (.06, .30) | .19 (.07, .46) | .13 (.05, .24) | .15 (.06, .29) | .27 (.09, .47) | .61 (.30, .83) |
| Intellect | | | | | | |
| 2 | .35 (.21, .68) | | | | .65 (.32, .79) | |
| 3 | .29 (.14, .52) | .28 (.14, .53) | | | .29 (.13, .55) | .52 (.27, .78) |
| 4 | .28 (.13, .57) | | .20 (.09, .33) | | .43 (.21, .65) | |
| 5 | .23 (.14, .53) | | | .22 (.10, .40) | .41 (.21, .64) | |
| 6 | .16 (.08, .35) | .15 (.08, .34) | .14 (.06, .25) | .21 (.09, .35) | .18 (.09, .38) | .51 (.23, .72) |
| Subjective well-being | | | | | | |
| 2 | .18 (.09, .64) | | | | .82 (.36, .91) | |
| 3 | .24 (.07, .47) | .38 (.15, .65) | | | .24 (.11, .60) | .78 (.37, .89) |
| 4 | .19 (.08, .51) | | .26 (.08, .47) | | .47 (.20, .72) | |
| 5 | .18 (.05, .52) | | | .16 (.07, .38) | .54 (.25, .77) | |
| 6 | .15 (.04, .33) | .21 (.05, .39) | .19 (.06, .34) | .14 (.07, .34) | .17 (.07, .40) | .55 (.25, .84) |

Heritability ($h^2$) and variance partition coefficients for nonadditive (dominance) genetic ($d^2$) and maternal ($m^2$), zoo ($z^2$) and unique ($e^2$) environments calculated relative to the repeatable variance, $V_{RPT} = V_A + V_D + V_M + V_Z + V_E$. $D_\alpha$ = proportion of nonadditive genetic variance

consistent with human findings that used a similarly specified, pedigree-based animal model (Pilia et al. 2006). This suggests that a high proportion of nonadditive genetic variance may be a common feature of personality in primates under long-term directional or stabilizing selection and not exclusively the result of evolutionary processes unique to the human lineage. Our low estimates of shared zoo environment effects on personality match results from chimpanzees (Weiss et al. 2000) and are consistent with findings from human personality research on the effect of the shared (family) environment (Bouchard and Loehlin 2001).

While we lacked enough power to get precise estimates of genetic correlations between personality and subjective well-being, the direction of the correlations matched results from chimpanzees (Weiss et al. 2002) and humans (Weiss et al. 2008). Human and great ape subjective well-being may therefore have a common genetic basis in personality

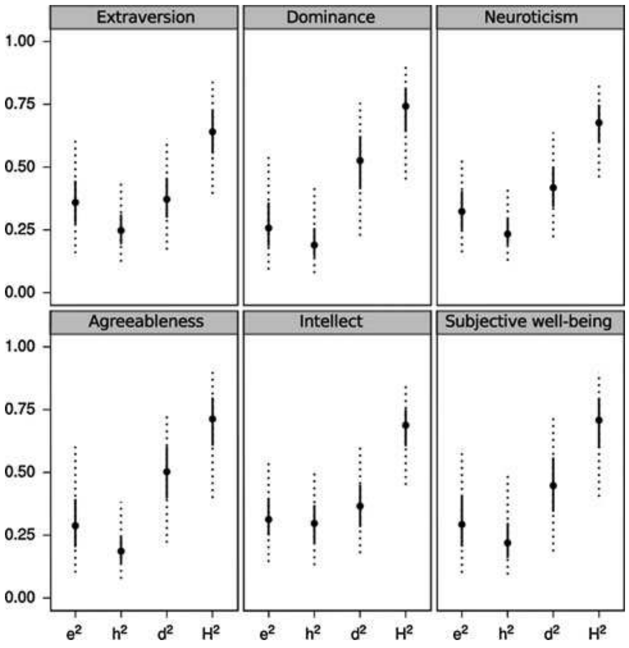

**Fig. 1** Variance proportion coefficients for repeatable variance. Points indicate posterior modes of each estimate with 50 % credible intervals in *solid* and 95% credible intervals in *dotted lines*. $h^2$ = (narrow-sense) heritability, $d^2$ = dominance, $H^2$ = broad-sense heritability, $e^2$ = unique environment. Figure by the authors, licensed under a Creative Commons Attribution Unported License and published under the terms of this license

traits related to emotional stability and social assertiveness. However, unlike chimpanzees and humans, less than half of the genetic variance in orangutan subjective well-being could be explained by genetic effects shared with personality. Thus, while the personality–subjective well-being link is likely ancestral in great apes, the greater genetic overlap in humans and chimpanzees may be a derived characteristic. Alternatively, personality and subjective well-being may have become more genetically uncoupled as orangutans diverged from these species.

In our models we used the dominance genetic relationship matrix, defined as the probability that two individuals share the same genotype at a locus (Lynch and Walsh 1998), to estimate nonadditive genetic variance. Dominance genetic variance comes from interactions between alleles at the same locus but additive × additive and other epistatic interactions could also contribute to nonadditive genetic variance. However, as only small fractions of variance from epistatic effects contributes to correlations among related individuals, the design matrix needed to estimate them will be very close to that used to estimate dominance genetic relationships. Therefore our estimate of nonadditive genetic variance would include some variance from any epistatic effects.

Our results also show the importance of conditioning on rater effects and other sources of measurement error when analyzing questionnaire-based assessments of animal personality. To wit, while raters were consistent in the scores they assigned to individual subjective well-being items, the interrater reliability of subjective well-being was lower than for the personality traits, which is consistent with the subjective well-being factor scores having a lower interrater agreement than those of personality (Weiss et al. 2006). Also, while rater variance was small compared to genetic and environmental variance, as shown by the high interrater reliability estimates, raters contributed to some of the covariance among personality traits and between personality traits and subjective well-being. Rater covariance effects that go in the same direction as the animal effects would tend to inflate the magnitude of the observed correlations. Thus, we found that the phenotypic correlations as estimated by the genetic and environmental covariances between subjective well-being and Extraversion, Neuroticism, and Agreeableness were smaller than the observed correlations previously reported (Weiss et al. 2006), which were inflated by covariance introduced by the raters. The opposite was true for Dominance; the animal and rater covariances went in opposite directions and cancelled out, explaining why no correlation was found between Dominance and subjective well-being at the phenotypic level (Weiss et al. 2006).

**Table 3** Heritability estimates for the combined sample and each species

| | $h^2$ | | | $H^2$ | | |
|---|---|---|---|---|---|---|
| | Combined | Bornean | Sumatran | Combined | Bornean | Sumatran |
| Extraversion | .23 (.13, .45) | .29 (.10, .55) | .22 (.09, .45) | .66 (.41, .86) | .67 (.43, .89) | .73 (.40, .87) |
| Dominance | .22 (.08, 42) | .26 (.08, .54) | .19 (.06, .46) | .78 (.49, .93) | .72 (.36, .91) | .78 (.43, .93) |
| Neuroticism | .22 (.12, .42) | .25 (.13, .53) | .29 (.14, .52) | .69 (.48, .85) | .68 (.40, .85) | .70 (.50, .87) |
| Agreeableness | .22 (.06, .38) | .25 (.09, .55) | .16 (.07, .43) | .82 (.41, .91) | .69 (.43, .90) | .71 (.40, .92) |
| Intellect | .29 (.14, .52) | .27 (.10, .53) | .28 (.15, .58) | .69 (47, .86) | .64 (.38, .88) | .73 (.46, .89) |
| SWB | .24 (.07, .47) | .19 (.06, .60) | .23 (.06, .48) | .77 (.44, .92) | .72 (.32, .90) | .78 (.40, .92) |

Posterior modes of narrow-sense, $h^2 = V_A/(V_A + V_D + V_E)$, and broad sense, $H^2 = (V_A + V_D)/(V_A + V_D + V_E)$, heritability with 95% credible intervals in parentheses

**Table 4** Genetic, environmental, and rater correlations

| | Extraversion | Dominance | Neuroticism | Agreeableness | Intellect |
|---|---|---|---|---|---|
| Additive genetic $r_{\mathrm{A}}$ | | | | | |
| Dominance | .14 (−.24, 37) | | | | |
| Neuroticism | −.01 (−.24, .37) | −.04 (−.30, .33) | | | |
| Agreeableness | .17 (−.12, .52) | −.20 (−.49, .19) | −.03 (−.38, .28) | | |
| Intellect | .08 (−.22, .39) | .17 (−.11, .50) | −.10 (−.42, .16) | .01 (−.38, .28) | |
| SWB | .23 (−.15, .45) | .13 (−.21, 43) | −.16 (−.47, .13) | .12 (−.19, .47) | .10 (−.18, 46) |
| Nonadditive (dominance) genetic $r_{\mathrm{D}}$ | | | | | |
| Dominance | .13 (−.20, .45) | | | | |
| Neuroticism | −.03 (−.29, .30) | .034 (−.29, .31) | | | |
| Agreeableness | .29 (−.02, .55) | −.22 (−.55, .12) | −.13 (−.48, .13) | | |
| Intellect | .15 (−.17, .40) | .20 (−.15, .47) | −.16 (−.47, .10) | .06 (−.23, .39) | |
| SWB | .22 (−.09, .51) | .14 (−.24, .44) | −.17 (−.48, .07) | .20 (−.07, .56) | .25 (−.11, .47) |
| Unique environment $r_{\mathrm{E}}$ | | | | | |
| Dominance | .16 (−.21, .44) | | | | |
| Neuroticism | −.03 (−.30, .31) | −.02 (−.31, 30) | | | |
| Agreeableness | .31 (.02, .59) | −.21 (−.52, .14) | −.16 (−.48, .13) | | |
| Intellect | .12 (−.12, .47) | .13 (−.18, .44) | −.15 (−.45, .11) | .16 (−.19, .46) | |
| SWB | .26 (−.07, .51) | .02 (−.30, .40) | −.25 (−.50, .04) | .30 (−.06, .54) | .20 (−.10, .50) |
| Rater $r_{\mathrm{J}}$ | | | | | |
| Dominance | .11 (−.15, .30) | | | | |
| Neuroticism | −.10 (−.30, .19) | .36 (.12, 55) | | | |
| Agreeableness | .41 (.16, 57) | −.10 (−.40, 10) | −.21 (−.38, .10) | | |
| Intellect | .20 (.06, .51) | −.17 (−.35, .13) | −.44 (−.54, −.09) | .30 (.04, .50) | |
| SWB | .24 (.00, .46) | −.17 (−.39, .13) | −.36 (−.55, −.09) | .30 (.06, .55) | .41 (.16, 61) |

Parameter estimates shows in 95% credible intervals in parentheses

*SWB* subjective well-being

**Table 5** Scale consistency and reliability of assessments by multiple raters

| | Consistency | Reliability |
|---|---|---|
| Extraversion | .28 (.24, .33) | .81 (.71, .87) |
| Dominance | .38 (.34, .44) | .87 (.81, .91) |
| Neuroticism | .23 (.20, .28) | .86 (.73, .90) |
| Agreeableness | .41 (.38, .48) | .77 (.64, .82) |
| Intellect | .31 (.25, .35) | .73 (.60, .83) |
| SWB | .49 (.42, .54) | .60 (.50, .74) |

Parameter estimates with 95% credible intervals in parentheses. *SWB* subjective well-being. Domain-scale consistency calculated as $(V_{\mathrm{RPT}} + V_{\mathrm{J}})/(V_{\mathrm{RPT}} + V_{\mathrm{J}} + V_{\mathrm{R}} + 1)$; latent reliability calculated as $V_{\mathrm{RPT}}/(V_{\mathrm{RPT}} + V_{\mathrm{J}})$ where $V_{\mathrm{RPT}} = V_{\mathrm{A}} + V_{\mathrm{D}} + V_{\mathrm{E}}$

While our analysis models rater effects or perceptions that introduce correlations among the personality and subjective well-being dimensions, it does not address to what extent the five personality dimensions themselves are products of rater beliefs and perceptions. The generalizability of chimpanzee personality dimensions across samples living in different environments (King et al. 2005; Weiss et al. 2007) and raters with different cultural backgrounds (Weiss et al. 2009), their relationship with observed behaviors (Pederson et al. 2005), and the recoverability when rater effects on chimpanzee and orangutan personality structure have been removed (Weiss et al. 2012) indicate that the structure of these nonhuman primate personality dimensions is inconsistent with them being solely an artifact of human perception. Furthermore, although similar, the personality structure of orangutans is not identical to that of humans and the personality structure of humans, chimpanzees, and orangutans differ in ways consistent with phylogeny (e.g., humans and chimpanzees share a personality domain, Conscientiousness, that is absent in orangutans) and social structure (e.g., the primacy of the chimpanzee Dominance domain) (Weiss and Adams 2008). However, even factor models of human personality can be understood in terms of our faculties for social perception (Srivastava 2010) and thus rater-based assessments of nonhuman primate personality may miss individual differences that are entirely absent in humans (Uher 2008a, b). Understanding the full genetic structure of orangutan personality may very well require multiple methods for measuring behavioral variation.

The quantitative genetic structure of personality within one species cannot act as strong evidence for past and current evolutionary scenarios (Gangestad 2011; Keller 2007). However, finding similar patterns of additive versus nonadditive genetic variation in human and orangutan personality suggests that similar processes of mutation and selection maintain variation in both species. A high proportion of nonadditive genetic variance is consistent with long-term selection on a trait (Crnokrak and Roff 1995; Merilä and Sheldon 1999) and while it may be a sign of strong selection reducing the additive genetic variance (Stirling et al. 2002) it is not indicative of recent selection (pace Figueredo and Rushton 2009; Penke et al. 2007). The recentness of novel selective pressures operating on human psychological characteristics since the agricultural revolution (~10 kya), which we interpret as the meaning of 'recent' in this context (see Figueredo et al. 2011), is a matter of perspective, as they are long-term compared to contemporary selection (Stearns et al. 2010) but recent relative to evolution before the split between human and chimpanzee lineages. Whether the large nonadditive genetic variance in orangutan and human personality evolved independently or is the result of long-term selection common in both species' ancestor could be investigated by estimating dominance or epistatic genetic sources of variation in chimpanzees. While we did not have the power to explore species differences in genetic structure between Bornean and Sumatran orangutans, future studies of orangutans or other closely related species (such as in macaques) or subspecies (such as in chimpanzees) may be informative. Such studies may also lead to an understanding of the genetic underpinnings of species divergence in personality dimensions, such as whether the genetic correlation we found between Extraversion and Agreeableness is related to the blend, at the phenotypic level, of these two domains in rhesus macaques (Weiss et al. 2011b). Furthermore, the presence of nonadditive genetic variance in bird personality (van Oers et al. 2004) suggests that this phenomenon may be a more general part of how personality evolves.

This study highlights how studying personality and subjective well-being heritability in other primates is a useful approach to understanding the evolution of these traits in humans. In doing so these findings suggest that evolutionary psychologists interested in these problems need to reach back further than the Pleistocene and grapple with an evolutionary story that is at least 15 million years old, and probably older.

**Acknowledgments** We thank Jarrod Hadfield for useful advice about genetic modeling and the personnel at the zoos for rating the orangutans. This work has made use of the resources provided by the Edinburgh Compute and Data Facility (ECDF).

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# Chapter 6
# Evolutionary Genetics of Personality in Nonhuman Primates

**Mark James Adams**

## 6.1 Introduction

Our whole conception and acknowledgement of personality – both scientific and quotidian – is based on the notion of difference. A personality is precisely that which distinguishes one individual from another. These differences have consequences for behavior, health, and well-being, but we are mostly ignorant of their evolutionary roots. For humans and other primates, evidence is coalescing around a common structure that describes personality differences usefully categorizable in terms of shared versus derived traits and consistent with known species differences (Gosling and John 1999; Weiss et al. 2006). Although functional and genomic studies begin to hint at the proximate genetic and environmental factors that mix to produce differences in personality, we are still left with this wondrous puzzle: Why do these basic differences persist over evolutionary time scales as primates have speciated and evolved?

This problem runs up against one of the unendingly contentious issues in quantitative genetics: How is trait variation maintained? This question comes out of a basic mathematical result in genetics with its origin in animal breeding. The result says that natural and artificial selection reduces the heritability of a trait in a population. Much ink has been spilled on theoretical treatments of variation in primate (mostly human) personality and other psychological traits (e.g., Tooby and Cosmides 1990a; Nettle 2006; Penke et al. 2007). What we need are good data.

But which way forward? Which data? In evolutionary psychology, the usual tact is to identify past conditions within a lineage that explain present-day adaptation and variation (Tooby and Cosmides 1990b). This is mistaken in that it ignores a key insight of evolutionary biology: it is only through a phylogenetically informed approach that we can determine when traits arose and changed within a lineage (Gosling and Graybeal 2007). For determining when different features of personality originated in each primate lineage, this comparative approach is sound. To explain why differences

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M. Inoue-Murayama et al. (eds.), *From Genes to Animal Behavior*,
Primatology Monographs, DOI 10.1007/978-4-431-53892-9_6, © Springer 2011

within populations persist, however, something else is needed. Evolutionary quantitative genetics fills this gap. This branch of biology deals with the effects of evolutionary processes on continuous traits and the genetic and environmental factors underlying them. Most promising and relevant for the explorations of primate personality is the development of techniques for studying evolution in wild populations using pedigree data (Kruuk and Hill 2008). Given the length of time many primate populations have been investigated (Goodall 1986; Rawlins and Kessler 1986; Fedigan and Asquith 1991; Nishida et al. 2002), the identification of individuals (de Waal 2003), and the resolution of pedigree structure (particularly through matrilineal kin e.g., Fairbanks et al. 2004; Blomquist 2009b), it is a wonder that these techniques have not been more widely applied to nonhuman primate behavior.

Revealing the evolution of nonhuman primate personality requires first understanding how personality variation is defined and how differences among species are informed by phylogenetic relations. The evolvability of personality within a species is proportional to the heritability of each personality trait, which has already been estimated in several primate species. Making usable inferences about the evolution of personality first requires choosing a method for estimating heritability appropriate to the data (Kruuk and Hadfield 2007). Knowing what heritability really is will lead to a consideration of the exact role that the resemblance between parents and offspring, as captured by heritability, plays in random drift and selection in wild populations. Pinning down the fitness implications of personality differences requires more than just the genetic structure of personality but offers the opportunity to integrate many threads from psychological and behavioral–ecological approaches to personality.

## 6.2 Nonhuman Primate Personalities

Nonhuman primate personality has been examined from a number of stances, but integrating these different attitudes is still a major challenge (Clarke and Boinski 1995; Itoh 2002; Uher 2008) (see Chap. 5 for a full discussion). These methods include, broadly, impressionistic ratings using adjectives describing personality; observational measures and codings of differences in the presence, frequency, and duration of behaviors; and impressionistic ratings of behavior–situation units (Uher and Asendorpf 2008). Although methodological differences can shroud comparisons among species, Gosling and John (1999) found broad support for the basic personality dimensions related to sociality, anxiety, and cooperativeness in a number of other animals, from octopuses to chimpanzees. Although species-specific dimensions outside of those that differentiate humans exist (Uher 2008; Uher and Asendorpf 2008) and personality should encompass not only people but also behaviors and situations (Funder 2009), descriptions of stable, between-human personality differences as rendered in factor models usefully orient explorations of nonhuman primate personality structure. Differentiating individuals along basic personality dimensions provides a platform of traits for initial quantitative genetic analyses of personality in primates. They are also good candidates for fitness correlates in evolutionary studies because these broad personality dimensions consistently relate to differences in health, longevity, and other social outcomes in humans (Roberts et al. 2007).

Studying multiple species with the same instrument also aids phylogenetic comparisons of personality structure by revealing the historical patterning of the emergence and modification of personality dimensions (Weiss and Adams 2008). This chapter next reviews factor model perspectives before considering how personality traits can evolve. However, behavioral and functional approaches make their appearance later when we need to causally connect broad personality variation to fitness (see Sect. 6.5.3). Assessments of behavioral profiles (Shoda and Mischel 2000; Uher et al. 2008), in particular, show promise for reaction-norm studies of personality evolution (see Sect. 6.6).

### *6.2.1 Models*

One of many models for human personality describes personality differences in five independent dimensions (Digman 1990): generally speaking, differences in sociability and assertiveness are called Extraversion; variation in trust and cooperation are grouped as Agreeableness; Conscientious describes differences in discipline, planning, and self-control; variation in curiosity and creativity is captured by Openness; and a dimension called Neuroticism differentiates individuals in terms of anxiety, emotional stability, and stress response. Reasonably, it is referred to as the Five-Factor Model (FFM). A single individual is characterized by a stable density distribution along each of these dimensions (Fleeson 2001). The FFM is robust across cultures (McCrae et al. 2005) and emerges whether people are measured on items that are adjectival descriptors (Digman 1990) or cognitive-affective reactions to situations (Denissen and Penke 2008). This factor-model description of human personality has served as the starting point of several investigations of nonhuman primate personality.

Chimpanzees share with humans the broad dimensions of the FFM, with the addition of Dominance, which describes differences in competitive facility (King and Figueredo 1997). As a personality trait in primates, Dominance should be distinguished from social dominance or rank as the latter is an outcome rather than an aspect of personality (Hinde 1978; Buss 1988; Gosling and John 1999). The chimpanzee dimensions Agreeableness and Openness were given names identical to their human homologues. Although the labels differ, the remaining three traits map human equivalents: Surgency onto Extraversion, Emotionality onto Neuroticism, and Dependability onto Conscientiousness. Although chimpanzee Conscientiousness is more narrowly defined than its counterpart in humans (it does not include facets related to trustworthiness and duty) the Conscientiousness personality dimension seems to be a derived character in humans and chimpanzees, as it has not appeared as a “pure” construct in any other species investigated (Gosling and John 1999; Weiss et al. 2006; Weiss et al. in press). Chimpanzees can also be differentiated from each other by their behavioral signatures, including propensities to set upon or affiliate with conspecifics, anxiety and arousal in stressful situations, curiosity toward novel foods and objects, impulsivity, goal pursuit, and physical and sexual activity (Pederson et al. 2005; Uher et al. 2008; Uher and Asendorpf 2008).

Gorillas likewise can be differentiated by their behavioral repertoires, similar to chimpanzees (Uher et al. 2008). Gorillas have also been described under the rubric of the human FFM using the dimensions Extroversion, Understanding (i.e., Agreeableness), Fearfulness (i.e., Neuroticism), and Dominance (Gold and Maple 1994). Salient in their absence from gorilla personality are homologues of human and chimpanzee Openness and Conscientiousness. Do gorillas really not differ in levels of curiosity and self-control, or were researchers just not looking for variation in these traits (Gosling and John 1999; Weiss et al. 2006)?

The importance of being more thorough can be seen in Weiss et al.’s (2006) portrayal of orangutan personality using a similarly broad instrument previously applied to chimpanzees (King and Figueredo 1997). Orangutans can be described with the dimensions Dominance, Extraversion, Agreeableness, Neuroticism, and Intellect. Intellect appears to be a blend of Openness and Conscientiousness.

A variety of models using impressionistic ratings have emerged to describe rhesus macaque personality. Some early studies revealed, alternatively, three dimensions: Fear, Hostility, Affiliation (Chamove et al. 1972) or Excitability, Sociability, Confidence (Stevenson-Hinde and Zunz 1978; Stevenson-Hinde et al. 1980). Later studies derived four dimensions: Tense–Fearful, Aggressive, Solitary, Curious–Playful (Bolig et al. 1992) or Sociability, Confidence, Excitability, Equability (Capitanio 1999). Rhesus macaques can even be described in as many as six dimensions: Confidence, Friendliness, Dominance, Anxiety, Openness, Activity (Weiss et al. in press). These results demonstrate the vagaries of measuring personality with instruments that have been incompletely adapted from studies of other species (Uher and Asendorpf 2008). That said, despite the various labels and differing numbers of components, many of these dimensions describe the same constructs. The primate dimensions of Extraversion are captured by Affiliation/Sociability/Solitary, Agreeableness by Hostility/Aggressive/Friendliness; Neuroticism by Fear/Excitability/Tense–Fearful/Confidence–Anxiety; Openness by Curious–Playful/Openness; and Dominance by Confidence/Dominance (Gosling and John 1999; Weiss et al. in press). This lumbering development matches the slow growth and refinement in characterizing broad dimensions of human personality chronicled by Digman (1990). We will not get there all in one go.

Using behavioral codings, Rouff et al. (2005) identified three dimensions of overall behavioral variation and four of between-individual differences in the personalities of lion-tailed macaques. The components that differentiated individuals (in contrast to behavioral occasions irrespective of the individual exhibiting them) map roughly onto the rhesus macaque dimensions Friendliness, Dominance, Activity/Confidence, and Anxiety. Although methodological and sample-size differences between these studies make for a knotty comparison, they suggest that several broad features are conserved in the genus *Macaca*. It also shows that basic dimensions can shine through even if the instrument or ethogram is not specifically designed to find them. For instance, Rouff et al. (2005) chose behaviors that defined Neuroticism-like bipolar facets, namely, Anxious–Relaxed and Reactive–Unreactive. Each pole of these facets, however, did not group together. Reactive clustered with the Confidence-like component, and Relaxed and Unreactive loaded on the Anxiety-like component. This tallies with the claim that primate Neuroticism can become uncoupled into two independent dimensions describing free-floating versus situationally determined anxiety (Weiss et al. in press). Further work on lion-tailed, rhesus, and other macaque species is needed to clarify personality structure within this genus.

Whole personality structures have been educed in other Old World monkeys. Vervet monkey personality consists of three dimensions – Social Competence, Playful, Curious, Opportunistic Self-Serving (McGuire et al. 1994) – which map to the great ape domains of Dominance, Openness, and Agreeableness, respectively (Gosling and John 1999).

Konečná et al. (2008) extended the search for nonhuman primate personality structure to colobines. They investigated male Hanuman langur personality using both impressionistic descriptors and behavioral codings. Male langur behavior exhibits a three-dimensional structure consisting of Dominance, Involvement, and Activity. Impressionistic ratings also revealed three dimensions, called Agreeableness, Confidence, and Extraversion. High Agreeableness was expressed behaviorally by low Dominance; high Confidence by high Dominance and Involvement and by low Activity; and high Extraversion by elevated Activity. Again, these dimensions broadly match those found in other primate species, and the absence of other distinct dimensions (such as Openness) have reasonable ecological explanations (e.g., langurs are opportunistic foragers).

Over the years other, more specific aspects of personality and temperament have been examined in nonhuman primates (Clarke and Boinski 1995). Factor models and behavioral profiles by no means cover all the facets of primate personality that have been discovered. Attempts to describe all the features of between-individual personality differences, however, are starting to pay dividends by distinguishing the separate threads that we need to weave the historical patterns of primate personality evolution.

### *6.2.2 Building Blocks*

Gosling and John (1999) showed that dimensions analogous (and perhaps homologous) to the five human factors appear in other species, with the addition of two dimensions, Dominance and Activity. Although Dominance is a salient dimension across many species, they found little evidence for Activity as a separate dimension. Nonetheless, activity is a common trait explored in behavioral–ecological investigations of personality (Réale et al. 2007) and was found to define a separate dimension in wild langurs (Konečná et al. 2008) and rhesus macaques (Weiss et al. in press). Furthermore, in humans, although this dimension is subsumed under Extraversion in adults, it can emerge as a separate feature in adolescent males (John et al. 1994).

As it is possible for traits that normally vary together to become uncoupled during development (Groothuis and Carere 2005), we can consider the developmental evolution and phenotypic integration of personality dimensions. Correlated variation in the rudimentary personality structures of humans, chimpanzees, orangutans, and rhesus macaques can be described with a set of eight "basic" and five "blended" personality traits (Weiss et al. in press). The basic traits are called Sociability, Activity, Altruism, Anxiety, Confidence, Dominance, Openness, and Conscientiousness. The other traits are combinations of these components. In humans, chimpanzees, and orangutans, Sociability and Activity positively covary to form Extraversion; and Anxiety and Confidence negatively covary as Neuroticism. In rhesus macaques, in contrast, Sociability fluctuates with Altruism and is denoted as Friendliness. Meanwhile, in humans, Altruism and Dominance negatively covary in the dimension that describes cooperative behavior (i.e., Agreeableness), whereas orangutans have an interesting blend of Openness and Conscientiousness called Intellect. Positing these different basic traits follows the suggestion of Réale et al. (2007) to start defining possible categories of correlated suites of behavior beyond those already considered in work on behavioral syndromes (i.e., shyness–boldness, exploration–avoidance, activity, aggressiveness, sociability). These basic traits may be the result of opportunities for adaptive behavioral variation for meeting the social, ecological, and developmental challenges faced by big-brained, gregarious, long-lived mammals. Factor models for each species are the first step in hypothesizing the building blocks constituting primate personality structures.

Why we should find this historical patterning in primates or even whether we have the right "basic" dimensions are big questions. When thinking about the evolution of personality dimensions, it might seem strange at first to consider the evolution of something that is only a construct describing differences between individuals. Extraversion, for instance, describes differences between individuals in their sociality and action. Unlike a new behavior or organ, a personality dimension is not an obvious thing that a single individual has. However, this thinking takes a rather narrow view of what evolution is or how it effects populations. Selection does not act only on the mean level of a trait. Evolutionary change can occur on higher moments (e.g., variance, skew, kurtosis) of the population distribution of a trait as well as its covariance with other traits (Rice 2004). The genetic and environmental factors contributing to personality can start and stop covarying as the population evolves.

Before worrying too much over these complications, let us start more simply. When a population experiences selection, how does it respond? Let us go into the wild and find a troop of apes that differ in Extraversion. We measure their personalities and find, as it happens, that only individuals who are a value of $S$ below the population mean in Extraversion are having children. For the moment, do not worry about why this might be the case. How sociable should we expect these offspring to be? Here, $S$ is the selection differential (the amount that the parents producing offspring deviate from the average trait value), and we want to know by how much the offspring will also differ from the parental average (or the response to selection, $R$). We are asking $R = ? \times S$ and the answer should have something to do about the resemblance between parents and their offspring.

## 6.3 Heritability

Heritability captures the resemblance between relatives. Heritability ($h^2$) is the proportion of the difference in phenotypes attributable to differences in inherited genes and thus ranges from 0 to 1.0. When considering two traits, we can also ask to what extent they are influenced by the same set of genes and what the direction of this relationship is. This is the genetic correlation ($r_A$) and can extend from −1.0 to +1.0. Behavioral traits are generally less heritable than morphological traits (Stirling et al. 2002). The heritability of personality and related traits has been established in several species of nonhuman primates. However, it is important to keep in mind that genes are not the only factor of interest in explaining variation: for certain problems, other types of environmental variance may be equally compelling to the researcher. As we shall see, although all sources of variation should be examined, differences caused by the additive effects of genes (called heritability) hold special status in the origin of both adaptive and neutral variation among individuals. The first step is to consider the extent of heritability in nonhuman primate personality.

Weiss et al. (2000) estimated the heritability of the six factors of chimpanzee personality. Of these factors, only Dominance was found to be significantly heritable ($h^2 = 0.63$). The estimate for Dependability was 0.21; although not detectably greater than 0, this suggests low to moderate heritability. The remaining traits showed little or no heritability. Importantly, this study of zoo-housed chimpanzees also established that very little of the differences in personality could be accounted for by differences among zoos. A later study using a different estimation technique (see Sect. 6.3.1) confirmed the high heritability of Dominance ($h^2 = 0.66$) and established the high genetic correlation with subjective well-being ($r_A = 1.00$) (Weiss et al. 2002).

The heritability of facets of personality and other related traits has also been investigated in nonhuman primates. Williamson et al. (2003) estimated the heritability of fearfulness and anxiety in rhesus macaques. Several aspects of their responses, such as a tendency to explore novel environments (latency to leave the protection of their mother during a Free Play Test) or to approach novel objects (in this case, a kiwi fruit) had estimated heritabilities of 1.0. These high estimates of heritability in these types of trait were confirmed in a later study with a similar measure of vigilance ($h^2 = 0.98$) (Rogers et al. 2008). Latency to approach strangers (measured as a Social Impulsivity Index) is also heritable in vervets, but only moderately so ($h^2 = 0.34 \pm 0.11$) (Fairbanks et al. 2004). There was no effect from the maternal environment, which given how it was estimated includes nonadditive genetic variance from dominance and epistatic effects as well as the influence of maternal care and the mother's genotype. The Social Impulsivity Index consisted of two subscales measuring approach–avoidance and aggressiveness that were themselves highly genetically correlated ($r_A = 0.78 \pm 0.12$), suggesting that the two facets are influenced by a similar set of genes.

These results are not surprising given that the heritability of personality dimensions in humans has been estimated to be in the range of 0.4–0.8 (Riemann et al. 1997; Bouchard and Loehlin 2001), depending on the population and whether personality is assessed with self-reports, peer-reports, or both and are of similar magnitude in other animal species (van Oers et al. 2005a). The lack of a maternal effect in vervet impulsivity is also consistent with the small influence of shared environment (e.g., maternal care experienced by siblings) on personality in humans (Bouchard 1994; Rowe 1994).

### 6.3.1 Estimating Heritability

It is worth taking a step back and considering what heritability is and how it can be estimated. The basic question is how do parents and offspring resemble each other; that is, what is the covariance between mean offspring and mean parental phenotypes? Second, what proportion of variation among the offspring is caused by variation inherited from their parents? This value is found in the coefficient from a linear regression of offspring on parental phenotypes (Falconer and Mackay 1996), or

$$\beta_{z_O, z_P} = \frac{\mathrm{cov}(z_O, z_P)}{\mathrm{var}(z_P)},$$

where $\mathrm{cov}(z_O, z_P)$ is the covariance between the phenotypes of offspring and their parents, and $\mathrm{var}(z_P)$ is the phenotypic variation of the parents. This quantity describes how traits are selected (see Sect. 6.3.2) (Rice 2004).

Like the derivation of many basic statistical terms (e.g., "split-plot") from agricultural experimentation, the meaning of many of the concepts surrounding the estimation of heritability are clearer once their origins in animal and plant breeding are understood. If you are raising livestock and are picking individuals to mate with one another to produce a new generation, what information do you want about these parents? What interests you is not the phenotype of each parent but, rather, the average phenotype of a parent's offspring. An individual's "breeding value" is a score representing their offspring's expected phenotype when mating is random (Falconer and Mackay 1996). Breeding values act additively – which is to say that an offspring's expected breeding value is the average of its parents' – and are thus thought of as caused by genes (not genotypes) that are passed from parents to their offspring. The effects of these genes act additively because they influence the phenotype independent of the constitution of the rest of the genotype, which is not the case for dominance or epistatic interactions.

The part of differences in phenotypes that can be attributed to breeding values is called the additive genetic variance of a trait. The ratio between additive genetic ($V_A$) and phenotypic variance ($V_P$) is an estimate of heritability

$$h^2 = \frac{V_A}{V_P}$$

because, assuming certain conditions apply, these genes are what determine the parent–offspring resemblance (Rice 2002). These assumptions are the following: (1) an individual's phenotype is a combination of the additive genetic effects from both its parents plus an effect from the environment (there is no influence from dominance or epistasis); (2) mating is random; (3) genotypes are independent of the environment in which they are expressed; and (4) parents do not transmit their environment to their offspring. To the extent that these conditions hold, $V_A/V_P$ can be used to estimate $\beta_{z_O, z_P}$, and in practice this is what is done.

Heritability can be estimated in a number of other ways, depending on the relationship between the individuals measured, such as twins (Martin and Eaves 1977) or half-siblings (Falconer and Mackay 1996). Entire pedigrees – describing not just the relatedness between parents and offspring or among siblings but between all relatives – can even be combined into a single analysis using the squared differences of phenotypes between all individuals (Grimes and Harvey 1980), which was shown to be an improvement over analysis of variance-based estimation techniques (Bruckner and Slanger 1986a, b). Like other, more advanced methods, this requires determining the relatedness of all individuals in the study population from a pedigree.

More recently, animal breeders and evolutionary quantitative geneticists have begun to favor variance component analysis, also known as random effects or mixed effects models, for estimating genetic and environmental sources of individual differences (Henderson 1950, 1975; Shaw 1987; Lynch and Walsh 1998; Kruuk 2004). These models still use all relationships in the pedigree; but, rather than pairing or nesting individuals together as in the techniques described above, breeding values are determined for each individual. Because the analysis occurs at the level of individual animals, this model was dubbed the "animal model" (Lynch and Walsh 1998). This set of equations can also be described as a mixed-effects model because it differentiates fixed effects (which account for mean differences among groups of individuals) from random effects (which partition the remaining variance between individuals). Breeding values are the typical random effect of interest. Although the meaning of "fixed" versus "random" effects are quite varied (and confused) in the literature (Gelman 2005), it is by these terms that evolutionary geneticists are trying to distinguish known causes of differences between classes of individuals (e.g., sex and age) from those that govern a trait's variance and for which each individual has its own value. An advantage of the animal model is that it can incorporate, and therefore estimate, other sources of variance. (See Chap. 7 for effects of interest in animal personality research.) Animal models have been used successfully on data from wild populations to estimate components of variance in addition to heritability (Kruuk 2004; Kruuk and Hadfield 2007) and are particularly suitable when trying to distinguish genetic from environment effects (Kruuk and Hadfield 2007). Variance components and breeding values for the animal model can be estimated with restricted maximum likelihood (REML) methods (Shaw 1987; Lynch and Walsh 1998) or using Bayesian analysis (Sorensen and Gianola 2007; O'Hara et al. 2008; Hadfield et al. 2010).

In quantitative genetics of natural populations, these effects can only be identified if they differ between individuals so variance component decomposition does not provide a complete causal account of how a trait comes to be (component terms such as $V_A$ or $V_E$ are also referred to as causal components of variance) (Falconer and Mackay 1996). Take a look at maternal effects such as those from early rearing experience: work by Harlow (1969) showed the importance of a mother's love for the behavior and adjustment of an individual later in life. The mother clearly has an "effect." Although such differences can be induced in experimental conditions, there still might not be any maternal effects in the wild. Just because close maternal contact is developmentally necessary for proper fear and anxiety reactivity does necessarily mean that differences in rearing style influence offspring phenotypes. This lack of difference is what is meant if no maternal effect is found on a trait.

Estimates of heritability in nonhuman primates have drawn on all of these techniques, but it pays to use the method most suited to the available pedigree data. For estimating heritability in primate populations, the animal model is to be preferred. This is primarily because it can handle the arbitrary but interconnected pedigree structure of primates in different zoos (Weiss et al. 2000) as well as tolerate unknown relatedness such as missing paternity information common in studies of wild primates (de Ruiter and Geffen 1998). Furthermore, using all relationships from a pedigree improves estimates of genetic correlations (Åkesson et al. 2008). The ability of Bayesian methods to handle small sample sizes (O'Hara et al. 2008) and confounding variables (Ovaskainen et al. 2008) makes it suitable for analyses involving the hundreds of subjects available for primate research rather than the thousands typical in agricultural settings, for which REML procedures have been developed and refined. Bayesian methods are also good for evolutionary questions because the uncertainty in the prediction of breeding values can more easily be carried on to estimates of evolutionary change (Hadfield et al. 2010).

Whichever technique is used, it is important to realize that these are simply models of the transmission of traits from parents to offspring (Rice 2004). Estimating heritability is a process of fitting statistical parameters to data, and these estimates are influenced by more than just the variation in additive genes (Stirling et al. 2002). Many of the modeling assumptions (random mating, no gene–environment correlations) required to estimate heritability from a parent–offspring regression are unlikely to hold in primates. Furthermore, variance from the environment in these models is actually just the residual variance, or the error. This error includes all the causes of differences between individuals for which we do not know how to account. Even when we are assigning a name to a key component of variance, such as $V_A$, the most general descriptions of the parent–offspring resemblance do not make any assumptions about what is being inherited. It is usually assumed that the transmission of DNA sequence variants accounts for this resemblance, but epigenetic sequences can be transmitted across generations and contribute to additive genetic variance in the same way (Johannes et al. 2008, 2009). Primate parents and offspring can resemble each other for nongenetic reasons as well, such as abusive rearing styles in rhesus macaques (Maestripieri 2005). That environments can be transmitted is a distinct possibility that is not without utility for evolutionary model building (Odling-Smee et al. 2003). As in the remake of a 1970s horror film, these snags in understanding heritability (Feldman and Lewontin 1975; Visscher et al. 2008) are the "undead" of quantitative genetics, particularly in the psychological sciences (Taylor 2010).

It is thus important in any discussion of heritability to have a handle on how it is being estimated and whether the model or design being used is appropriate to the data (Kruuk and Hadfield 2007; Hadfield et al. 2010). Similarly, animal models can be sensitive to the inclusion of fixed effects (Wilson 2008). Additive genetic variance estimates can change when adding a fixed effect that is genetically correlated with the trait.

When interpreting heritability as a statistic, there is little practical use in $P$ values associated with testing the hypothesis that $h^2 > 0$. First, almost all psychological traits are heritable (Turkheimer and Gottesman 1991), so finding significant additive genetic variance should not come as a shock. Second, the sample sizes available for most primate populations often do not give enough power to distinguish heritability from zero, even if heritability is actually moderate. Finally, evolutionary geneticists are not interested in the predictive utility of heritability as it is practiced in animal and plant breeding, where a particular point estimate for $h^2$ is sought. What we are, instead, interested in is the range of likely values for $h^2$ that are supported by the data and by the model (typically the 95% coverage or confidence interval) to indicate whether heritability is low, moderate, or high.

