Phylogenetic Comparative Investigations of Sexual Selection and Cognitive Evolution in Primates

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Contributions

Chapter 4

Dr. Catharine Cross provided advice on implementation of meta-analysis and interpretation of results. All other work was carried out by myself.

Chapter 5

Prof. Charles Nunn provided feedback on the hypothesis and advice on implementation of analyses and interpretation of the results. All other work was carried out by myself.

Chapter 6

Dr. Ana Navarrete provided access to an unpublished primate brain dataset, and advice on its use in comparative analyses. All other work was carried out by myself.

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Thesis abstract

A full understanding of any biological trait requires investigation of its evolutionary origin. Primates inspire great curiosity amongst researchers due to the remarkable diversity across species in both anatomical and behavioural traits, including sociality, sexual behaviour, life histories, neuro-anatomy, cognitive abilities and behavioural repertoires. The study of primates has involved comparative approaches since its inception, however, the necessary tools for statistically investigating the macro-evolutionary processes responsible for current diversity in biological traits have been developed only in the last 30 years or so, namely phylogenetic reconstruction and phylogenetic comparative methods. Amongst a multitude of evolutionary questions that can be addressed by phylogenetic comparative analyses, this thesis attempts to address two in particular, concerning primates. First, chapters 3 and 4 use meta-analysis and phylogenetic comparative analyses to investigate the evolution of large, brightly coloured ‘exaggerated sexual swellings’ in female Catarrhine (‘Old World’) primates. Together, chapters 3 and 4 show that such swellings are signals of temporal fertility, and present evidence to suggest that swellings co-evolved with conditions favouring male mate choice and cryptic female choice, therefore shedding light on the general conditions under which female signals of temporal fertility should evolve. Second, chapters 5 and 6 use phylogenetic comparative analyses investigate the evolution of enlarged brain size in the primate order. Together, chapters 5 and 6 suggest that multiple selection pressures have contributed to diversity in brain size and cognitive traits across primates, including sociality, intra-sexual competition and extended life history. Further, analyses presented in chapter 6 suggest that reliance on learned behaviour is a self-reinforcing evolutionary process, favouring ‘runaway’ increases in cognitive abilities and reliance on culture in some primate lineages, which parallels increases in brain size, cognitive ability and reliance on culture in human evolution.

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Chapter 1: General Introduction

1.1 The comparative method

"It is second nature for evolutionary biologists to think comparatively because comparisons establish the generality of evolutionary phenomena." - Harvey & Pagel (1991)

In the Origin of Species (1859), Darwin proposed that the fit of biological traits to environments was the result of natural selection over geological time-scales. For example, Darwin explained the co-occurrence of winglessness with exposed environments across beetle species as follows: "*For during thousands of successive generations each individual beetle which flew least [...]will have had the best chance of surviving from not being blown out to sea.".* The associations between anatomical, behavioural and ecological traits across species, in combination with estimated phylogenetic relationships between species, form the basis of the 'comparative method' – the inference of the evolutionary history of biological traits from their distribution across species – which remains integral to the study of evolution to the present day (Harvey & Pagel, 1991; Nunn, 2011). The modern comparative method is empowered by methodologies and technology unavailable to Darwin, including online, globally available species datasets, molecular phylogenies and specialised phylogenetic statistical methods, which enable comparative studies to draw broad conclusions about macro-evolutionary processes. In particular, 'phylogenetic comparative methods' integrate phylogenetic relationships into statistical analyses of cross-species datasets, allowing for the investigation of not simply variation in extant characters across species, but of the evolutionary processes that account for the origin of such characters (Pagel, 1999).