### 6.3.2 Why Care About $h^2$?

In the age of molecular genetics, heritability may seem like an old fashioned or even outdated concept (Visscher et al. 2008). It may also appear quirky to put so much focus on genes (without naming specific ones) rather than on genotypes. Would we not like to know the specific genes that interact with each other and with the environment to determine an individual's personality? On a practical level, even if an investigation revolves around nongenetic variables, carrying out an analysis within an animal model framework allows estimates of the effects of these variables to be conditioned on familial resemblance. For answering evolutionary questions, heritability gets at those differences in genes that are required for the change of phenotypes through both random drift and natural selection and are therefore fundamental to the debate over how phenotypic differences are maintained in populations.

Going back to our hypothetical troop of more-or-less extraverted primates, heritability captures how much offspring are expected to resemble their parents. A linear regression, such as that of offspring on mid-parent phenotype, is also a model for predicting an offspring's phenotype from those of its parents. It can be used to predict the average personality level of the next generation from the mean level of the selected parents. Heritability thus answers our question of how the offspring of the less Extraverted parents will differ from their parents' generation. The potential for the mean phenotypic value of a trait to respond to selection is proportional to the magnitude of selection on the trait times its heritability. The equation expressing this relationship is called the breeder's equation,

$$R = h^2 S,$$

stating that a population's response ($R$) to selection ($S$) is limited by the heritability of the trait being selected. This equation can be expanded to more than one trait, in which case the response to selection of one trait is a function of its genetic variance and its covariance with other traits being selected (Lande 1979; Turelli 1988; Falconer and Mackay 1996), given by

$$\Delta z = \mathbf{G}\beta,$$

the multivariate breeder's equation, where $\mathbf{G}$ is a matrix of additive genetic variances and covariances of the traits, $\beta$ is a vector of selection gradients on each trait, and $\Delta z$ is a vector of responses to selection for each trait (see Blows 2007 for a review). When studying the evolution of personality, then, it is important to estimate not just the heritability of each dimension but also the genetic correlations among the dimensions and between personality and other traits (see Chap. 7). Thus, genetic correlations between behaviors is one way in which personality traits can be defined (Dingemanse and Réale 2005).

The centrality of heritability to the problem of quantitative variation comes from a basic mathematical result: both random drift and selection reduce additive genetic variance (Falconer and Mackay 1996). Much work on the evolution of personality has gone into developing theories about how individual differences in personality are maintained.

## 6.4 Persistence of Variation in Psychological Traits

The maintenance of heritable variation in traits is a long-standing problem in biology (Barton and Turelli 1989; Barton and Keightley 2002). Processes that maintain additive genetic variation in a trait may come through direct action on the trait or through indirect action on a genetically correlated trait (Robertson 1967).

In discussions of the "amount" of additive genetic variation, it is often pointed out that, as a ratio, the magnitude of heritability is as much a function of all other sources of variance (nonadditive genetic and environmental) as it is of $V_A$. To make heritability comparable between traits and species, Houle (1992) defined the coefficient of additive genetic variation as

$$CV_{\mathrm{A}} = 100\frac{\sqrt{V_{\mathrm{A}}}}{\bar{X}},$$

which standardizes $V_{\mathrm{A}}$ by the phenotypic mean, $\bar{X}$. However, calculating $CV_{\mathrm{A}}$ requires that the phenotype is measured on a ratio scale, meaning that it has a true zero value. Personality constructs in primates are typically formed on ordinal or interval scales, however. This coefficient, therefore, has little utility for comparisons among the heritability of many psychological traits. Furthermore, it loses the key interpretation of heritability as the covariation of parent and offspring phenotype, which is so key to the evolvability of a trait.

### 6.4.1 Processes Maintaining Variation

All genetic differences ultimately arise through mutation, so it is possible for genetic variance to be maintained by a balance between its introduction by mutation and its removal by selection (Lande 1979) or random drift (Barton and Turelli 1989). In biology, most of the debate involves theoretical considerations about the distribution of mutation effect sizes, the number of loci influencing the trait, and the extent of pleiotropy (Johnson and Barton 2005; see Penke et al. 2007 for a review of alternative models from the perspective of human personality evolutionary genetics). The problem with applying these models to the maintenance of genetic variation in nonhuman primate personality traits is that the data required to evaluate them are not available so the arguments are restricted to theoretical considerations. Until such a time as data are available, evolutionary studies of personality will focus on phenotypic and quantitative genetic data.

Even without comprehensive molecular genetic data, fitness trade-offs are essential to consider in the evolution of any trait (Lande 1982; Charnov 1989; Roff and Fairbairn 2007). Such incompatibilities arise when a change in one trait that increases fitness is accompanied by a change in a second trait that decreases fitness. Trade-offs are a particular focus of life-history theory where, for example, there might be alternative choices between fecundity and survival (Williams 1966b; Partridge and Sibly 1991). Because selection will have eroded variation that influences both traits positively, components of fitness tend to have negative genetic correlations even if the phenotypes are positively correlated (Lande 1982). The evolutionary effect that such trade-offs have is typically explored through genetic covariations (Roff and Fairbairn 2007). This brings us back to the multivariate breeder's equation (see Sect. 6.3.2): the potential response of a trait to selection is constrained by selection on other, correlated characters, expressed in the **G** matrix.

The interpretation of **G** as an expression of trade-offs between traits is not without controversy (Pigliucci 2006) because functional trade-offs between two traits (e.g., in resource allocation) can sometimes have a positive genetic correlation

(Houle 1991). In personality research, some of these broader problems can be avoided because we are not interested in predicting long-term responses to selection, which is the crux of much of Pigliucci's (2006) critique of evolutionary quantitative genetics. Trade-offs that can be posited by considering genetic covariances can also be seen when selection of correlated characters produces scenarios where different combinations of traits have equal fitness, potentially maintaining genetic variation in each trait (Roff and Fairbairn 2007). Beyond this, traits can be entangled developmentally through higher orders of epistasis in addition to genetic correlation (Rice 2004).

### 6.4.2 Evolving and Resolving Explanations

Evolutionary psychologists have given many explanations for the persistence of variation in human personality. These explanations have been grouped into three categories: adaptive, nonadaptive, and maladaptive differences (Buss and Greiling 1999). In evolutionary genetic terms, the categories can be rephrased. When speaking of adaptive or maladaptive differences, one is interested in traits that are causally related to fitness, without regard for "where" the variation is coming from (genes or the environment). Nonadaptive sources of difference include neutral variation that, although it may correlate with fitness, does not cause fitness differences; and "by-products of adaptive variation" (Buss and Greiling 1999) that come about through the correlated selection of some other trait. Given the recent shared ancestry and common personality structures between humans and nonhuman primates, explanations offered by evolutionary psychologists are a reasonable starting point for addressing variation in nonhuman primate personality.

Tooby and Cosmides (1990a) were the first to place personality squarely within a modern evolutionary framework, arguing that individual variation was the result of neutral evolution. Most of the variation in the traits that psychologists consider as personality would evolve by drift if behavioral tendencies that are stable across situations are not adaptive; this is because such general tendencies would not be solving any particular problem and thus be causally unconnected with fitness, that is, evolving neutrally. Although the effective population size in humans is large enough that drift is inadequate at reducing genetic variance in neutral traits, all the evidence connecting personality to differences in health, longevity, and reproductive success contradicts the required complete selective neutrality (Penke et al. 2007). MacDonald (1995, 1998) and Nettle (2006) argued instead that variation is maintained by balancing selection for personality differences as alternative behavioral strategies. Human personality dimensions can be cast as trade-offs (Nettle 2006) between mating success and exploration versus risk (Extraversion); vigilance versus the health consequences of stress (Neuroticism), mate attraction versus psychosis (Openness); short-term versus long-term fitness benefits (Conscientiousness); and altruism versus selfishness (Agreeableness). If this is the case, similar trade-offs are likely to manifest in nonhuman primates. As several of these mechanisms are being investigated in primates (e.g., stress and cooperative behavior), an appreciation of individual differences would reveal whether these fitness trade-offs exist. For example, most primate interaction networks support the emergence of cooperation (Voelkl and Kasper 2009), so primate societies might contain a mix of cooperators and defectors who differ in Agreeableness. Other trade-offs that have not been put forward for humans have been observed in primates, such as decreased vigilance over infants displayed by rhesus macaque mothers while engaged in allogrooming (Maestripieri 1993).

A basic life-history trade-off has also been theorized to underlie human personality and intelligence differences (Rushton 1985; Figueredo et al. 2005; Rushton et al. 2008). This within-species difference in a developmental strategy of investing in fecundity or survival was theorized to extend in humans to family size, interbirth interval, and parental care (Rushton 1985). An individual would either pursue a risky life of multiple mates, large families, and little parental investment or a slow-paced existence with one mate, few children, and long life. Humans disposed toward the latter strategy were found to be less neurotic, more extraverted, more agreeable, and more conscientious (Figueredo et al. 2005). Rushton et al. (2008) combined this with the postulation of a general factor of personality (GFP) underlying the five human dimensions (Musek 2007) to suggest this single factor (capturing differences in cooperativeness and prosociality) is under directional selection along with the associated life-history traits (contra Figueredo et al. 2005, who proposed balancing selection). Although selection has not been estimated for the GFP, genetic analysis of twins showed that all of the genetic variance was attributable to dominance effects (Rushton et al. 2008), which matches a theoretical prediction of long-term directional selection (Falconer and Mackay 1996) and the finding that life-history traits have higher dominance variance (Crnokrak and Roff 1995).

The existence of a general personality factor in humans is a bit tender in its psychometric joints (Ashton et al. 2009), but this does not invalidate the study of life-history traits and personality in nonhuman primates. Personality traits may be separately linked to different life-history variables. In comparison with most other mammals of the same size, primates take longer to gestate and mature, have fewer offspring, and live longer lives (Strier 2003). There is also a significant amount of variation in life-history variables among primate species concerning the speed of gestation, development, and maturation adjusting to fit differences in body size, which is an adaptation to local ecology (Harvey and Clutton-Brock 1985). Trade-offs, then, exist at the within-species level. This can be seen in rhesus macaques, which exhibit a positive genetic correlation between age at primiparity and longevity, so females who start reproducing earlier have a shorter lifespan (Blomquist 2009b), suggesting that a fitness trade-off in life-history strategies potentially exists in nonhuman primates.

The life-history perspective on personality is also favored in theoretical work by behavioral ecologists (Dall et al. 2004; Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008). Personality differences are again conceived of as distinct behavioral strategies (Dall et al. 2004). This body of theory allows us to imagine under what conditions we would not have personalities at all. Two basic "personalities" can coexist as stable types of competing strategies under frequency-dependent selection (Maynard Smith 1982). However, the same stable situation can emerge if each individual plays a mixture of both strategies. In this case, no personalities exist because each individual is expressing exactly the same behavioral tendency. Individual differences in behavior that can be dubbed personality can emerge, however, if these differences are tied to life-history trade-offs (Wolf et al. 2007; Biro and Stamps 2008). More generally, the fitness of a particular trait may depend on the frequency of other traits being expressed in the population rather than on the frequency of alleles affecting the target trait (Reeve and Dugatkin 1998). For example, the fitness implications of exploratory behavior might depend on conspecifics' aggression rather than on one's own level of exploration–avoidance. The output of such theory has so far been applied exclusively to studies of nonprimate animal personality from the framework of behavioral syndromes (Sih et al. 2004).

For rhetorical reasons, explanations of the persistence of variation in personality are often set up as mutually exclusive possibilities. This need not be the case and is probably an artifact of how selection is usually presented and contrasted (Rice 2004). Directional and stabilizing selection can co-occur on the same trait, changing different moments of the phenotypic distribution. Such possibilities should be exploited when considering how personality evolves (see Sect. 6.6).

Which approach is applicable for nonhuman primates? Both their close affinity with humans and the rich literature on their behavioral ecology (Strier 2003) suggest that combining methodologies from evolutionary psychology and behavioral ecology perspectives are feasible. From an evolutionary genetic perspective, the apparent commonality of several aspects of primate personality structure, such as dimensions related to sociality and anxiety, suggest that certain evolutionary equilibria are maintained over long periods of time in primates. If true, evolutionary genetic processes can be fruitfully investigated using phenotypic data (see Chap. 7). Resolving alternative explanations for the persistence of variation in nonhuman primate personality is particularly exciting because we can compare species that are closely allied because of phylogenetic affinity (e.g., macaques) or socioecological similarity (e.g., chimpanzees and spider monkeys). Nonhuman primates also offer a window through which to chase the evolutionary genetics of personality into the wild.

## 6.5 Evolution in the Wild

Studying the evolution of personality in primates means eventually studying personality in wild primates. Investigating the selection of personality can proceed along two courses: by relating personality to fitness differences or by indirect inference in comparing how correlations among personality traits differ between populations in varying environments (Dingemanse and Réale 2005). Evolutionary genetic studies in the wild have progressed tremendously through the use of extensive pedigree information, long-term data collection, and the identification of individuals (Kruuk and Hill 2008). Recognizing individual animals in the wild has been central to traditions in primatology for at least 60 years (Matsuzawa and McGrew 2008). This acknowledgment of individuality and family life eventually led some primatologists to start tracking familial lineages (Kawai 1958; Kawamura 1958; DeVore 1962; Yamada 1963; Carpenter 1964; Goodall 1986). Given the many decades these pedigrees have been curated at some wild primate sites (e.g., Arashiyama, Cayo Santiago, Gombe, and Koshima), it is a wonder that this information has been used only sparingly for evolutionary and quantitative genetic research (the exceptions are, notably, captive populations, those at the Vervet Research Colony and the Southwest National Primate Research Center). More typically, pedigree information is used for the purpose of determining reproductive success, mate choice, and social relationships among kin (see Chap. 3). Quantitative genetic studies of wild primates offer rich, low-hanging fruit of which primatologists are now beginning to partake (Blomquist 2009a, b).

### *6.5.1 Pedigree Construction*

In primates, maternity can be reliably inferred from behavioral data, as infants initially associate exclusively with their mothers (Strier 2003). Paternity is more tricky and typically requires exclusion or likelihood assignment using genetic markers. Currently, the most prevalent molecular markers for pedigree construction are microsatellites (Jones and Ardren 2003). The advantages of microsatellites are that they are relatively easy to discover in new species, are codominant (both alleles can always be recognized, if they differ), are highly variable (making it easier to distinguish individuals), and can be obtained from wild samples (Pemberton 2008). With these markers, a number of algorithms and statistical techniques can be used to assign paternity (Jones and Ardren 2003; Pemberton 2008). For evolutionary genetics, pedigree accuracy is a constant concern because errors lead to imprecision in heritability estimates (Kruuk 2004).

Building pedigrees also allows detection of inbreeding. In primates, inbreeding is primarily a concern in isolated, endangered, or captive populations (e.g., Alvarez et al. 2009). Although the role of inbreeding depression in personality has not been investigated directly (Penke et al. 2007), there is evidence suggesting that it is a possibility (Rebello and Boomsma 2007).

### *6.5.2 Fitness Is Not What You Think It Is; Rather, It Is Exactly What You Think It Is*

“Fitness” is an inconsistently used term in evolutionary studies, with evolutionary psychology being no exception. Many workers have taken definitions of fitness that attempt to distinguish the effect of random drift from that of natural selection. Writing on the subject, authors often adopt, knowingly or unknowingly, Williams’s (1966a) definition of fitness as the average reproductive success of a given “design.” For example, Grafen (1988) acknowledged Williams in distinguishing individual lifetime reproductive success from fitness, and Penke et al. (2007, p. 553) described fitness as a property of a genotype, with “its statistical propensity for successful reproduction.” Yet these distinctions are not necessary. The cleanest definition marks fitness as an individual’s contribution to the next generation, and it is thus a property of individuals and not of genotypes or of alleles (Rice 2004). This interpretation includes both selection and drift in an individual’s reproductive success, the difference being whether the covariance between genotype and fitness is random (drift) or nonrandom (selection). It is thus a question of causality.

Lifetime reproductive success is therefore the canonical measure of fitness, but individual differences leading to reproductive success can enter at any stage in an organism’s life – the where and when having considerable practical import. Four general components of fitness include survival to breeding age, reproductive lifespan, fecundity, and offspring survival (Brown 1988). Assuming parentage can be assigned, these data can be (and are being) tracked in wild primates. Whichever component of fitness is used, selection is measured with it in the same way. The first step is to test whether the trait of focus is significantly related to fitness (Mitchell-Olds and Shaw 1987) by regressing the trait on fitness. Because annual and lifetime breeding success are not normally distributed but, rather, follow a zero-inflated Poisson or negative binomial distribution, where each year in an animal’s life is a chance to “fail” at having an offspring, a generalized linear model should be used instead of an ordinary least-squares regression (Kruuk et al. 2002). The next step is to estimate the strength and mode of selection by regressing the standardized trait on relative fitness as the linear coefficient (for directional selection) or twice the quadratic coefficient (for stabilizing or disruptive selection) using an ordinary least-squares method (Arnold and Wade 1984; Stinchcombe et al. 2008). Because there are competing hypotheses about the role of selection in maintaining variation in personality, it is essential to avoid the publication bias that plagues estimates of the strength of selection (Kingsolver et al. 2001). Given the present state of knowledge on personality in the wild, the absence of selection is as interesting as its presence (Dingemanse and Réale 2005) because we would like to know under what ecological conditions personality differences are adaptive in primates and when they are only neutral.

Selection coefficients of personality traits are already being estimated in wild populations of nonprimate animals (Dingemanse and Réale 2005), so primatologists should follow the lead of behavioral ecologists in applying the tools of evolutionary biology to personality (in contrast to doing psychology with their evolutionary-paradigm beanie on). A difficulty in following this path is that in current studies of nonhuman primate personality, lifetime reproductive success is usually not available simply because the study subjects are still alive. Research on living individuals must then use other components of fitness, such as age at primiparity, interbirth interval, annual reproductive success, or infant survival. Investigations of personality in populations of wild primates are barely embryonic, but a future goal of this research should be longitudinal studies that ultimately measure the implications of personality differences for lifetime reproductive success.

### 6.5.3 G Matrices Gone Wild

The use of the additive genetic variance–covariance matrix runs into a spot of trouble when taken out of the farm and into the jungle. In agricultural and laboratory conditions, the predictive value of the breeder's equation works because we decide which traits to select. In the wild, however, we can never be certain that we are including all the characteristics that are being selected (Lande and Arnold 1983; Endler 1986). This is one explanation for why, in wild populations, the phenotypic response to selection can be either zero or even opposite of what is predicted from the **G** matrix and the vector of selection gradients (Merilä et al. 2001).

Another general difficulty that must be resolved in the particular is the leap from the estimation of selection gradients to inferences about adaptation (Grafen 1988). Here, we are seeking functional and causative accounts for how personality and life-history variables lead to differences in reproductive success (Pigliucci 2006). In the troop of primates where we find only the introverts having children, is the negative correlation between Extraversion and breeding success chance sampling variation (i.e., genetic drift), or is this connection causal, meaning that there is selection for low Extraversion? In building causal models to distinguish direct selection from indirect selection or random drift, it is essential to have a more complete functional and behavioral understanding of personality differences. In nonhuman primates, personality dimensions based on adjectival descriptors do not enjoy a one-to-one mapping with independent aspects of behavior (Konečná et al. 2008). In langurs, both Confidence and Extraversion correlate with the behavioral dimension Activity, but Confidence is also related to the Dominance and Involvement behavioral components. It is likely that impressionistic dimensions capture personality traits that can be expressed through different aspects of the same behavior, such as the frequency and bout length of grooming sessions. This is precisely the point where behavioral repertoire and syndrome approaches will be of most use in the evolutionary genetics of nonhuman primate behavior, where a syndrome or profile can identify the situational and behavioral units that correlate. Such procedures promise to untangle the ecological variables defining the situations in which personality is differentially expressed and provide testable paths through which trait personality differences might be affecting life-history outcomes and reproductive success.

### 6.5.4 Into the Wilds of Personality

Although personality researchers can borrow techniques for estimating heritability and selection from evolutionary quantitative geneticists, they are still faced with the problem of collecting personality data on wild animals. Studies that specifically take ecological or evolutionary paths to discovering and defining personality traits are sorely lacking on nonhuman primates (Uher 2008). In addition to highlighting the need to investigate species-specific differences in personality constructs (Uher 2008; Uher et al. 2008), we also need to be open to the possibility of the same species exhibiting alternative personality structures in different ecological environments (Bell 2005; Uher 2008). Another barrier to educing a whole personality structure of a species in the wild is the number of different populations that can be studied. The incorporation of Openness-like facets into the Extraversion dimension of Hanuman langurs (Konečná et al. 2008) could be peculiar to the population rather than to the species. The small sample of langurs ($n=27$) is not necessarily fatal, as a fully informative factor structure can be recovered from small samples if the number of factors is small and the number of items large (de Winter et al. 2009). Furthermore, as the chimpanzee factor model replicated in different populations (King et al. 2005; Weiss et al. 2007, 2009), there are unlikely to be broad structural differences between primate populations of the same species, as defined by factor models of personality. Understanding the ecologically relevant differences in primate personality expression, then, requires the finer lens of behavioral repertoire and allied approaches.

A standard adjective rating instrument, such as the Hominoid Personality Questionnaire,[1] can be used to obtain an initial impression of species whose personality has not been previously measured. First, this allows initial integration into other findings about personality structure and will help resolve unknown questions about the historical patterns of personality evolution. Second, as a practical matter, impressionistic ratings can be gathered from raters who, although familiar with the individual animals in the study population, may not have been studying their behavior. Finally, behavioral repertoires might differ between populations (because of slight differences in ecological situations) more than the personality structure is likely to differ.

## 6.6 Personality As a Norm of Reaction

An interaction between a genotype and a set of environments is called a reaction norm (Dobzhansky 1955; Platt and Sanislow 1998 and references therein). Plots showing hypothetical reaction norms of different genotypes in different environments litter psychology textbooks (Platt and Sanislow 1998) and come up repeatedly in contentious debates about nature and nurture (e.g., Sternberg and Grigorenko 1997). Accounting for these effects will take real work, not just chatter about *Arabadopsis*, *Drosophila*, and *Mus*. Models that estimate variance from $G \times E$ interactions have started making their way into psychological research (Johnson 2007). The concept of a behavioral syndrome explicitly incorporates the idea of personalities as norms of reaction (i.e., a correlated suite of responses across environments) (Sih et al. 2004) and captures the idea that personality depends on context (van Oers et al. 2005b). Envisioning personality in this way may allow behavioral ecologists

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[1] Available from Alexander Weiss.

to bypass much of debate between person–situation and ordinary trait perspectives on personality (Penke et al. 2007). However, a norm-of-reaction approach offers a much greater potential for integrating between- and within-individual variation in personality to the intrepid primate psychologist willing to grapple with a few more complexities in their models.

Looking at personality as a reaction norm may fuse various perspectives on personality when we incorporate tools from quantitative genetics (van Oers et al. 2005a). Mischel and Shoda's (1995) person × situation perspective on personality, which looks for stable behavioral profiles, can be recast in terms of reaction norms (Penke et al. 2007). Penke et al. (2007) also noted that Mischel and Shoda (1995) focused their theory on describing individual reaction norms but that as aspects of these behavioral profiles are heritable (Borkenau et al. 2006) it is more appropriate to examine the $G \times E$ level of reaction norm differences. However, the individual reaction norm should not be discarded, even if what we are interested in is genetics.

The $G \times E$ reaction norms are typically investigated using experimental designs that subject a set of genotypes to different environments to assess the phenotypic plasticity of each genotype (Via et al. 1993). What do we do with primates, however, who are generally not keen on being cloned or grown in experimental plots? To the extent that a personality trait varies within an individual, it is a labile trait, changing throughout the course of life (Gomulkiewicz and Kirkpatrick 1992; Lynch and Walsh 1998).

Because personality can be measured multiple times, either in different situations or as the individual ages, it can also be examined using individual reaction norms (Nussey et al. 2007). Individual reaction norms encompass all of the situations and environments in which an individual expresses a trait throughout life. Reaction norms can be scrutinized at both the individual phenotypic and genotypic levels. An individual reaction norm covers person × situation (or environment) variance at the phenotypic level, whereas the genetic reaction norm describes $G \times E$ interactions. Differences in reaction norms may exist at either level (or none or both). These reaction norms have a physiological basis, as seen in rhesus macaques, who have stable serotonin concentrations in early life as they experience a number of stressful events during emigration (Mehlman et al. 1995). The nongenetic variance in individual reaction norms is attributed to permanent environment effects, which for personality could include the influence of early development or of learning. Individual reaction norms can be studied with quantitative genetics using a random regression animal model (Gomulkiewicz and Kirkpatrick 1992; Nussey et al. 2007), which, using repeated measures of personality in different situations and pedigree data, can distinguish the permanent from the genetic sources of interaction variance.

The chief practical difficulties of this approach for the evolutionary genetics of primate personality are twofold. The first is the partition of environments. What situations are considered the same environment in which a personality trait is being expressed? Plus what is a situation? Second, the sample sizes needed to obtain good estimates of these parameters will be arduous to muster for nonhuman primates. Hopefully, primatologists are up to this challenge (van Oers et al. 2005a).

## 6.7 Conclusion

Reaction-norm representations of the expression, development, and evolution of behavior may be able to separate out the genes, situations, and vagaries of existence that go into determining an individual primate's personality. However, these approaches by themselves have little hope of putting an end to the nature–nurture debate because we cannot fathom that nature + nurture is a model.

The focus here has been on variance component models that break down the causes of personality and of measuring selection on the phenotypic level because this is what the data from most current studies of wild nonhuman primates can support. Researchers familiar with their primate subjects, even if they do not study behavior, are a resource for getting initial impressionistic ratings from which a personality structure can be defined. Once this structure is known and compared within its phylogenetic context, researchers can ask the salient behavioral and ecological questions of why we find a particular personality structure in each species. Many primates live together in groups where kin can be identified and tracked as individuals throughout their lives, supplying information about genetic relatedness and life history needed for evolutionary genetic studies of personality. Ethological investigations of more specific aspects of personality can be used to connect personality differences to fitness-relevant outcomes. To the extent that personality hinders or helps individual or group adaptation to habitat disruption, a thorough understanding of nonhuman primate personality may aid conservation efforts.

Taking evolutionary quantitative genetics more broadly, we should aim to investigate primate personality through population genetics, genomics, and molecular ecology. These techniques are already being used to study the evolution of primate phenotypes, such as coloration, for which specific gene variants have been identified (see Chap. 14). Comparing homologous and convergent personality traits among primate taxa would highlight ecological conditions that pattern structural divergence between species as well as guide the evolutionary study of psychological traits out of the morass of "environments of evolutionary adaptedness" (Symons 1979; Tooby and Cosmides 2005). This would further involve finding gene variants and quantitative loci underlying personality differences, detecting differences in gene frequencies among populations of the same species, and looking for molecular signatures of past selection and demographic changes that explain extant variation in primate personality.

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Journal of Comparative Psychology
2011, Vol. 125, No. 1, 72–83

0735-7036/11/$12.00 DOI: 10.1037/a0021187

# Rhesus Macaques (*Macaca mulatta*) as Living Fossils of Hominoid Personality and Subjective Well-Being

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Personality dimensions capturing individual differences in behavior, cognition, and affect have been described in several species, including humans, chimpanzees, and orangutans. However, comparisons between species are limited by the use of different questionnaires. We asked raters to assess free-ranging rhesus macaques at two time points on personality and subjective well-being questionnaires used earlier to rate chimpanzees and orangutans. Principal-components analysis yielded domains we labeled Confidence, Friendliness, Dominance, Anxiety, Openness, and Activity. The presence of Openness in rhesus macaques suggests it is an ancestral characteristic. The absence of Conscientiousness suggests it is a derived characteristic in African apes. Higher Confidence and Friendliness, and lower Anxiety were prospectively related to subjective well-being, indicating that the connection between personality and subjective well-being in humans, chimpanzees, and orangutans is ancestral in catarrhine primates. As demonstrated here, each additional species studied adds another fold to the rich, historical story of primate personality evolution.

*Keywords:* rhesus macaque, primate, personality, stability, well-being

Nonhuman primate personality traits capture impressions that are reliable in that they are consistent across raters and time (King & Figueredo, 1997; King, Weiss, & Sisco, 2008; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Uher, Asendorpf, & Call, 2008; Weiss, King, & Perkins, 2006). Nonhuman primate personality traits are also valid in that they are related to other measures, including observed behavior (Capitanio, 1999; Konečná et al., 2008; Pederson, King, & Landau, 2005; Stevenson-Hinde et al., 1980; Uher & Asendorpf, 2008).

Like the study of physical characteristics in different species, the comparative method can address questions concerning the evolution of stable personality traits (Gosling & Graybeal, 2007; Harvey & Pagel, 1991). King and Figueredo (1997) examined personality phylogeny by obtaining ratings of zoo chimpanzees on a questionnaire based on measures of the five major dimensions along which humans differ — Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness (Digman, 1990). They found a broad chimpanzee-specific Dominance domain, and five additional domains that, while differing slightly on the trait level, were analogous to human personality domains (King & Figueredo, 1997). Thus, precursors of human personality were likely present in the common chimpanzee-human ancestor and early hominids, though dominance was no longer a key domain upon which members of the latter could be distinguished. A study of orangutan

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This study complies with the current laws of Puerto Rico and the United States. The IACUC of the University of Puerto Rico, Medical Sciences Campus approved this investigation. The rhesus macaque population of Cayo Santiago is supported by the University of Puerto Rico, Medical Sciences Campus and by the National Center for Research Resources (NCRR), a component of the National Institutes of Health (NIH) (NCRR Grant P40RR003640 Award to the CPRC). The content of this publication is solely the responsibility of all of the authors and does not necessarily represent the official views of NCRR, NIH, or the United States Government. We thank Amanda K. Accamando, Lauren J. N. Brent, Julie Cascio, Camille Guillier, Doreen Hess, Constance Dubuc, Veronique Martel, Jennifer L. Danzy, Joyce Moewius, Maggie Chivavetta, Veronica Gutierrez, Claude Richer, Agnieszka Sukiennik Koniec, and Akie Yanagi for rating the monkeys. Without their cooperation, this project would not have been possible. We also thank Edgar Davíla and Julio Resto for maintaining a daily census of the rhesus macaques of Cayo Santiago. We thank Jana Uher and Michael Tomasello for their helpful comments on a draft. Finally, we would like to thank one anonymous reviewer for suggesting the analyses depicted in Table 3 and both anonymous reviewers for several helpful comments which have improved the manuscript.

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personality using an expanded version of the same questionnaire as that used to rate chimpanzees found variants of human and chimpanzee Neuroticism, Extraversion, and Agreeableness domains as well as a Dominance domain, suggesting that these domains may have existed in the common ancestors of great apes and humans (Weiss et al., 2006). In addition, this same study found that, instead of making up separate domains, traits defining Openness and Conscientiousness defined a single domain in orangutans named Intellect, suggesting that selection may have favored separate Openness and Conscientiousness domains in species such as humans and chimpanzees, which have more complex social structures.

Although personality differences have been described in great apes and humans, the historical patterns of personality evolution cannot be deduced from examining this taxon alone. Studying personality in Old World monkeys, which split off from hominoids between 25 and 30 mya (Andrews, 1986), could offer insights into the evolutionary origins of personality and selective factors which contribute to phylogenetic divergences in personality. Their distant relatedness to humans relative to hominoids makes Old World monkeys an important study species for understanding human evolution.

Rhesus macaques have been the most widely used nonhuman primate in behavioral research. Unlike hominoids, and what is often assumed to be the ancestral social structure for early hominids (Foley & Lee, 1989; Wrangham, 1987), rhesus macaque social structure is largely based on male dispersal (Colvin, 1986; Manson, 1995; Melnick & Pearl, 1987) with female philopatry (Gouzoules & Gouzoules, 1987). Like other macaque species, rhesus macaques live in multimale, multifemale groups, which are characterized as matrilineal societies, with a matriline defined as all descendants of a founder female (Melnick & Pearl, 1987).

Early personality research on captive rhesus macaques using a questionnaire containing 33 behaviorally defined adjectives identified three reliable and stable domains: Confident, which describes differences in boldness and submissiveness; Excitable, representing differences in curiosity, activity, and reactions to change; and Sociable, which captures differences in how much time individuals spends with others (Stevenson-Hinde et al., 1980; Stevenson-Hinde & Zunz, 1978). Later studies using this same questionnaire identified an additional rhesus macaque personality domain labeled Equable (Bolig, Price, O'Neill, & Suomi, 1992; Capitanio, 1999), comprised of individual differences in reactions to conspecifics, the appropriateness of behaviors displayed toward conspecifics, and being slow, deliberate, and not hurried (Capitanio, 1999).

These four rhesus macaque personality domains roughly approximate personality domains of other species. Confident is described by items similar to those which describe chimpanzee Dominance (Dutton, 2008; King & Figueredo, 1997) and orangutan Neuroticism (Weiss et al., 2006). Traits similar to those making up the Excitable, Sociable, and Equable domains are found in the Neuroticism, Extraversion, and Agreeableness domains, respectively, of humans (Costa & McCrae, 1992), chimpanzees (Dutton, 2008; King & Figueredo, 1997), and orangutans (Weiss et al., 2006). In addition to predicting behavior (Capitanio, 1999), these domains predicted immunocompetence (Capitanio, Mendoza, & Baroncelli, 1999; Maninger, Capitanio, Mendoza, & Mason, 2003) and corticosteroid response (Capitanio, Mendoza, & Bentson, 2004).

Subjective well-being or "happiness" is a construct closely related to personality and describes individual differences in positive affect (Diener, 2000). The study of subjective well-being was, in part, a reaction to the near exclusive focus of much psychological research on the study of psychopathology (Seligman & Csikszentmihalyi, 2000). Like human personality domains (McCrae & Costa, 2003), subjective well-being is mostly stable throughout life (Diener, 2000). Moreover, humans who are higher in subjective well-being tend to be lower in Neuroticism and higher in Extraversion (Steel, Schmidt, & Shultz, 2008). This personality-well-being nexus is partially genetic, as the genetic variance in subjective well-being can be accounted for by genes also influencing personality (Weiss, Bates, & Luciano, 2008).

Research on rater assessed chimpanzee subjective well-being also found high interrater reliability, stability over time, and correlations with personality like those described in human research (King & Landau, 2003; Weiss et al., 2009). A study of subjective well-being in orangutans using the same questionnaire also found correlations like those described in humans and chimpanzees (Weiss et al., 2006). Finally, as in humans, chimpanzee subjective well-being is genetically correlated with personality (Weiss, King, & Enns, 2002).

The above findings regarding human, chimpanzee, orangutan, and rhesus macaque personality suggest conservation of some basic personality dimensions over evolutionary time. We therefore expect to find rhesus macaque variants of traits similar to the Sociable, Excitable, Equable, and Confident domains identified in prior studies (Bolig et al., 1992; Capitanio, 1999; Stevenson-Hinde et al., 1980; Stevenson-Hinde & Zunz, 1978). However, these previous studies of rhesus macaque personality did not identify distinct Conscientiousness or Openness domains. There are three possible explanations for the failure to find such domains in rhesus macaques. The first possibility is that the earlier assessment instrument was developed prior to the adoption of what has come to be known as the human Five-Factor Model (Digman, 1990) and may therefore not have been comprehensive enough to capture all rhesus macaque personality domains (Uher, 2008). The second possibility is that prior studies were based on captive samples which may not have been able to fully express their behavioral repertoires (Uher, 2008). The third possibility is that rhesus macaques cannot be differentiated on these domains and that the distinct clustering of individual differences in exploratory behavior and predictability is a more recent adaptation.

As such, our primary goal was to investigate which personality domains are present in rhesus macaques, and, in particular, whether distinct Conscientiousness or Openness domains are present. To rule out the possibility that limitations of previous rhesus macaque personality studies led to the absence of separable Conscientiousness or Openness domains, we used a broad instrument which identified these domains in chimpanzees. To exclude the possibility that the limited behavioral repertoires of small samples of captive rhesus macaques did not permit the detection of Conscientiousness and Openness, we conducted this study with a large sample of free-ranging individuals. These results could therefore address the third possibility, that these personality differences are the result of adaptation, and thus yield valuable insights into the evolutionary origins of personality. For example, if we find distinct Conscientiousness or Openness domains, this would suggest that they were present in the common ancestor of Old World monkeys and hominoids and that the orangutan Intellect domain is derived. On the other hand, if we fail to find distinct Conscientiousness or Openness domains this would suggest that these domains arose in the common ancestor of chimpanzees and humans before they speciated some 5–6 mya (Chimpanzee Sequencing & Analysis Consortium, 2005).

The subjective well-being findings in humans and great apes strongly suggest that the relationship between personality traits such as Extraversion and Neuroticism and higher and lower subjective well-being, respectively, is ancestral. This possibility is strongly supported by the fact that these relationships are genetically mediated in humans (Weiss et al., 2008) and chimpanzees (Weiss et al., 2002). Thus, we asked several raters to assess the same set of rhesus macaques on the subjective well-being measure used in previous studies of chimpanzees (King & Landau, 2003; Weiss et al., 2009) and orangutans (Weiss et al., 2006). If personality and subjective well-being are related in the same way as they are in humans, chimpanzees, and orangutans, this would suggest that these relationships existed in the common ancestor of cercopithecoids and hominoids and were conserved.

One defining characteristic of human personality traits (Roberts & DelVecchio, 2000) and subjective well-being is that they are mostly stable over time (Eid & Diener, 2004). Thus, for the present study, personality and subjective well-being ratings were collected in two waves separated in time by over 1 year. These data will therefore enable us to determine how stable these constructs are in rhesus macaques and whether the relationship between these constructs is also stable. Thus, they will offer further insight into how rhesus macaque personality and subjective well-being compare to like constructs in chimpanzees, orangutans, and humans.

## Methods

### Subjects and Raters

Subjects were 125 rhesus macaques (*Macaca mulatta*) from the free-ranging population on Cayo Santiago (for more details see Rawlins & Kessler, 1986) who were rated in two waves. The Wave 1 sample consisted of 124 subjects (51 males and 73 females) rated between February 2006 and July 2007. The mean age of Wave 1 subjects was 7.71 years ($SD = 6.21$). Wave 1 males had a mean age of 7.17 years ($SD = 6.48$) and Wave 1 females had a mean age of 8.08 years ($SD = 6.03$). The Wave 2 sample consisted of 71 subjects (26 males and 45 females) rated 13.9 to 18.0 months later between August, 2007 and May, 2008. Of the Wave 2 subjects, all but one male had been rated in Wave 1. The mean age of Wave 2 subjects was 6.26 years ($SD = 5.53$). Wave 2 males had a mean age of 3.09 years ($SD = 0.09$) and Wave 2 females had a mean age of 8.09 years ($SD = 6.27$).

Subjects were rated by multiple raters who, for 3 to 24 months prior to this study, had been conducting unrelated research, and could reliably identify individual subjects. There were 11 raters in Wave 1. Ratings in Wave 2 were made by three raters from Wave 1 and three new raters.

### Instruments

We modified questionnaires used to rate the personality and subjective well-being of captive chimpanzees (King & Figueredo, 1997; King & Landau, 2003; Weiss et al., 2009) and orangutans (Weiss et al., 2006) for use in rating free-ranging monkeys. Modification involved changing the words “enclosure” and “chimpanzee” to “environment” and “monkey,” respectively. Raters were instructed to base ratings on overall impressions of the subjects and to not discuss their ratings. Ratings were made on a 7-point Likert scale.

**Personality measure.** The Hominoid Personality Questionnaire consists of 54 adjectives, each followed by one to three sentences defining the adjective within the context of nonhuman primate behavior. For example, the item *fearful* is “FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.” The original version included 43 items and was used to rate chimpanzees (King & Figueredo, 1997). Of these items, 41 were sampled from the factors of Goldberg’s (1990) taxonomy of the Big Five and two (*autistic* and *clumsy*) were created by the King and Figueredo. This questionnaire was later increased by five items for a study of orangutan personality (Weiss et al., 2006). Of these new items, *anxious* and *vulnerable* were based on facets of the Revised NEO Personality Inventory Neuroticism domain (Costa & McCrae, 1992), *curious* and *conventional* were based on markers of Openness from an adjectival questionnaire (McCrae & Costa, 1985), and *cool* was created by the researchers to capture low Neuroticism. In a later revision (Weiss et al., 2009) the 48 item version of the questionnaire was expanded by adding three Conscientiousness and three Openness items. Two Conscientiousness items (*thoughtless* and *quitting*) were from an adjectival questionnaire (McCrae and Costa, 1985) and one (*distractible*) was devised by the researchers. All three Openness markers (*individualistic*, *innovative*, and *unperceptive*) were created by these researchers.

**Subjective well-being measure.** This questionnaire includes four items derived from measures of human subjective well-being, which assessed the balance of positive and negative moods, pleasure derived from social interactions, the ability to achieve personal goals, and how “happy” raters think they would be if they were the target individual. Because of a clerical error, the third item of this questionnaire referred to “enclosure”; it was thus left out of all analyses.

### Missing Data

At Wave 1 one subject was missing one item (*curious*) while 13 subjects were missing 18 to 39 items. Data were not missing at random but came from raters who did not provide ratings for any subject on a subset of items. Twenty-three subjects were not assessed by one of their raters on a single subjective well-being item, although every subject had a rating from at least one rater on each item.

### Statistical Analyses

**Interrater reliabilities of items.** Interrater reliabilities of personality and subjective well-being ratings were calculated from scores at Wave 1 for the 91 macaques judged by two or more raters. We measured interrater reliabilities of personality and subjective well-being ratings using two intraclass correlations (Shrout & Fleiss, 1979): *ICC*(3, 1) and *ICC*(3, *k*).

**Principal-components analysis.** To determine the factors underlying ratings, we conducted principal-components analyses[1] using the principal procedure (Revelle, 2009) from the R statistics package (R Development Core Team, 2008) and determined the number of components by examining the scree plot and by using R's paran function (Dinno, 2008) to conduct a parallel analysis (Horn, 1965). We then used a varimax rotation to obtain orthogonal components and a promax procedure to obtain oblique components. The latter rotation was conducted because it enabled us to estimate correlations among components and to determine whether allowing components to correlate altered the structure.

The principal-components analysis of personality ratings was based on the mean scores across raters for the 52 personality items at Wave 1 which displayed some consistency across raters. For this analysis we dropped 13 subjects that were missing scores on nine or more items. The principal-components analysis of subjective well-being items was based on the mean scores across raters for the three subjective well-being items.

We created personality domain scores using unit-weighting. This involved assigning items with salient loadings (defined as $\geq .40$) on a component weights of $+ 1$ or $-1$ depending on whether the loading was positive or negative, respectively, and assigning a weight of 0 to items which did not have salient loadings. If an item had salient loadings on more than one component, it was assigned to the component on which it had the highest loading. The sum of the weighted item scores defined the domain score. The same procedure was used to create domain scores for any subjective well-being components.

It is important to note that creating scores via unit-weighting does not preserve the independence of varimax-rotated components. However, we chose to use unit-weighting because results derived from these scores are more generalizable than those derived from differentially weighted scores (Gorsuch, 1983; p. 267). This advantage stems from the fact that, unless sample sizes are very large, the exact component loadings used to create differentially weighted scores will reflect some degree of capitalization on chance (Gorsuch, 1983; p. 266).

To interpret rhesus macaque personality factors, we examined the items that had salient loadings on those factors in light of the content of those items, the relationship between those items and the five human dimensions, and the rhesus macaque personality literature (Bolig et al., 1992; Capitanio, 1999; Stevenson-Hinde et al., 1980; Stevenson-Hinde & Zunz, 1978). To help interpret factors we also created unit-weighted domain scores for the rhesus macaques rated in Wave 1 using the definitions of the six chimpanzee (King & Figueredo, 1997) and five orangutan (Weiss et al., 2006) personality factors and examined the correlations between domain scores based on rhesus macaque personality structure and those based on the chimpanzee and orangutan personality structures.

**Reliabilities of personality domains and subjective well-being.** We measured interrater reliabilities of personality domain and subjective well-being scores using two intraclass correlation coefficients described by Shrout and Fleiss (1979): *ICC*(3, 1) and *ICC*(3, *k*). Personality domain scores in these analyses were based on unit-weighted scores with mean substitution from individual judgments on the 81 subjects at Wave 1 and 49 subjects at Wave 2 that were assessed by multiple raters who did not miss more than eight items. Subjective well-being scores for these analyses were generated by summing the three subjective well-being items from individual judgments of each animal. Internal consistency reliabilities for personality domains and subjective well-being were calculated via Cronbach's alpha on mean ratings of 111 macaques at Wave 1 and 71 at Wave 2. Retest reliabilities were measured using Pearson correlations between the Wave 1 and Wave 2 mean unit-weighted personality domain and subjective well-being scores for the 70 subjects assessed in both waves.

**Personality and subjective well-being correlations.** To examine the cross-sectional relationship between personality domains and subjective well-being we computed correlations between personality and subjective well-being scores for the 111 subjects assessed in Wave 1 and the 71 subjects assessed in Wave 2 with fewer than nine missing items. For the 70 subjects assessed at both time points we examined correlations between Wave 1 personality domains and Wave 2 subjective well-being as well as correlations between Wave 1 subjective well-being and Wave 2 personality domains.

## Results

### Interrater Reliabilities of Items

**Personality.** The reliability of single ratings (*ICC*[3, 1]) ranged from −0.05 for *autistic* to 0.63 for *dominant* and had a mean of 0.26. The reliability of mean ratings (*ICC*[3, *k*]) ranged from −0.17 for *autistic* to 0.86 for *dominant* with a mean of 0.52. We excluded the items *autistic* and *unperceptive* from further analysis as unreliable because their interrater reliabilities were less than zero.

**Subjective well-being.** All three subjective well-being items were reliable. The *ICC*(3, 1) for the items assessing balance of positive and negative moods, pleasure derived from social interactions, and how "happy" raters think they would be if they were the monkey were 0.41, 0.44, and 0.43, respectively. The *ICC*(3, *k*) values for the same three items were .72, .73, and .72, respectively.

### Personality Structure

Principal-components analysis of the 52 reliable items indicated 10 components with eigenvalues exceeding 1.00. Examination of the scree plot suggested there were six components and parallel analysis indicated that only the first six eigenvalues (10.47, 7.21, 7.05, 4.11, 2.74, and 2.24) were greater than expected by chance at the 95% confidence level. We therefore extracted six components and subjected these components to a varimax rotation (see Table 1).

A promax rotation[2] revealed that the correlations among components were modest with the mean of the absolute correlations being .14 (see Table 2) and correlations between the six components' varimax- and promax-rotated loadings were all uniformly

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[1] Previous studies have found that principal-components analysis yields nearly identical structures as those derived from principal axis factor analysis (Velicer, 1977; Weiss et al., 2006, footnote 4). For the present study, use of principal axis factor analysis yielded a virtually identical personality structure as that derived via principal-components analysis.

[2] The table of loadings derived via promax rotation is available from Alexander Weiss upon request.

Table 1

*Comparison of Rhesus Macaque Personality Domains to Those of Humans, Chimpanzees, and Orangutans*

| | Rhesus macaque components[a] | | | | | | Classification in other species[c] | | |
|---|---|---|---|---|---|---|---|---|---|
| Item | Cnf | Opn | Dom | Frd | Act[b] | Anx[b] | Humans | Chimpanzees[h] | Orangutans[i] |
| Fearful | **−0.86** | −0.13 | −0.14 | 0.03 | −0.08 | 0.21 | N+[d] | D− | N+ |
| Submissive | **−0.81** | 0.10 | −0.28 | −0.03 | 0.06 | −0.06 | A+[d] | D− | D− |
| Timid | **−0.73** | −0.03 | −0.07 | −0.09 | −0.17 | 0.13 | E−[d] | D− | N+ |
| Cautious | **−0.73** | −0.22 | −0.36 | −0.21 | −0.01 | 0.06 | E−[d] | D− | N+ |
| Stable | **0.66** | 0.15 | −0.17 | 0.25 | −0.05 | **−0.43** | N−[d] | N− | N− |
| Distractible | **−0.56** | 0.01 | **0.45** | 0.05 | 0.20 | 0.16 | C−[e] | C− | — |
| Disorganized | **−0.55** | −0.14 | **0.41** | 0.02 | 0.04 | 0.05 | C−[d] | C− | I− |
| Dependent/follower | **−0.54** | 0.10 | −0.26 | 0.32 | −0.37 | 0.24 | N+[d] | D− | I− |
| Vulnerable | **−0.50** | **0.43** | −0.35 | −0.10 | −0.06 | 0.39 | N+[f] | D− | N+ |
| Inquisitive | 0.17 | **0.85** | −0.06 | 0.14 | 0.14 | 0.09 | O+[d] | O+ | E+ |
| Thoughtless | −0.04 | **0.81** | −0.02 | −0.03 | −0.22 | 0.12 | C−[g] | C− | — |
| Innovative | 0.15 | **0.66** | −0.09 | −0.05 | **0.50** | −0.06 | O+[e] | O+ | — |
| Inventive | 0.18 | **0.64** | −0.17 | −0.07 | **0.49** | −0.05 | O+[d] | O+ | E+ |
| Curious | 0.10 | **0.64** | 0.13 | **0.42** | 0.22 | 0.05 | O+[g] | O+ | E+ |
| Imitative | −0.15 | **0.58** | −0.31 | 0.02 | −0.20 | 0.37 | O−[d] | E+ | E+ |
| Impulsive | −0.14 | **0.55** | 0.35 | 0.04 | 0.09 | **0.43** | E+[d] | C− | N+ |
| Bullying | 0.18 | −0.06 | **0.87** | 0.03 | 0.09 | −0.01 | A−[d] | D+ | D+ |
| Stingy/greedy | 0.11 | −0.15 | **0.84** | 0.02 | −0.03 | −0.07 | A−[d] | D+ | D+ |
| Aggressive | 0.09 | 0.18 | **0.83** | 0.01 | 0.12 | 0.12 | A−[d] | C− | D+ |
| Irritable | 0.06 | −0.28 | **0.78** | −0.10 | −0.17 | 0.22 | A−[d] | C− | D+ |
| Manipulative | 0.01 | −0.17 | **0.75** | 0.14 | 0.10 | −0.23 | A−[d] | D+ | D+ |
| Defiant | −0.05 | 0.38 | **0.69** | 0.06 | 0.19 | −0.09 | A−[d] | C− | D+ |
| Excitable | −0.35 | 0.09 | **0.67** | 0.21 | 0.12 | 0.31 | N+[d] | N+ | N+ |
| Reckless | 0.20 | 0.33 | **0.61** | 0.00 | 0.22 | 0.37 | C−[d] | C− | D+ |
| Gentle | −0.28 | 0.08 | **−0.60** | **0.40** | −0.12 | **−0.44** | A+[d] | A+ | D− |
| Dominant | **0.55** | −0.23 | **0.57** | 0.20 | −0.11 | −0.14 | A−[d] | D+ | D+ |
| Independent | 0.37 | 0.05 | **0.51** | −0.19 | 0.34 | −0.22 | N−[d] | D+ | I+ |
| Individualistic | 0.19 | −0.10 | **0.41** | −0.09 | 0.32 | −0.07 | O+[e] | E− | — |
| Helpful | −0.08 | −0.08 | 0.17 | **0.81** | 0.05 | 0.04 | A+[d] | A+ | A+ |
| Friendly | 0.00 | 0.24 | −0.30 | **0.73** | 0.12 | −0.26 | A+[d] | E+ | A+ |
| Affectionate | −0.05 | 0.12 | −0.28 | **0.73** | 0.05 | −0.12 | A+[d] | E+ | A+ |
| Sociable | 0.30 | 0.35 | 0.02 | **0.70** | 0.13 | −0.04 | E+[d] | E+ | A+ |
| Sensitive | −0.34 | 0.13 | −0.01 | **0.67** | −0.14 | 0.14 | A+[d] | A+ | A+ |
| Depressed | **−0.48** | 0.11 | −0.13 | **−0.64** | −0.31 | −0.04 | E−[d] | E− | E− |
| Protective | 0.11 | −0.21 | 0.27 | **0.63** | 0.13 | −0.06 | A+[d] | A+ | A+ |
| Solitary | **−0.42** | −0.08 | 0.11 | **−0.58** | −0.14 | −0.26 | E−[d] | E− | E− |
| Sympathetic | −0.06 | **0.45** | **−0.42** | **0.55** | −0.01 | 0.08 | A+[d] | A+ | A+ |
| Intelligent | 0.22 | −0.17 | 0.30 | **0.50** | 0.06 | −0.06 | O+[d] | D+ | I+ |
| Persistent | **0.40** | 0.04 | 0.36 | **0.50** | −0.14 | 0.00 | C+[d] | D+ | D+ |
| Decisive | 0.39 | −0.15 | **0.41** | **0.44** | 0.03 | −0.20 | C+[d] | D+ | I+ |
| Conventional | −0.14 | −0.24 | −0.18 | 0.12 | **−0.75** | 0.03 | O−[g] | A+ | E− |
| Predictable | 0.11 | −0.10 | −0.25 | −0.06 | **−0.72** | −0.23 | C+[d] | C+ | N− |
| Lazy | 0.14 | 0.06 | 0.03 | −0.30 | **−0.71** | −0.17 | C−[d] | E− | E− |
| Active | 0.01 | 0.11 | 0.26 | 0.37 | **0.69** | −0.05 | E+[d] | E+ | E+ |
| Clumsy | −0.33 | 0.36 | 0.18 | −0.25 | **−0.52** | −0.20 | C−[e] | C− | I− |
| Playful | −0.08 | **0.42** | −0.01 | **0.42** | **0.48** | 0.11 | E+[d] | E+ | E+ |
| Cool | **0.40** | −0.13 | 0.12 | 0.10 | −0.23 | **−0.76** | N−[e] | N− | N− |
| Quitting | −0.05 | 0.13 | 0.02 | −0.02 | −0.03 | **0.66** | C−[g] | C− | — |
| Anxious | **−0.48** | 0.04 | −0.17 | −0.07 | −0.01 | **0.63** | N+[f] | D− | N+ |
| Erratic | 0.03 | **0.40** | 0.14 | −0.10 | 0.38 | **0.59** | C−[d] | C− | N+ |
| Unemotional | 0.22 | 0.16 | −0.10 | −0.18 | −0.21 | **−0.45** | N−[d] | N− | E− |
| Jealous | −0.08 | 0.30 | **0.41** | 0.12 | −0.27 | **0.44** | A−[d] | C− | D+ |

*Note*. Salient loadings (≥ |.40|) are in boldface.

[a] Cnf = Confidence; Opn = Openness; Dom = Dominance; Frd = Friendliness; Act = Activity; Anx = Anxiety. [b] Loadings were reflected. [c] N = Neuroticism; E = Extraversion; O = Openness; A = Agreeableness; C = Conscientiousness; D = Dominance; I = Intellect; + = positive loadings; − = negative loadings. [d] Classification from Goldberg (1990). [e] Classification from Weiss et al. (2006, 2009). [f] Classification from Costa and McCrae (1992). [g] Classification from McCrae and Costa (1985). [h] Classification from King and Figuredo (1997) and Weiss et al. (2009). [i] Classification from Weiss et al. (2006).

high (*r*s ≥ 0.97). Inspection of the loadings after promax rotation revealed some minor differences: three items (*vulnerable*, *imitative*, and *intelligent*) did not have salient loadings on any component and eight items (*stable*, *impulsive*, *gentle*, *dominant*, *solitary*, *playful*, *jealous*, and *persistent*) loaded on different components. Of the latter eight items, only one (*persistent*) loaded onto a component where it did not have a salient loading in the varimax structure. These changes in loadings did not appear to alter the

Table 2
*Component Intercorrelations Derived via Promax Rotation*

| Component | Confidence | Openness | Dominance | Friendliness | Activity |
|---|---|---|---|---|---|
| Confidence | | | | | |
| Openness | 0.06 | | | | |
| Dominance | 0.19 | 0.06 | | | |
| Friendliness | 0.06 | 0.21 | 0.04 | | |
| Activity | 0.32 | 0.01 | 0.30 | 0.00 | |
| Anxiety | −0.36 | 0.15 | 0.03 | 0.11 | −0.25 |

nature of the components. Given these results, we decided to interpret and base our scores on the varimax solution.

The first component was defined by negative loadings on items such as *fearful*, which described adverse reactions to the physical or social environment and is related to human Neuroticism (Goldberg, 1990). The first component was also comprised of negative loadings on items such as *disorganized*, which suggest low focus and poor self control and is thus related to low human Conscientiousness (Goldberg, 1990). High scoring individuals are thus seemingly more confident in the presence of potential threats and stressors as well as more directed and in control of their behavior. Low scoring individuals are thus more vigilant, highly reactive to these stressors, and exhibit poorer internal controls. The previously identified rhesus macaque Confidence domain (Stevenson-Hinde & Zunz, 1978) described variation along traits similar to or related to those which define this component. We therefore named this component Confidence. When the subjects were assigned unit-weighted scores as defined by the chimpanzee and orangutan structures (see Table 3), Confidence was positively correlated with chimpanzee and orangutan Dominance as well as orangutan Intellect and was negatively correlated with chimpanzee and orangutan Neuroticism.

The second component exhibited positive loadings on items related to exploratory and inquiring behavior, such as *curious* which is related to human Openness (McCrae & Costa, 1985). This component also loaded on items related to imprudence and poor behavioral controls, such as *thoughtless* and *impulsive*, which are markers of low human Conscientiousness (McCrae & Costa, 1985) and either high Neuroticism (Costa & McCrae, 1992) or low Conscientiousness (Goldberg, 1990), respectively. High scoring rhesus macaques would therefore be explorers of their physical and social surroundings, willing to engage in new behaviors, and curious. These same individuals were also perceived as being more forgetful and prone to act on impulse. Low scoring rhesus macaques would thus be less curious about their surroundings and conspecifics but less imprudent and impulse-ridden. Similar domains have not been previously described in rhesus macaques. However, human (Digman, 1990) and chimpanzee (King & Figueredo, 1997) Openness are comprised of sets of traits similar to or related to those making up this domain. Furthermore, the Openness domain in rhesus macaques closely resembled the one identified in chimpanzees (see Table 3). We therefore labeled this component Openness.

The third component was manifested by positive loadings on items indicating aggressive tendencies, such as *bullying* and items related to social potency and Machiavellianism (Maestripieri, 2007), such as *dominant* and *manipulative*, respectively. Such items are typically markers of low human Agreeableness (Goldberg, 1990). This component also positively loaded on items related to unpredictability in behavior or affect, such as *reckless* and *excitable*, which have been identified in human studies as indicators of low Conscientiousness and high Neuroticism, respectively (Goldberg, 1990). High scoring individuals would therefore be advantaged in social status competitions; low scoring individuals would be disadvantaged in social status competitions. Similar dimensions were not previously identified in studies of rhesus macaque personality. However, this component closely resembles the chimpanzee (King & Figueredo, 1997) and orangutan (Weiss et al., 2006) Dominance domains (see Table 3). We therefore named this component Dominance.

The fourth component was made up of positive and negative loadings on items related to social engagement, including *sociable* and *solitary*, respectively. Similar items are related to high or low human Extraversion (Goldberg, 1990). Other loadings were on items indicating cooperative behavior and positive social interactions, such as *helpful* and *friendly*, respectively, which are indicative of Agreeableness in humans (Goldberg, 1990). This domain also positively loaded on *persistent* and *intelligent*, which are indicative of purposefulness and perception as they are markers of human Conscientiousness and Openness, respectively (Goldberg, 1990). High scorers would thus be sociable and cooperative. Low scoring macaques would be more solitary, unresponsive to social interaction, and inattentive to the dispositions and intentions of conspecifics. In that this domain captured traits related to sociality, it resembled the Sociable–Solitary (Stevenson-Hinde & Zunz, 1978) and Sociability (Capitanio et al., 1999) domains previously identified in rhesus macaques. The domain score for this component was highly similar to the Extraversion and Agreeableness domains of chimpanzees and orangutans (see Table 3). We therefore labeled this component Friendliness.

After reflecting the fifth component by multiplying loadings by −1, it had negative and positive loadings on items related to low (*lazy*) and high (*active*) energy, respectively. Items such as these are often markers of low human Extraversion (Costa & McCrae, 1992; Goldberg, 1990). This component also negatively loaded on items related to behavioral and social conformity and consistency, such as *conventional* and thus included aspects of low human Openness (McCrae & Costa, 1985). Individuals high on this component would be vigorous, playful, and spontaneous whereas low-scoring macaques would tend to be inactive, placid, and predictable. Comparable dimensions were not previously identified in studies of rhesus macaque personality. This domain is most similar to orangutan Extraversion though it also describes a blend of the six chimpanzee personality domains (see Table 3). We therefore named this domain Activity.

Table 3

*Correlations Between Unit-Weighted Scores as Defined by the Rhesus Macaque, Chimpanzee, and Orangutan Structures*

| | Rhesus macaque | | | | | |
|---|---|---|---|---|---|---|
| Domains | Confidence | Openness | Dominance | Friendliness | Activity | Anxiety |
| Chimpanzee | | | | | | |
| Dominance | **0.85 (0.78, 0.89)** | −0.10 (−0.28, 0.09) | **0.84 (0.77, 0.89)** | **0.35 (0.18, 0.50)** | **0.48 (0.32, 0.61)** | **−0.40 (−0.54, −0.23)** |
| Extraversion | 0.26 (0.07, 0.42) | **0.53 (0.42, 0.67)** | −0.01 (−0.18, 0.19) | **0.88 (0.83, 0.91)** | **0.63 (0.51, 0.73)** | 0.12 (−0.07, 0.30) |
| Agreeableness | −0.03 (−0.22, 0.15) | 0.28 (0.11, 0.45) | −0.19 (−0.36, 0.00) | **0.80 (0.72, 0.86)** | 0.15 (−0.03, 0.33) | −0.01 (−0.19, 0.18) |
| Neuroticism | **−0.51 (−0.64, −0.36)** | 0.04 (−0.13, 0.24) | **0.29 (0.11, 0.45)** | 0.00 (−0.19, 0.19) | 0.17 (−0.02, 0.35) | **0.73 (0.63, 0.80)** |
| Openness | 0.24 (0.05, 0.41) | **0.84 (0.78, 0.89)** | −0.07 (−0.26, 0.11) | 0.30 (0.12, 0.46) | **0.54 (0.39, 0.66)** | 0.08 (−0.11, 0.26) |
| Conscientiousness | 0.11 (−0.08, 0.29) | **−0.37 (−0.52, −0.20)** | **−0.67 (−0.76, −0.55)** | −0.07 (−0.25, 0.12) | **−0.38 (−0.53, −0.21)** | **−0.59 (−0.70, −0.45)** |
| Orangutan | | | | | | |
| Dominance | **0.49 (0.34, 0.62)** | −0.07 (−0.26, 0.11) | **0.97 (0.95, 0.98)** | 0.19 (0.00, 0.36) | **0.37 (0.19, 0.52)** | 0.00 (−0.19, 0.18) |
| Extraversion | 0.26 (0.07, 0.42) | **0.57 (0.46, 0.71)** | 0.15 (−0.04, 0.33) | **0.58 (0.44, 0.69)** | **0.82 (0.75, 0.87)** | 0.25 (0.06, 0.42) |
| Agreeableness | 0.18 (0.00, 0.36) | 0.29 (0.11, 0.45) | 0.04 (−0.15, 0.22) | **0.92 (0.88, 0.94)** | 0.33 (0.16, 0.49) | −0.05 (−0.23, 0.14) |
| Neuroticism | **−0.83 (−0.88, −0.76)** | 0.27 (0.08, 0.43) | −0.09 (−0.27, 0.10) | −0.21 (−0.38, −0.02) | −0.01 (−0.19, 0.18) | **0.90 (0.86, 0.93)** |
| Intellect | **0.77 (0.68, 0.84)** | −0.12 (−0.30, 0.07) | **0.37 (0.20, 0.52)** | **0.34 (0.16, 0.49)** | **0.50 (0.34, 0.63)** | **−0.49 (−0.62, −0.34)** |

*Note.* $N = 111$. Correlations in boldface are significant at $p < .001$. 95% confidence intervals in parentheses.

After reflecting the sixth component, it loaded positively on items reflecting high degrees of anxiety or distress (*anxious*) and negatively on items reflecting low degrees of anxiety or distress (*cool*). The former item is similar to a facet of human Neuroticism (Costa & McCrae, 1992) and, based on its behavioral description, the latter is likely a marker of low Neuroticism. This component also loaded positively on items reflecting low consistency, such as *erratic*, which is a low Conscientiousness marker in humans (Goldberg, 1990). Unlike Confidence, items loading on this component reflect general as opposed to situationally determined levels of anxiety and distress. High scoring individuals would therefore be tense, anxious, and generally not calm, whereas low scoring individuals would be relaxed, calm, and predictable. It is therefore not surprising that domain scores based on this component were highly similar to those based on definitions of chimpanzee and orangutan Neuroticism, though it was also similar to low chimpanzee Conscientiousness (see Table 3). Previous studies identified a rhesus macaque personality dimension named Excitable, which is made up of some similar and related traits (Stevenson-Hinde & Zunz, 1978). However, because the item *excitable* was, in fact, related to Dominance, we felt that naming this component Anxiety better captured its meaning.

## Subjective Well-Being

Principal-components analysis indicated that only the first eigenvalue (2.50) was greater than 1.00. We therefore extracted a single component which described individual differences in subjective well-being. The loadings of this component on all three items exceeded 0.90.

## Reliabilities of Personality Domains and Subjective Well-Being

The interrater reliabilities, internal consistencies, and stabilities of the personality domains and subjective well-being are presented in Table 4. For personality domains at both time points, interrater reliabilities ranged from poor (Anxiety) to good (Friendliness, Dominance, and Confidence) and internal consistencies were excellent. Retest reliabilities for the personality domains ranged from good (Openness and Activity) to excellent (Friendliness, Dominance, and Confidence).

For subjective well-being at both time points, interrater reliabilities and internal consistencies were excellent. The retest reliability of subjective well-being was also excellent.

## Personality Predictors of Subjective Well-Being

Three of the personality domains were consistently related to subjective well-being in all four sets of analyses (see Table 5). Higher subjective well-being was related to higher Confidence, and Friendliness. Lower subjective well-being was related to higher Anxiety. One explanation for the high correlations among Friendliness and subjective well-being scores is content similarity. Namely, the presence of the item *depressed* in Friendliness, because of its similarity in meaning to the items making up subjective well-being, may inflate the correlations between scores. If this is the case, removing the item *depressed* from the scale should reduce the correlation. To test this, we recomputed Friendliness

Table 4
*Interrater Reliabilities, Internal Consistencies, and Stabilities of Personality Domains and Subjective Well-Being*

| | *ICC*(3, 1) | | *ICC*(3, *k*)[a] | | Alpha | | |
|---|---|---|---|---|---|---|---|
| | Wave 1 | Wave 2 | Wave 1 | Wave 2 | Wave 1 | Wave 2 | $r_{W1,W2}$[b] |
| Confidence | 0.35 | 0.40 | 0.54 | 0.60 | 0.90 | 0.87 | 0.75 |
| Openness | 0.32 | 0.20 | 0.50 | 0.36 | 0.86 | 0.76 | 0.63 |
| Dominance | 0.40 | 0.47 | 0.59 | 0.67 | 0.90 | 0.89 | 0.78 |
| Friendliness | 0.45 | 0.58 | 0.64 | 0.76 | 0.86 | 0.85 | 0.71 |
| Activity | 0.27 | 0.32 | 0.44 | 0.52 | 0.81 | 0.81 | 0.67 |
| Anxiety | 0.10 | 0.16 | 0.19 | 0.30 | 0.86 | 0.79 | 0.70 |
| Subjective well-being | 0.45 | 0.51 | 0.65 | 0.70 | 0.86 | 0.86 | 0.77 |

*Note*. $r_{W1,W2}$ = Correlation between Wave 1 and Wave 2 ($N$ = 70).
[a] Based on a mean of 2.31 raters per subject. [b] All $ps < .05$.

scores without *depressed* and reran the correlations with concurrent and prospective subjective well-being. The correlations did not change significantly (Hotelling-Williams tests, $p$'s = .76–.95).

## Discussion

The results of our study suggest that ratings on 52 adjectival traits in a large sample of free-ranging rhesus macaques could be reduced to six components named Confidence, Openness, Dominance, Friendliness, Activity, and Anxiety. An oblique (promax) rotation indicated that the components were modestly correlated. However, the range of absolute correlations and their mean were in line with those of chimpanzee ($M$ = .135; see Table 2 and p. 264 of King & Figueredo, 1997) and orangutan ($M$ = .18; Weiss et al., 2006; p. 507) personality dimensions. Moreover, they were lower than the unweighted mean of absolute correlations from 14 studies of human personality ($M$ = .29; computed from Appendix A in Digman, 1997). Finally, the components and loadings of a promax solution were highly similar to those of a varimax solution.

The interrater reliabilities of the six components were acceptable, but somewhat lower than those in prior studies (Capitanio et al., 1999; King & Figueredo, 1997; Weiss et al., 2006). This might be explained by the fact that each rater had to rate far more subjects ($M$ = 25.2) and knew subjects for a shorter period of time than raters in previous studies. On the other hand, the retest reliabilities were excellent.

Confidence, Dominance, Anxiety, and Friendliness were similar to dimensions identified in previous studies of rhesus macaque personality that used different questionnaires (Bolig et al., 1992; Capitanio et al., 1999; Stevenson-Hinde et al., 1980; Stevenson-Hinde & Zunz, 1978). Specifically, Friendliness matched the Sociable dimension, though it was broader, incorporating traits related to chimpanzee (King & Figueredo, 1997) and orangutan (Weiss et al., 2006) Agreeableness, such as *protective*. Traits indicative of aggression, vulnerability, and competitive prowess, which were subsumed under Confidence dimensions in previous studies of rhesus macaques, defined Confidence, Dominance, and Anxiety in this study. Furthermore, we did not find components similar to the Equable and Excitable dimensions identified in previous studies (Bolig et al., 1992; Capitanio et al., 1999; Stevenson-Hinde et al., 1980; Stevenson-Hinde & Zunz, 1978) as the traits making up these dimensions were markers of Dominance in the present study. We also found two previously unidentified dimensions. The first, Activity, consisted of items usually found in Extraversion domains in humans (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et al., 2006). The second, Openness, was similar to the Openness domain described in humans (Costa & McCrae, 1992) and chimpanzees (King & Figueredo, 1997).

The dimensions identified in this study also differed in five ways from those identified in studies of humans (Digman, 1990),

Table 5
*Correlations Between Personality and Subjective Well-Being*

| | Wave 1 personality | | Wave 2 personality | |
|---|---|---|---|---|
| | $SWB_{W1}$ | $SWB_{W2}$ | $SWB_{W1}$ | $SWB_{W2}$ |
| Confidence | 0.59 (0.45, 0.70)$^{***}$ | 0.48 (0.28, 0.64)$^{***}$ | 0.58 (0.40, 0.71)$^{***}$ | 0.51 (0.31, 0.66)$^{***}$ |
| Openness | 0.11 (−0.07, 0.30) | 0.17 (−0.07, 0.39) | 0.23 (−0.01, 0.44) | 0.22 (−0.01, 0.43) |
| Dominance | 0.20 (0.00, 0.37)$^{*}$ | 0.19 (−0.05, 0.41) | 0.25 (0.01, 0.46)$^{*}$ | 0.08 (−0.15, 0.31) |
| Friendliness | 0.60 (0.46, 0.71)$^{***}$ | 0.48 (0.28, 0.64)$^{***}$ | 0.57 (0.39, 0.71)$^{***}$ | 0.63 (0.47, 0.76)$^{***}$ |
| Activity | 0.25 (0.06, 0.42)$^{**}$ | 0.12 (−0.11, 0.34) | 0.10 (−0.14, 0.33) | 0.14 (−0.10, 0.36)$^{*}$ |
| Anxiety | −0.46 (−0.60, −0.30)$^{***}$ | −0.38 (−0.56, −0.15)$^{**}$ | −0.38 (−0.56, −0.16)$^{***}$ | −0.46 (−0.63, −0.26)$^{***}$ |
| $N$ | 111 | 70 | 70 | 71 |

*Note*. 95% confidence intervals in parentheses. $SWB_{W1}$ = Wave 1 subjective well-being; $SWB_{W2}$ = Wave 2 subjective well-being.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et al., 2006). First, traits related to Neuroticism in these other species defined two dimensions in rhesus macaques: Confidence which was related to reactions to external stimuli and events, including social events; and Anxiety which could be described as general levels of distress and unease. These two dimensions can also be distinguished, as although both were similar to chimpanzee and orangutan Neuroticism, Confidence was composed of items that in chimpanzees and orangutans make up Dominance. Second, traits related to Extraversion in these species defined a dimension related to sociability (Friendliness) and a dimension related to activity levels (Activity). These dimensions were thus similar to the Gregariousness and Activity facets of human Extraversion (Costa & McCrae, 1992). Third, we did not find a Conscientiousness dimension similar to that of humans or chimpanzees. Items composing chimpanzee Conscientiousness instead were part of the rhesus macaque Dominance and Anxiety dimensions. Fourth, unlike orangutans, but like chimpanzees and humans, we found a clear Openness dimension. Fifth, unlike humans, but like the great ape species we have data on, we found a Dominance dimension.

The similarities and differences between personality in rhesus macaques and those identified in hominoids are informative about personality phylogeny (see Figure 1). Why would it be useful to describe the origin and evolution personality dimensions in the same way that morphological or fixed behavioral traits are characterized, that is, as being ancestral or derived? After all, personality dimensions describe differences between individuals and are not species-typical characteristics like thumbs or wings. Furthermore, if a personality trait is constructed out of the covariance of numerous items or behaviors, how does it evolve? Both of these issues arise out of a limitation in evolutionary theorizing rather than being problems unique to the evolution of personality structures. First, every biological trait, whether specific to a species or differing among individuals, is the result of a host of underlying

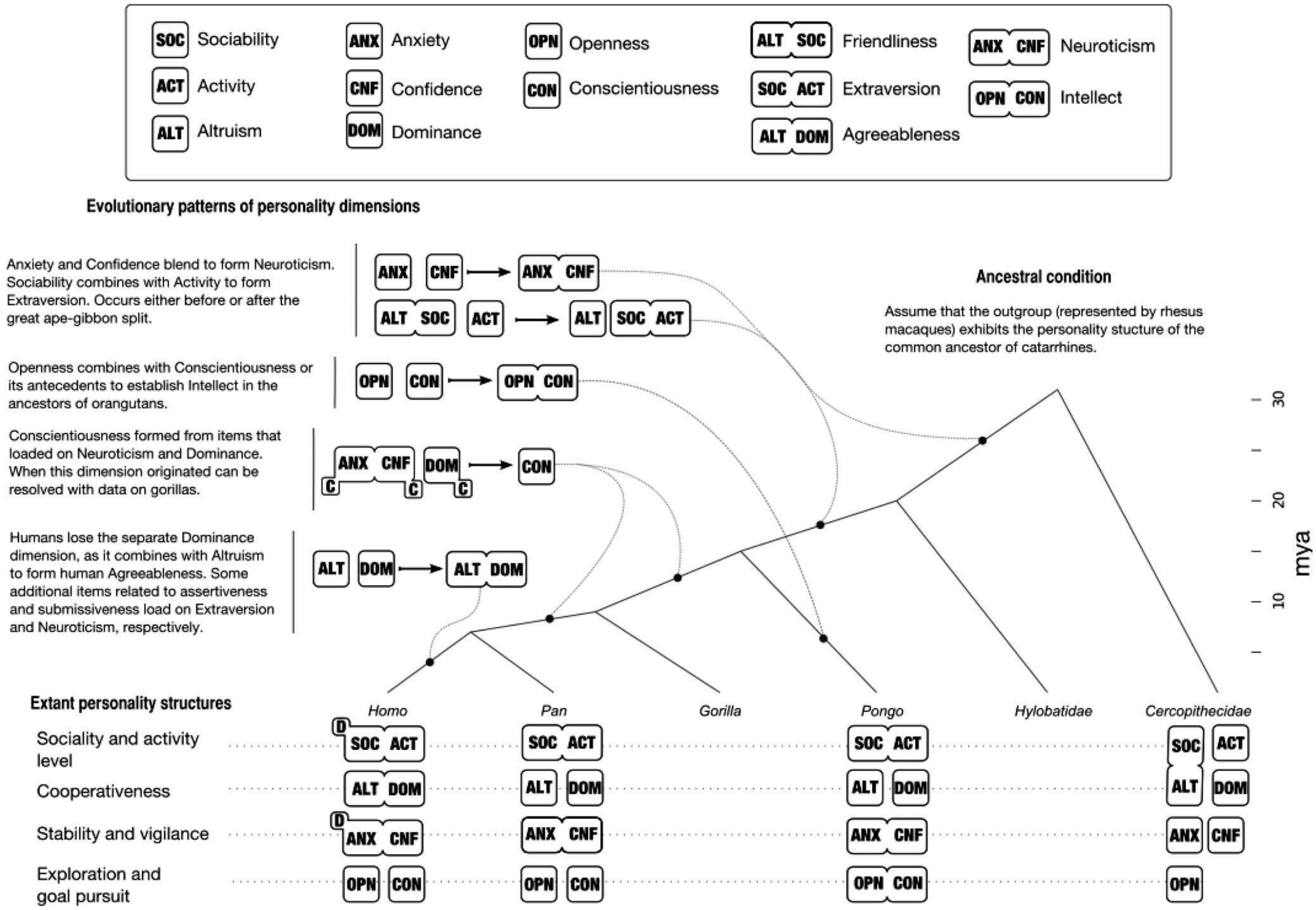

*Figure 1.* Cladogram of the hypothesized patterns of personality evolution in the parvorder Catarrhini. Personality structures are described as a combination of "basic" or "blended" dimensions, for example, Friendliness in rhesus macaques is a blend of Altruism and Sociability. The evolutionary transitions are interpreted as the integration or disintegration of these dimensions, shown by horizontal arrows between groups of dimensions. The possible transition points, indicated by the dashed lines, are placed according to phylogenetic parsimony. This picture is likely to change as more species are assessed. The structure of the genus Pan is represented by chimpanzees and the family Cercopithecidae by rhesus macaques. Figure by the authors, licensed under a Creative Commons Attribution Unported License and published under the terms of this license.

genetic and environmental factors (Rice, 2004). Selection can act directly on the joint distribution of the factors contributing to each trait as well as to those among traits, allowing traits to become developmentally integrated or disassociated from one another. Genetic covariances between traits are both the result of natural selection and a constraint on evolution. Second, selection does not operate only on trait means, but can also influence higher moments of a trait's distribution, such as variance (Rice, 2004). Thus, personality differences can evolve within a species. Finally, our phylogeny, while parsimonious and consistent with the data, describes only one possible set of evolutionary patterns. Casting personality dimensions as explicitly ancestral or derived might hopefully motivate further work in this area, and lead to the exploration of personality and subjective well-being in additional, distantly related taxa, permitting formal, comparative analyses.

Given the known primate personality structures, Openness appears to be an ancestral characteristic present in the ancestor of Hominoidea and Cercopithecoidea. Finding Openness in rhesus macaques is not surprising given their relatively large neocortex, which probably evolved in response to their large group sizes and complex social system (Dunbar, 1998). The presence of Openness may have enabled rhesus macaques to survive in a wide range of habitats including different ecological conditions (Seth & Seth, 1986). Future studies of less widely distributed macaque species could be used to test whether the presence of Openness is one explanation for the successful distribution of rhesus macaques as a species. In contrast, Openness traits in orangutans are more closely related to traits defining Conscientiousness with which they form the Intellect domain and to traits defining Extraversion. This pattern of loadings is likely derived, having evolved in response to their semisolitary social structures (Galdikas, 1985) as encountering unrelated conspecifics would be highly novel experiences. Future studies should test this hypothesis by comparing the personalities of related solitary and social species. These findings also support earlier suggestions that Conscientiousness is a derived domain (Gosling & John, 1999), possibly exclusive to African apes or at least Pan and Homo (Weiss et al., 2006). To address this requires studying gorilla and bonobo personality with a similar questionnaire, which remains to be done.

These findings also suggest that the unidimensional Neuroticism and Extraversion domains found in humans, chimpanzees, and orangutans are derived from multidimensional ancestral variants: Confidence and Anxiety in the case of Neuroticism; Friendliness and Activity in the case of Extraversion. The presence of lower-order facets in the human Five-Factor Model (Costa & McCrae, 1992) is consistent with this possibility. However, research on other macaque species is needed to determine whether the configuration of traits responsible for this multidimensionality are a derived characteristic of rhesus or ancestral and shared with other macaque species.

These results also affirm perhaps the key characteristic of human personality that sets it apart from that of nonhuman primates, that is, the absence of a specific Dominance domain in five-factor personality space (Gosling & John, 1999). This does not mean humans do not have dominance relationships. In fact, some aspects of human personality such as the assertiveness facet of Extraversion (Costa & McCrae, 1992), social potency (Patrick, Curtin, & Tellegen, 2002), and the Dominance factor of Cattell's 16 PF (Conn & Rieke, 1994) clearly indicate that individual differences in human dominance can be assessed. Moreover, a personality style (Leaders) defined by a combination of high Extraversion and low Agreeableness (Costa & McCrae, 1998) describes a similar construct. One possible reason for this difference between humans on the one hand and nonhuman primates on the other was hinted at by Hinde (1978) who argued that human dominance may be context-specific, that is, humans dominant in one domain of life or society are not necessarily dominant in another. However, this explanation is unlikely as the dominance rank a rhesus macaque occupies also varies across contexts (Bernstein & Gordon, 1980). A second possibility is that the absence of a dominance-related domain is a consequence of selection for increasing egalitarianism in human evolution (Boehm, 1999). One way to test this last possibility is by comparing macaque species that, while occupying similar ecological niches, vary to the extent to which they are egalitarian as opposed to despotic (Matsumura, 1999; Sterck, Watts, & van Schaik, 1997; Thierry, 1985, 2000). A third possibility is that humans might be unique in achieving dominance by different means, such as intelligence or accrued resources, which could tap into different personality facets across different domains, rather than a singular one. A fourth possibility is that human societies may offer multiple dominance hierarchies in which individuals can participate (Gosling & John, 1999).