1.1.1 Comparative primatology

By comparing biological characteristics across primate species, Darwin paved the way for the first comparative primatologists. For example, Darwin observed that presentation by male monkeys tended to occur in species with "brightly coloured hinder-ends" and suggested therefore that the bright colouration was an example of sexual ornamentation (Darwin, 1876). Today, primatologists continue to investigate the origin of variation in skin colouration across primates (e.g. Santana et al., 2012). By describing differences in mental 'faculties', such as imitation, reason and memory, between humans and other primates, as a matter of degree and not kind (Darwin, 1871), Darwin recognised that cognitive as well as biological traits evolve, varying across species due partly to both adaptation and shared ancestry, which remains central to animal cognition research today (MacLean et al., 2011). Researchers began to compare primate species in both anatomy (e.g. Zuckerman, 1930), and behaviour (e.g. Köhler, 1925; Yerkes, 1916) in the early 20th century, and ever since, primatologists have increasingly employed systematic comparative studies in their research (Nunn & Barton, 2001). Over the past ~30 years, comparative studies of primates have addressed such diverse topics as sociality, foraging ecology, sexual selection, parasitism and cognition (Kappeler & van Schaik, 2004; Lee, 1999; Nunn & Alitzer, 2006; Smuts et al., 1987; Tomasello & Call, 1997) (see **Table 1.1** for specific examples).

Topic	**Sub-topic**	**Associated traits**	**Species sample**	**Reference**
Sociality	Social network size	Neocortex ratio & grooming clique size	N=32, across order	(Kudo & Dunbar, 2001)
	Group composition	Female group size & male group size	N=49, across order	(Nunn, 1999)
Foraging	Diet composition	Diet quality & relative brain size	N=44, across order	(Fish & Lockwood, 2003)
	Frugivory	No. parvocellular neurons & % frugivory in diet	Diurnal species	(Barton, 1998)
Sexual selection	Size dimorphism	Operational sex ratio & size dimorphism	N=18, anthropoid species	(Mitani et al. 1996)
	Sperm competition	Testes mass & multi-male mating systems	N=58, across order	(Harcourt et al.1995)
Disease	Disease risk	Population density & parasite species richness	N=101, anthropoid species	(Nunn et al., 2003)
	Immune system	Mating promiscuity & white blood cell counts	N=15, across order	(Nunn, 2000)
Communication	Vocal communication	Home range size & male call carrying distance	N=43, across order	(Wich & Nunn, 2002)
	Facial colouration	Complexity of facial colour pattern & no. sympatric congener species	N=129, neotropical species	(Santana et al., 2012)
Cognition	Brain size	Positive selection on microcephaly genes & neonatal brain mass	N=21, anthropoid species	(Montgomery et al.,2011)
	Inhibitory control	Fission-fusion social systems & performance on inhibitory control tasks	N=7, anthropoid species	(Amici et al., 2008)

Table 1.1: *Examples of recent comparative studies of primates reporting positive associations between traits across species.*

1.1.2 Significance of comparative primatology

Comparative studies attempt to identify the macro-evolutionary processes responsible for current cross-species diversity in biological traits (Harvey & Pagel, 1991). Therefore, comparative studies of primates can have broad implications for evolutionary biology far beyond the primate order. Amongst diverse applications, the comparative method can be used in the study of adaptation, by investigating evidence for co-evolution of biological, behavioural or environmental traits in multiple independent lineages (Nunn, 2011). Although statistical approaches used by comparative studies often do not explicitly reveal the macro-evolutionary processes responsible for co-variation of traits across species (Martins, 2000), comparative studies can be used to test predictions of hypothesised relationships between traits (Harvey & Pagel, 1991; Nunn, 2011). As a non-primate example, consistent with the hypothesis that felid coat patterns are adaptations for camouflage, tropical forest habitats are associated with irregular-patterned coats across felid species (Allen et al., 2011). However, in addition to adaptation, other processes may account for cross species relationships between biological variables, such as biological constraints, by-products or the response of multiple traits to a further selection pressure (Harvey & Pagel, 1991). Therefore, co-variations between traits across species can more appropriately be interpreted as evidence of 'co-evolution', consistent with specific evolutionary scenarios, in the absence of additional evidence for causal directionality (Nunn, 2011).