Ratings related to the balance of moods, pleasure derived from social interactions, and global well-being were highly intercorrelated and described a domain similar to human (Diener, Suh, Lucas, & Smith, 1999), chimpanzee (King & Landau, 2003), and orangutan (Weiss et al., 2006) subjective well-being. At Waves 1 and 2 this domain displayed high interrater reliabilities; the stability of this domain was also high. Higher Confidence and Friendliness and lower Anxiety were consistently related to greater subjective well-being. Thus, like humans (Steel et al., 2008), chimpanzees (King & Landau, 2003; Weiss et al., 2009), and orangutans (Weiss et al., 2006), rhesus macaques that are more social, sympathetic, and equable and less anxious, timid, and erratic exhibit more positive affect. It therefore appears that the nexus of positive affect, low Neuroticism, and high Extraversion are phylogenetically ancestral, and may have been present in the common ancestor of Old World monkeys, great apes, and humans some 31 mya (Steiper & Young, 2006).

We also found differences in how positive affect is related to personality in rhesus macaques. Unlike chimpanzees (King & Landau, 2003; Weiss et al., 2009) though like orangutans (Weiss et al., 2006), Dominance and Openness were not consistently related to rhesus macaque subjective well-being. These results suggest that, ancestrally, there was no relationship between personality dimensions similar to Dominance or Openness and positive affect and that the interrelationship between chimpanzee Dominance, Openness, and subjective well-being may be evolutionarily more recent.

In addition to possibly being a product of environmental consistency across time, the high correlations between Wave 1 personality domains and Wave 2 subjective well-being may reflect, as they do in humans (Lykken, Bouchard, McGue, & Tellegen, 1990; Lykken & Tellegen, 1996; Nes, Røysamb, Tambs, Harris, & Reichborn-Kjennerud, 2006), common genetic influences at both time points. Similarly, as is the case for humans (Weiss, Bates, & Luciano, 2008) and chimpanzees (Weiss, King, & Enns, 2002), the relationships between personality and subjective well-being may also be genetically mediated in rhesus macaques.

One potential limitation of the present study is that, like other studies of nonhuman primate personality (e.g., King & Figueredo, 1997), the ratio of sample size to items (2.13) is considerably smaller than that typically recommended for principal-components analysis (5.00 or 10.00). However, in a series of simulation studies Guadagnoli and Velicer (1988) demonstrated that there was little support for the sample size to ratio rules. Instead they found that the stability of structures was mostly a function of the size of component or factor loadings with absolute sample sizes of 150 yielding stable structures in most cases. While the sample size in the present study fell slightly below 150, items were based on multiple ratings, thus making them more reliable. However, as in studies of chimpanzee personality (King, Weiss, & Farmer, 2005; Weiss, King, & Hopkins, 2007; Weiss et al., 2009), there should be attempts to replicate this structure in other samples.

Our findings also speak to the validity of using questionnaires to assess animal personality and subjective well-being. Critics may argue that questionnaire-based measures are compromised by anthropomorphic projection, but we found domains similar to those found in studies of rhesus macaques using different questionnaires which also differed from those identified in other species rated on the same questionnaire. Critics might further claim that differences reflect situational artifacts, such as the background of the raters or the environment in which the rhesus macaques were observed. However, previous research has shown that the same species-typical domains emerge even in differing environments or when ratings are made by raters with different cultural backgrounds (King et al., 2005; Weiss et al., 2009; Weiss et al., 2007). Thus, these findings build upon a rich set of findings indicating that personality ratings probably do not reflect anthropomorphic projections or other artifacts (Capitanio, 1999; Konečná et al., 2008; Uher & Asendorpf, 2008; Uher et al., 2008; Weinstein & Capitanio, 2008).

In light of findings in humans (Digman, 1990), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et al., 2006), our results indicate that intense sociality may have been a potent selective pressure driving personality trait evolution and coevolution. On the other hand, these same forces appear not to have impacted the evolution of positive affect or its coevolution with personality.

Assessing multiple related species using similar instruments is an effective tool with which to better understand the phylogeny of personality as well as the relationship of personality domains to affect. In the future, these measures, together with similarly standardized measures of behavior, ecology, and social structure, could help develop a fuller understanding of personality in nonhuman primates such as macaques, and even ourselves.

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Received October 30, 2009
Revision received June 22, 2010
Accepted July 14, 2010 ■

*Published as*

**Weiss, A., Adams, M. J., & Johnson, W. (2011). The Big None: No Evidence for a General Factor of Personality in Chimpanzees, Orangutans, or Rhesus Macaques. Journal of Research in Personality, 45, 393–397. doi:10.1016/j.jrp.2011.04.006**

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# The Big None: No Evidence for a General Factor of Personality in Chimpanzees, Orangutans, or Rhesus Macaques

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**Acknowledgements:** This project could not have been achieved without the cooperation of the raters, zoological parks, or the Caribbean Primate Research Center. We thank James E. King for allowing us to use the chimpanzee personality data and Aurelio J. Figueredo and Tom Booth for useful discussions on the topic. We would also like to thank Melissa S. Gerald and Anja Widdig for their assistance in coordinating the rhesus macaque data collection.

**Note:** This study complies with the current laws of Puerto Rico and the United States. The IACUC of the University of Puerto Rico, Medical Sciences Campus approved the investigation

of rhesus macaque personality. The rhesus macaque population of Cayo Santiago is supported by the University of Puerto Rico, Medical Sciences Campus and by the National Center for Research Resources (NCRR), a component of the National Institutes of Health (NIH) (NCRR grant P40RR003640 award to the CPRC). The content of this publication is solely the responsibility of all of the authors and does not necessarily represent the official views of NCRR, NIH, or the United States Government.

Word Count: 2595

## Abstract

Higher-order factor analyses of human personality dimensions have revealed what appears to be a general factor of personality (GFP). We examined whether a GFP was present in chimpanzees, orangutans, or rhesus macaques. We used confirmatory factor analysis (CFA) to model correlations among first-order factors as arising from a GFP. We then conducted two principal-axis factor analyses (PFA). In the first we extracted a single higher-order factor from each of the first-order factor scores. In the second we extracted two oblique factors from the first-order factor scores. Model fit was poor for the CFA in chimpanzees and orangutans, but not rhesus macaques. The single higher-order factor extracted via PFA did not resemble the GFP in any of the samples. Moreover, the two oblique higher-order factors extracted via PFA were only weakly correlated in all three samples. These results do not support the existence of a GFP in nonhuman primates.

# The Big None: No Evidence for a General Factor of Personality in Chimpanzees, Orangutans, or Rhesus Macaques

There has recently been a renewal of interest in higher-order factors of personality. Musek (2007) and others (e.g., Rushton & Irwing, 2008) seemingly uncovered a single higher-order personality factor (the general factor of personality or GFP) underlying first- or second-order structures of a variety of personality measures. Figueredo and Rushton (2009) found that the GFP was genetically correlated with questionnaire-based measures of life-history strategies and that some of the shared genetic effects were nonadditive. These results led Figueredo and Rushton (2009) to conclude that the GFP evolved in response to needs for a coordinated suite of behavioral and life-history traits related to greater pro-sociality, reduced mating effort, and increased offspring investment.

This evolutionary explanation of the GFP can be challenged given that balancing selection and mutation load are more likely than directional selection to be forces in personality evolution (Penke, Denissen, & Miller, 2007). Critics have also questioned the psychometric validity of the GFP and suggested that it is an artifact arising from, for example, common method variance (Riemann & Kandler, 2010), self-presentation bias (Bäckström, Björklund, & Larsson, 2009), or blends of orthogonal factors (Ashton, Lee, Goldberg, & de Vries, 2009). A way to concurrently address both evolutionary and methodological issues stemming from the GFP is to test for higher-order factors in closely allied nonhuman species that resemble humans in personality structure and life-history patterns.

For the present study we conducted a series of analyses to examine whether the GFP was present in chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). Its presence in these species would provide evidence that it was present in the ancestor species we share with them. We therefore tested whether correlations among the previously described first-order personality dimensions in these species (King & Figueredo, 1997; Weiss, Adams, Widdig, & Gerald, 2011; Weiss, King, & Perkins, 2006) could be explained by a GFP.

We shared a common ancestor with chimpanzees approximately 6 million years ago (Steiper & Young, 2006). Like humans, chimpanzees live in complex social groups, have a slow life-history strategy and exhibit many human-like behaviors, characteristics, and abilities. Among others, these include theory of mind, moral behaviors, empathy, cooperative hunting, culture, and warfare (Goodall, 1990). In addition, five of the six chimpanzee personality factors that were reported in these data are comparable to the five human factors in several respects and the sixth factor, Dominance, was a broad factor and likely related to competitive prowess or rank (King & Figueredo, 1997).

On the other hand, of the great apes, we are most distantly related to orangutans, with whom we shared a common ancestor some 18 million years ago (Steiper & Young, 2006). Orangutan social structure differs considerably from that of humans and most nonhuman primate species in that orangutans are semi-solitary (Mackinnon, 1974). As such, it is not surprising that the structure that was reported in this species differed more from that in humans than did that reported for chimpanzees. While human-like Extraversion, Agreeableness, and Neuroticism dimensions were reported for orangutans, factors corresponding to human or chimpanzee Conscientiousness and Openness were not observed (Weiss, et al., 2006). Instead, Intellect, a dimension which loaded on markers of Conscientiousness and Openness was reported (Weiss, et al., 2006). Finally, like chimpanzees, there was a Dominance dimension (Weiss, et al., 2006).

Rhesus macaques are Old World monkeys and split from the hominoids, i.e., the great apes and humans, 27 to 36 million years ago (Steiper & Young, 2006). While rhesus macaques are a social species, their social structure differs from that of humans, chimpanzees, and orangutans in that their troops are comprised of descendents of a founding female (Melnick & Pearl, 1987). The personality structure reported for rhesus macaques differed even more from that of humans than did those reported for orangutans and chimpanzees. The only personality factor rhesus macaques clearly shared with humans was Openness; traits related to Neuroticism and traits related to Extraversion loaded on two different factors each, and Agreeableness markers were related to a factor similar to Extraversion (Weiss, et al., 2011). Finally, like the chimpanzees and orangutans, they also exhibited a personality dimension that could best be described as Dominance (Weiss, et al., 2011).

Given the phylogenetic relationships among these species and humans, comparing higher-order factor structures across species is instructive with respect to understanding the GFP's place in personality evolution. If selection for slower life-histories and more sociality led to the evolution of the GFP in the primate lineage, we would expect that chimpanzees would be most likely among the three nonhuman primates to exhibit it. Moreover, given the differences among chimpanzee, orangutan, and rhesus macaque social structures, testing for a GFP in these species can provide insight into whether the GFP evolved as a response to selection for individuals that were better equipped for the demands of more complex social environments. In this case, we might expect a GFP in rhesus macaques as well.

To test for the presence of a GFP we conducted a series of confirmatory and exploratory factor analyses. We first used confirmatory factor analysis (CFA) to fit a model that posited a single higher-order factor. If the GFP is present in any of the samples we would predict that model fit would be acceptable and that all of the first-order factors would have significant loadings. We then used exploratory factor analysis and extracted a single higher order factor. If the GFP is present in any of the samples, we would predict that all of the first-order factors would have salient loadings on this higher-order factor. Finally, we tested whether the GFP emerged from higher-order factors by using exploratory factor analysis to extract two oblique higher-order factors. If there is a GFP in any of these samples, we would expect that the correlation among the two higher-order factors would be substantial.

Finally, studying the GFP in nonhuman primates offers an additional advantage. Because the personality dimensions were based on rater-reports, self-enhancement effects are unlikely to contribute to any covariation of the first-order factors. Also, the personality ratings of these individuals were aggregated across multiple raters, which would cancel out specific rater effects (Rushton, Brainerd, & Pressley, 1983). Thus, a GFP in any of these species would not likely stem from methodological artifacts.

## Methods

### Samples and Ratings

The analyses in the present study are re-analyses of three existing datasets. Previous studies using these data have focused on the structure of personality in nonhuman primates (King & Figueredo, 1997; Weiss, et al., 2011; Weiss, et al., 2006), though other studies have also used these data.

**Chimpanzees.** This sample was comprised of 100 chimpanzees (*Pan troglodytes*) housed in 12 zoological parks. The chimpanzees ranged in age from 2.4 to 55.2 with a mean age of 18.8 (*SD* = 11.9). The mean age for the 41 males was 18.5 (*SD* = 12.5) and the mean age for the 59 females was 19.0 (*SD* = 11.6). Thus, this sample included individuals ranging from infants to old adults.

Questionnaire items were 43 adjectives sampled from Goldberg's taxonomy of the Big Five (see King & Figueredo, 1997 for details). Each item was paired with one to three sentences that placed the adjective in the context of nonhuman primate behavior. For example, the item *fearful* was "**FEARFUL:** Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress." Questionnaires were completed by 53 raters who were zoo employees or volunteers and highly familiar with the individuals. Each chimpanzee was rated by a mean of 4.05 raters (King & Figueredo, 1997).

In the original study of chimpanzee personality using these data, principal axis factor analysis was used to extract six orthogonal factors --- Dominance, Surgency, Dependability, Agreeableness, Emotionality, and Openness[1] --- from the 42 items with the highest interrater reliabilities (King & Figueredo, 1997). All six factors were reliable across raters (King & Figueredo, 1997; Table 3) and subsequent studies have shown that they generalize to other chimpanzee samples (e.g., Weiss et al., 2009). In addition to subjecting the factors to a varimax rotation, King and Figueredo used a promax rotation to obtain inter-factor correlations, which ranged from |.00| to |.45| with a mean of .13 (King & Figueredo, 1997; Table 2).

**Orangutans.** This sample was comprised of 152 orangutans (*Pongo spp*.) housed in 41 zoological parks. The orangutans ranged in age from 1.5 to 51.6 years with a mean age of 21.4 (*SD* = 11.5). The mean age for the 58 males was 19.1 (*SD* = 10.7) and the mean age for the 94 females was 22.9 (*SD* = 11.8). Thus, this sample included individuals ranging from infants to old adults.

The questionnaire items included the same 43 used to rate chimpanzees and 5 additional items (see Weiss, et al., 2006 for details). Questionnaires were completed by 105 raters who were zoo employees. Each orangutan was rated by a mean of 2.64 raters. In this study, principal-components analysis was used to extract 5 orthogonal components from all 48 items. The components were labeled Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect (see Weiss, et al., 2006 for more details). Like the chimpanzee factors, these dimensions were reliable across raters (Weiss, et al., 2006, p. 507). As with the study of chimpanzees, Weiss and his colleagues used promax rotation to obtain inter-factor correlations, which ranged from .03 to .36. The mean of the absolute inter-factor correlations was .18 (Weiss, et al., 2006).

**Rhesus macaques.** This sample was comprised of 111 of the free-ranging rhesus macaques (*Macaca mulatta*) living on Cayo Santiago. They ranged in age from 1.6 to 24.4 years with a mean age of 7.3 (*SD* = 6.3). The mean age for the 45 males was 6.9 (*SD* = 6.8) and the mean age for the 66 females was 7.6 (*SD* = 6.0). Thus, this sample included individuals ranging from infants to old adults, as their lifespan is approximately 25 years.

The rhesus macaques were rated on the 48 questionnaire items used to rate orangutans and 6 additional items (Weiss, et al., 2011). Questionnaires were completed by 14 raters who had been conducting research unrelated to this project and were thus highly familiar with the subjects. Each macaque was rated by a mean of 2.31 raters (see Weiss, et al., 2011 for details).

Weiss et al. (2011) used principal components analysis to extract six orthogonal components from the 52 reliable items. The components were Confidence, Openness, Dominance, Friendliness, Activity, and Anxiety (Weiss, et al., 2011; Table 1). The reliabilities of these components ranged from poor to good (Weiss, et al., 2011; Table 4). In addition to the varimax rotation, Weiss and his colleagues used promax rotation to determine the inter-factor correlations. These correlations ranged from |.00| to |.36| with a mean of .14 (Weiss, et al., 2011; Table 2).

## Data Preparation and Analysis[2]

Different extraction methods were used in the previous studies, though when the results of different factor extraction techniques were compared within the same sample or species, they were found to yield similar structures (Weiss, et al., 2011; Weiss, et al., 2009; Weiss, et al., 2006). For the present study we used the differentially-weighted factor scores derived from each sample. To derive these factor scores, for each sample we conducted a principal-axis factor analysis (PFA) with promax rotations (SAS Institute, 1999) on the mean ratings of the items. Communalities were estimated using squared multiple correlations. For the chimpanzee sample only, as in King and Figueredo's (1997) study, we weighted the covariance matrix by number of raters.

We conducted three analyses on each sample's factor scores. In the first analysis we used M*plus* 6.1 (L. K. Muthén & Muthén, 1998-2010) to conduct a confirmatory factor analysis (CFA) using a Bayesian estimator. Because the default convergence criterion yielded parameter estimates that showed high autocorrelations, for these analyses we ran 200,000 iterations and discarded the first half. For each CFA we modeled all first-order factors as being manifestations of a higher-order GFP.

We switched to Bayesian analysis after encountering estimation problems using maximum likelihood. Bayesian analysis combines prior information about model parameters with the likelihood of the data to yield a posterior distribution for each parameter estimate (Gelman, Carlin, Stern, & Rubin, 2004; B. O. Muthén & Asparouhov, 2010). Bayesian estimators offer several advantages over maximum likelihood techniques such as better handling of small sample sizes and flexibility in assessing model fit (B. O. Muthén & Asparouhov, 2010). We assessed model fit using posterior-predictive *p*-values (*PPP*s) which yield the proportion of times that the fit of the estimated model against the data is worse than against data simulated from the model. Values close to .5 indicate good fit while low values indicate poor fit.

In the next two analyses, we used PFA to extract higher-order factors; communalities were estimated via squared multiple correlations (SAS Institute, 1999). Salient loadings were defined as those greater than or equal to |.40|. In the second analysis we extracted a single higher-order factor from the lower-order factors. In the third analysis, we extracted two higher-order factors from the lower-order factors. We used exploratory factor analyses to extract two higher-order factors because we did not have a priori expectations regarding higher-order structures other than the GFP. After extracting these factors, we used a promax rotation to estimate the correlation between the higher-order dimensions.

## Results

### Confirmatory Factor Analyses

**Chimpanzees.** The GFP model for chimpanzees indicated poor fit (*PPP* = .000). The GFP had significant positive loadings on Agreeableness and a significant negative loading on Neuroticism (see top panel of Table 1).

**Orangutans.** The GFP model for orangutans also indicated poor fit (*PPP* = .000). The GFP had significant positive loadings on Extraversion and significant negative loadings on Dominance and Neuroticism (see middle panel of Table 1).

**Rhesus macaques.** The GFP model for rhesus macaques had adequate fit (*PPP* = .203). The GFP had significant positive loadings on Dominance and Activity and significant negative loadings on Anxiety (see bottom panel of Table 1).

## Exploratory Factor Analyses

**Chimpanzees.** None of the eigenvalues of the reduced correlation matrix reached 1, indicating that any higher-order factor accounted for less than a single first-order factor. The results of the first higher-order PFA analysis are presented in the left panel of the top half of Table 2. The higher-order factor only had salient and positive loadings on Conscientiousness and Agreeableness. The results of the second higher-order PFA are in the left panel of the bottom half of Table 2. The first factor had salient positive loadings on Conscientiousness and Agreeableness. The second factor had salient loadings on Extraversion and Openness. The correlation between these higher-order factors was low and thus suggested there were no further higher-order factors.

**Orangutans.** None of the eigenvalues of the reduced correlation matrix reached 1, indicating that any higher-order factor accounted for less than a single first-order factor. The results of the first higher-order PFA are presented in the middle panel of the top half of Table 2. The higher-order factor had a salient, positive loading on Agreeableness and salient, negative loadings on Dominance and Intellect. The results of the higher-order PFA are shown in the middle panel of the bottom half of Table 2. The first factor had a salient negative loading on Dominance and a salient positive loading on Agreeableness. The second factor had a salient positive loading on Neuroticism and a salient negative loading on Intellect. The correlation between these higher-order factors was low and thus suggested there were no further higher-order factors.

**Rhesus macaques.** None of the eigenvalues of the reduced correlation matrix reached 1, indicating that any higher-order factor accounted for less than a single lower-order factor. The results of the first higher-order PFA are presented in the right panel of the top half of Table 2.

The higher-order factor only had salient and positive loadings on Confidence and Activity. The results of the higher-order PFA are shown in the right panel of the bottom half of Table 2. The first factor had salient positive loadings on Confidence, and Activity. The second factor had no salient loadings. The correlation between these higher-order factors was low and thus suggested there were no further higher-order factors.

## Discussion

The results from the CFAs and PFAs did not support the presence of a GFP in chimpanzees, orangutans, or rhesus macaques. For the CFAs, only the GFP model for rhesus macaques had adequate fit. However, of the 14 freely estimated loadings, only 8 were statistically significant. Extracting a single higher-order GFP via PFA yielded similar results, namely, of the 17 possible loadings, only 7 were salient. Finally, when we extracted two higher-order factors via PFA, the correlations between the two higher-order factors we extracted for all three species were small.

These findings were contrary to the prediction that, given their phylogenetic proximity to humans, their slow life-histories, and the fact that, early in their evolutionary history, they may have faced many of the same problems as early humans, we would find the GFP in chimpanzees and not the other species. One way to reconcile these findings with the findings of GFP in human studies is to argue that the GFP is a recent product of evolution, emerging after the chimpanzee-human split (Figueredo & Rushton, 2009). A second way to reconcile these two sets of findings is to argue that the GFP in humans is an artifact. As noted earlier, given that we studied independent ratings of individual subjects, there were likely no presentation bias effects. Moreover, by aggregating across multiple raters, we reduced artifacts related to either presentation bias or shared method variance. Human studies which control for these effects also have not yielded GFPs (Bäckström, et al., 2009; Riemann & Kandler, 2010). Thus, the latter explanation accounts for the present findings and those of human studies which do and do not find a GFP. Moreover, it is a more parsimonious explanation in that it does not require that such large differences among two very behaviorally and genetically similar species arose out of very rapid evolution. One shortcoming of this explanation is that we have not been able to test all of the alternative evolutionary scenarios for the origins of the GFP. For example,unlike humans, the species examined in the present study are not cooperative breeders. Thus, studies of nonhuman primates that are cooperative breeders (e.g., marmosets) are needed to provide further evidence regarding the evolutionary explanations for the GFP.

This paper should not be seen as a critique of the search for higher-order factors of personality in humans or nonhuman animals. In fact, we believe that careful studies of higher-order personality dimensions, and especially those which use multitrait-multimethod data, can yield extremely important insights into personality structure and how we judge our own personalities or those of other animals. However, our findings do not support the present evolutionary explanations for the GFP.

# Footnotes

[1] To maintain consistency with other personality studies the chimpanzee personality factors named Surgency, Dependability, and Emotionality in this study have since been renamed Extraversion, Conscientiousness, and Neuroticism, respectively.

[2] Correlation matrices of the three data sets are provided in Supplementary Tables A, B, and C.

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Table 1

*Factor Loadings for Confirmatory Factor Analysis of Lower-Order Chimpanzee, Orangutan, and Rhesus Macaque Personality Factors*

| First-order Factors | λ | 95% *CI* | *p* | $R^2$ |
|---|---|---|---|---|
| **Chimpanzees** | | | | |
| Dominance | -.288 | -.578, .105 | .073 | .084 |
| Extraversion | -.108 | -.455, .286 | .300 | .025 |
| Conscientiousness[a] | .991 | .956, 1.000 | .000 | .983 |
| Agreeableness | .690 | .463, .818 | < .001 | .477 |
| Neuroticism | -.374 | -.632, .004 | .026 | .140 |
| Openness | -.233 | -.543, .166 | .124 | .057 |
| **Orangutans** | | | | |
| Extraversion | .257 | .086, .414 | .002 | .066 |
| Dominance | -.416 | -.564, -.257 | < .001 | .173 |
| Neuroticism | -.180 | -.343, -.002 | .024 | .032 |
| Agreeableness[a] | .965 | .956, 1.000 | .000 | .931 |
| Intellect | -.107 | -.286, .071 | .119 | .012 |
| **Rhesus Macaques** | | | | |
| Dominance | .298 | .090, .490 | .003 | .089 |
| Confidence[a] | .942 | .839, .997 | .000 | .888 |
| Openness | .083 | -.135, .290 | .227 | .009 |
| Friendliness | .071 | -.144, .282 | .257 | .008 |
| Anxiety | -.379 | -.558, -.180 | < .001 | .144 |

| | | | | |
|---|---|---|---|---|
| Activity | .280 | .069, .486 | .005 | .078 |

*Note*. $\lambda$ = GFP loading for standardized solutions; 95% CI = 95% Credibility Interval; $p$ = one-tailed $p$-value. [a]The unstandardized parameter estimate of the loading was fixed to 1.

Table 2

*Loadings of the Two Higher-Order Chimpanzee, Orangutan, and Rhesus Macaque Personality Factors Onto First-Order Factors*

| Chimpanzees | | Orangutans | | Rhesus macaques | |
|---|---|---|---|---|---|
| | Factor | | Factor | | Factor |
| First-order Factors | GFP | First-order factors | GFP | First-order factors | GFP |
| Dominance | -.129 | Extraversion | .339 | Dominance | .351 |
| Extraversion | .258 | Dominance | -.498 | Confidence | .597 |
| Conscientiousness | .522 | Neuroticism | .175 | Openness | .039 |
| Agreeableness | .554 | Agreeableness | .483 | Friendliness | .062 |
| Neuroticism | -.290 | Intellect | -.471 | Anxiety | -.380 |
| Openness | .217 | | | Activity | .403 |

| | Factors | | | Factors | | | Factors | |
|---|---|---|---|---|---|---|---|---|
| First-order Factors | I | II | First-order factors | I | II | First-order factors | I | II |
| Dominance | -.132 | -.018 | Extraversion | .123 | .359 | Dominance | .374 | .240 |
| Extraversion | .063 | .533 | Dominance | -.538 | -.074 | Confidence | .598 | .010 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Conscientiousness | .621 | -.145 | Neuroticism | -.209 | .531 | Openness | .072 | .334 |
| Agreeableness | .549 | .119 | Agreeableness | .603 | -.032 | Friendliness | .084 | .230 |
| Neuroticism | -.254 | -.145 | Intellect | -.171 | -.499 | Anxiety | -.346 | .353 |
| Openness | .006 | .566 | | | | Activity | .414 | .104 |
| $r_{I,II}$ | -.004 | | | .136 | | | -.129 | |

*Note*. Loadings are standardized regression coefficients. $r_{I,II}$ = Correlation between factors I and II.

Published as

**Weiss, A., Adams, M. J., & King, J. E. (2011). Happy orang-utans live longer lives. Biology Letters, 7(6). doi:10.1098/rsbl.2011.0543**

# Happy Orangutans Live Longer Lives

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Nonhuman primates show similar aging profiles to humans (1). Is it also the case that relationships between psychological factors and mortality are conserved across phyla? Lay persons may see happiness, or its scientific cousin subjective well-being, as indicating the presence of positive events and the absence of negative events in the lives of individuals. Increasingly, studies are showing that this is true, although these same studies are also showing that subjective well-being has a genetic basis (2) and foretells better health and longevity (3).

The link between subjective well-being and longevity is strong and even appears when subjective well-being measures are expressions of spontaneous moods in the form of the personal diary entries of nuns (4), or the judged smile intensities in photographs of baseball players (5). Given that physical and behavioral cues signal subjective well-being, it is not surprising that independent judges are consistent in their questionnaire-based ratings of ‘subjective well-being’ in a great ape (6).

To test the hypothesis that orangutan subjective well-being is related to longevity, we examined whether ratings of 172 captive orangutans on a 4-item subjective well-being measure predicted mortality. The time between the date an animal was rated and either their date of death or the censoring date ranged from 217 days to 7.5 years. We examined the relationship between measured subjective well-being and longevity using discrete time hazard analysis. We statistically adjusted the analysis to control for sex, age, species, and number of transfers to new facilities.

Male orangutans were more than twice as likely to die as females over the follow-up period (Odds Ratio [OR] = 2.38; 95% Confidence Interval [$CI_{95\%}$] = 1.18,4.82; P = .042). Older orangutans were at significantly greater risk with each year being related to a ~10% increase in risk (OR = 1.10; $CI_{95\%}$ = 1.07,1.14; $P < .001$). There was no significant difference in mortality risk between Sumatran and Bornean orangutans (OR = 1.14; $CI_{95\%}$ = 0.75,1.75; P = .603) or between purebred and hybrid orangutans (OR = 0.88; $CI_{95\%}$ = 0.42,1.82; P = . 772). Number of transfers were also not significantly related to increased risk of death (OR = 1.20; $CI_{95\%}$ = 0.94,1.53; P = .210).

After controlling for sex, age, species, and transfer effects, orangutans rated as higher in subjective well-being were less likely to die over the follow-up period: each standard deviation was associated with a ~40% reduction in risk (OR = 0.58; $CI_{95\%}$ = 0.41,0.83; P = .012). In terms of risk reduction, this effect was equivalent to being more than 5 years younger (Fig. 1).

These results demonstrate that, as in humans, indicators of positive affect in orangutans are related to longer life. Thus, the relationship between human subjective well-being and longevity likely has deep phylogenetic roots and that, like humans in fairy tales (and real life), orangutans also live happily ever after.

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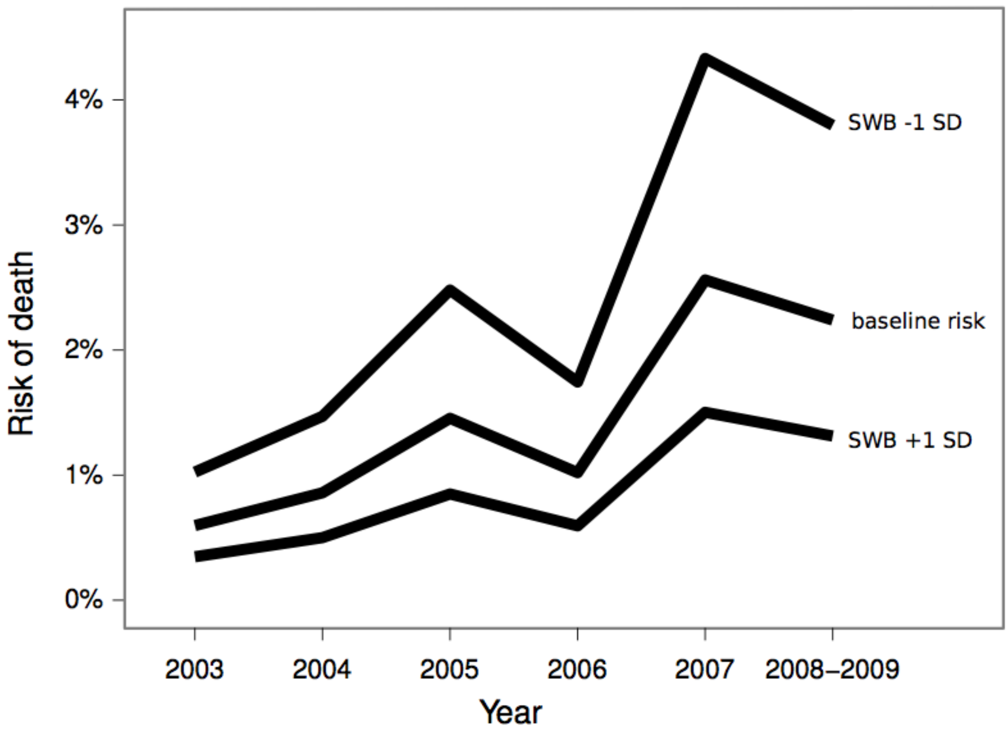
Fig. 1: Predicted risk of death over follow-up periods. Solid green line is risk for subjects with mean age and mean subjective well-being (SWB). The solid red and blue lines represent risk associated with SWB that is one standard deviation below (-1 SD) and above (+1 SD) the mean, respectively. The dashed red and blue lines represent risk associated with being older and younger in age, respectively.


4%
3%
2%
1%
0%
Risk of death
SWB -1 SD
baseline risk
SWB +1 SD
2003
2004
2005
2006
2007
2008–2009
Year

*Published as*

**Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012). All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. Animal Behaviour. http://www.sciencedirect.com/science/article/pii/S0003347212001157**

# All too Human? Chimpanzee and Orang-utan Personalities are not Anthropomorphic Projections

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Running head: Anthropomorphism

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## Abstract

Ratings of chimpanzee and orang-utan personality reveal dimensions resembling those found in humans. Critics have argued that this similarity derives from anthropomorphic projection or other rater-based effects. We developed two forms of data reduction analyses to determine whether these dimensions can best be explained by the inherent tendencies of the animals (e.g., orang-utans that are curious *are* playful) or anthropomorphic projections of raters (e.g., believing that orang-utans that are curious *should be* playful). We found that personality dimensions derived after differences between rater means and rater by item interactions had been removed from ratings replicated the previously discovered dimensions. Conversely, we found a different set of dimensions when analyzing items from which differences between animal means and animal by item interactions had been removed. Finally, we used multilevel factor analysis to examine whether the published structure replicated when we extracted factors based on the within-level animal differences in item scores effects while allowing between rater differences to covary freely. Again, the personality dimensions were similar to those described in previous studies. These analyses can be used in combination with interrater reliability, temporal stability, and correlations between personality and other external variables to validate animal personality ratings. These analyses confirmed that personality similarities between humans and great apes are best explained by genetic and phylogenetic affinity and not by anthropomorphic artifacts.

## Introduction

When Jane Goodall described the personalities of the wild chimpanzees, her observations were criticized as being anthropomorphic (Goodall 1990). Decades after Goodall first presented her findings critics continue to warn that ascribing human-like traits such as personality to animals, including nonhuman primates, is contaminated by anthropomorphism (Uher 2008; Wynne 2009). This caution is understandable. Attribution of human characteristics to animals and other nonhuman entities is common among laypersons and scientists alike and possibly reflects a basic process underlying social cognition (Andrews 2009; Waytz et al. 2010). However, no empirical studies support claims that anthropomorphism is always inconsistent with valid scientific inquiry. Moreover, when anthropomorphism is used to generate testable hypotheses, an approach referred to as "critical anthropomorphism," it can lead to a better understanding of complex animal behaviour (Burghardt 2007) of which personality is one example. The use of critical anthropomorphism in the study of animal personality has produced findings contrary to what one would expect if anthropomorphism had an inimical influence upon animal personality ratings (Gosling 2001; Konečná et al. 2008; Kwan et al. 2008; Maninger et al. 2003; Pederson et al. 2005; Uher and Asendorpf 2008).

We examined whether ratings-based personality dimensions of chimpanzees and orang-utans are products of anthropomorphic projections of individual raters or other rater biases. Previous studies using ratings to study the personalities of chimpanzees revealed six dimensions (King and Figueredo 1997). The first dimension was labelled Dominance as it was apparently indicative of competitive prowess. The five remaining dimensions were similar to the five personality dimensions found in humans (Digman 1990) --- Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness --- and thus labelled similarly. A study of orang-utans with a slightly expanded rating form yielded only five dimensions. One of these dimensions (the second) was labelled Dominance as it appeared to be a more narrowly defined version of the chimpanzee Dominance dimension. Three dimensions resembled the human and chimpanzee Extraversion, Neuroticism, and Agreeableness dimensions. The fifth dimension was specific to orang-utans and labelled Intellect as it consisted of traits related to Openness and Conscientiousness (Weiss et al. 2006).

Considerable evidence suggests that these chimpanzee and orang-utan personality dimensions are real. First, chimpanzee and orang-utan personality dimensions exhibit interrater reliabilities comparable to those of human personality dimensions (King and Figueredo 1997; Weiss et al. 2006; Weiss et al. 2007; Weiss et al. 2009). Second, the chimpanzee personality dimensions are stable over time (Dutton 2008; King et al. 2008). Third, chimpanzee personality dimensions generalize across samples living in different environments and raters from different cultural backgrounds (King et al. 2005; Weiss et al. 2007; Weiss et al. 2009). Fourth, these dimensions are related to observed behaviours (Pederson et al. 2005) and affect (King and Landau 2003; Weiss et al. 2006; Weiss et al. 2009). Finally, chimpanzee and orang-utan personality dimensions are heritable (Adams et al. under review; Weiss et al. 2000), and chimpanzee personality dimensions are related to neuroanatomical structures (Blatchley and Hopkins 2010) and genetic polymorphisms (Hong et al. 2011).

There is thus little doubt that personality ratings assess real characteristics of individual animals. However, this does not rule out the possibility that the striking similarities between human personality dimensions, on the one hand, and those of chimpanzees or orang-utans on the other hand are at least partially products of anthropomorphic projections. This possibility arises when ratings on multiple items are used. Correlations between items should reflect individual differences in the personality characteristics of animals. The correlations, however, could also reflect prior anthropomorphic assumptions by individual raters about species-wide characteristics. For example, some raters may believe that chimpanzees in general are both “active” and “friendly.” This assumption would cause those raters to assign similar ratings to the “active” and the “friendly” descriptors, thus spuriously increasing the correlation that would have otherwise have occurred between “active” and “friendly.” In addition, if the strength of the anthropomorphic belief about the linkage between active and friendly varied among raters, a rater by item interaction would occur. A similar bias towards a negative correlation would occur if some raters have an anthropomorphic belief that two descriptors are negatively related.

Raters’ species-wide belief about the linkage of paired personality descriptors could emerge from global assumptions about the personality of chimpanzees or possibly assumptions about chimpanzees generalized from an implicit personality theory about humans. A failure to find effects of such biases would support the view that these dimensions are not mere anthropomorphic artefacts but offshoots of ancestral variants in the common ancestor of great apes and humans 15 million years ago.

## Methods

### Subjects

The first sample (the ChimpanZoo sample) was comprised of 78 male and 124 female chimpanzees ranging in age from .8 to 55.2 years (*M* = 16.5; *SD* = 12.2). This sample was housed in 17 U.S. zoos and 1 Australian zoo (King et al. 2008) that participated in the ChimpanZoo project of the Jane Goodall Institute.

The second sample (the Japanese sample) was comprised of 64 male and 91 female chimpanzees ranging in age from .2 to 51.7 years (*M* = 22.3; *SD* = 10.6). This sample was housed in 9 zoos, 1 sanctuary, and 2 research centres in Japan. Of this sample, 60 males and 86 females were described in a previous study (Weiss et al. 2009). The additional chimpanzees included two males and three females housed in the Higashiyama Zoo and two males and two females housed in the Fukuoka Zoo.

The third sample (the orang-utan sample) was comprised of 70 male and 104 female orang-utans ranging in age from 1.8 to 51.2 years (*M* = 21.7; *SD* = 12.1). Of this sample, 58 males and 94 females were housed in 34 U.S., 2 Canadian, and 1 Australian zoo and were described in a previous study (Weiss et al. 2006). The additional 12 males and 10 females were housed in the Singapore Zoo.

**Personality Ratings**

Raters of all three samples were employees, volunteers or researchers at the institutions who regularly interacted with the apes. For the ChimpanZoo sample, there were 90 raters. Each chimpanzee was rated by 1 to 8 raters (*M* = 3.9). Length of time raters knew the chimpanzees before rating them (*M* = 5.4 years; *SD* = 4.2) was available for 43 raters of 141 chimpanzees.

For the Japanese sample, there were 52 raters. Each chimpanzee was rated by 2 to 5 raters (*M* = 3.2). Length of time raters knew the chimpanzees before rating them (*M* = 5.1 years; *SD* = 4.8) was available for 52 raters of the entire sample.

For the orang-utan sample, there were 107 raters. Each orang-utan was rated by 1 to 6 raters (*M* = 2.6). Length of time raters knew the orang-utans before rating them (*M* = 5.9 years; *SD* = 5.6) was available for 107 raters of the entire sample.

Questionnaires instructed raters to base ratings on their impressions of individuals and to use a seven-point scale in which 1 indicated “Displays either total absence or negligible amounts of the trait.” and 7 indicated “Displays extremely large amounts of the trait.” The ChimpanZoo sample was rated on the Chimpanzee Personality Questionnaire (King and Figueredo 1997). This questionnaire contains 43 personality descriptor adjectives taken from the human literature (Goldberg 1990). To place adjectives within the context of primate behaviour, each was defined by one to three sentences (e.g., “FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress.”). Each orang-utan was rated on one of two expanded and slightly modified versions the questionnaire used to rate chimpanzees. Most of these subjects were rated on a 48 item questionnaire that included the 43 original items used to rate chimpanzees and 5 new items. A smaller number of subjects in this sample were assessed on a questionnaire that included the 48 items used to rate most of the subjects and 6 additional items. To maximize our sample size, we only used the 48 items on which all orang-utans in our sample were rated. The Japanese sample was rated on a Japanese-language version of the questionnaire that included all 54 items (Weiss et al. 2009).

While the original item set was sampled from markers of the human Five-Factor Model (Goldberg 1990), the purpose of selecting these items was not to impose the human personality dimensions on nonhuman species. Instead, these items were chosen because they represented a broad range of different traits relevant to the behaviour of nonhuman primates. Moreover, using a common set of items enables one to directly compare the dimensions arising in different samples and species (Weiss and Adams 2008).

**Analyses**

The standard approach to analyzing animal personality ratings involves first computing each animal’s mean of the ratings across raters. In other words, each subject’s score on each item is equal to the mean of the ratings by raters on that item. Then, to determine the personality dimensions of that species, those mean ratings are subjected to principal-components analysis or factor analysis. This approach has the virtue of eliminating the effects of individual raters’ non-systematic deviations from the mean of all raters’s scores for each combination of animal and item (Rushton et al. 1983). However, this approach cannot reduce the effects of individual differences in raters’ systematic deviations from mean ratings as noted in the introduction. In other words, it would not eliminate rater by item interactions which could lead to spurious between-item correlations.

The three analyses in the present study differ from this standard approach. These analyses can be illustrated using a modified version of a framework developed by Cattell (1966). This framework acknowledges that, because multiple animals are rated on multiple items by multiple judges (the raters) ratings reflect the animal's behavioural tendencies, item content, and rater effects (Fig. 1a). As described below, it is possible to adjust ratings and remove the effects of individual differences in raters systematic deviations as described above. It is also possible to remove a comparable effect to obtain correlations based on rater scores independent of differences among or animals.

**M-Type analysis.** The first analysis using Cattell's (1966) framework is depicted in Figure 1b. Here, each rating of an animal on an item by a judge is adjusted by subtracting that judge's average rating across all animals that they rated on that item (for details see Appendix A). These adjusted ratings no longer include rater effects, i.e. the mean scores of all raters across animals will be identical. Therefore, any distortion of between-item correlations resulting from between-rater differences in overall item means or from rater by item interactions, as described by the example above, must be zero. Thus, principal-components analyses or factor analyses of these adjusted ratings yield personality dimensions that are based on rater discriminations among individual animals and not by between-rater differences in item means or rater by item interactions. If the personality dimensions derived via the standard approach were products of anthropomorphism or implicit personality theories about global prior assumptions about species wide personality correlations then principal-components analysis or factor analysis of the adjusted ratings should derive different dimensions than the standard approach. On the other hand, if the personality dimensions derived using the standard approach are based mainly on characteristics of individual animals not raters' implicit or global assumptions about the species in general, then dimensions derived from adjusted ratings should not differ.

We conducted four of these analyses to determine whether these anthropomorphic rater effects were responsible for the previously described chimpanzee personality dimensions (King and Figueredo 1997; Weiss et al. 2009). In all four we used parallel analysis to determine the number of statistically significant dimensions derived from the adjusted scores (Dinno 2008; Horn 1965). If the number of dimensions were the same as the number of dimensions obtained via the standard approach for that species, we compared the dimensions based on adjusted scores and dimensions based on the standard approach. In these cases, we used targeted orthogonal Procrustes rotations (McCrae et al. 1996) to compare the dimensions. Targeted orthogonal Procrustes rotation provides congruence coefficients, which indicate the degree to which the two sets of dimensions are similar (Haven and ten Berge 1977). Congruence coefficients greater than .85 indicate that the dimensions are comparable. If the number of components differed from those derived from the standard approach, we rotated the dimensions using the promax procedure. In addition, we extracted the same number of components as derived via the standard approach and used a targeted orthogonal Procrustes rotation to compare the dimensions based on adjusted scores and those based on the standard approach.

In the first analysis we compared dimensions derived via principal-components analysis of the adjusted ratings of the ChimpanZoo sample to dimensions derived using the standard approach. We derived the latter dimensions using the same 100 chimpanzees and factor analysis procedures described by King and Figueredo (1997). In the second analysis we compared the dimensions derived via principal-components analysis of the adjusted ratings of the Japanese sample to the dimensions derived using the standard approach for this sample. In the third M-Type analysis, to conduct a more stringent test, we compared the dimensions derived via principal-components analysis of the Japanese sample to the dimensions derived using the same 100 chimpanzees and factor analysis procedures, i.e., the standard approach, described by King and Figueredo (1997). This analysis was limited to the 43 items both samples shared in common. In the fourth analysis we compared the dimensions derived from the adjusted ratings of the 174 orang-utans to the dimensions derived via the standard approach. We derived the latter dimensions using the same 152 orang-utans and principal-components analysis procedures as in Weiss et al. (2006).

**G-Type analysis.** The second analysis using Cattell's (1966) framework is shown in Figure 1c. Here, each rating of an animal on an item by a judge is adjusted by subtracting the average rating of that item for that animal by all judges that rated the animal (for technical details see Appendix). These adjusted ratings do not include animal effects. Thus, principal-components analysis or factor analysis of these adjusted ratings yield personality dimensions defined by characteristics of the judges and not the animals. We interpreted and assessed these dimensions based on an inspection of the component loadings and likewise compared them to existing dimensions. If the personality dimensions arrived at using the standard approach reflected anthropomorphism or implicit personality theories, the dimensions derived from the adjusted scores should be similar. If the personality dimensions derived using the adjusted scores differ, it would suggest that the personality dimensions derived via the standard approach cannot be attributed to anthropomorphism or implicit personality theories. Finally, by examining whether G-Type dimensions are similar or dissimilar across different species rated within the same culture (the ChimpanZoo sample and the orang-utan sample) or the same species rated within different cultures (the ChimpanZoo sample and the Japanese sample) can lead to insights regarding the sources of rater effects.

We conducted one such analysis for each of our three samples. In all three we used parallel analysis to determine the number of significant dimensions (Dinno 2008; Horn

1965). Moreover, in all three cases, because these analyses were exploratory, we simply rotated the resulting dimensions using the promax procedure. Similarly, we did not label the rater-based dimensions because without understanding the processes involved in rating animal personality that are unrelated to the animal's dispositions, it would be premature to interpret these dimensions.

**Multilevel exploratory factor analysis.** The third analysis can also be understood within Cattell's (1966) framework. However, instead of adjusting scores by holding the effects of raters or animals constant to determine the dimensions defined by animal or raters, respectively, this approach uses maximum likelihood to find the parameters at both the animal and the rater level that best fit the data (Muthén and Muthén 1998-2010; Reise et al. 2005). In other words, this approach enables us to estimate the factor loadings for the animal effects and the covariances among rater effects simultaneously.

To allow for model convergence, for each species, we analyzed one dimension at a time. In addition we combined the ChimpanZoo and Japanese samples into a single sample. There were thus six analyses on the chimpanzees and five analyses on the orang-utans. In each analysis we extracted a single within-rater, i.e., animal-based, factor from items that had been identified as defining that dimension in previous studies (King and Figueredo 1997; Weiss et al. 2006; Weiss et al. 2009). In the case of chimpanzee Openness, because exploratory factor analysis requires at least three items, we defined this factor by the two items (*inventive* and *inquisitive*) identified by King and Figueredo (1997) and the item *imitative*.

We compared the animal-based factor loadings obtained via multilevel exploratory factor analysis to the loadings on dimensions derived from unadjusted ratings (King and Figueredo 1997; Weiss et al. 2006). We used two methods to compare the dimensions derived using multilevel exploratory factor analysis and those derived via the standard approach. The first method was to compare the two sets of loadings with Tucker's congruence coefficients (Gorsuch 1983, p. 285). The second method involved comparing correlations between factor scores of individual animals generated using factor definitions from the standard approach and those generated using the animal-based factor definitions derived via the the multilevel factor analyses (Nunnally and Bernstein 1994, p. 550).

## Results

### Relation Matrix Analysis

**M-Type analysis.** The adjusted ratings of the ChimpanZoo sample defined six significant dimensions. The Procrustes rotation revealed that four of these dimensions were clearly similar to those derived via the standard approach (see first row of Table 1). Neuroticism and Openness were not congruent, probably reflecting the small number of items defining these dimensions (King et al. 2005, pp. 401-402).

The adjusted ratings of the Japanese sample defined seven dimensions. The first was recognizable as Dominance. The second was a blend of Extraversion and Openness. The next three were recognizable as Agreeableness, Conscientiousness, and Neuroticism, respectively. The final two reflected Social Confidence and Negative Affect, respectively. Extraction of six dimensions from the adjusted ratings of the Japanese sample yielded dimensions that replicated those derived in the Japanese sample using the standard approach (see second row of Table 1). Comparison of dimensions derived from adjusted ratings of the Japanese sample to the dimensions derived from the original 100 chimpanzees using the standard approach indicated that the entire structure and Dominance, Extraversion, Conscientiousness, and Agreeableness replicated. Again, Neuroticism and Openness did not clearly replicate (see third row of Table 1). These congruences were virtually identical to those obtained when comparing dimensions derived in the Japanese and ChimpanZoo samples using the standard approach (see Table I in Weiss et al. 2009).

For the orang-utan sample, Procrustes rotation revealed that, after adjusting ratings, principal-components analysis defined the same personality dimensions as those found using the standard approach (Weiss et al. 2006). In fact, the five dimensions that emerged from adjusted ratings were almost identical to those derived from unadjusted ratings (see fourth row of Table 1).

**G-Type analysis.** For the ChimpanZoo sample, after adjustment of ratings for animal effects, the intercorrelations among items defined seven dimensions (see Tables 2 and 3). Upon inspecting the rater-based structure, the most striking feature was the lack of a Dominance dimension which had been a pronounced feature of chimpanzee personality in prior studies (Dutton 2008; King and Figueredo 1997). If the loadings are reflected, i.e. multiplied by -1, component I resembled the Agreeableness dimensions found in previous studies (Dutton 2008; King and Figueredo 1997). Component II described individual differences in aggression or hostility. Component III described individual differences in timidity. Component IV was seemingly indicative of negative affect. After reflecting its loadings, component V closely resembled Neuroticism dimensions found in previous studies (Dutton 2008; King and Figueredo 1997). After their loadings were reflected, components VI and VII bore similarities to the Conscientiousness and Openness dimensions, respectively, that were identified in previous studies (King and Figueredo 1997).

The adjusted ratings of the Japanese sample contained eight dimensions (see Tables 4 and 5). Unlike the rater-based dimensions of the ChimpanZoo sample, there was a Dominance dimension (component I), which resembled Dominance dimensions in previous studies (Dutton 2008; King and Figueredo 1997). Component IV was somewhat similar to the previously described Conscientiousness dimension (King and Figueredo 1997). Components V and VI could be best described as dimensions related to individual differences in excitability and timidity, respectively. Component VII, after reflection, and component VIII were similar to the Openness and Agreeableness dimensions described in prior studies (Dutton 2008; King and Figueredo 1997). Components II and III were not easily interpretable.

For the orang-utan sample, principal-components analysis of the adjusted yielded six dimensions (see Tables 6 and 7). Components I, II, and IV were similar to the Dominance, Agreeableness, and Neuroticism dimensions, respectively, that were identified using the standard approach (Weiss et al. 2006). Component III appeared to resemble Openness dimension identified in chimpanzees (King and Figueredo 1997) and partly resembled Extraversion dimensions identified in orang-utans (Weiss et al. 2006). When reflected, component V appeared to capture individual differences in tameness, which had been identified as a subcomponent of chimpanzee Conscientiousness (King et al. 2008). Component VI was also not previously identified in chimpanzees or orang-utans. This dimension described individual differences in a combination of low activity and low or negative affect.

**Multilevel Exploratory Factor Analysis**

The animal-based factor loadings replicated those derived using the standard approach (see Tables 8 and 9). The animal-based loadings defining the combined chimpanzee sample were highly congruent with unadjusted loadings: .99, 1.00, .98, .99, .98, and 1.00 for Dominance, Extraversion, Conscientiousness, Agreeableness, Neuroticism, and Openness, respectively. The animal-based loadings defining the orang-utan sample were also highly congruent: .99, .99, .99, .96, and .93 for Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect, respectively.

Comparison of factor scores computed using the animal-based loadings from the multilevel exploratory factor analysis and factor scores derived from the unadjusted loadings shows that the factor scores are comparable for chimpanzees and orang-utans (Figs. 2 and 3, respectively). The correlations for chimpanzee Dominance (*r* = 1.00), Extraversion (*r* = 1.00), Conscientiousness (*r* = 1.00), Agreeableness (*r* = 1.00), Neuroticism (*r* = .99), and Openness (*r* = 1.00) were all significant (all *p*s < .001). The correlations for orang-utan Extraversion (*r* = .81), Dominance (*r* = .97), Neuroticism (*r* = .93), Agreeableness (*r* = 1.00), and Intellect (*r* = .98) were significant (all *p*s < .001).

## Discussion

The previously described personality dimensions based on ratings of two great ape species were not appreciably affected by removal of rater effects via the M-Type analysis or via multilevel exploratory factor analysis. If the expectations of raters influenced their assessment of the personalities of nonhuman primates, we would expect a lower congruence between the animal-based factors and conventionally defined factors. Thus, biases, preconceptions, and projections (anthropomorphic and otherwise) cannot account for the personality dimensions in these three samples.

These findings are consistent with studies which demonstrated interrater reliability and those showing that ratings are related to behaviours and other outcomes (Freeman and Gosling 2010). These findings also agree with studies showing that personality dimensions derived using behavioural observations and measures are comparable to those derived from ratings (Bergvall et al. 2011; Konečná et al. 2008). Finally, these findings are consistent with those showing that humans do not project their personalities onto their dogs (Kwan et al. 2008) and that human personality dimensions reflect genetic correlations among lower-order traits and not implicit personality theories or correlations based entirely on semantic meaning of items (McCrae et al. 2001; Rowe 1982).

Our findings therefore suggest that similarities among great ape and human personality dimensions are most parsimoniously explained as evolutionarily conserved features. The conservation of behavioural dispositions across species suggests that processes of balancing selection (environmental heterogeneity, negative frequency-dependent selection, and migration) that have been implicated in the evolution of human personality (Penke et al. 2007) have also maintained variation in chimpanzee and orang-utan personality.

While the present study describes dimensions related to effects related to between rater-differences, it cannot explain the processes that give rise to these dimensions. One possibility is that these rater-based dimensions arise via the semantic similarity of the items (D'Andrade 1965). However, our finding that the rater-based dimensions for the ChimpanZoo and orang-utan samples differ diminishes the likelihood of this possibility. Another possibility is that the rater-based dimensions describe raters' general prior beliefs about the species that is being rated. However, our finding of different rater-based dimensions in raters from Western and Eastern cultures seems to rule against this possibility, too. This difference suggests the possibility is that the rater-based dimensions reflect culturally-specific views and expectations about the personalities of these species. Future studies comparing the beliefs about the personalities of great apes in Japan and in English-speaking countries are needed to test this possibility.

Rater-based dimensions can aid researchers in understanding how people perceive animal personality in other ways. Because the effects of the animals have been removed from the rater-based dimensions, they potentially reflect the diversity among raters in their dispositions and assumptions. Future studies should therefore examine correlations between rater-based dimensions and characteristics of raters, including their personalities, dispositions toward primates, or preconceptions concerning the personality structure of given species.

Our study does not suggest that ratings based approaches should replace behavioural observations or tests. Instead, ratings should be viewed as complementing behavioural observations or tests and used alongside such tests (Bergvall et al. 2011; Konečná et al. 2008; Nettle and Penke 2010; Uher and Asendorpf 2008) or used when behavioural observations or tests would not be feasible.

The present study is not without shortcomings. The M-Type factor analysis only removes the main effects of raters and rater by item interactions. As such, the remaining covariances describe animal effects and the interaction of rater and animal effects. This interaction may be responsible for some or all of the consistency of the animal-based dimensions and those described in previous studies. However, we found similar results using multilevel exploratory factor analysis, which does not suffer from this shortcoming. Another shortcoming is that, given the sample size, number of items, and the unbalanced design, conducting the multilevel exploratory factor analysis required examining one personality dimension at a time. As such, information about cross-loadings of items onto different dimensions was lost. We therefore recommend that future studies of this sort use more subjects and a balanced design.

These findings strongly rule out the possibility that similarities between the personalities of humans and great apes derived via ratings are anthropomorphic projections. Instead, they suggest that Jane Goodall's (1990) impressions of the human-like personalities of the chimpanzees she studied reflected the chimpanzees' individual behavioural differences. Naturally, researchers should remain leery of attributing human-like personality traits such as "thoughtlessness" to invertebrates or other distantly related species (Hebb 1946). However, researchers should also avoid engaging in "anthropodenial" (de Waal 2009), i.e., rejecting, without evidence, and even in the face contradictory evidence, the possibility that the genetic similarity of closely-related species may be expressed in behavioural similarities.

Even though 50 years have passed since Jane Goodall's observations of chimpanzee personalities were criticized as being anthropomorphic, critics have not tested their claims. By conducting this study, we took up the mantle that critics refused to don themselves. In doing so, we found evidence refuting their worst fears and concerns over anthropomorphism, which, in fact, casts nary a shadow over great ape personality.

## Acknowledgements

We would like to express our thanks to Miho Honjyo, Ryota Matsukawa, Nami Suzuki, Shin’ichi Ito, Toshikazu Hasegawa, Gen’ichi Idani, Kazuhide Hashiya, Koichiro Zamma, Toshisada Nishida, Virginia Landau, and Lori Perkins. Without their assistance and cooperation, this project would not have been possible. We would also like to thank the raters at the zoos, research centres, and sanctuaries for their evaluations of the personalities of the chimpanzees and orang-utans. We would also like to express our thanks to Roy Welensky who created Figure 1. Alexander Weiss was supported by a Small Project Grant from The University of Edinburgh Development Trust (]2828) and a Daiwa Foundation Small Grant (6515/6818). Miho Inoue-Murayama was supported by a University Grant, Ministry of Education, Science, Sports and Culture, Grant-in-Aid for Scientific Research (B) (]18310152 to MIM) and the Cooperation Research Program of the Primate Research Institute, Kyoto University.

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## Figure Captions

Figure 1. Representation of data using Cattell's data cube. a) Ratings before adjustment are comprised of item, subject, and rater effects. b) After rater effects are removed, ratings are only comprised of subject and item effects. c) After subject effects are removed, ratings are only comprised of rater and item effects. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license.

Figure 2. Chimpanzee factor scores. A factor score in each personality domain was calculated for all individuals weighted by the factor loadings derived via the standard approach or by the within-rater factor loadings. Raw scores were converted to *T*-scores (*M* = 50; *SD* = 10). Strong correlations between the two factor scores indicate high congruence in structure before and after covariances attributable to raters were removed. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license.

Figure 3. Orang-utan factor scores. A factor score in each personality domain was calculated for all individuals weighted by the factor loadings derived via the standard approach or by the within-rater factor loadings. Raw scores were converted to *T*-scores (*M* = 50; *SD* = 10). Strong correlations between the two factor scores indicate high congruence in structure before and after covariances attributable to raters were removed. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license.

Table 1

*Congruence Coefficients Between Animal-Based Structures Derived via the Standard Approach and M-Type Structures and*

| Comparison | | Congruences | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Standard | Adjusted | Dom | Ext | Agr | Neu | Con | Opn | Int | Total |
| ChimpanZoo | ChimpanZoo | .99 | .98 | .97 | .78 | .98 | .82 | --- | .95 |
| Japan (54-item) | Japan (54-item) | .99 | .97 | .99 | .94 | .95 | .99 | --- | .97 |
| ChimpanZoo | Japan (43-item) | .89 | .92 | .90 | .75 | .90 | .69 | --- | .87 |
| Orang-utan | Orang-utan | .99 | 1.00 | .97 | .99 | --- | --- | .97 | .99 |

*Note*. Dom = Dominance, Ext = Extraversion, Agr = Agreeableness, Neu = Neuroticism, Con = Conscientiousness, Opn = Openness, Int = Intellect, Total = Total structure.

Table 2

*Rater-based G-Type Structure of Ratings for Chimpanzees (ChimpanZoo Sample)*

| | Component | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | I | II | III | IV | V | VI | VII |
| Affectionate | **-.74** | -.02 | .05 | -.25 | -.01 | .06 | .07 |
| Sympathetic | **-.70** | -.16 | .09 | -.05 | -.04 | -.02 | -.14 |
| Friendly | **-.68** | -.11 | .01 | -.29 | -.08 | .04 | .03 |
| Helpful | **-.65** | -.16 | -.03 | -.04 | .07 | .02 | -.22 |
| Sociable | **-.62** | .08 | -.03 | **-.50** | -.05 | .01 | .05 |
| Protective | **-.62** | .05 | -.09 | -.01 | .01 | -.05 | -.18 |
| Sensitive | **-.59** | .04 | .08 | .01 | .05 | .22 | .10 |
| Gentle | **-.58** | **-.43** | .16 | .07 | -.12 | .03 | .02 |
| Intelligent | **-.47** | .07 | -.15 | .00 | .06 | .47 | .04 |
| Jealous | .09 | **.67** | .11 | .02 | .01 | -.03 | -.08 |
| Stingy/Greedy | .18 | **.65** | -.01 | .16 | -.10 | .04 | .17 |
| Bullying | .14 | **.63** | -.14 | -.08 | .15 | -.05 | -.08 |
| Defiant | -.02 | **.61** | -.20 | .02 | .25 | .02 | -.22 |
| Aggressive | .23 | **.60** | -.14 | -.04 | .25 | -.14 | -.07 |
| Manipulative | -.17 | **.59** | .02 | -.20 | .02 | .03 | -.09 |
| Irritable | .18 | **.56** | -.04 | .18 | .16 | -.30 | .02 |
| Persistent | -.22 | **.46** | -.26 | -.08 | .02 | .09 | -.09 |
| Reckless | .02 | **.45** | -.30 | .12 | .36 | -.16 | .13 |
| Timid | .11 | .02 | **.68** | .20 | -.01 | -.20 | -.09 |
| Dependent/Follower | -.24 | -.02 | **.66** | -.07 | .02 | -.11 | .06 |
| Fearful | .03 | .09 | **.63** | .11 | .31 | -.03 | -.06 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Cautious | -.07 | -.13 | **.63** | .12 | -.15 | .12 | -.04 |
| Submissive | -.03 | -.08 | **.62** | .04 | .09 | -.09 | .11 |
| Independent | -.10 | .17 | **-.53** | .13 | .04 | .26 | -.05 |
| Dominant | -.02 | **.46** | **-.50** | -.08 | -.18 | .07 | -.18 |
| Solitary | .16 | -.07 | .13 | **.69** | -.03 | .03 | -.25 |
| Depressed | .19 | .13 | .11 | **.64** | .03 | -.16 | -.08 |
| Active | -.16 | .29 | -.02 | **-.55** | .03 | -.01 | -.33 |
| Lazy | -.03 | .05 | .02 | **.54** | -.14 | -.25 | .23 |
| Playful | -.33 | .19 | .14 | **-.48** | -.04 | .00 | -.34 |
| Excitable | -.05 | .38 | .17 | -.04 | **.61** | -.10 | .02 |
| Unemotional | .09 | .05 | .02 | .35 | **-.59** | -.16 | -.12 |
| Impulsive | -.07 | **.43** | .00 | .10 | **.56** | -.17 | -.20 |
| Stable | -.33 | -.05 | -.29 | -.02 | **-.52** | .06 | .09 |
| Disorganized | .03 | .24 | .16 | .15 | .09 | **-.71** | .06 |
| Decisive | -.22 | .21 | -.29 | .06 | -.03 | **.56** | .14 |
| Clumsy | -.05 | .09 | .12 | .24 | -.02 | **-.55** | .16 |
| Erratic | .05 | **.43** | .01 | .16 | .35 | **-.50** | -.04 |
| Inventive | -.34 | .23 | -.13 | .07 | -.01 | .18 | **-.62** |
| Predictable | -.18 | -.11 | .04 | .15 | -.34 | .35 | **.50** |
| Inquisitive | **-.45** | .27 | .03 | -.11 | -.06 | .11 | **-.46** |
| Imitative | -.21 | .34 | .30 | -.02 | -.08 | -.09 | -.29 |
| Autistic | -.03 | .27 | .15 | .33 | -.02 | -.09 | .25 |

*Note*. Salient loadings (≥ .40) are in boldface.

Table 3

*Inter-factor Correlations of Rater-Based G-Type Components of Chimpanzees (ChimpanZoo Sample)*

| Component | I | II | III | IV | V | VI |
|---|---|---|---|---|---|---|
| I | | | | | | |
| II | .09 | | | | | |
| III | .02 | -.22 | | | | |
| IV | -.11 | .12 | .02 | | | |
| V | -.18 | .22 | -.06 | .00 | | |
| VI | -.33 | .13 | .22 | .18 | .28 | |
| VII | .08 | .18 | .02 | -.35 | .11 | .05 |

Table 4

*Rater-based G-Type Structure of Ratings for Chimpanzees (Japanese Sample)*

| Item | Component | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | VII | VIII |
| Aggressive | **.73** | .21 | -.03 | .02 | .11 | -.02 | -.13 | -.11 |
| Bullying | **.65** | .19 | -.02 | .04 | .05 | .18 | -.09 | -.24 |
| Dominant | **.65** | .10 | -.03 | .21 | -.14 | -.23 | -.09 | -.08 |
| Defiant | **.64** | -.02 | -.10 | -.03 | .18 | -.11 | -.09 | -.06 |
| Irritable | **.64** | -.09 | .08 | -.15 | .11 | .12 | -.04 | -.07 |
| Jealous | **.62** | -.14 | -.03 | .07 | -.04 | .31 | -.13 | -.07 |
| Manipulative | **.59** | .23 | .00 | .19 | -.07 | -.04 | -.31 | .13 |
| Excitable | **.57** | -.21 | .05 | -.11 | .28 | .13 | .03 | .07 |
| Reckless | **.55** | -.02 | .22 | -.33 | .17 | -.01 | .04 | .17 |
| Stingy/Greedy | **.53** | -.33 | .19 | .06 | -.01 | .04 | .06 | -.05 |
| Thoughtless | **.46** | -.23 | .12 | -.12 | .13 | .09 | .10 | .30 |
| Impulsive | **.44** | -.18 | .07 | -.19 | .34 | .10 | -.02 | .09 |
| Distractible | **.43** | -.07 | .03 | -.38 | .17 | .17 | .13 | .24 |
| Cautious | **-.42** | -.03 | .13 | .35 | .02 | .37 | -.14 | -.01 |
| Unemotional | -.14 | **.58** | .12 | .03 | -.13 | .16 | -.04 | .20 |
| Cool | -.22 | **.50** | .19 | .14 | -.26 | .06 | -.18 | .10 |
| Helpful | .18 | **.47** | -.15 | .12 | .05 | -.13 | -.23 | .38 |
| Clumsy | .17 | **.41** | .31 | -.25 | .27 | .19 | .03 | .11 |
| Solitary | .00 | .06 | **.72** | .04 | .13 | .09 | -.04 | -.07 |
| Individualistic | .18 | .00 | **.63** | -.01 | .06 | .01 | -.02 | -.04 |
| Lazy | .02 | .21 | **.46** | -.17 | .18 | .13 | .23 | .16 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Sensitive | .07 | -.05 | -.05 | **.68** | -.03 | -.06 | -.03 | .25 |
| Intelligent | .05 | .19 | -.14 | **.64** | -.05 | -.07 | -.18 | .16 |
| Decisive | .01 | .14 | .22 | **.50** | -.11 | -.01 | -.30 | .12 |
| Unperceptive | .17 | .33 | .16 | **-.46** | .02 | .33 | .06 | .11 |
| Predictable | -.23 | .29 | .29 | **.42** | -.30 | .19 | .12 | .05 |
| Conventional | -.18 | .21 | .13 | **.40** | -.26 | .20 | .29 | .06 |
| Erratic | .10 | -.10 | .12 | -.08 | **.73** | .04 | .02 | -.05 |
| Disorganized | .16 | .15 | .03 | -.17 | **.60** | .21 | .02 | .09 |
| Anxious | .09 | .06 | .11 | -.14 | **.54** | .19 | .04 | .00 |
| Autistic | .10 | -.15 | .09 | .07 | **.51** | -.13 | .01 | -.14 |
| Timid | .15 | -.04 | .09 | -.16 | .14 | **.64** | .08 | -.01 |
| Vulnerable | .09 | .15 | .11 | .00 | .06 | **.57** | .00 | -.12 |
| Dependent | -.01 | .11 | -.09 | -.08 | -.20 | **.51** | -.13 | .35 |
| Fearful | .02 | -.28 | -.09 | .25 | .35 | **.44** | .06 | -.13 |
| Depressed | -.05 | -.07 | .38 | .00 | .26 | **.42** | .06 | -.08 |
| Inventive | .00 | .00 | .01 | -.02 | .00 | .01 | **-.76** | .19 |
| Inquisitive | .03 | .05 | .01 | .10 | -.13 | .02 | **-.72** | .16 |
| Innovative | .13 | .26 | .06 | -.01 | -.01 | .01 | **-.68** | .21 |
| Curious | .00 | -.10 | -.11 | .23 | .08 | -.09 | **-.67** | .09 |
| Playful | .16 | **.42** | -.32 | .03 | -.03 | .01 | **-.44** | .25 |
| Affectionate | .03 | .08 | -.06 | .19 | .00 | -.16 | -.14 | **.70** |
| Sociable | .07 | .18 | -.28 | .15 | -.07 | -.03 | -.21 | **.61** |
| Gentle | -.29 | .14 | .19 | .08 | -.02 | -.09 | -.16 | **.61** |
| Friendly | -.31 | .04 | .13 | .13 | -.06 | .09 | -.15 | **.57** |
| Sympathetic | .00 | **.42** | -.33 | .10 | .05 | -.10 | -.14 | **.54** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Imitative | .17 | .13 | -.05 | -.05 | .08 | .17 | -.34 | **.50** |
| Submissive | -.06 | -.02 | .10 | -.06 | -.12 | **.44** | -.07 | **.50** |
| Active | .28 | .26 | -.31 | -.02 | .13 | .19 | -.36 | .07 |
| Independent | -.10 | .36 | .25 | .19 | .39 | -.09 | -.09 | -.01 |
| Persistent | .27 | .22 | .06 | .22 | -.16 | -.13 | -.39 | .02 |
| Protective | -.05 | .38 | -.10 | .31 | .20 | .17 | -.09 | .20 |
| Quitting | .18 | .27 | -.05 | .06 | .28 | .37 | .21 | .13 |
| Stable | -.29 | .38 | .08 | .26 | -.29 | -.18 | -.09 | -.02 |

*Note.* Salient loadings (≥ .40) are in boldface.

Table 5

*Inter-factor Correlations of Rater-Based G-Type Components of Chimpanzees (Japanese Sample)*

| Component | I | II | III | IV | V | VI | VII |
|---|---|---|---|---|---|---|---|
| I | | | | | | | |
| II | .19 | | | | | | |
| III | -.12 | .25 | | | | | |
| IV | -.26 | .17 | .21 | | | | |
| V | .29 | -.03 | .03 | -.22 | | | |
| VI | .14 | -.09 | -.01 | -.09 | .22 | | |
| VII | -.03 | -.27 | -.17 | -.07 | .03 | .25 | |
| VIII | .29 | .29 | .26 | -.22 | .10 | .23 | .02 |

Table 6

*Rater-based G-Type Structure of Ratings for Orang-utans*

| Item | Component I | II | III | IV | V | VI |
|---|---|---|---|---|---|---|
| Bullying | **.64** | -.06 | -.11 | .03 | -.07 | .02 |
| Aggressive | **.62** | -.05 | -.10 | .11 | .18 | -.14 |
| Stingy/Greedy | **.59** | -.15 | .08 | .18 | .07 | -.03 |
| Dominant | **.53** | -.01 | .09 | -.20 | -.02 | .05 |
| Jealous | **.51** | .01 | .13 | .24 | .18 | -.08 |
| Manipulative | **.46** | .37 | -.07 | -.13 | .16 | -.12 |
| Independent | **.47** | -.12 | .29 | -.25 | -.08 | .21 |
| Submissive | **-.46** | .16 | .00 | .33 | .09 | .10 |
| Persistent | **.41** | -.09 | .35 | -.07 | .21 | -.05 |
| Sympathetic | -.12 | **.70** | .24 | -.13 | -.14 | .00 |
| Helpful | -.12 | **.68** | .08 | -.10 | -.01 | -.19 |
| Sensitive | -.02 | **.56** | .06 | .14 | -.17 | .04 |
| Protective | .12 | **.54** | .15 | -.09 | .01 | -.03 |
| Affectionate | -.34 | **.51** | **.43** | -.07 | .02 | -.09 |
| Gentle | **-.45** | **.46** | .10 | -.27 | -.11 | -.02 |
| Imitative | -.02 | **.45** | .09 | .06 | .07 | -.06 |
| Curious | .01 | .01 | **.68** | -.03 | -.04 | -.08 |
| Inquisitive | .04 | .18 | **.62** | -.15 | -.08 | -.05 |
| Inventive | .22 | .24 | **.53** | .01 | -.13 | -.05 |
| Sociable | -.23 | .27 | **.52** | -.06 | -.10 | -.11 |
| Intelligent | .14 | .35 | **.46** | -.12 | -.05 | -.09 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Friendly | -.24 | .33 | **.45** | .09 | -.20 | -.18 |
| Decisive | **.40** | .06 | **.44** | -.13 | -.19 | .25 |
| Fearful | .08 | .02 | .00 | **.74** | -.06 | .07 |
| Timid | -.11 | -.03 | -.22 | **.60** | .12 | .07 |
| Cool | -.16 | .17 | .09 | **-.60** | -.03 | .29 |
| Stable | -.04 | .14 | .27 | **-.59** | .17 | .12 |
| Excitable | .19 | .02 | .15 | **.55** | .21 | -.26 |
| Anxious | .03 | .06 | -.06 | **.54** | .21 | .16 |
| Erratic | .14 | -.10 | .00 | .15 | **.71** | -.14 |
| Clumsy | .00 | .03 | -.08 | .00 | **.63** | .24 |
| Disorganized | -.02 | -.04 | -.14 | .09 | **.58** | .15 |
| Irritable | **.45** | -.09 | -.16 | .09 | **.52** | -.01 |
| Defiant | **.43** | .09 | -.07 | -.12 | **.50** | -.14 |
| Predictable | -.03 | .13 | .06 | -.09 | **-.46** | .29 |
| Impulsive | .27 | -.01 | .18 | .33 | **.40** | -.27 |
| Lazy | .00 | -.09 | -.18 | .08 | .10 | **.66** |
| Active | .02 | .28 | .19 | -.09 | .17 | **-.58** |
| Conventional | -.13 | -.03 | .08 | .04 | .00 | **.56** |
| Unemotional | -.06 | .01 | .02 | -.21 | .11 | **.56** |
| Playful | .00 | .23 | .25 | .00 | .11 | **-.45** |
| Depressed | .09 | .03 | **-.42** | .28 | .16 | **.44** |
| Cautious | -.14 | .29 | -.11 | .25 | -.07 | .13 |
| Autistic | .13 | .26 | -.25 | .12 | .30 | .08 |
| Reckless | .37 | .02 | -.08 | .14 | .13 | -.03 |
| Solitary | .19 | .16 | -.36 | .07 | -.11 | .35 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Vulnerable | -.12 | .03 | -.02 | .38 | .22 | .15 |
| Dependent | -.27 | .38 | -.11 | .19 | .23 | -.07 |

*Note*. Salient loadings (≥ .40) are in boldface.

Table 7

*Inter-factor Correlations of Rater-Based G-Type Components of Orang-utans*

| Component | I | II | III | IV | V |
|---|---|---|---|---|---|
| I | | | | | |
| II | .09 | | | | |
| III | .12 | .44 | | | |
| IV | .08 | .26 | .04 | | |
| V | .18 | -.30 | -.13 | -.11 | |
| VI | -.13 | .18 | -.15 | .34 | -.30 |

Table 8

*Comparison of Within-Rater Factor Loadings and Factor Loadings Derived Using the Standard Approach for Chimpanzees (combined ChimpanZoo and Japanese Sample)*

| Item | Loading | |
|---|---|---|
| **Dominance** | Standard | Within-Rater |
| Dominant | .90 | .82 |
| Submissive | -.86 | -.76 |
| Dependent | -.86 | -.70 |
| Independent | .83 | .57 |
| Fearful | -.82 | -.54 |
| Decisive | .82 | .50 |
| Timid | -.81 | -.63 |
| Cautious | -.63 | -.52 |
| Intelligent | .63 | .33 |
| Persistent | .61 | .51 |
| Bullying | .58 | .55 |
| Stingy | .52 | .41 |
| **Extraversion** | Standard | Within-Rater |
| Solitary | -.85 | -.67 |
| Lazy | -.83 | -.65 |
| Active | .83 | .77 |
| Playful | .81 | .78 |
| Sociable | .80 | .72 |
| Depressed | -.78 | -.59 |
| Friendly | .65 | .51 |

|  |  |  |
|---|---|---|
| Affectionate | .60 | .52 |
| Imitative | .52 | .52 |
| **Conscientiousness** | Standard | Within-Rater[a] |
| Impulsive | -.78 | -.66 |
| Defiant | -.74 | -.71 |
| Reckless | -.73 | -.64 |
| Erratic | -.72 | -.53 |
| Irritable | -.62 | -.64 |
| Predictable | .61 | .42 |
| Aggressive | -.60 | -.73 |
| Jealous | -.58 | -.58 |
| Disorganized | -.53 | -.33 |
| **Agreeableness** | Standard | Within-Rater |
| Sympathetic | .84 | .86 |
| Helpful | .74 | .70 |
| Sensitive | .74 | .53 |
| Protective | .70 | .57 |
| Gentle | .61 | .62 |
| **Neuroticism** | Standard | Within-Rater |
| Stable | .73 | .60 |
| Excitable | -.71 | -.80 |
| Unemotional | .57 | .40 |
| **Openness** | Standard | Within-Rater |
| Inventive | .65 | .77 |
| Inquisitive | .64 | .89 |

*Note*. [a]Loadings were reflected.

Table 9

*Comparison of Within-Rater Factor Loadings and Factor Loadings Derived Using the Standard Approach for Orang-utans*

| Item | Loading | |
|---|---|---|
| **Extraversion** | Unadjusted | Within-Rater |
| Playful | .84 | .84 |
| Active | .83 | .90 |
| Lazy | -.80 | -.85 |
| Curious | .77 | .62 |
| Conventional | -.76 | -.56 |
| Inquisitive | .70 | .58 |
| Inventive | .69 | .53 |
| Depressed | -.64 | -.56 |
| Imitative | .63 | .63 |
| Solitary | -.59 | -.54 |
| Unemotional | -.53 | -.46 |
| **Dominance** | Unadjusted | Within-Rater |
| Bullying | .87 | .88 |
| Aggressive | .82 | .81 |
| Stingy | .78 | .72 |
| Jealous | .75 | .62 |
| Dominant | .75 | .72 |
| Gentle | -.72 | -.68 |
| Defiant | .68 | .55 |
| Submissive | -.67 | -.63 |

| | | |
|---|---|---|
| Manipulative | .66 | .46 |
| Persistent | .62 | .59 |
| Irritable | .60 | .58 |
| Reckless | .56 | .37 |
| **Neuroticism** | Unadjusted | Within-Rater |
| Anxious | .83 | .67 |
| Fearful | .82 | .72 |
| Cool | -.73 | -.77 |
| Timid | .70 | .56 |
| Stable | -.66 | -.61 |
| Excitable | .58 | .62 |
| Impulsive | .56 | .53 |
| Cautious | .55 | .37 |
| Vulnerable | .48 | .38 |
| Erratic | .48 | .42 |
| Predictable | -.47 | -.48 |
| **Agreeableness** | Unadjusted | Within-Rater |
| Sympathetic | .82 | .71 |
| Helpful | .79 | .70 |
| Protective | .73 | .35 |
| Affectionate | .67 | .81 |
| Sensitive | .63 | .47 |
| Friendly | .63 | .80 |
| Sociable | .61 | .77 |
| **Intellect** | Unadjusted | Within-Rater |

| | | |
|---|---|---|
| Intelligent | .72 | .38 |
| Decisive | .70 | .69 |
| Clumsy | -.66 | -.37 |
| Disorganized | -.66 | -.36 |
| Independent | .64 | .79 |
| Dependent | -.52 | -.74 |

Figure 1

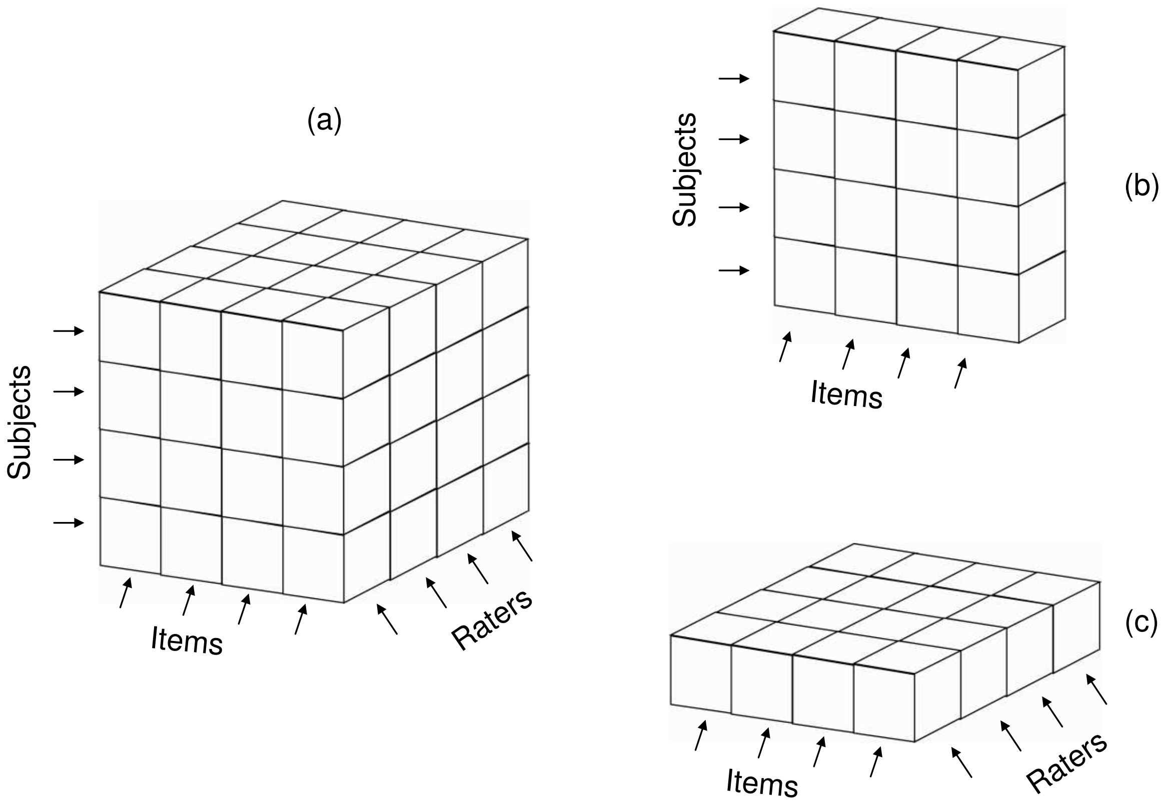


Figure 2

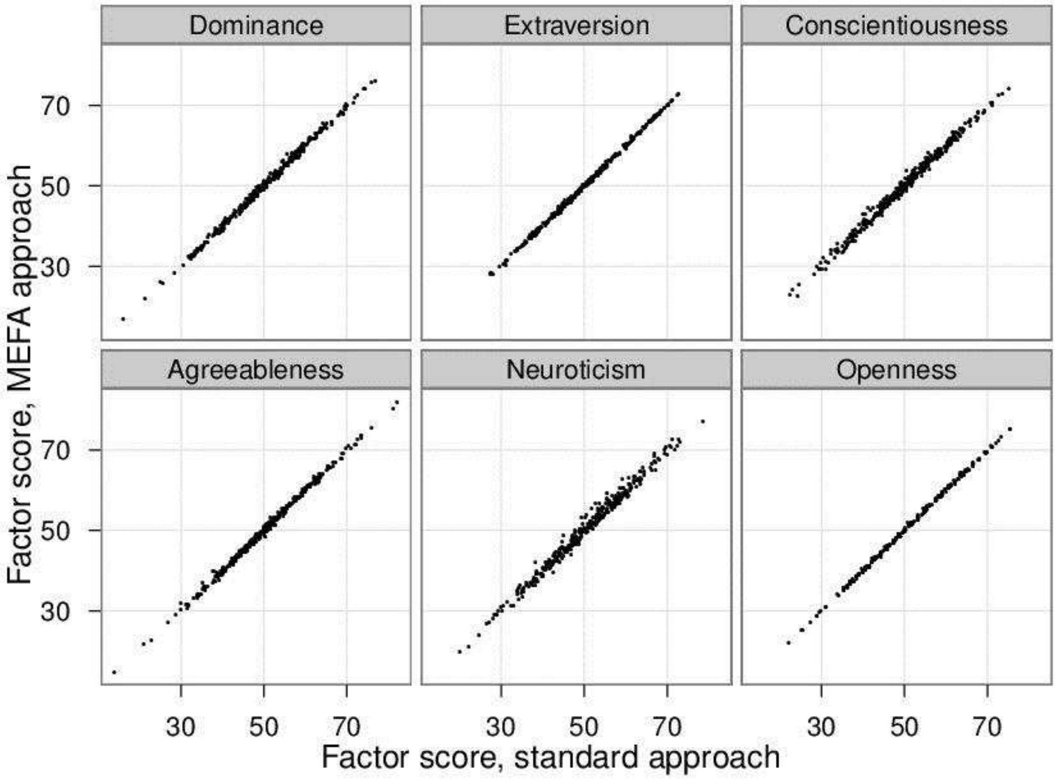
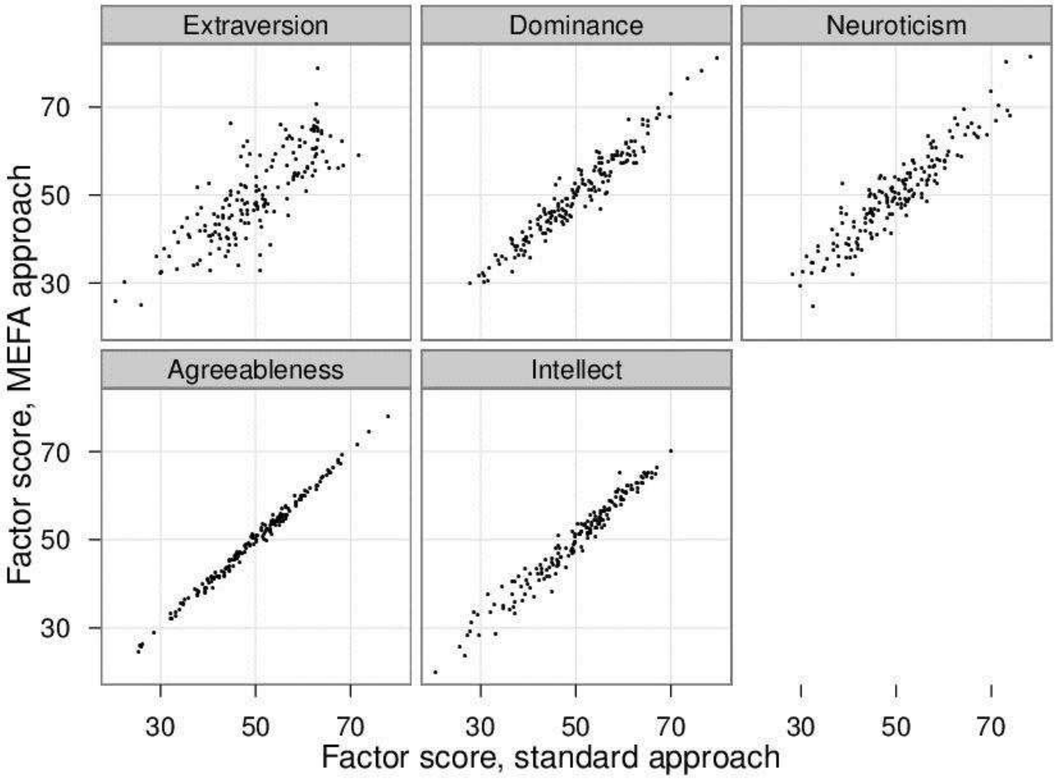

Dominance
Extraversion
Conscientiousness
Agreeableness
Neuroticism
Openness
Factor score, MEFA approach
30
50
70
Factor score, standard approach

Figure 3


Extraversion
Dominance
Neuroticism
Agreeableness
Intellect
Factor score, MEFA approach
30
50
70
Factor score, standard approach

# Appendix A

## M-Type and G-Type Analysis

The analyses used are based on the nested nature of the data, i.e., the fact that each animal is rated by more than one knowledgeable rater on multiple items. When data are nested in this manner, items may correlate with each other for multiple reasons (Cattell 1966). In these analyses, we can statistically remove sources of covariance among items related to raters or animals.

The **M-Type** analysis involves extracting dimensions that describe the animals. We calculated the deviation of each rater j's raw score of animal s on item i ($x_{sji}$) from the rater's mean score for that item across all animals

$$m_{sji} = x_{sji} - \sum_{l=1}^{n_j} \frac{x_{lji}}{n_j} \qquad (1)$$

where rater j rated $n_j$ subjects and $x_{lji}$ is the rater's rating of their lth subject. Raters' mean scores are equal to the predicted score of rater j on item i from a regression on a rater identity matrix

$$m_{sji} = x_{sji} - \hat{x}_{ji} \qquad (2)$$

$$\hat{x}_{ji} = \mu_i + u_{ji0} \qquad (3)$$

We then subjected the $m_{sji}$ scores to a parallel and principal components analysis. We used a corresponding procedure for the **G-Type** analysis to extract the rater dimensions, subtracting each animal's predicted score on an item from the raw score. This, too, can be derived in a similar way from regression

$$g_{sji} = x_{sji} - \sum_{m=1}^{k_j} \frac{x_{smi}}{k_j} \qquad (4)$$

$$g_{sji} = x_{sji} - \hat{x}_{si} \qquad (5)$$

$$\hat{x}_{si} = \mu_i + u_{si0} \tag{6}$$

**R Code**

For the **M-Type** analysis, let `Scores` be a data frame with columns `subject` and `rater` of type factor and numeric columns with names `item.names` of the rater’s score of the subject on each item. For convenience we massage the vector `item.names` into a list

```
items <- as.list(item.names)
names(items) <- item.names
```

and transform this list into a list of formulae of the form `item ~ rater`

```
item.formulae <- lapply(items,
                        function(x) {formula(paste(x, '~ rater'))})
```

We then have a function that runs a linear model using each formula on the `Scores` data and returns the residuals

```
m.lm <- function(item.formula, data) {

  model <- lm(item.formula, data=data);
  m <- model$residuals

  return(m)
}
```

We apply this function to each formula and turn the resulting list of residuals back into a data frame

```
M <- as.data.frame(lapply(item.formulae, m.lm, data=Scores))
```

The data frame `M` is then suitable as an input to functions for parallel and principal components analyses

```
library(paran)
library(psych)

m.pa <- paran(M, graph=TRUE)
m.pca <- principal(M, nfactors=m.pa$Retained)
```

The **G-Type** analysis proceeds as above except that the formula construction is of the form

```
item.formulae <- lapply(items,
                  function(x) {formula(paste(x, '~ subject'))})
```

**SAS Code**

For the **M-Type** analysis, let `Scores` be a dataset with columns `subject` and `rater` which are nominal variables and numeric columns with names `item_1`, `item_2, ...` `item_i` of the rater's score of the subject on each of i items. We will output the residuals to a temporary dataset named `m_Scores`

```
proc glm data=Scores;
        class rater;
        model item_1--item_i = rater;
                output out=m_Scores r=m_item_1-m_item_i;
run;
```

The residualized variables stored in the temporary dataset `m_Scores` can then be subjected to parallel analysis and principal components analyses.

We can use a similar method to obtain the variables for the **G-Type** analysis

```
proc glm data=Scores;
        class subject;
        model item_1--item_i = subject;
                output out=g_Scores r=g_item_1-g_item_i;
run;
```

**SPSS Code**

For the **M-Type** analysis, let `Scores` be a dataset with columns `subject` and `rater` which are nominal variables and numeric columns with names `item_1`, `item_2, ...` `item_i` of the rater's score of the subject on each of i items

```
DATASET ACTIVATE Scores.
UNIANOVA item_1 to item_i BY rater
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
```

```
  /SAVE=ZRESID
  /CRITERIA=ALPHA(0.05)
  /DESIGN=rater.
```

The residualized variables, i.e., the `m_scores` will be stored at the end of the `Scores` data set. These variables can be subjected to parallel analysis and principal components analyses.

We can use a similar approach to obtain the variables for the **G-Type** analysis

```
DATASET ACTIVATE Scores.
UNIANOVA item_1 to item_i BY subject
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=ZRESID
  /CRITERIA=ALPHA(0.05)
  /DESIGN=subject.
```

Running Head: DIFFERENTIAL BEHAVIORAL ECOLOGY

# Differential Behavioral Ecology

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# Behavioral Variation

Behavioral variation is of import to evolution. Behavioral differences in, for example, courtship, can lead to reproductive isolation and speciation, a process referred to as ethological isolation (Dobzhansky, 1970, ch 10). As such, the study of behavioral variation can yield important clues about other kinds of diversity. While the study of human behavioral variation in the form of personality research is a mature field with a distinguished record of accomplishments, there has only recently been renewed interest in studying individual differences in nonhuman animal behavior. Research in this area has appeared under various guises, including temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), behavioral syndromes (Sih, Bell, Johnson, & Ziemba, 2004), and personality (Gosling, 2001). While these frameworks all concern individual differences in behavior, they differ in several critical ways. Notably, compared to animal personality research based in human differential psychology, animal personality research arising from behavioral ecology prominently features evolutionary theory as a unifying theme. Other differences include basic assumptions, central research questions, methods, and measurement. Much like behavioral differences that act as barriers to reproduction between individuals within a species we think that these differences between research programs may lead to a less ‘fruitful’ evolutionary science of personality.

The realization by scientists that nonhuman primates are individually recognizable and behaviorally distinct probably began in early laboratory colonies and preceded the formal study of their personality (Crawford, 1938, p. 79; Yerkes, 1939). Later contributions came from researchers such as Itani (1957) who considered introversion and extraversion in Japanese macaques, and Goodall (1986) who described the personalities of the chimpanzees she studied at Gombe. Rather than being simple anthropomorphism (a charge that Yerkes anticipated), the assumption that primate personality should resemble our own has a strong phylogenetic basis. Without evidence to the contrary, we assume that closely related species will be more similar to each other than more distantly related species (Darwin, 1859, ch 13). Thus, how nonhuman primates differ behaviorally should resemble how we differ.

Our own research on nonhuman primate personality led us to believe that the approaches of human differential psychology can benefit research on personality conducted by behavioral ecologists. This revelation came about because nonhuman primates are ideal subjects for studies that link approaches from differential psychology and behavioral ecology. To wit, compared to other animals, our phylogenetic affinity with nonhuman primates, and especially the great apes, makes us more able to 'read' a primate's personality and thus provide reliable and valid ratings (Uher & Asendorpf, 2008). This, and the fact that their social lives and behaviors are complex and distinct, readily lends these species to more comprehensive measures that can educe a whole personality structure. In addition, while practical and ethical barriers prevent studying humans with some of the behavioral ecologists' experimental manipulations (see, e.g. Réale et al., 2007) or conducting "field" research, such barriers in studying nonhuman primates are few. Finally, this also means that tools for assessment adapted from human studies will capture much of the variety present in nonhuman primates.

Compared to findings in studies of fish or birds, results from nonhuman primate personality research are also more likely to be informative to human studies. This point is underscored by a study on the genetic correlation of human personality and subjective well-being (Weiss, Bates, & Luciano, 2008) which replicated the findings of an earlier chimpanzee study (Weiss, King, & Enns, 2002). Also, recent studies on the relationship between human personality and immune functioning (Ironson & Hayward, 2008; Ironson, O'Cleirigh, Weiss, Schneiderman, & Costa, 2008; O'Cleirigh, Ironson, Weiss, & Costa, 2007) were anticipated by studies in rhesus macaques (Capitanio, Mendoza, & Baroncelli, 1999; Maninger, Capitanio, Mendoza, & Mason, 2003).

We hope to show that, while each of these research programs asks interesting questions, to understand the nature of personality, i.e., its ultimate origins in humans and other species, requires a combination of approaches. Based on studies of personality ratings in humans and in nonhuman primates, we believe that nonhuman personality research in other animals would benefit by incorporating approaches from differential psychology research. These approaches include more broadly defining and measuring traits, conducting epidemiological studies in natural communities, looking at personality profiles, and examining the covariance among traits or structure.

## The Study of Personality in Behavioral Ecology

### Research Questions

#### Trade-Offs and Life-History Strategies

Behavioral ecologists who study nonhuman personality follow the approach outlined by Tinbergen (2005); they formulate and test hypotheses concerning ultimate causation or how a particular behavior is adaptive. This research program also posits that existing behaviors represent an optimal trade-off between fitness costs (e.g., energy expended) and benefits (e.g., reproductive outcomes). The study of optimization in classical ethology or behavioral ecology has typically been at the species level. For example, one might test whether the pattern of foraging within a species is such that individuals switch to another patch when the amount of energy from food they gain from one patch is exceeded by the cost of continued foraging in that patch (MacArthur & Pianka, 1966). Studies of personality variation by behavioral ecologists have brought this focus on trade-offs to the study of intra-specific behavioral variation.

Behavioral ecology also concerns the study of life-history strategies (Pianka, 1970). Life-history strategies comprise a suite of traits that are co-adapted for particular environments. These traits reflect trade-offs between reproductive and somatic effort. Unstable environments lead to species that are r-selected, that is, characterized by reproductive effort. These r-selected species (e.g., rabbits) have short generation times, a lower probability of offspring survival, and small body size. On the other hand, stable environments lead to species that are characterized by somatic effort or K-selected. Individuals within K-selected species (e.g., elephants) possess traits indicative of somatic effort, namely larger body size, high parental investment, and greater longevity.

Dall, Houston, and McNamara (2004) conceptualized personality as alternative behavioral strategies and Wolf, van Doorn, Leimar, and Weissing (2007) placed it within the context of life-history evolution. An individual’s optimal behavior depends both on its own condition and behavioral history as well as on the behaviors of others in the population. For example, an animal with poor body condition and, therefore, a low potential for reproductive success, would do better to invest in foraging, even if this increases predation risk. Likewise, the advantage of behaviors like aggression depends both on how others are behaving and on population density. Normally, aggression leads an individual to out-compete its neighbors for resources, but at low population densities with moderate competition, high aggression might be counter-productive, leading to lower fitness (Dingemanse, Both, Drent, & Tinbergen, 2004; Sih et al., 2004).

Personality may also become co-adapted with life-history traits such as the trade-off between growth and mortality (Biro & Stamps, 2008; Stamps, 2007). As growth rate is known to vary consistently between individuals in many different species, individuals that require an increased food intake benefit from a personality style suitable for high foraging rates, e.g., by being bold, aggressive, or explorative. The maintenance of variation in both productivity and behavioral traits require and reinforce each other.

This approach to the study of personality and life-history strategies should be distinguished from that typically conducted in humans or other primates. In the study of humans and nonhuman primates the focus is typically on how individual differences in some personality dimension are related to individual differences in life-history outcomes. In the non-primate personality literature researchers are less interested in species-typical behaviors or fixed action patterns than in how personality is expressed, the relation between personality and fitness, how combinations of personality traits may be adaptations for particular ecological niches, how the presence or absence of variation can be explained by ecological factors, and the maintenance of heritable genetic variation. On a methodological level, the phylogenetically-informed inferences and arguments from theory made by workers coming from the tradition of human psychology (Gosling, 2008; Gosling & Graybeal, 2007; Gosling & John, 1999; Penke, Denissen, & Miller, 2007b) are distinct from the heavy lifting of measuring the strength and mode of natural selection practiced by behavioral ecologists (Dingemanse & Réale, 2005). While both traditions are engaged with evolutionary theory, empirical analyses from evolutionary biology are featured more frequently and more prominently in behavioral ecology (Dingemanse & Réale, 2005; Open Peer Commentary, 2007) than in differential psychology (Eaves, Martin, Heath, Hewitt, & Neale, 1990).

## The Persistence of Heritable Variation

Personality variation in humans and other animals is, in part, genetic. The heritability of personality traits has been estimated for a number of animal species (van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005). Both behavioral ecologists and differential psychologists have adopted a number of methods for estimating heritability, although a method uniquely available to studies of nonprimate animals is realized heritability via selection experiments. Behavioral ecology research has also examined the genetic variance of personality in wild populations and has gone beyond estimating heritability by attempting to understand how genetic variation in personality traits are maintained within specific populations. If personality traits in primates show similar levels of heritability, then differential psychologists should share a concern for how this variation is maintained.

A review of the literature suggested that approximately 50% of the variance of all five human domains was heritable with little to no variance being accounted for by the shared family environment (Bouchard & Loehlin, 2001). There have also been several recent studies on the genetics of personality in nonhuman primates. One study which examined the heritability of personality in 145 zoo chimpanzees found that, of the six personality dimensions identified by personality ratings (King & Figueredo, 1997), only Dominance was significantly heritable ($h^2 = .62$; Weiss, King, & Figueredo, 2000). A later study of rhesus macaques examined the heritability of seven factors derived from reactions to anxiety tests (Williamson et al., 2003). They found that individual differences on the Movement ($h^2 = 1.00$), Distress cues ($h^2 = .58$), Early independence ($h^2 = .83$), Explore familiar environment ($h^2 = .47$), and Explore novelty ($h^2 = 1.00$) factors were heritable; neither the Distress vocalizations nor Delayed independence factors were heritable. In a study of vervet monkeys, Fairbanks et al. (2004) found that Social Impulsivity was heritable ($h^2 = .35$). Fairbanks and her colleagues also found evidence for the heritability of the two facets of Social Impulsivity: Impulsive Approach ($h^2 = .25$) and Aggression ($h^2 = .61$). Finally, Rogers, Shelton, Shelledy, Garcia, and Kalin (2008) found evidence that two measures of behavioral inhibition (likely related to Neuroticism) in juvenile rhesus macaques were influenced by additive genetic effects (freezing: $h^2 = .38$; vigilance: $h^2 = .91$).

Molecular genetic research in nonhuman primates supports the findings of quantitative geneticists. Bethea et al. (2004) found evidence linking the serotonin transporter linked polymorphic region (5HTTLPR) and reactions to several tests of anxious behavior or Neuroticism: monkeys that had two short forms of this allele (s/s) displayed greater anxiety than monkeys who had two long forms of the allele (l/l) or who were heterozygous (s/l). A molecular genetic study of a heritable phenotype related to Neuroticism (novelty seeking) found that latency to approach a novel object was lower in vervet monkeys that had the five- as opposed to six-repeat polymorphism of the dopamine D4 receptor gene (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007). Interestingly, experimental studies of genotyped rhesus macaques suggests that the effects of genetic polymorphisms on behavioral indicators of personality differs as a function of early environmental stressors (Champoux et al., 2002; Kraemer, Moore, Newman, Barr, & Schneider, 2008; Newman et al., 2005).

How this additive genetic variation is maintained remains a puzzle for under directional or stabilizing selection, one would expect that the heritable variance in any given trait to be negligible (Barton & Turelli, 1989; Falconer & Mackay, 1996). This has led to considerable debate. Some theorists have suggested that variation in human psychological traits is maintained by neutral selection (Tooby & Cosmides, 1990). The neutral theory states that most mutations have neither beneficial nor deleterious fitness consequences (Kimura, 1983, 1986) leading to a balance between the input of new variation by mutation and its removal by drift (Lynch & Hill, 1986). Others have taken an adaptationist stance, and see individual differences in humans and other animals as arising from mechanisms such as frequency-dependent selection, sexual selection, or any number of mechanisms by which individual differences emerge because there are multiple niches or that what is ‘optimal’ depends on the social and non-social context (see Open Peer Commentary, 2007 for a discussion; Penke, Denissen, & Miller, 2007a; Penke et al., 2007b).

To explore these hypotheses necessitates adopting additional methods from behavioral ecology to examine micro-evolutionary trends such as fluctuations in selection pressure across time (Dingemanse et al., 2004) or across environments (Dingemanse et al., 2007). Unlike research on primates, these ecologically informed studies have measured selection on temperament (Bell & Sih, 2007; Réale & Festa-Bianchet, 2003) rather than relating personality to fitness in only the broadest terms.

## Personality Measures

Behavioral ecologists who study personality typically use similar methods as one another. While there are notable exceptions (e.g., Réale & Festa-Bianchet, 2003), one methodological feature common to much of this research is the use of small numbers of subjects that are easily (and safely) subjected to behavioral tests or experimental manipulations. Another common methodological feature is a preference for behaviorally-based measures of personality, which has its roots in the traditional ethological emphasis on observation and the aversion to seeming anthropomorphism (Tinbergen, 1951). Finally, these studies typically focus on one or two rigidly-defined traits such as boldness, aggressiveness, or exploratory behavior. The definitions of these traits does not constrain how they are measured, which might include behavioral or physiological (hormonal, serotonergic, etc.) indicators. This framework does not assume that intercorrelations among traits are the product of underlying latent constructs née personality factors, and leaves this as a question to be investigated (Réale et al., 2007). Instead, the approach typically taken by many behavioral ecologists is to measure several behaviors thought to indicate a particular personality trait and test whether they are correlated (Stamps, 2007).

In one example of this approach, Réale, Gallant, Leblanc, and Festa-Bianchet (2000) measured boldness (in terms of trappability) and docility (behavior during handling) in female sheep, found they were weakly correlated, and concluded that they represented two separate traits. Sometimes a single trait is examined, as in Daniewski's and Jezierski's (2003) study of exploratory behavior in rabbits using an open field test.

In short, the behavioral differences currently studied by ecologists were never meant to be comprehensive. Instead, these studies rely on hypothesis-driven observations and experiments that attempt to assess how a few narrowly defined traits are related to ecological or social variables. It will be necessary to add further traits to fully define most of the intra-specific behavioral variation present, particularly in species with more complex social lives.

# The Study of Personality in Differential Psychology

## Personality Measures

### Historical Precedents

The study of human—and to some extent primate—personality has different origins. While early biographers such as Plutarch (46 AD-120 AD) ascribed personality characteristics to their subjects, the study of human personality as a science has a shorter history. Research in human personality originated from Francis Galton's (1822-1911) study of human individual differences, which also led to the development of modern psychometrics, statistics, behavior genetics, and cognitive abilities research.

The insight that personality descriptors may be found in natural languages and can be used to construct personality inventories came later (Allport & Odbert, 1936), and is still one of the most popular way of studying human personality. These data are most commonly analyzed using factor or principal components analysis (Gorsuch, 1983), which involve examining covariances among variables to determine whether groups of variables cluster together, i.e., are indicative of one or more latent underlying constructs (factors or components). Each factor or component can be described with respect to the amount of variance it accounts for (its eigenvalue) and the degree to which each variable is related to the factors or components (loadings).

## Debates About Traits

The study of human personality via ratings was and is still not without debate. The most serious charge by critics was that personality traits did a poor job of predicting behavior and were inconsistent across situations (Mischel, 1968). In fact, like early (and some contemporary) ethologists and behavioral ecologists, Mischel favored using behavioral measures. This challenge was later answered by research showing that personality measures were related to behavior if behavior was aggregated over time (Epstein, 1979). Personality researchers also showed that self-ratings and observer-ratings were correlated (McCrae et al., 2004), that personality was mostly stable in adulthood (Costa & McCrae, 2002), and that personality predicted a broad range of important outcomes (Ozer & Benet-Martínez, 2006; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007).

Other debates, many of which are still ongoing, revolved around the number of personality dimensions needed to explain human personality differences (Costa & McCrae, 1992a, 1992b; Eysenck, 1992a, 1992b; Lee, Ogunfowora, & Ashton, 2005). For the purpose of this chapter, we will focus our discussion on the Five-Factor Model (FFM; Digman, 1990), as it is the dominant model in human personality research, which contends that five normally-distributed dimensions or domains---Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness---describe human personality differences.

While it is not possible to comprehensively summarize each of the five personality domains, we feel it is useful to highlight some of their cardinal characteristics as described by Costa and McCrae (1992c). Individuals on the low end of Neuroticism are emotionally stable, well-adjusted, and exhibit low levels of negative affect; individuals on the high end tend to be emotionally unstable, have problems with adjustment, and have high levels negative affect. Individuals high in Extraversion are more sociable, assertive, active, and experience more positive affect whereas those low in Extraversion do not seek out others' company and are independent, less active, and experience less positive affect. Individuals scoring higher in Openness to Experience tend to be curious, value new experiences and feelings, and unconventional whereas individuals scoring on the low tend to be less curious, prefer the familiar to the novel, and are more conventional in their outlooks and behavior. Individuals higher in Agreeableness tend to be helpful, trusting, and more inclined to cooperate rather than compete. On the other hand, individuals lower in Agreeableness tend to be less inclined to help others, suspicious and cynical, and more competitive. Finally, individuals ranking high in Conscientiousness will be reliable, organized, directed, and self-disciplined whereas those lower in Conscientiousness will often be less reliable, disorganized, directionless, and lacking in self-discipline.

While laymen would be inclined to see one end of each personality domain as a desirable state of affairs, when considered within the framework of evolution, it is easy to imagine the advantages and disadvantages presented by various levels of each of these five domains. In fact, Nettle (2006; Table 1) has outlined possible benefits and costs to the high end of each domain which we briefly detail. While high Neuroticism could offer benefits such as increased vigilance, it might also carry costs including poorer interpersonal relationships which are critical in social species. Extraversion, while possibly leading to benefits such as mating success might also cost in terms of harm from risk taking behaviors. High Openness to Experience, while being related to benefits such as increased creativity carries the possible costs of having unusual or even harmful beliefs. High Agreeableness may benefit individuals by making them more valued partners in coalitions, though it may also lead to individuals being at greater risk from social cheaters. Finally, while Conscientiousness may benefit individuals by helping them meet long-term goals, it can potentially cost them the benefits of more immediate fitness gains.

This framework offers fascinating possibilities for considering the evolution basis of heritable variation in the FFM. Recent research which couches personality differences within evolutionary theory has made progress in understanding the ultimate causes of personality. Moreover, prior and ongoing research in seemingly unrelated areas has also yielded insights relevant to personality evolution.

## Is the Five-Factor Model Related to Life-History Strategies?

One reason why the differential psychology approach may appeal to behavioral ecologists is that the measures derived using this approach are likely related to evolutionarily-relevant characteristics such as life-history strategies. Figueredo, Vásquez, Brumbach, and Schneider (2004; 2007) argued that, although life-history strategy is typically used to differentiate species, it is also a dimension on which individuals within a species differ. In other words, while humans are generally suited to a long-term (K-selected) strategy, there is still considerable variation. To test whether human personality dimensions were related to how K-selected individuals were, Figueredo et al. (2004; 2007) conducted two analyses. In the first they showed that factor analysis of either the phenotypic or genetic covariance among questionnaire items concerning altruism, reproductive effort, parenting effort, and other aspects of life history revealed a single factor, which they named K. Figueredo et al. also conducted a second factor analysis on the covariance among K and the five human personality factors and found a single higher order factor. These findings are certainly suggestive. However, these studies are limited in that they are cross-sectional and do not rule out the possibility that correlations may have arisen because personality and outcome measures were assessed using the same method, i.e., questionnaires (see Campbell & Fiske, 1959 for a detailed discussion).

Behavioral ecologists used to objectively measured life history variables will be understandably skeptical of these cross-sectional questionnaire-based results. However, prospective epidemiological studies linking personality to real-world health outcomes also suggest a relationship between human personality dimensions and life-history strategy. This is especially true for Conscientiousness, which, of the five human dimensions, is most consistently related to a wide variety of health outcomes (Bogg & Roberts, 2004; Roberts et al., 2007). One set of findings demonstrates that, across studies of samples differing widely in health, age, socioeconomic status, culture, cognitive ability, and other characteristics, people who are high in Conscientiousness live longer (Kern & Friedman, 2008). Conscientiousness is also related to slower disease progression; research on HIV infected persons has shown that higher Conscientiousness was related to reductions in viral load and increases in CD4 counts (Ironson et al., 2008; O'Cleirigh et al., 2007). Moreover, recent research has shown that higher Conscientiousness is associated with a reduced risk of Alzheimer's disease and cognitive decline, suggesting slower senescence (Wilson, Schneider, Arnold, Bienias, & Bennett, 2007).

The fact that Conscientiousness is a particularly robust and strong predictor of mortality and other health outcomes is interesting. More interesting still is the fact that, despite the fact that Conscientiousness leads to health behaviors (Bogg & Roberts, 2004), these possible mediating variables only explain only part of the relationship between Conscientiousness and mortality (Martin, Friedman, & Schwartz, 2007). Thus, the protective effect of Conscientiousness may be due to Conscientiousness reflecting a more long-term or K-selected orientation, including facets of competence, order, dutifulness, achievement striving, self-discipline, and deliberation (Costa & McCrae, 1992c). This suggests that Conscientiousness may be particularly well-positioned to capture individual differences in life history.

If Conscientiousness were the only personality domain related to these variables, it would be problematic. This is because, to date, Conscientiousness dimensions have only been identified in chimpanzees and humans (Gosling & John, 1999). It is therefore good that other personality domains are also related to health outcomes. Agreeableness is comprised of facets such as altruism and compliance (Costa & McCrae, 1992c), which are related to the K-selected end of the life-history strategy spectrum (Pianka, 1970). Epidemiological research has generally found that Agreeableness is related to reduced cardiovascular disease risk (see Whiteman, Deary, & Fowkes, 2000 for a review) and longevity (e.g., Weiss & Costa, 2005). However, these findings have not been replicated in all studies (e.g., Iwasa et al., 2008).

Neuroticism, too, may reflect some aspects of life-history strategy, especially in terms of short-term orientation, e.g., the impulsiveness facet. However, the relationship between Neuroticism and mortality is markedly less clear: some studies show that it is a risk factor (e.g., Wilson, de Leon, Bienias, Evans, & Bennett, 2004), others have found that it is protective (e.g., Weiss & Costa, 2005), and still others find no significant relationship (e.g., Iwasa et al., 2008).

The reduced fidelity among studies examining the relationship between personality domains other than Conscientiousness and mortality should give one pause; it suggests that the association between personality and life-history strategy is probably more complex than suggested by the results of questionnaire-based studies (e.g., Figueredo et al., 2004; 2007). There are several possible explanations for why personality dimensions potentially related to life history are not related to health outcomes. Among these explanations are that effect sizes are smaller, and, as such, it might be difficult to replicate these findings. However, failures to find this effect have occurred in some studies (Almada et al., 1991) that used very large samples. This also does not explain why in some studies of Neuroticism and mortality, the effects are significant, but in the opposite direction (e.g., Weiss & Costa, 2005). A final possibility is that contextual or environmental factors, such as population density or resource availability may attenuate or modify the way in which human personality domains are related to these outcomes.

## How Differential Psychology Can Enrich Studies of Personality in Behavioral Ecology

As pointed out by Gosling (see chapter X this volume) and Capitanio (in press), researchers can gain insight into human personality from studies of animal personality. We echo this sentiment, but add that animal personality studies, especially those conducted by behavioral ecologists, can benefit from human personality research. In particular, we emphasize the benefits of adopting a multivariate approach to measurement, asking questions about the impact of multiple dimensions, and examining personality structure.

### Improving Measures

As we previously indicated, there are marked differences in how personality is measured in these disciplines. While neither approach possesses an absolute advantage, we feel that behavioral ecologists could benefit from using the some tools developed by differential psychologists. To do so we will first highlight the advantages and disadvantages of behavioral measures. we will then offer several recommendations.

#### Advantages of Behavioral Measures: Uniformity

As noted previously, behavioral ecology research on personality typically relies on single ‘item’ measures of one or two aspects of personality. There are multiple advantages to this approach. First, these measures are easily replicable within and across species, thus facilitating their use by multiple investigators. Second, unlike rating scales, individuals within a sample can be quickly assessed. Third, unlike using rating scales, where raters need to know individuals for a considerable period of time, responses to behavioral tests can be assessed by naïve individuals who have had little or no experience with the individual animals. Finally, these measures benefit those wishing to conduct meta-analyses as the uniformity in personality measures makes comparing studies straightforward.

## Disadvantages of Behavioral Measures: The Lack of Context

Like all methods, there are drawbacks to this approach. One drawback is that this method assumes that a behavior measured in one species has the same meaning in other species. While this assumption might very well hold, it is impossible to know unless there are multiple measures of multiple personality domains (Cronbach & Meehl, 1955; Uher, 2008a, 2008b).

To illustrate the problem, consider the bold-timid dimension often studied by behavioral ecologists (Réale et al., 2007). Behavioral ecologists usually define this dimension as an individual's reaction to risky yet non-novel situations and have drawn broad conclusions concerning the evolutionary importance of individual differences in the bold-timid dimension based on this definition. However, an examination of a related measure in studies of zoo chimpanzees (King & Figueredo, 1997) and orangutans (Weiss, King, & Perkins, 2006) suggests that this assumption does not always hold. Both studies used comparable questionnaires, which only differed in that the questionnaire used to assess orangutan personality included five additional items (for more details see Weiss et al., 2006; pp. 504-505). The item timid is common to both questionnaires and defined as “Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.” In chimpanzees, this item is a clear marker of the Dominance factor, having a loading of -.81. By examining the other items that load on Dominance, we see that individuals described as timid are also, for example, less persistent and more dependent (see Table 1 in King & Figueredo, 1997). On the other hand, in orangutans timid is a clear marker of the Neuroticism factor, its loading being .70. Orangutans described as timid are more likely to be excitable and impulsive, but less likely to be cool (see Table 3 in Weiss et al., 2006).

Clearly, without the context of other items, the meaning of timid would be misunderstood in chimpanzees, orangutans, or both. Worse for the study of nonhuman personality is that, without this context, researchers may be led down blind alleys and comparisons of results across studies may be misleading.

### Recommendations

It is not our intention to be scolds, and, given their advantages, we think it would be foolish for behavioral ecologists to abandon their measures. Instead we advocate that, where feasible, researchers use multiple types of measures (e.g., ratings, experimental tests, behavioral observations) of multiple personality constructs (e.g., Neuroticism, Extraversion, Agreeableness). This method, first advanced by Campbell and Fiske (1959), later expanded upon by others (see, e.g. Shadish, 1992; Widaman, 1985), and applied in a study of great ape personality (Uher & Asendorpf, 2008) is based on the premise that traits may be correlated because they reflect the same underlying trait (e.g., Neuroticism) or method (e.g., an experimental paradigm). Thus, by measuring multiple constructs using multiple methods, one can better understand and more reliably measure the traits of interest. Once we understand the species-specific contexts in which a trait such as timid is expressed, we can begin to place it within the behavioral and social ecology of the species. Under what ecological conditions or social organizations, for instance, does boldness versus timidity become a facet related to social dominance rather than anxiety?

## Adopting Multidimensional and Multivariate Approaches

In addition to our recommendations concerning measures, we also feel that behavioral ecology could reap great rewards and insights by studying multiple traits. To support this suggestion we will highlight research in psychology suggesting that individual traits or dimensions do not always act alone. More fundamentally, we will next highlight how studies of personality structure may benefit behavioral ecology.

## Profiles

Personality profiles in differential psychology. Until relatively recently, like behavioral ecology research in personality, human personality research has focused on examining a single dimension at a time. However, sometimes it may be useful to study or understand the “whole person” (or animal in this case). That is, one wishes to examine how the combination of an individual’s traits may be related to important outcomes. At present, the study of personality profiles has been focused on mental as opposed to physical health outcomes, including subjective well-being and happiness, affective disorders such as depression, and personality disorders.

The study of subjective well-being or happiness has shown major advances since the advent of interest in the area (Diener, Lucas, & Scollon, 2006; Diener, Suh, Lucas, & Smith, 1999). While there is also growing evidence from large longitudinal panel studies that subjective well-being can be changed by major life events, e.g., marriage (Lucas, Clark, Georgellis, & Diener, 2003), a consistent finding across several studies has been that subjective well-being is reliably predicted by all five human personality dimensions, especially low Neuroticism and high Extraversion (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008).

Some may wish to dismiss the study of happiness and related personality profiles as merely reflecting whether fortune (genetic or environmental) smiles upon an individual. However, a recent review of the literature suggests that this may be premature as subjective well-being actual predicts numerous positive outcomes such as more successful marriages and higher income (Lyubomirsky, King, & Diener, 2005) as well as longevity (Danner, Snowdon, & Friesen, 2001). As such, one could hypothesize that subjective well-being and associated personality profiles predict outcomes reflecting adjustment to one’s environment.

As suggested by its relationship with mortality (Kinder et al., 2008), major depression may have high fitness costs or be related to life-history strategy. Prospective studies have highlighted the depression risk conferred by high Neuroticism and low Extraversion over long periods of time and that this relationship is mediated by common genetic factors (Kendler, Gatz, Gardner, & Pedersen, 2006).

Even though high Neuroticism and low Extraversion are risk factors for depression, many individuals exhibiting either or both of these risk factors do not become depressed. To study how other personality dimensions moderate this risk, Weiss et al. (2009) studied the relationship between the five personality dimensions and 28 of the personality styles and depression in older adults. Their results indicated that, while high Neuroticism and low Conscientiousness were risk factors, they only predicted depression in the context of the individual’s standing on other personality dimensions.

Personality disorders refer to underlying and persistent sets of behaviors, cognitions, and affective dispositions that can lead individuals and those close to them to experience many difficulties and general impairment (American Psychiatric Association, 2004). Unlike personality measures, personality disorders have traditionally been operationalized as categories or types. This conceptualization is captured in the major classification manuals used by psychiatry, such as the Fourth Edition Text Revision of the Diagnostic and Statistical Manual (DSM-IV-TR; American Psychiatric Association, 2004). For example, individuals exhibiting antisocial personality disorder may encounter repeated legal difficulties because of their violation of social norms and rules. The DSM-IV-TR criteria used to classify individuals as having antisocial personality disorder are that they demonstrate:

> A. A pervasive pattern of disregard for and violation of the rights of others occurring since age 15, as indicated by at least three of the following:
> (1) Failure to comform to social norms and repeated lawbreaking.
> (2) Deceitfulness.
> (3) Impulsivity of failure to plan ahead.
> (4) Irritability and aggressiveness.

(5) Reckless disregard for safety of self or others.
(6) Consistent irresponsibility.
(7) Lack or remorse.

B. The individual is at least 18 years of age.
C. There is evidence of Conduct Disorder with onset before age 15.

It is beyond the present chapter's scope to detail the problems with this typological approach. However, these problems have led to a growing unease with its use and advocacy for a dimensional approach based on the FFM (Widiger & Frances, 2002).

The research supporting the move toward a dimensional approach suggests that personality disorders are, in fact, reflections of maladaptive combinations of extremely high or low standings on the five personality dimensions. A recent meta-analysis on the relationship between the five human personality dimensions and ten DSM-IV-TR personality disorders revealed that high Neuroticism and low Agreeableness were consistent across most disorders (Saulsman & Page, 2004). This same meta-analysis also found that, for the most part, personality disorders can be distinguished by standings on the other dimensions. For example, antisocial personality disorder is also characterized by low Conscientiousness, whereas avoidant personality disorder is characterized by low Extraversion.

Personality profiles in behavioral ecology. The accumulated research suggests that personality profiles are critical to understanding potentially fitness-related outcomes in humans such as health and adjustment. Although it might be difficult or impossible to study phenomena as complex as personality or affective disorders in many nonhuman species, including primates, incorporating personality profiles could expand the scope of nonhuman personality research and may yield numerous insights. In the case of the role of different environmental or ecological contexts in maintaining genetic personality variance (e.g., Dingemanse et al., 2004), personality dimensions other than the one of interest in a particular study may be an additional contextual background in which the personality dimension of interest operates. This would provide yet another means by which heritable variation may be maintained through selection on correlated traits (Lande & Arnold, 1983; Merilä, Sheldon, & Kruuk, 2001). A hypothetical example might be a species with a positive genetic correlation between exploratory behavior and boldness (great tits; van Oers, de Jong, Drent, & van Noordwijk, 2004). In an environment with a high population density but also significant predation, these two traits could be selected in the opposite direction. While a fast exploring individual would be able to outcompete conspecifics for access to food, its high boldness would raise its risk to predation. Access to food and mates is usually compared with rank, which in primates is captured by personality dimensions such as Dominance. For a primate, the social networks through which influence operates can be equally effective for controlling group dynamics, so high Extraversion and Agreeableness would be beneficial.

## Structure

Why ask questions about structure? Another way in which a multivariate approach can advance the study of nonhuman personality research is via the elucidation of personality, i.e., the way in which traits cluster together as revealed by their loadings on different factors. Instead of focusing on the relationship of each individual's standing on one or more personality traits to life-history strategy or context and how heritable personality variation is maintained, the study of personality structure would permit researchers to examine personality at higher levels of organization, including species.

The universality of structure in humans. Human personality research strongly indicates that while variation on any number of personality traits is the norm, the nature of the covariance among these traits is a human universal. The majority of this evidence is based on cross-cultural studies of human personality in which a well-validated measure developed in one culture is administered to members of another culture to see whether a similar factor structure emerges. The most ambitious study to date examined ratings on a well-validated measure of the FFM, the Revised NEO Personality Inventory (NEO-PI-R; Costa & McCrae, 1992c). The participants were college students who were members of 50 Western and non-Western cultures spanning six continents and were asked to rate other members of the culture whom they knew well (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005). Overall, McCrae and his colleagues found evidence that the five factors found in American samples were reliably replicated in all of the cultures, with poorer replicability being mostly attributable to problems with data quality and smaller sample sizes.

The universality of structure in chimpanzees. Evidence showing that personality structure may also be stable across different populations of nonhuman primates in different settings is accumulating. King and Figueredo (1997) obtained ratings from zoo keepers and volunteers on 100 zoo-housed chimpanzees. The 43-item questionnaire was based on human personality questionnaires and attempted to sample items from all five human domains; factor analysis of the ratings revealed a broad chimpanzee-specific factor labeled Dominance as it reflected dominance and competitive prowess and five factors similar, though not identical, to the five human factors.

Three studies using identical or comparable questionnaires have examined whether the factor structure derived by King and Figueredo (1997) replicated in different samples. The first study used a sample comprised of ratings on 43 chimpanzees living in a naturalistic sanctuary in the Republic of the Congo rated on a French-language translation of the questionnaire and 74 zoo chimpanzees rated on the same questionnaire (King, Weiss, & Farmer, 2005). The second study (Weiss, King, & Hopkins, 2007) involved 175 chimpanzees housed at Yerkes National Primate Research Center rated using the same questionnaire as the original 100 chimpanzees. The third study was based on ratings of 146 chimpanzees housed in zoos, research centers, and a sanctuary in Japan (Weiss, Inoue-Murayama et al., 2009). The chimpanzees in this last study were rated on a translated version of the questionnaire and their factor structure was compared to that of the original 100 chimpanzees. In all three studies high congruence coefficients (Haven & ten Berge, 1977) suggested that Dominance, Extraversion, Conscientiousness, and Agreeableness clearly replicated and that the overall structures of the original chimpanzee personality structure was replicated. On the other hand, considerably lower congruence coefficients indicated that neither Neuroticism nor Openness was replicated in these studies. However, loadings on these two factors were not at odds with definitions of Neuroticism or Openness and a follow-up analysis revealed that these factors also did not replicate in a second sample of zoo chimpanzees. These findings suggest that the failure to replicate the Neuroticism and Openness dimensions is probably attributable to properties of the questionnaire and not their absence in other samples (see King et al., 2005 for more details).

Top-down versus bottom-up approaches. Saucier and Goldberg (2001) have argued that the apparent universality of personality structure is an artifact reflecting the top-down or etic approach used by McCrae and his colleagues (2005), i.e., the structure is imposed by virtue of the items within the questionnaire. Saucier and Goldberg favor bottom-up or emic approaches, such as the lexical approach, which involve assessing individuals within cultures using personality descriptive adjectives derived from within those cultures. A similar criticism could, of course, be raised to question the seeming universality of chimpanzee personality structure or rating nonhuman primates and other animals on questionnaires based on the FFM (Uher, 2008a, 2008b). Uher’s alternative approach is also a bottom-up approach in that she recommends that one base measures or questionnaires of nonhuman personality on a species’ naturally occurring behaviors.

However, there is evidence that these criticisms of the top-down approach may be overstated and that use of the same questionnaire items will not obscure species differences. For example, while the questionnaire King and Figueredo (1997) used to study chimpanzees was based on the FFM, the structure that emerged in chimpanzees differed from the human structure: it included a sixth factor, Dominance, and the other factors were not identical to their human analogues. Similarly, when a slightly expanded version of this questionnaire was used to assess orangutan personality (Weiss et al., 2006), the structure differed from that of chimpanzees and humans: Conscientiousness and Openness items loaded on a single factor named Intellect and Dominance was more narrowly defined.

Studies using a personality questionnaire designed by Stevenson-Hinde and Zunz (1978) have also revealed differences. A study of rhesus macaque personality found four factors: Sociable, Equable, Confident, and Excitable (Capitanio, 1999). On the other hand, a study of gorillas found four seemingly different factors: Extroverted, Dominant, Fearful, and Understanding (Gold & Maple, 1994).

Of course, in the latter example, different names may obscure similarities between the rhesus macaque and gorilla personality structures. However, a visual inspection of the loadings suggests that these factors differ (Capitanio, 1999, Table II; Gold & Maple, 1994, Table 1). To test how similar these factors were, we conducted an orthogonal targeted Procrustes rotation on the published results of these studies; this type of factor rotation involves rotating the structure derived from one sample so that it maximally resembles that of another structure (McCrae, Zonderman, Bond, Costa, & Paunonen, 1996). For the present analysis we rotated the gorilla factor structure to the rhesus macaque factor structure using only the loadings of the 12 items that were in common between the two studies. Also, because exact factor loadings were not provided for the gorilla data, we defined loadings in both samples as being equal to 0, 1, or -1 depending on whether the item was not associated with the factor, positively associated with the factor, or negatively associated with the factor, respectively. The congruence coefficients suggest that rhesus structure was not replicated in gorillas (.73); only the Equable factor replicated (.86), and that the loadings of only five items (equable, understanding, sociable, playful, and curious) replicated (see Table 1). In short, this analysis suggested that the factor structures of gorillas and rhesus macaques differed.

What can be learned from a study of structure? Once a sufficient number of personality structures are determined using comparable instruments, researchers can begin comparing them in a phylogenetic context to infer the historical patterns (when, where, and why) of personality evolution (Gosling & Graybeal, 2007). For example, while the broad personality domains found in the great apes are similar, we are still left to puzzle out the ultimate causes of structural differences, e.g., why orangutans share no domain equivalent to Conscientiousness or why humans lack a Dominance domain. Presumably these structural differences will be related to adaptations by each species to their ecological and social environments. A challenge in phylogenetic inference about personality structures is that personality dimensions are not species-typical traits (as a new anatomical feature or behavior might be), but rather a feature that differs among individuals. Orangutans lack of a distinct Conscientious domain but this does not mean they are unconscientious. The maintenance of variation of personality within species can also be informed by the determination of structure. If dimensions of a species' personality structure are genetically correlated, then knowing the whole structure (not just one or two dimensions) would be necessary to understand how personality traits respond to correlated selection and relate to life-history trade-offs.

## Conclusions

We are pleased to see the recent growth and development of research in nonhuman animal personality research. However, we think that the relatively minor schism between behavioral ecologists and differential psychologists, if allowed to grow wider, can potentially threaten progress in this endeavor. If this occurs, such an event would not be without precedent in the study of animal behavior (see, e.g., the early rift, now mostly healed, between ethology and comparative psychology). As in biological evolution, we think that when research programs become overly-specialized and rigid, i.e., lack diversity, they are threatened with extinction, or, at the very least, becoming a degenerating research program (Lakatos, 1976).

While these potential consequences are dire, preventing this form of ethological isolation may be relatively simple. The present chapter and volume represent two such efforts. In addition, we suggest that behavioral ecologists and differential psychologists try to incorporate each other's methods, publish in each other's respective journals, and attend each other's conferences. Also, when appropriate, graduating Ph.D.s in behavioral ecology should consider seeking placements in differential psychology labs.

Thus, researchers studying personality could opt to follow their own ways and end up as the ring-tailed lemurs of animal behavior research, whiling away on isolated scientific islands. Alternatively, these researchers could choose to increase their behavioral diversity and spread over a wide range of environments, much like rhesus macaques, or even humans.

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# Acknowledgements

Alexander Weiss would also like to thank Jim King, Paul Costa, and Jeff McCrae for their invaluable advice, collaborations, support, collegiality, and wisdom that eventually led to many of the thoughts presented in this chapter. Mark James Adams thanks Michael Huffman and Goro Hanya for fostering his interest in primate behavior and Nina Won for all her encouragement. In addition, we think this chapter was markedly improved by comments and suggestions offered by Jim King, Melissa Gerald, and the two reviewers. Finally, we wish to express our gratitude to the editors of the present volume for inviting us to contribute to this exciting work.

Table 1

Gorilla Personality Factor Structure Rotated to Rhesus Macaque Factor Structure

| | Factor | | | | |
|---|---|---|---|---|---|
| Item | Equable | Confidence | Excitable | Sociable | Congruence |
| Equable | .98 | .00 | .03 | .19 | .98 |
| Understanding | .98 | .00 | .03 | .19 | .98 |
| Slow | .19 | .01 | -.22 | -.96 | .19 |
| Confident | -.01 | .55 | -.81 | .19 | .55 |
| Aggressive | .01 | .83 | .54 | -.11 | .83 |
| Effective | .01 | .83 | .54 | -.11 | .83 |
| Excitable | .01 | .83 | .54 | -.11 | .54 |
| Active | -.19 | -.01 | .22 | .96 | .22 |
| Subordinate | .01 | -.55 | .81 | -.19 | .81 |
| Sociable | -.19 | -.01 | .22 | .96 | .96 |
| Playful | -.19 | -.01 | .22 | .96 | .96 |
| Curious | -.19 | -.01 | .22 | .96 | .96 |
| Congruence | .86 | .78 | .58 | .76 | .73 |

Note. Gorilla structure derived from Table 1 in Gold and Maple (1994). Macaque structure derived from Table II in Capitanio (1999). Congruence coefficients ≥ .85 indicate replication of factors, item loadings, or the structure.

Published as
**Encyclopedia of Behavioral Neuroscience, 2010, Vol. 3, 47-53**

# Personality, temperament, and behavioral syndromes

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**Keywords**: balancing selection, behavioral syndromes, ethology, individual differences, natural selection, personality, psychometrics, ratings, temperament, variation, well-being

**Synopsis**:

Research into animal personality, temperament, or behavioral syndromes is finding that, like humans, there are stable individual differences in dimensions related to behavior, affect, and even cognitions among a wide array of taxa. While debates about how to best measure personality in animals are ongoing, animal models of personality offer intriguing insights into the neural, molecular, and genetic bases of human personality as well as the relationship between personality and health, well-being, and even psychopathology. Moreover, these studies enable researchers to develop new insights into the means by which behavioral variation in humans and other animals is maintained.

## Glossary

**Factor analysis:** A data reduction technique to re-describe the correlations among observed variables with a smaller set of unobserved latent variables.

**Orthologous genes:** Genes in separate species that are descended from a common ancestral gene.

**Proximate causation:** Genetic, developmental, physiological, and environmental reasons for why a particular phenotype exists.

**Quantitative trait locus:** Regions of DNA containing or closely linked to genes or transcription regulators that influence a trait.

**Ultimate causation:** Evolutionary explanation of why a particular phenotype exists.

I. Introduction

II. Measurement of Personality, Temperament, and Behavioral Syndromes

  a) Rating approaches

  b) Behavioral coding approaches

  c) Reliability

  d) Validity

    1. Convergent validity

    2. Divergent validity

  e) Comprehensiveness

III. Factor analysis

  a) Exploratory factor analysis

  b) Confirmatory factor analysis

III. Correlates of animal personality measures

  a) Behavior

  b) Well-being

  c) Health

  d) Corticosteroids

  e) Reproduction

IV. Causes

  a) Proximate causes

    1. Genetic influences

      i. Heritability

      ii. Genomics

    2. Neurotransmitters and enzymes

    3. Gene x Environment interactions

b) Ultimate causes

1. Neutral theory

2. Mutation-seletion balance and balancing selection

3. Environmental niches

V. Conclusion

## Introduction

That animals, like humans, exhibit consistent individual differences in “character” or “personality” has been a long-standing observation among pet-owners and researchers alike. Personality refers to mostly stable individual differences in behavioral, affective, and cognitive predispositions. More narrow terms used to describe stable individual differences include temperament and behavioral syndromes, which emphasize measured or observed behaviors to the exclusion of possible cognitive or affective traits. Temperament is an older term which derives from human psychology research and is used to refer to individual behavioral differences that are stable across time and situations, e.g., activity. The term behavioral syndrome is more recent and has its roots in the study of behavioral ecology. Behavioral syndromes are defined as sets of correlated behaviors that are consistent across multiple situations. This paradigm explicitly ties behavioral variation to differences in growth, reproduction, and survival. While the approaches encompassed by these three terms differ broadly in the kinds of data considered, the species they are used to study, the traits they are compared with, and the background of researches who practice them, they share a common goal of understanding and explaining differences on the individual level.

One characteristic that distinguishes animal personality, temperament, or behavioral syndromes from other aspects of animal behavior include their bases within individuals. That is to say, these characteristics of individuals are not elicited or caused by environmental situations or schedules of reinforcement, but, instead, indicate how an individual animal typically behaves across a variety of situations. A second characteristics is their relative stability over time; while there is a considerable amount of debate about how to interpret the magnitude of the effects, most researchers studying human personality would agree that, in adulthood, while there is some change, an individual's standing on a particular personality dimension at one point in time is a fairly good predictor of their standing on that personality dimension at a later point in time. A final, though not often mentioned, characteristic is the emphasis, at least in animal personality or behavioral syndromes research, of studying multiple correlated traits or facets that make up broader dimensions, sometimes referred to as factors, domains, or dimensions.

## Measurement of Personality, Temperament, and Behavioral Syndromes

How to measure dimensions of personality, temperament, or behavioral syndromes as well as how to distinguish between relatively good and relatively poor dimensions is crucial to the study of personality in all species. Broadly, there are two approaches to assessing animal personality: ratings and behavioral coding.

### Rating approaches

Ratings-based approaches originate from methods often used in human personality research. They share in common a reliance on judges familiar with the individual animals, the use of questionnaires for rating personality, and asking judges to base their ratings on their overall impressions of the animals. Typically ratings on these questionnaires are made on 5- or 7-point Likert scales, true-false questions, or similarly quantitative responses. Some questionnaires are based on psycholexical approaches to studying human personality and ask judges to rate the degree to which each animal can be characterized by a series of personality descriptor adjectives (e.g., anxious). In some questionnaires, these adjectives are supplemented by sentences which attempt to resolve ambiguity or define the descriptor within the context of the species' behavior. Other questionnaires are more behaviorally-oriented, i.e., they ask raters to describe the animal with respect to specific behaviors, such as rate of aggressive interactions, as opposed to descriptor adjectives.

### Behavioral coding approaches

Behavioral coding is rooted in ethological approaches to the study of behavior and are more commonly used in animal personality research than ratings approaches. They involve actually objectively measuring behaviors, for example by recording their frequency or assessing the strength of the response to some stimuli. There are two major subtypes of behavioral coding approaches. One approach can be described as naturalistic. Here, observers watch an animal in its natural environment or a captive setting and record its spontaneously emitted behavior on an ethogram. The second approach can be described as experimental. This method involves changing the animal's environment in some way and recording the animal's response. For example, in "novel-object tests" a new or unusual object may be introduced into an animal's natural environment or enclosure and the reactions of the animal to the object as well as how closely it approaches the object are recorded. A similar method may categorize the animal's behavior when handled by experimenters.

### Reliability

Prior to using a particular measure of animal personality, one must determine its reliability. Reliability refers to the proportion of the animal personality score that is accounted for by the characteristics of the subject, sometimes referred to as "true score" variance. The remaining variance is referred to as "error" and is accounted for by any other factors, including specific judges, time of measurement, situational effects, and any other effects.

A common misconception is that the behavioral coding approaches are more reliable than ratings approaches. No studies support this view, and, in fact, a recent study of captive chimpanzee personality directly compared the reliabilities of ratings and behavioral coding methods. This study found that the mean reliability of ratings was substantially higher than the mean reliability of codings derived from focal animal sampling.

### Validity

In studying animal personality it is also important to show that a personality measure demonstrates convergent and divergent validity. That is to say, is a personality measure related in expected ways to other measures or outcomes?

### Convergent validity

Convergent validity refers to the degree to which a personality measure is correlated with measures or tasks that should tap the same construct. For example, we would expect that a rating measure of extraversion and a behavioral coding measure of time spent in proximity to conspecifics should be positively correlated. In short, measures of the same construct should be related.

### Divergent validity

Divergent or discriminant validity refers to the degree to which a personality measure is not correlated with measures or tasks that reflect different constructs. That is to say, it is indicative of the extent to which supposedly different constructs are distinct. For example, we would expect that a rating measure of neuroticism should only show negligible correlations with measures such as time spent in proximity to conspecifics.

### Comprehensiveness

Recently, some have emphasized the importance of comprehensiveness as another criterion by which to judge personality ratings. This criteria asks whether a measure captures all the personality differences of the animal or is limited to a select number of domains. A bottom-up behavioral repertoire approach to studying animal personality is one way to address these issues. This method involves behavioral coding and may enable researchers to find domains or dimensions of personality differences that are not revealed by the use of top-down ratings-based approaches, which are seen to impose a personality structure from one species (typically humans) onto another.

### Factor analysis

Factor analysis refers to a family of data analytic methods that can reduce a large number of variables into a smaller set of variables. It is based on the premise that the relationships among a set of manifest variables or traits arise because of a common underlying set of causes or latent variables, which cannot be directly measured. In the study of personality, manifest variables refer to the individual items making up the rating scale or individual behaviors whereas latent variables are personality dimensions such as five-human like domains found in chimpanzees and the chimpanzee-specific domain of Dominance. These analyses are used in the study of personality in humans and nonhuman animals, and are more commonly used in studies that measure personality via ratings as opposed to behavioral codings.

## Exploratory factor analysis

Of the two types of factor analytic techniques, exploratory factor analysis is the most commonly used. These techniques consist of methods such as principal components analysis and principal axes analysis. These approaches have in common that the researcher does not pre-specify the nature of the latent variables, i.e., which items they define. Instead, he or she determines the number of factors believed to be sufficient to explain the intercorrelations among variables, extracts these factors, and then interprets factors based on how strongly items reflect or load on which factors. This last procedure often first involves rotating the factors, which serves to rescale the loadings so that high loadings are as close to 1 or -1 as possible and low loadings are as close to 0 as possible.

## Confirmatory factor analysis

An equally important but more seldom used technique is confirmatory factor analysis. Here the researcher pre-specifies the nature of the latent variables, i.e., indicates which manifest variables they believe will be explained by which latent factors. The researcher then tests whether the pre-specified factors adequately explain the intercorrelations among items.

A researcher may also wish to compare multiple sets of pre-specified factors to determine which best explains the intercorrelations of the items with the fewest possible parameters.

This technique is most commonly used when researchers, based on prior studies using exploratory factor analysis, already have strong ideas concerning the nature of the factors or if they wish to compare the factors of two different samples or species. For example, confirmatory factor analysis was recently used to test whether the rhesus macaque personality factors identified in one sample replicated in a new sample.

## Correlates of animal personality measures

### Behavior

A fundamental question regarding measures of animal personality, particular those based on ratings, is whether they are related to behavior. There is considerable evidence in a range of primate species that measures of personality obtained via ratings are, in fact, correlated with behaviors in ways consistent with the definitions of the factors. For example, extraverted zoo chimpanzees are more oriented towards their conspecifics than they are to members of the viewing public whereas this pattern is reversed for introverted chimpanzees; langur monkeys rated as more agreeable engaged in less aggressive behavior and more grooming; and rhesus macaques rated high in sociability in one context engaged in more affiliative behaviors in another context up to 4.5 years later.

In non-primate species, because measurements are usually made using behavioral coding, the interest instead is finding ecologically meaningful correlates between behavioral domains. In stickleback fish, aggression, activity level, and exploratory behavior were strongly correlated only in populations that were subject to predation. Recently, this research has been extended to include birdsong: male collared flycatchers who scored higher in tests of exploratory behavior or risk-taking behavior sang from lower and higher posts, respectively.

## Well-being

One well-known feature of human personality is its relationship to measures of subjective well-being. Although it is correlated with other personality dimensions, too, on average, more emotionally stable and more extraverted people are happier than less emotionally stable and less extraverted people. The nonhuman work on personality and well-being has been limited to studies of chimpanzees and orangutans. In the case of chimpanzees, greater well-being was positively related to the chimpanzee-specific personality domain, Dominance, a broad factor that incorporates aspects of low neuroticism, high extraversion, low agreeableness, and low conscientiousness. More extraverted and conscientious chimpanzees also were rated as being higher on well-being than their introverted and unconscientious counterparts. A later study of orangutan personality revealed that orangutans who were rated as extraverted, emotionally stable, and agreeable had higher well-being scores than their introverted, neurotic, and disagreeable counterparts.

## Health

Human personality is related to health outcomes and in several studies with long follow-up periods, personality dimensions have been related to all-cause mortality. In particular, low conscientiousness is strongly related to earlier death, though high neuroticism, low agreeableness, and low extraversion have also been linked to greater mortality risk. Studies of the relationship between human personality and health outcomes are limited in that ethical considerations bar the experimental procedures that could elucidate the mechanisms underlying the relationships. However, work on this relationship in primate models is making progress in revealing the causal mechanisms underlying these associations.[1]

## Corticosteroids

Studies of personality dimensions in nonhuman species have revealed relationships between these dimensions and hormone levels. For example, one study examined adult male rhesus macaques that were assessed on four personality dimensions and plasma cortisol concentration. Consistent with some studies of human neuroticism, this study found that monkeys rated as being higher in excitability had lower levels of basal cortisol in the PM phase. This study also found higher levels of the confidence dimension were related to significantly higher levels of cortisol throughout the AM phase and higher levels of cortisol throughout the beginning, but not end, of the PM phase.

Also, in a study of cortisol and sedation stress in young chimpanzees, individuals who scored higher on the behavioral dimension mellow showed higher peak cortisol levels and a more substantial increase in cortisol over time. Another study of juvenile chimpanzees showed some evidence that the same dimension was related to testosterone levels, though the effects of the chimpanzees' actual rank may have been a confound.

Studies of great tit lines selected for being fast explorers or slow explorers that were exposed to stressors (a social defeat in this case), showed that the fast explorers displayed a greater reduction in activity levels than slow explorers. However, slow explorers also showed increases in fecal corticosteroid metabolites whereas no such increase was revealed among the fast explorers.

### Reproduction

Evidence from several studies suggests that personality may be related to variables associated with successful reproduction. Captive-born cheetahs that were rated as being higher in a dimension named tense-fearful were more likely not to breed than those who were rated as being lower on this dimension. Also, in an experimental study, successful mate pairings in dumpling squid were those in which females with intermediate or high scores on a shy-bold dimension were paired with males who also displayed intermediate or high scores on this dimension. On the other hand, shy females were able to successfully mate with shy, intermediate, and bold males. A similar boldness-shyness dimension also leads to differential reproductive success in bighorn sheep; bold ewes exhibit an earlier age at primiparity and greater weaning success. Among red squirrels, female activity level was related to their offspring's growth rate but did not influence dates of birth or litter size. In common lizards, clutch size was found to correlate positively with the ability of females to tolerate conspecifics (a measure of sociality). Social females that can deal with high population densities have more opportunities to mate and reproduce.

## Causes

### Proximate Causes

### Genetic influences

#### Heritability

Human personality dimensions are approximately 50% heritable[2], but what does this mean? Roughly, heritability is the proportion of variation in a trait between individuals in the same population that is due to genes that are passed down from parents. Heritability is not a measure of how "biological" a trait is, only how much of the differences between individuals can be accounted for by differences in genes.

The importance of heritability for the study of personality is in informing both the proximate and ultimate causes of individual differences. Low heritability may suggest strong selection for a particular level of a personality trait. Estimates of heritability vary wildly between species, traits, and even between studies of the same trait in the same species. On the low end, boldness and aggression in three-spined sticklebacks has been found to have no heritability while dominance in chimpanzees was estimated to be 66%. Like any trait, the heritability of personality is a function of both selection and the amount of genetic and environmental variability underlying it.

#### Genomics

Two genome-wide scans have been carried out on humans to detect quantitative trait loci (QTL) connected with personality differences. One study used linkage with microsatellite markers to detect larger regions of each chromosome that explained variance in Psychoticism, Extraversion, Neuroticism, and social desirability as measured by the Junior Eysenck Personality Questionnaire. A second study conducted a genome-wide association scan and measured the personality traits Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness using the Revised NEO Personality Inventory and identified several biologically-plausible genes associated with each dimension.

Several other studies have considered personality or personality-like traits individually, particularly in conjunction with psychiatric disorders. The inability to replicate results from genome-wide association studies is not a fatal flaw for this type of research but simply an indication that other physiological and developmental evidence will be needed to determine how specific genetic variants result in personality and behavioral differences. A larger challenge is that the genes identified thus far explain such a small amount of phenotypic variance (on the order of 1%). Personality is indeed a complex trait in this sense, a product of many genes interacting with the environment.

Because of the complex genetic architecture of personality in humans, researchers often turn to model organisms, particularly mice. The strategy is to identify genes in the model species that are descended from a common ancestor with humans (that is, the genes are orthologs). The assumption is that the orthologous genes carry out the same (or similar) functions in both species. Because the ultimate aim of studying individual differences with model organisms is usually in understanding psychiatric disorders, the focus is usually on traits such as neuroticism (sometimes called emotionality) that have strong correlates with anxiety- and depression-related disorders. For example, a region of chromosome 1 associated with emotionality in mice (as measured in novel-environment tests) was compared with the orthologous region that has been implicated in human neuroticism. A key result from this comparison was that the exact disease-causing gene variants are unlikely to be shared across species.

A further outcome of investigations with mice is to separate genetically clusters of related behavioral phenotypes such as activity in open-field tests and mazes that all assumed to measure a single trait: anxiety. QTL analysis revealed a dimensionality of anxiety-related behavors that was lost in a factor analysis of the phenotypic data.

## Neurotransmitters and enzymes

There is mixed evidence for the role that variation in specific neurotransmitter transporters and receptors and related enzymes play in personality and behavior. Most work has centered around a small set of genes and their promotors: serotonin transporter (5-HTT or SLC6A4), dopamine receptor D4 (DRD4), and monoamine oxidase A (MAOA). Polymorphism in the serotonin transporter gene and its promoter region (5-HTTLPR) have been linked to neuroticism in humans and emotion in rhesus macaques. Variation in DRD4 has been associated with novelty-seeking in great tits, humans, and vervet monkeys, among other species. MAOA is a catalyst that breaks down the neurotransmitters serotonin, epinephrine, and noepinephrine. It has been linked to aggressive behavior in humans and several species of macaques.

However, various follow-up studies with humans have failed to replicate a link betweeen 5-HTT and neuroticism and DRD4 and novelty seeking or extraversion. Rather than completely overturning the behavioral associations of these genes, these mixed results suggest that the pathway between genes and behavior is more complicated and not the action of single genes. Similarly, populations may differ in which gene variants are responsible for differences in personality and behavior.

## Gene × Environment interactions

The possibility that the environment may moderate the influence of genes on personality development has often been discussed and recently been explored. One area of emphasis has been on the MAOA gene. Low activity MAOA genotypes have been related to aggression, antisocial behavior, and conduct disorder in humans. An orthologous gene (rhMAOA-LPR) was subsequently identified in rhesus macaques. A recent study of male rhesus macaques suggested that the effect the low activity genotype may be sensitive to the early rearing environment: mother-reared macaques with the low activity genotype had higher aggression scores than mother-reared macaques with the high activity genotype; peer-reared macaques with the high activity genotype had higher aggression scores than peer-reared macaques with the low activity genotype.

### Ultimate causes

Understanding variation in personality involves not just dissecting the genetic and environmental influences, but in discovering why such differences exist in the first place. This is a puzzle, namely because under direct selection one would expect the additive genetic the variance of a trait to decrease. As such, multiple hypotheses have been offered to explain the maintenance of heritable variation in personality.

### Neutral theory

The first possibility is that variation in behavioral, affective, and cognitive predispositions is the result of neutral evolution. Under this mode, all differences in a trait are due to mutations that are fixed or lost in the population through random genetic drift. The phenotypes resulting from each allele all have equal fitness, so there is no selection on the trait. However, the evidence connecting personality with differences in reproduction and health outcomes makes it unlikely that personality differences have zero fitness costs or benefits. Selection would have to be extremely weak to be overcome by genetic drift. More directly, there are many cases where, when measured, selection on personality traits have been found to be moderate. However, the neutral theory is not completely irrelevant for the evolution of personality. Firstly, it reminds us that the origin of all genetic variation lies ultimately with mutation. Secondly, the neutral theory remains the null hypothesis against which all evolutionary propositions are tested.

### Mutation-selection balance and balancing selection

After random drift, the next mechanism to consider is a balance between selection and mutation. If there is an optimal value of a personality trait (for example, being moderate in neuroticism) that maximizes fitness, selection will move the population mean toward that optimal value. This elimination of genetic variation in the trait is balanced by the introduction of new variation via mutation. However, many characteristics of personality variation do not fit with the predictions of this explanation.

Another possibility that is better supported by the evidence is that some form of balancing selection accounts for the variation in personality traits. Thus, differing levels of the personality trait exist because each is related, in some way, to fitness benefits and costs. For example, in a species where females favor aggressive males, the benefit of being higher in some aggression-related trait may be offset by the higher likelihood of injury or death resulting from fights. Another example involves differences in life history within species, i.e., that different levels of personality dimensions are related to trade-offs between number of offspring reproduced and lifespan of the parent or viability of the offspring.

### Environmental niches

Another possible way in which genetic variation in personality might be maintained is because the environment offers a multitude of niches in which different levels of personality may be successful. Thus, in a population there may be ways for individuals along all levels of extraversion or any other dimension to successfully survive and reproduce. Environmental heterogeneity can also lead to differing selection pressures among populations, such as whether stickleback behaviors were correlated resulted from differing predation rates. In addition to spatial variation, individual differences can also be maintained by temporal variation in selection pressure. For example, bold ewes are less susceptible to predation by cougars, but this only results in appreciable fitness differences when predation is high.

## Conclusion

The abundance of individual differences is the only clear result that is consistent across all species where personality has been examined. The genetic architecture underlying personality and how its variation is being maintained are likely to differ between species, and a major goal will be to identify the broad patterns that explain the ultimate and proximate causes of individual behavioral proclivities. Measuring and validating personality and dissecting its complex genetic basis are key challenges in this area. What personality is and how best to study it will continue to provide much fuel for debate.

## Acknowledgements

We wish to thank Jana Uher for the continuing dialogue which has provided much food for thought here and elsewhere.

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Suggested Cross References

1. See chapter 196 by Capitanio and Jiang

2. See chapter 28 by Canli and Dunam

JOURNAL OF Evolutionary Biology

doi: 10.1111/j.1420-9101.2010.02212.x

# Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*

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*Keywords:*

competition;
dominance;
indirect genetic effect;
quantitative genetics;
selection.

## Abstract

By determining access to limited resources, social dominance is often an important determinant of fitness. Thus, if heritable, standard theory predicts mean dominance should evolve. However, dominance is usually inferred from the tendency to win contests, and given one winner and one loser in any dyadic contest, the mean proportion won will always equal 0.5. Here, we argue that the apparent conflict between quantitative genetic theory and common sense is resolved by recognition of indirect genetic effects (IGEs). We estimate selection on, and genetic (co)variance structures for, social dominance, in a wild population of red deer *Cervus elaphus*, on the Scottish island of Rum. While dominance is heritable and positively correlated with lifetime fitness, contest outcomes depend as much on the genes carried by an opponent as on the genotype of a focal individual. We show how this dependency imposes an absolute evolutionary constraint on the phenotypic mean, thus reconciling theoretical predictions with common sense. More generally, we argue that IGEs likely provide a widespread but poorly recognized source of evolutionary constraint for traits influenced by competition.

## Introduction

In animal societies, it is widely expected that social dominance is positively associated with fitness. This is because dominant individuals, by definition, should have greater access to limiting resources such as food (Herberholz *et al.*, 2007), mates (Willisch & Neuhaus, 2010) or territories (Franck & Ribowski, 1993). In organisms that might loosely be classified as displaying higher levels of ‘sociality’ (Costa & Fitzgerald, 2005), it is also common for dominant individuals to monopolize reproduction and receive benefits from subordinate helpers (Clutton-Brock *et al.*, 2001). Thus, social dominance is generally viewed as being under positive selection, although empirical studies have highlighted that exceptions can and do occur (Ellis, 1995; Qvarnström & Forsgren, 1998; Verhulst & Salomons, 2004).

A critical requirement for adaptive evolution is that trait variation within populations is, at least in part, caused by heritable differences among individuals. If selection acts on such a heritable trait, then quantitative genetic theory states that the population mean of that trait should evolve over time (Falconer & Mackay, 1996). However, common sense tells us that mean dominance cannot evolve in this way, because the trait is always observed through contests with one or more other individuals in a group (Barrette, 1987; Drews, 1993). For the case of dyadic interactions, there must be one ‘winner’ and one ‘loser’ in every contest, such that the mean rate of winning must always be equal to one half.

Here, we conduct a quantitative genetic analysis to estimate the genetic basis of variation in dominance among wild red deer, *Cervus elaphus*, on the Isle of Rum,

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Scotland. We show that social dominance is both heritable and under positive selection, but also that phenotypic expression is subject to indirect genetic effects (IGEs) that arise from interactions among individuals (Moore *et al.*, 1997). It has previously been argued that incorporating these IGEs into quantitative genetic models is essential for understanding the evolution of social dominance (Moore *et al.*, 2002). Here, we estimate these effects, show that their presence resolves the apparent conflict between theory and common sense and provide an empirical demonstration of a potentially widespread source of evolutionary constraint.

Social dominance is generally inferred from consistent differences between individuals in their ability to win contests (Drews, 1993) and has been studied in wild populations across a wide range of animal taxa. In some cases, there is evidence that dominance rank can be passed from parent to offspring (e.g. 'maternal rank inheritance' in primates and spotted hyenas, Holekamp & Smale, 1991). However, it has not generally been possible to demonstrate a genetic basis to such patterns in the wild, and there is clear evidence that they can arise from social rather than genetic mechanisms (e.g. East *et al.*, 2009). Thus, to our knowledge, no study has demonstrated a genetic basis of variation to dominance rank *per se* in the wild, although two strong lines of evidence suggest that genetic effects are likely. First, work under laboratory conditions has demonstrated genetic variance for dominance, for example through selection experiments (Craig *et al.*, 1965; Moore *et al.*, 2002) or through directly estimating heritabilities (Nol *et al.*, 1996). Secondly, dominance is often correlated with (and believed to be causally related to) aspects of morphology (e.g. body size, weapon size) and behaviour (e.g. aggression) that are generally found to be heritable in natural populations as well as in the laboratory (Horne & Ylönen, 1998; Kruuk *et al.*, 2008).

Numerous indices have been proposed to rank individuals within a hierarchy, and while debate continues as to their relative merits (Bayly *et al.*, 2006; Bang *et al.*, 2010), a feature common to most is a recognition that the probability of success in any contest depends on the relative strengths of the focal individual and the opponent. Dyadic contest outcomes can therefore be viewed as arising from the interaction of two phenotypes and by extension (if there is genetic variance for dominance) of two genotypes (Moore *et al.*, 1997; Wilson *et al.*, 2009a). An important consequence of this is that if social dominance is a heritable trait, then contest outcomes are likely subject to both direct and IGEs.

Indirect genetic effects, or 'associative effects' (following, Griffing, 1967), occur when the genotype of one individual has a causal influence on the phenotype of another (Moore *et al.*, 1997). As has long been recognized, such effects can have major consequences for the evolution of phenotypic traits under selection – whether artificial or natural (Griffing, 1981a,b; Wolf, 2003; Bijma & Wade, 2008). In the current context IGEs, genetic variation for competitive ability (or contest winning) is expected to result in IGEs on the observed phenotype (i.e. an individual's success in contests, Moore *et al.*, 2002). Moreover, there is an expectation of a negative covariance between direct and IGEs associated with competition (Wolf, 2003; Bijma *et al.*, 2007b). This is because a gene that predisposes to winning a contest when carried by a focal individual will predispose to losing if that gene is carried by the focal individual's opponent instead. Theoretical models show that this source of negative genetic covariance could provide an important source of evolutionary constraint, reducing (or even reversing) the expected phenotypic change for a trait under selection (Moore *et al.*, 1997; Wolf *et al.*, 1998; Bijma *et al.*, 2007b). Recent empirical studies on laboratory and livestock systems have provided convincing evidence that IGEs can influence a range of traits (Bijma *et al.*, 2007a; Mutic & Wolf, 2007; Bleakley & Brodie, 2009; Wilson *et al.*, 2009a). However, apart from the specific case of maternal genetic effects (e.g. Wilson *et al.*, 2005), the role of IGEs in natural populations has received limited empirical scrutiny to date (but see e.g. Brommer & Rattiste, 2008).

In what follows we perform quantitative genetic analyses to test the genetic basis of variance in social dominance, defined as success in pairwise contests, in red deer on the Scottish island of Rum (Clutton-Brock *et al.*, 1982). We first test the *a priori* expectation that social dominance is positively correlated with fitness in this population before testing for genetic variation in dominance and IGEs on contest outcomes. Finally, we parameterize a recently proposed model of IGEs (Bijma *et al.*, 2007b) to test the hypothesis that IGEs on social dominance must exist if the trait is heritable, and show that these provide a source of absolute evolutionary constraint that resolves the apparent conflict between common sense and quantitative genetic prediction.

## Materials and methods

### Phenotypic data

The red deer population in the North Block of the Isle of Rum, Scotland, has been the subject of an individual-based study since 1971, with detailed life-history and behavioural data collected on individually identifiable animals from birth to death (Clutton-Brock *et al.*, 1982). Here, we used data from observations of dyadic dominance interactions recorded between 1974 and 1995. The available data relate to low-level interactions among females and (predominantly) young males outside of the breeding season. Adult stags are very poorly represented in the data as they are largely nonresident in the study area and spend little time in association with female groups outside of the annual rut period. Thus, the available data are limited in that they include neither observations of contests between stags during the rut nor interactions between adult males out with this period. Across all interactions recorded, the mean age of individuals observed was 5.57 years in females but just 1.75 years in males.

At the time of observation, one member of each dyad was scored as the winner based on agonistic behaviours including nose and ear threats, displacements, kicking, boxing, bites and chases (see, Clutton-Brock *et al.*, 1982 for a full description of these behaviours). Note that in what follows we analyse the observed data on contest outcomes directly, rather than by using these observations to first estimate a measure of dominance rank for each individual. Although the latter may seem more intuitive, our approach is statistically advantageous because dominance ranks should themselves be recognized as individual-level statistics that are estimated with error (Poisbleau *et al.*, 2006). Consequently, investigations into the causes or consequences of dominance rank variation must find a way to incorporate this error if statistical analyses are to be considered robust. Here, we avoid the pitfall of doing 'statistics on statistics' by using a mixed-model framework that allows our hypotheses to be tested by modelling the observed data in a single step (see e.g. Hadfield *et al.*, 2010, for further discussion). In total, the data comprise 10 517 observations of dyadic interactions (6215 female–female, 3771 female–male, 516 male–male and 15 involving one individual of unknown sex). About 1278 distinct individuals were observed in at least one contest, with a mean of 16.5, and a maximum of 179, observations per individual.

## Pedigree structure

The red deer pedigree has been constructed from a combination of behavioural observation and molecular paternity analysis using microsatellite data (full details are presented in Walling *et al.*, 2010). On average, individual paternity assignments are made with 97.6% confidence. Within the entire red deer pedigree, 1336 individuals are informative with respect to the genetics of dominance, either by virtue of being observed in one or more phenotypic records from contests ($N = 1278$) and/or because their pedigree position provides information on the relatedness among phenotyped individuals. Among this informative subset, 1184 maternities and 648 paternities are known. With respect to the genetics of social dominance, the informative portion of the pedigree is defined by many pairwise pedigree relationships, including 2459 and 3132 maternal and paternal pairwise sibling relationships, respectively. The pedigree is highly convoluted, with many known relationships both within and among cohorts (Fig. 1). Pedigree statistics and the graphical representation of the pedigree were generated using the R package pedantics (Morrissey & Wilson, 2010).

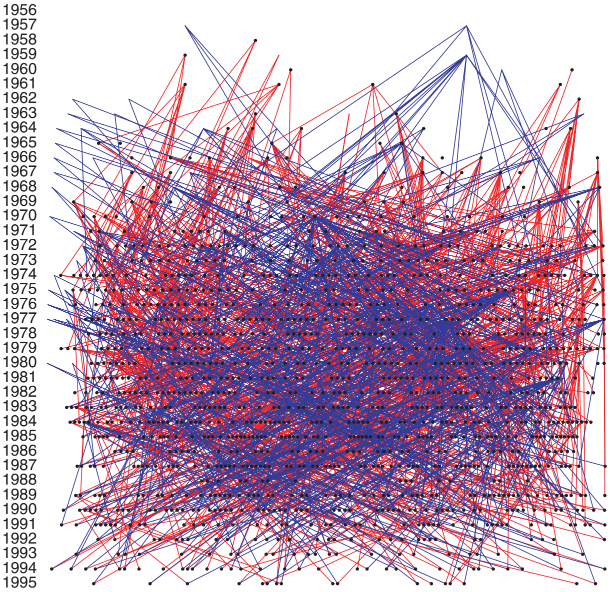

**Fig. 1** The structure of the portion of the red deer pedigree that is informative with respect to the genetics of variation in dominance ($N = 1336$). Numbers on the left-hand side indicate cohort affinities, some of which are estimated based on age at first known reproduction and typical sex- and age-specific patterns of reproductive success. Red lines denote maternal links, and blue lines denote paternal links. Individuals with one or more records from dominance interactions are denoted with black dots.

## Selection on social dominance

To confirm our *a priori* expectation that dominance is under positive selection, we formally tested its relationship with fitness, estimated as the number of offspring produced by an individual over its lifetime (lifetime breeding success, LBS). Because the distribution of LBS differs greatly between the sexes (i.e. the male distributions are much more highly skewed) analyses were performed separately for males ($N = 456$) and females ($N = 579$). Note that for males, fitness values were estimated as the number of offspring assigned in the pedigree structure on the basis of microsatellite genotype data. Each individual was assigned an estimate of fitness, and individuals observed as juveniles were included regardless of whether they survived to breeding age. Note, however, that individuals could only be included in the analysis if they were phenotypically informative (i.e. had been observed in dominance interactions), and our data are therefore not informative with respect to the potential fitness consequences of avoiding interactions. Any animal known to have died an unnatural death (i.e. to have been shot) was excluded prior to analysis.

For each sex, selection was estimated in two ways. First, for each individual *i*, we simply determined mean contest success as the proportion of interactions observed across *i*'s lifetime in which *i* was scored as the winner. We then estimated selection as the ordinary least-squares regression coefficient of fitness (LBS) on mean contest success. To facilitate comparison with selection estimates in the literature, we also regressed relative fitness (i.e. $\mathrm{LBS}_i/\overline{\mathrm{LBS}}$) on mean contest outcome scaled to standard deviation units to obtain the standardized linear selection differential (Endler, 1986). Whereas the simple linear regression is appropriate for estimating the selection differentials, statistical inference is not valid in the absence of residual normality. Consequently, we also fitted negative binomial regressions in each sex to test the hypothesized positive association between mean dominance. This approach is appropriate given that LBS is a count and has positively skewed distributions in both sexes.

Secondly, we estimated (for each sex separately) the within-individual covariance between dominance and fitness using a bivariate linear mixed effects model with individual identity fitted as a random effect. For each observed interaction, one (randomly chosen) individual within the pair of animals was assigned a phenotypic value of 0 or 1 according to the contest outcome. Henceforth, we refer to this individual as the *focal* animal and the other individual as the *opponent*. This approach was taken such that each dyadic observation contributes a single phenotypic record to the analysis, which is appropriate as the phenotypic status of the focal completely determines that of the opponent and *vice versa*. We modelled fitness (LBS) and contest outcome as response variables, with identity of the focal individual as a random effect on both traits. In addition to controlling for pseudoreplication, the random effect of focal individual allows us to model dominance as a latent individual-level variable that influences observed contest outcomes and is assumed to vary among animals. It also allows us to estimate the covariance between this latent variable (dominance) and fitness.

Our second approach has the advantage of allowing the fitness-phenotype covariance estimate to be conditioned on known sources of trait variation. Here, we included age difference (focal individual's age in years minus opponent's age in years) and sex code as fixed effects on observed phenotype. We included a linear effect of age difference as older individuals are (on average) dominant to younger ones (Clutton-Brock *et al.*, 1982; Thouless & Guinness, 1986; Fig. 2). This represents a potential source of bias in the first simple regression estimate of selection because individuals that live longer will be the older individual in a higher proportion of their dyadic interactions and will also have (on average) higher fitness (even if dominance is not causally related to longevity or fecundity). Thus, the age effect could in itself be sufficient to cause apparent positive selection on dominance. Preliminary data analysis also revealed that while females tended to win more often in cross-sex contests, this is likely due to the different age distributions between the sexes. In fact, considering only interactions between animals of the same age, males were significantly more likely to win in contests against females than *vice versa* (Fig. 2). We therefore included an additional fixed effect of sex code as a three-level factor corresponding to the possible dyadic interaction types (1 = same sex dyad, 2 = female focal with male opponent, 3 = male focal with female opponent).

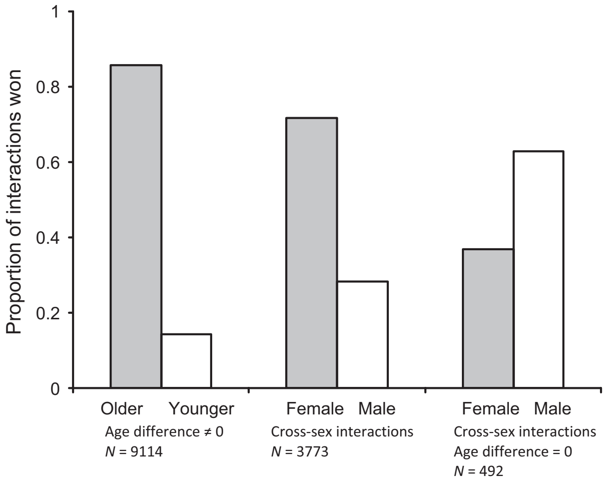

**Fig. 2** Proportion of observed dominance interactions won in encounters between animals of differing age or sex. Older individuals tend to be dominant to younger ones, and while females are more likely to dominate males overall, this is because of differences in average age between the sexes (see text); males tend to dominate females of the same age. Deviations from null expectations (i.e. 50 : 50 proportions) are highly significant with binomial probabilities < 0.0001 for all three comparisons.

A limitation of this analysis is that we are currently unable to fit the multivariate generalized linear mixed effect model that would be most appropriate to these two response variables (as contest outcomes are binary observations and LBS is best modelled using a negative binomial or quasi-Poisson distribution). We therefore fitted the model assuming errors follow a multivariate normal distribution and note that statistical inferences drawn from the model should be treated as provisional.

## Repeatability and genetic variance for social dominance

Genetic and environmental components of variance for social dominance were estimated from phenotypic and pedigree data. Models were formulated to test for repeatability of social dominance, the presence of additive genetic variance and finally the presence of IGEs. Testing repeatability requires that the total variance in a trait can be partitioned into within- and among-individual components. Because this is only possible given repeated measurements on individuals, all quantitative genetic analyses were carried out on the observed data (i.e. contests) rather than on summary lifetime statistics for each individual. Dominance was therefore modelled with generalized linear mixed effect models (GLMM) using a logit link function to relate binary observations to an underlying (normal) latent scale.

### *Models fitted*

Each dyadic interaction contributes a single record to the data analysis. For observation $x$ of focal individual $i$ with opponent $j$, the observed contest outcome (0/1) is given as:

$$Outcome_{ijx} = \delta[logit^{-1}(l_{ijx})]$$

where $\delta$ is a draw from a Bernoulli distribution with probability $logit^{-1}(l_{ijx})$, $l_{ijx}$ is thus the liability on the logit scale of $i$ winning the contest. We fitted a series of models, identical in their fixed effects but differing in their random effects, to predict $l_{ijx}$:

$$l_{ijx} \sim age\ difference + sex\ code + focal_i + opponent_j \qquad \text{(model 1)}$$

$$l_{ijx} \sim age\ difference + sex\ code + (pe_{\mathrm{F}i} + a_{\mathrm{F}i}) + opponent_j \qquad \text{(model 2)}$$

$$l_{ijx} \sim age\ difference + sex\ code + (pe_{\mathrm{F}i} + a_{\mathrm{F}i}) + (pe_{\mathrm{O}j} + a_{\mathrm{O}j}) \qquad \text{(model 3)}$$

Fixed effects included the linear function of *age difference* (years) and sex code (as described earlier).

In model 1, we included a random effect of focal identity $focal_i$ to estimate the between focal individual variance ($V_{\mathrm{F}}$). If scaled by the total phenotypic variance, $V_{\mathrm{F}}$ can be interpreted as the repeatability of focal dominance. Model 1 also contained a random effect of opponent identity $opponent_j$ to estimate the variance in opponent effects ($V_{\mathrm{O}}$), the extent to which different opponents have repeatable effects on contest outcomes. Under model 2, the influence of the focal individual $i$ is partitioned into an additive genetic effect ($a_{\mathrm{F}i}$) and a nongenetic 'permanent environment' effect $pe_{\mathrm{F}i}$, allowing estimation of the corresponding variance components $V_{\mathrm{F.A}}$ and $V_{\mathrm{F.PE}}$ Under this model, only direct genetic effects are included and $V_{\mathrm{F.A}}$ is simply the conventional additive genetic variance. Model 2 is therefore a standard animal model (Wilson *et al.*, 2009b) for a trait with repeated measures, in which the opponent effect is treated as a purely environmental source of variance. In model 3, we apply a similar decomposition of $opponent_j$ to test for IGEs. This allows partitioning of $V_{\mathrm{O}}$ into additive genetic ($V_{\mathrm{O.A}}$) and nongenetic ($V_{\mathrm{O.PE}}$) components, where $V_{\mathrm{O.A}}$ is the variance attributable to IGEs.

Models 1–3 allow focal and opponent influences to be estimated and partitioned into genetic and environmental components and they also contain an implicit but likely erroneous assumption that no correlations exist between the direct and indirect effects. As the designation of focal and opponent individuals is in fact completely arbitrary for each observation $x$, it follows that focal and opponent effects should be perfectly correlated within individuals. Thus, for any individual $i$, it can be argued that $focal_i = -opponent_i$, and therefore, $a_{\mathrm{F}i} = -a_{\mathrm{O}i}$, and $pe_{\mathrm{F}i} = -pe_{\mathrm{O}i}$. From this it follows logically that we expect equalities to exist among the variances such that $V_{\mathrm{F.A}} = V_{\mathrm{F.O}}$ and $V_{\mathrm{PE.A}} = V_{\mathrm{PE.O}}$ whereas the correlations between direct and indirect effects (denoted $r_{\mathrm{G.FO}}$ and $r_{\mathrm{PE.FO}}$ for genetic and permanent environment correlations, respectively) should equal −1. To test this expectation, we fitted two further models. Model 4 was specified as model 3 but with a potentially nonzero correlation between direct and IGEs directly estimated to test our expectation that they would equal −1. Finally, we compared the effect size estimates under model 4 to those in a model constrained to be consistent with our expectations described elsewhere (Model 5). Thus, we estimated the magnitude of genetic and permanent environment effects under the forced conditions that $V_{\mathrm{F.A}} = V_{\mathrm{O.A}}$, $r_{\mathrm{G.FO}} = -1$, $V_{\mathrm{F.PE}} = V_{\mathrm{O.PE}}$, $r_{\mathrm{PE.FO}} = -1$.

Random effects were assumed to be drawn from normal distributions with means of zero and variance/covariance matrices among individuals of $\mathbf{I}\sigma^2_{\mathrm{F}}, \mathbf{I}\sigma^2_{\mathrm{O}}, \mathbf{I}\sigma^2_{\mathrm{F.PE}}, \mathbf{I}\sigma^2_{\mathrm{O.PE}}, \mathbf{A}\sigma^2_{\mathrm{F.A}}$, and $\mathbf{A}\sigma^2_{\mathrm{O.A}}$. Variance components are as described earlier (note that here we use $\sigma^2$ to denote a true variance as opposed to V to denote its estimate above) and are assumed to be homogeneous across sexes. **I** is an identity matrix with order equal to the number of individuals; **A** is the additive numerator relationship matrix containing the individual elements $A_{ik} = 2\Theta_{ik}$; and $\Theta_{ik}$ is the coefficient of coancestry between any pair of individuals $i$ and $k$ in the pedigree.

### *Validation of quantitative genetic analyses*

All quantitative genetic models were solved by penalized quasi-likelihood (PQL) implemented in the program ASREML v2 (Gilmour *et al.*, 2006). This method is appropriate for the binary observations of contest outcomes but is not without difficulties. First, estimates of random effects can be biased when GLMMs are solved by PQL approximations (Goldstein & Rasbash, 1996; Rodriquez & Goldman, 2001; Bolker *et al.*, 2009). We therefore undertook power and sensitivity analyses, using simulation-based approaches advocated by Morrissey *et al.*, (2007) to assess the performance of the GLMMs, as fitted in our dataset. Specifically we sought to determine whether biases could exist in our analyses, given the particular conditions of our analyses (i.e. size and structure of the pedigree, number of observations and distribution of observations among individuals). A second difficulty is that appropriate statistics for hypothesis tests of random effects in GLMMs solved by PQL are unknown. We therefore used the simulations to determine, again under the particular conditions of our analyses, whether evaluation of the ratio of the estimate to its estimated standard error, as reported by ASReml, provided practical means of evaluating statistical significance.

Full details of these simulation-based analyses are presented in Appendix 1. In brief, the results indicated that our estimates of genetic variance components are likely to be downwardly biased (a known problem with PQL approximations, Bolker *et al.*, 2009). However, under simulation conditions designed to mimic the actual analyses of dominance in red deer, these biases are not large enough to hinder the biological interpretation of our model-based estimates (see Appendix 1). Simulations also demonstrated that the common 'rule of thumb' of assuming statistical significance when the ratio variance/standard error ≥ 2 is justifiable here (and is expected to be conservative with respect to a nominal significance level of $\alpha = 0.05$). Lacking a method to generate exact *P*-values, we have therefore used this criterion as a *de facto* test of statistical significance for (co)variance components in what follows. Note that we do not advocate the application of this criterion to other studies unless simulations specifically tailored to the appropriate data structures can be shown to provide similar support.

## Results

### Selection on social dominance

Consistent with our *a priori* expectation of positive selection, regression analyses showed positive relationships between fitness and social dominance. Ordinary least-squares regression analysis of *LBS* on *mean dominance* suggested a significant relationship in females [$\beta = 5.94$ (SE 0.466), $P < 0.001$] though not in males [$\beta = 1.07$ (SE 0.693), $P = 0.125$]. These estimates correspond to standardized linear selection differential estimates (SE) of 0.400 (0.032) for females and 0.207 (0.135) for males, respectively. The *P*-values from simple linear regression given earlier are not strictly valid given the deviation from residual normality, but negative binomial regressions of *LBS* on *mean dominance* yielded qualitatively similar results (females: coefficient = 1.398 (SE = 0.117), $P < 0.001$; males: coefficient = 0.647 (SE = 0.511), $P = 0.206$).

Under the bivariate mixed model we estimated the within-individual covariance (SE) between *focal dominance* (conditioned on *age difference* and *sex code*) and *LBS* as 0.057 (0.032) in females. Although positive as expected, this effect was marginally nonsignificant under a two-tailed test (likelihood ratio test comparison to a reduced model with covariance fixed at zero: $\chi^2_1 = 2.98$, $P = 0.084$). Dividing by the among-individual variance estimate for *focal dominance* yielded a regression coefficient of $\beta = 2.88$ (1.61) and a corresponding standardized selection differential of 0.333 (0.187). A positive covariance term was also estimated in males and was found to be statistically significant using a likelihood ratio test [within-individual covariance (SE) = 0.139 (0.060); $\chi^2_{1\mathrm{DF}} = 5.47$, $P = 0.019$], with a regression coefficient of $\beta = 5.65$ (2.45) and a standardized selection differential of 1.639 (0.712). As a caveat to these results, we reiterate that the standard assumption of multivariate residual normality was violated, and *P*-values associated with these bivariate models should therefore be treated with appropriate caution.

Thus, estimates of the strength of selection do differ under the two approaches used. This is primarily because of accounting for age effects in the bivariate mixed model, which were significant predictors of contest outcome for both focal females [*age difference coefficient* (SE) = 0.058 (0.001), $F_{1,7468.1} = 3615$, $P < 0.001$] and focal males [age difference coefficient (SE) = 0.045 (0.002), $F_{1,2389.4} = 324.7$, $P < 0.001$]. In contrast, *sex code* was not a significant predictor of contest outcome for either sex. For focal females, the predicted mean outcome (SE) was 0.461 (0.009) against a female opponent and 0.447 (0.012) against a male ($F_{2,7915} = 1.67$, $P = 0.189$). For focal males, the corresponding predicted means were 0.497 (0.020) against a male opponent and 0.453 (0.016) against a female ($F_{2,2279.6} = 2.43$, $P = 0.089$).

### Genetic influences on social dominance

#### *Repeatability and genetic (co)variances for social dominance*

Under model 1, we found evidence for significant effects on focal dominance of both the focal and opponent identities (Table 1). Thus, both individuals in the interaction have a repeatable effect on the observed phenotype consistent with among-individual variance in social dominance. Furthermore, we found evidence for a heritable component of variance in focal dominance (Table 1). Under model 2, the estimated direct additive genetic variance was estimated as 0.314 (0.106), yielding an estimated direct heritability of 0.095 (0.032) if we make the standard assumption for the logit link that residual variance = $\Pi^2/3$.

Because it is widely known that social inheritance of dominance rank can occur (Holekamp & Smale, 1991), we tested for nongenetic maternal effects that, if present, are expected to cause upward bias in $\mathrm{V_{A.F}}$ by adding a random effect of maternal identity to Model 2. Maternal variance was low and nonsignificant [$V_M = 0.077$ (0.061)], and the estimate of $\mathrm{V_{A.F}}$ showed virtually no reduction on the inclusion of $V_M$ [$V_{A.F} = 0.312$ (0.113)]. Based on these results, we concluded that nongenetic maternal effects are unlikely to represent an important bias on additive effects here and we did not include them in subsequent models (but see later for important discussion relating to this issue). In comparison with the GLMM results, we also estimated heritability under

**Table 1** Components of variance (on the liability scale) for social dominance estimated from models 1–4.

| Model | $V_{F}$ | $V_{F.A}$ | $V_{F.PE}$ | $V_{O}$ | $V_{O.A}$ | $V_{O.PE}$ | $r_{G,FO}$ | $r_{PE.FO}$ | Parameter constraints |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.02 (0.094) | | | 0.836 (0.082) | | | 0 | 0 | No direct–indirect effect covariance |
| 2 | | 0.314 (0.106) | 0.706 (0.113) | 0.849 (0.083) | | | 0 | 0 | No direct–indirect effect covariance |
| 3 | | 0.366 (0.113) | 0.677 (0.113) | | 0.269 (0.093) | 0.575 (0.099) | 0 | 0 | No direct–indirect effect covariance |
| 4 | | 0.364 (0.119) | 0.956 (0.129) | | 0.363 (0.112) | 0.819 (0.118) | −0.913 (0.065) | −1.080 (0.030) | No constraints |
| 5 | | 0.346 (0.105) | 0.910 (0.110) | | 0.346 | 0.910 | −1 | −1 | $r_{G.FO}$, $r_{PE.FO} = -1$,<br>$V_{F.A} = V_{O.A}$,<br>$V_{F.PE} = V_{F.PE}$ |

Variance components for focal individual ($V_F$) and opponent ($V_O$) estimated under model 1 are partitioned into additive genetic ($V_{F.A}$, $V_{O.A}$) and permanent environment ($V_{F.PE}$, $V_{O.PE}$) in models 2–5. Estimated standard errors are indicated in parentheses and indicate statistical significance at the nominal level ($\alpha = 0.05$) for all variance component estimates (and the direct–indirect genetic correlation ($r_{G,FO}$) under Model 4). $r_{PE.FO}$ denotes the within-individual correlation between direct and indirect permanent environment effects. Absence of a standard error indicates a parameter is fixed because of a model constraint and is therefore not freely estimated (see text for details).

model 2 using data on the observed (0/1) scale and a normal animal model and then transformed this estimate to the liability scale following Dempster & Lerner, (1950). This approach gave slightly lower estimates of $h^2 = 0.041$ (0.013) on the observed scale and 0.064 (0.020) for the liability scale.

Models 3 and 4 indicate that the opponent variance contains a significantly heritable component consistent with the presence of IGEs on the expected contest success of focal individuals (Table 1). Furthermore, under Model 4, we estimated a statistically significant genetic correlation between direct and IGEs of −0.913 (0.065), in close accordance with our expectation of a negative genetic correlation of −1. Under Model 4, direct and indirect additive components were of nearly identical magnitude; the permanent environment variance components associated with focal and opponent individuals were also very similar (Table 1). These results are therefore quantitatively consistent with our logical argument that focal and opponent effects must be drawn from the same distribution but be perfectly negatively correlated. Under this scenario (model 5), additive and permanent environment variance estimates were again significant with $V_{F.A} = V_{O.A} = 0.346$ (0.105) and $V_{F.PE} = V_{O.PE} = 0.910$ (0.110). Although parameter estimates are very similar under models 4 and 5, it is difficult to formally compare models 4 and 5 as likelihood-based methods (e.g. likelihood ratio test, AIC) are not valid using the PQL solutions obtained here. As a way to informally compare model fits, we calculated the variance in working residuals (on the observed data scale, i.e. observed contest outcome – predicted contest outcome). For model 4 we estimated $V_{\text{working residuals}}$ as 0.103 whereas the corresponding estimate for model 5 was 0.101. Thus, while the variances in working residuals were almost identical, a lower estimate was actually obtained under model 5 despite the fact that fewer parameters were estimated.

## Discussion

Our analyses support the *a priori* expectation that dominance is positively associated with fitness, estimated here as LBS, in red deer. This conclusion is qualitatively consistent across the various complementary selection analyses that we conducted, although statistical support was equivocal in some cases. For example, the simple regression approach yielded an estimate of very strong directional selection in females, but this may be upwardly biased by age effects. Specifically, females that live longer will have higher lifetime fitness (on average), but may also have higher mean dominance by simple virtue of being the older individual in more of their dyadic interactions. The correlation between age and dominance rank was previously known in this population (Clutton-Brock *et al.*, 1982; Thouless & Guinness, 1986) and has also been reported in other ungulate populations (Festa-Bianchet, 1991). Accordingly, with age controlled for in the bivariate model of female LBS and focal dominance, the estimated strength of selection was reduced by approximately half (though the standardized selection differential estimate of 0.333 remains high relative to the distribution of estimates in the literature, Kingsolver *et al.*, 2001). Conditioning the selection estimates on age effects in this way reduces the potential bias from age effects but will be overly conservative if higher dominance does causally influence lifetime fitness by effects on survival and hence longevity.

In males, the relationship between dominance and fitness was also positive, although much weaker (and nonsignificant) when selection on mean dominance was estimated from simple regression. However, in males, age effects may induce downward (rather than upward) bias in the selection estimate given that only young focal males were included in the data. Accordingly, with age difference effects accounted for, the estimated strength of selection on dominance in males was actually stronger in males (standardized selection differential of 1.639) than in females, a finding that has been reported elsewhere (Ellis, 1995). Although direct comparison between the sexes is complicated by the differing age distributions of females (all ages) and males (primarily juveniles), a similar result was obtained if the dominance data for females were restricted to observations of juveniles (< 3 years; results not shown). Although adult male–male interactions during the rut were not included in our study, one possibility is that strong selection on male focal dominance results, at least in part, from a high within-individual correlation between dominance during feeding interactions as a juvenile and success in adult male–male contests later in life. The ability to hold a harem and defend it from other males during the rut is a key determinant fitness in adult males (Clutton-Brock *et al.*, 1982).

Thus, our results are largely consistent with positive selection on focal dominance in both sexes although our data certainly do not allow us to prove a causal relationship between the trait and fitness (particularly as we have considered only a single phenotypic trait, Lande & Arnold, 1983). Nonetheless, plausible mechanistic hypotheses linking dominance to fitness do exist. For example, previous analyses of female–female interactions in the Rum red deer population have shown that feeding rate is decreased in subordinates by the close proximity of dominant neighbours, most likely due to movements away by the subordinates that require a break from feeding (Thouless, 1989). Correlations between feeding time and social rank have also been shown in female red deer elsewhere (Veiberg *et al.*, 2004), whereas female–female aggression has been linked to resource competition in other ungulates (Festa-Bianchet, 1991; Robinson & Kruuk, 2007).

Our models of focal dominance also provided evidence that the outcome of dyadic interactions is repeatable within individuals. In other words, there is evidence that, after conditioning on age difference and sex, there is among-individual variance in the likelihood of winning interactions. This finding is broadly consistent with earlier conclusions relating to this population (Thouless & Guinness, 1986). Consistent differences among individuals may arise from a variety of nonmutually exclusive processes including ‘winner’ and ‘loser’ effects (when current contest outcome depends on, and is positively correlated with, prior contest outcomes, Dugatkin, 1997), differences in morphological traits (e.g. size) associated with assessment of resource holding potential (Parker, 1974) or among-individual variation in agonistic behaviours involved in mediating contest outcomes. Whereas our data do not allow us to disentangle these mechanisms, previous analyses have shown a correlation between female dominance rank and body size in this population, suggesting that this is likely to be an important trait (Clutton-Brock *et al.*, 1984).

Our analyses also indicate that a substantial proportion (approximately 27% under model 4) of the among-focal individual variance in dominance is attributable to direct additive genetic effects. Furthermore, our results also supported the final hypothesis that contest outcomes are subject to IGEs. Thus, the dominance status of a focal individual will depend to some extent upon its genotype, but whether a focal individual wins any given contest will also depend upon the genotype of the opponent with which it interacts.

It is important to acknowledge that there is abundant evidence for social inheritance of maternal dominance rank in some taxa (most notably primates and hyenas, Holekamp & Smale, 1991). In the absence of experimental manipulation, it would be foolish to completely rule out the possibility of unmodelled mechanisms of social inheritance upwardly biasing our estimated genetic parameters. However, we note that the animal model framework is far more robust in this regard than classical approaches such as mother–daughter regression. This is because estimates of the genetic parameters are informed by distant relatives (including many that share ancestry through paternal relationships only). Furthermore, the model can be extended to explicitly model maternal effects (Kruuk & Hadfield, 2007), allowing a direct test of the hypothesis that maternal identity explains variation in contest success. Here, there was no statistical support for the presence of (nongenetic) maternal effects and inclusion of maternal identity as a random effect in the model had little impact on genetic parameter estimates. We therefore believe our conclusion that dominance is heritable to be statistically robust.

Accepting that dominance is indeed under direct selection (i.e. there is a causal relationship between focal dominance and fitness) and heritable, then the presence of IGEs provides a resolution to the apparent paradox that a heritable trait is unable to respond to selection (i.e. with one winner and one loser in each contest, the mean contest outcome must always equal 1/2). Recent theoretical work has shown that the expected response to selection depends not just on the conventional additive genetic variance, but also on the indirect genetic variance, the genetic covariance between direct and indirect effects and the relatedness structure among interacting individuals (Wolf *et al.*, 1998; Bijma *et al.*, 2007b; Bijma & Wade, 2008). We have argued that in a contest between two animals there is only one independent observation. If the focal individual is observed to win the contest, then it follows that the opponent must have lost. As our designation of focal and opponent individuals is arbitrary, it is necessarily true that if the focal genotype influences contest outcome (i.e. there are direct genetic effects), then so must the opponent genotype (i.e. there must be IGEs). This argument is supported by the results of our empirical analyses.

Furthermore, if direct and IGEs on dominance must have equal variances and a perfect negative correlation, the sum of $V_{\mathrm{A.F}}$ and $\mathrm{COV}_{\mathrm{A.FO}}$ must equal zero. For the case of two interacting individuals, the sum of $V_{\mathrm{A.F}}$ and $\mathrm{COV}_{\mathrm{A.FO}}$ determines the amount of heritable variation on which selection among individuals can act (from equation 15 of Bijma & Wade, 2008, for $n = 2$). Under the constraints imposed in model 5, this sum must necessarily equal zero, whereas under model 4 we estimated this sum (with SE) as 0.032 (0.052). Note also that under model 5 the variance in total breeding values (*sensu*, Bijma *et al.*, 2007b) is also zero, and therefore, a response in the mean phenotype is not expected, regardless of whether multilevel selection is present and irrespective of the relatedness structure (Bijma & Wade, 2008). Thus, model 5 posits a zero-sum game in which the perfect negative correlation between direct and IGEs creates an absolute constraint on mean contest winning rate, a trait that is both heritable and under selection. We note that although formulated and parameterized somewhat differently, model 5 is essentially equivalent to a theoretical model proposed by (Wolf *et al.*, 2008) as a resolution for the lek paradox. In both contexts, competition among individuals is predicted to cause maintenance of additive genetic variance and an absence of observable phenotypic evolution.

While there is an absolute constraint on the evolution of mean observed phenotype (i.e. contest outcome), this should not be taken to mean that a constraint on genetic change is present. Neither does it follow that the phenotypic means of traits contributing to dominance are evolutionarily constrained (discussed further later). In fact breeding values for, and gene frequencies at loci influencing, dominance are free to evolve. Verbally, the argument here is that a gene predisposing a focal individual to dominance should be selected and so increase in frequency. However, while a focal individual in a subsequent generation will be more likely to carry that gene, it will also be more likely to encounter an opponent carrying it (thus negating any advantage with respect to contest outcome). This represents a particular case of 'environmental deterioration' (Fisher, 1958; Frank & Slatkin, 1992) or the 'treadmill of competition' (Wolf, 2003), which occurs when the phenotypic gains naively expected from selection on (and spread of) a more competitive genotype are not realized because of increased competition in the social environment (Bijma, 2010; Hadfield, J. D., Wilson, A. J. and Kruuk, L. E. B., submitted). Although it is not feasible to conduct such an experiment in red deer, the phenotypic consequences of an underlying genetic response can be made apparent if individuals are transplanted to a different social environment. This was demonstrated by Moore *et al.* (2002) who found that despite little change in agonistic behaviour within selected lines of cockroaches, after seven generations individuals from high-selected lines were consistently dominant in trials against individuals from low-selected and control lines.

In providing an explanation for what we already know must be true (i.e. that the mean proportion of contests won cannot evolve), it could be argued that our analyses provide relatively little biological insight into the evolutionary dynamics of social dominance in red deer on Rum. We also note that quantitative genetic models of the sort developed here are intended to predict the per generation selection response for a phenotypic mean, not changes in higher-order moments (e.g. variance or skew in dominance), or evolutionary stable strategies (Maynard Smith & Price, 1973).

However, aside from the point that we are now able to empirically estimate the genetic components of (co)variance and so recover this 'truth', we hope that the present result also highlights the need for wider recognition of IGEs and their consequences. For instance, although indirect effects (genetic or otherwise) must exist for dominance interactions, the same logic can be extended to any resource-limited trait where phenotype is determined, at least in part, by competitive interactions among individuals. Thus, if competitive ability (i.e. ability to acquire and/or monopolize a limited resource) is heritable, then we expect IGEs to act as evolutionary

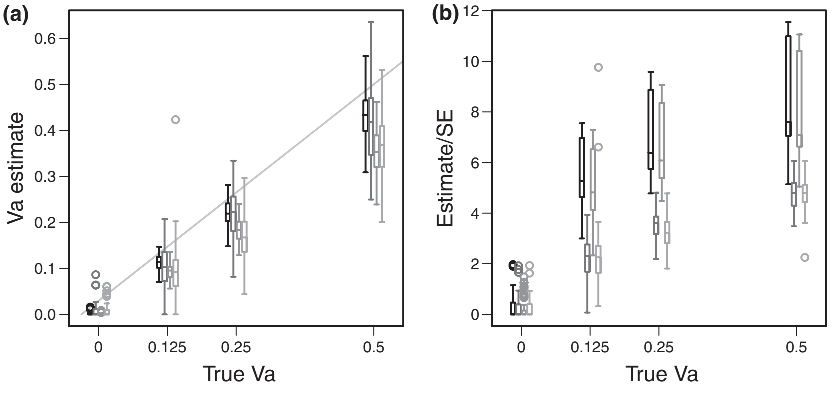

**Fig. 3** Evaluation of (a) bias and (b) power in penalized quasi-likelihood solutions to generalized linear mixed model analyses of dominance in red deer, Cervus elaphus. Each cluster of four bars with decreasing shading represents results from simulations with values of nongenetic repeatable variance ($Vb$) and within-individual variance ($Ve$) set to (i) $Vb = 0$, $Ve = 0$, (ii) $Vb = 0.5$, $Ve = 0$, (iii) $Vb = 0$, $Ve = 0.5$, (iv) $Vb = 0.5$, $Ve = 0.5$. The 1 : 1 line on panel (a) indicates where unbiased estimates should lie.

constraints on resource-limited traits (e.g. growth). Under the IGE modelling framework employed here (i.e. Muir & Craig, 1998; Bijma *et al.*, 2007b), genetic variance in competitive ability should be manifest as a negative covariance between direct and IGEs on resource-limited traits.

We also note that the advantages of directly modelling the observed data using mixed effects models are certainly not limited to genetic studies. For example, in contrast to derived dominance metrics, the observed data come from a defined and known distribution, whereas effects such as age or sex are readily incorporated as explanatory covariates. Furthermore, by testing the causes and consequences of dominance interactions directly, we can avoid the widespread, but statistically unfortunate practice of analysing dominance metrics under the assumption they are known without error (Poisbleau *et al.*, 2006).

A further point of interest is that if dominance (or in a more general context simply competitive ability) is under selection, then the evolutionary consequence of IGE-based constraints will vary among correlated traits according to their causal relationships. For instance, consider a (purely hypothetical) situation in which a morphological trait (e.g. weapon size) was a strong determinant of success in contesting for access to a limited food resource and therefore a strong determinant of growth. If weapon size were heritable, then we would expect positive (direct) genetic correlations between it and both dominance and growth rate. Consequently, we might naively predict that direct selection on dominance would induce positively correlated responses in the other two traits. However, with an IGE-based constraint on dominance recognized then this expectation changes. Whereas the trait causal for dominance (i.e. weapon size) would still evolve as a correlated response to the selection, the downstream trait dependent on contest outcomes (i.e. growth) would be constrained.

In conclusion, our results highlight that social dominance can be a heritable trait. However, it is also a latent trait that, rather than being directly measured, is inferred through observations of contest outcomes. Winning or losing a contest is not a phenotypic observation that can be treated as belonging to a single individual. Rather contest outcomes result from interacting phenotypes and – so by extension – from interacting genotypes (Moore *et al.*, 1997). If the outcomes of these interactions are influenced by additive genetic effects, then they must also be influenced by IGEs. It has been argued that IGEs arising from competitive interactions could represent a widespread, but poorly recognized source of evolutionary constraint for resource-limited traits under natural selection (Cooke *et al.*, 1990; Hadfield, J. D., Wilson, A. J. and Kruuk, L. E. B., submitted). For the particular case of dominance as defined here, we know *a priori* that no amount of selection can result in an increase in the mean observed phenotype, but it is only by explicit recognition and estimation of IGEs that we can demonstrate the genetic basis of this constraint.

## Acknowledgments

We are grateful to Scottish Natural Heritage for allowing us to work on Rum and to the Rum community for their support. Our particular thanks go to the field assistants on Rum and to the Natural Environment Research Council, the Biotechnology and Biological Sciences Research Council (BBSRC), and the Royal Society for supporting the long-term data collection on Rum. AJW is funded by a BBSRC David Phillips fellowship, MM by the Natural Sciences and Engineering Research Council of Canada and LK by the Royal Society.

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## Appendix 1: validation of GLMM methodology

### Simulation approach

We simulated varying rates of additive genetic variance, repeatable among-individual variation and within-individual variation (essentially overdispersion in the context of GLMM analyses) for social dominance. The currently available pedigree for the red deer system has an estimated overall confidence level of 97.6%, and because most remaining null assignments are likely to unsampled individuals from outside of the study area (Walling *et al.*, 2010), we simulated breeding values over the available pedigree, assuming that it is complete and correct. In doing so, we effectively treat all null parentage links in the pedigree as links to unrelated founders, and we deemed this a safe approximation because the population outside the study area is relatively large compared to the number of immigrants to the study area. We composed simulated outcomes of each contest in the real data according to the probabilistic formula

$$z_{ijx} = \delta[logit^{-1}(l_{ijx})]$$

where $z_{ijx}$ is the observed phenotype on the 0/1 scale, $\delta$ is a draw from a binomial distribution, and $l_{ijx}$ is the latent scale probability of that individual $i$ wins contest $x$ against opponent $j$ and is calculated as

$$l_{ijx} = a_i + b_i + e_{ix} - a_j - b_j - e_{jx}$$

where $a$ represents breeding values, $b$ represents nongenetic repeatable individual effects, and $e$ represents a residual error on the latent scale. We simulated data for 100 replicates of each of 16 parameter sets, comprising all possible combinations of *Va*, *Vb* and *Ve* with the following values: *Va* of 0, 0.125, 0.25 or 0.5; *Vb* of 0 or 0.5; and *Ve* of 0 or 0.5. We analysed each simulated data set using model 4 (as described above). For every replicate analysis, we recorded the estimate of *Va* and the ratio of the estimate to its estimated standard error, so that we could subsequently evaluate both bias in *Va* and the utility of comparison of the magnitudes of the estimate to its estimated standard error for hypothesis testing.

### Simulation results

We observed an overall trend for estimates of *Va* to be downwardly biased by about 10% across all nonzero simulated levels of additive genetic variance for dominance (Fig. 3a). The presence of simulated environmental variation had a tendency to very slightly increase this bias (Fig. 3a). These two patterns in bias are expected for PQL solutions to GLMMs of a binary trait (Bolker *et al.* 2009, Rodriquez & Goldman, 2001; Goldstein & Rasbash, 1996), but under the conditions of our analyses of variation in dominance in red deer, these biases are not large enough to hinder the biological interpretation of our model-based estimate.

Under the null hypothesis with respect to additive genetic variance, the ratio of estimated *Va* to the estimated standard error of *Va* proved to be a conservative test statistic. Application of the common 'rule of thumb' that ratios over 2 are statistically justifiable, no false positives occurred in the simulated data for the four combinations of magnitudes of nongenetic sources of variance that we simulated. Given that hypothesis testing of *Va* is a one-tailed test, i.e. we typically do not attach biological meaning to negative *Va*, threshold *Z*-value of 1.64 corresponds to $\alpha = 0.05$ may be justifiable. At this threshold significance level, false-positive rates ranged between 0% and 3%. When we simulated the presence of additive genetic variation for dominance, our study design proved to provide substantial power to detect even modest levels of *Va* (Fig. 3b). Whereas estimates of *Va* were largely unbiased by *Vb* (Fig. 3a), the presence of nonzero *Vb* did reduce power to detect *Va* (Fig. 1b). At the lowest level of *Va* that we simulated (i.e. *Va* = 0.125), average power (i.e. the rate of significant tests) was estimated as 1 in the absence of repeatable among-individual variation and 0.755 when *Vb* = 0.5, at the threshold values of the ratio of the estimate to estimated standard error of 1.64. The corresponding estimates of power were 1 and 0.655 at the 'rule of thumb' threshold of 2 for this ratio.

*Received 1 September 2010; revised 22 November 2010; accepted 29 November 2010*

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