1.2 Current projects

The following thesis investigates two evolutionary questions in non-human primates (henceforth referred to as 'primates'), to which comparative studies have already been applied, but where major issues remain unresolved. Chapter 2 introduces modern phylogenetic comparative methods, particularly the phylogenetic generalised least squares (PGLS) regression approach. Chapters 3 and 4 address sexual selection on female primates and use meta-analyses and comparative analyses to investigate the evolution of brightly-coloured, conspicuous anogenital swellings, and chapters 5 and 6 use comparative analyses to investigate the evolution of brain size, cognition and culture in primates.

Chapter 2: General methods

In Chapter 2, I discuss the technological developments that have permitted the routine use of phylogenetic comparative statistical analyses to address macro-evolutionary questions in primate anatomy and behaviour. I explain why ordinary statistical methods are typically unsuitable for the analysis of cross-species datasets (Harvey & Pagel, 1991; Nunn, 2011), describe the primate phylogenies used in comparative analyses throughout the thesis and explain the PGLS approach, employed in all the proceeding chapters. I explain that PGLS should be preferred over independent contrasts because PGLS scales phylogenetic signal – the extent to which variation in cross-species data is influenced by phylogenetic relatedness – according to the signal estimated for a given analysis, whilst the independent contrasts approach effectively assumes maximum phylogenetic signal. PGLS is a flexible method in that, where phylogenetic signal is zero, PGLS analyses are equivalent to ordinary least squares (OLS) regression, and where phylogenetic signal is maximal, PGLS analyses are equivalent to independent contrasts analyses (Blomberg et al., 2012). Therefore, using PGLS negates the issue of whether 'phylogenetic or non-phylogenetic' methods should be used to analyse cross-species datasets. Further, additional methodological concerns related to comparative analyses, including a historical reliance on bi-variate correlations and the influence of confounding variables, can be addressed using multiple PGLS regression.

1.2.1 Sexual selection on female primates

Comparative analyses of primates have demonstrated that sexual selection shapes the evolution of male anatomical traits at the macro-evolutionary scale. For example, across anthropoid primates, male-biased size dimorphism is greatest in species where intra-sexual competition between males is expected to be most intense, such as those with polygynous mating systems (Leutenegger & Kelly, 1977; Lindenfors & Tullberg, 1998) and male-biased operational sex ratios (Mitani et al., 1996). These associations support the broader hypothesis that male-male competition selects for ‘armaments’ used in physical confrontations over mates (Andersson, 1994; Darwin, 1871). Accordingly, male-biased size dimorphism is associated with polygyny not only in primates, but across a sample of ~1000 bird species (Dunn et al., 2001). In addition to competition through pre-copulatory mechanisms such as aggressive defence of mates, comparative analyses of primate species suggest that post-copulatory competition shapes the evolution of anatomical traits in males. Mating systems in which females mate multiply are associated with enlarged relative testes mass in males (Harcourt et al., 1995), supporting the general hypothesis that sperm competition selects for traits that increase insemination probability (Birkhead & Møller, 1998). Again, this association is not limited to primates, but rather, enlarged testes mass is also associated with non-monogamous mating systems in birds (Pitcher et al., 2005).

The extent to which sexual selection shapes the evolution of anatomical traits in female animals is currently less well understood than for males, which may be partly attributable to a history of anthropomorphic assumptions about female passivity and ‘coyness’ in mating (Hrdy, 1997; Karlsson Green & Madjidian, 2011). In females, the possibility that ‘ornaments’ – which can be defined broadly as conspicuous, decorative traits with no apparent survival value, result from sexual selection on females, has until recently, received far less attention from evolutionary biologists than have similar traits in males (Amundsen, 2000). Darwin considered bright plumage colouration in female birds as ‘anomalous cases’ resulting from correlated inheritance of male ornaments (Darwin, 1876). Although Darwin proposed that bright skin colouration in male monkeys was an example of sexual ornamentation, favoured by female mate choice, he did not consider the possibility that the similarly bright, conspicuous skin colouration in some female primates was the result of male mate choice

(Darwin, 1876). Today, females of species from a wide taxonomic range are known to exhibit ornamentation, including mammals, reptiles, birds, fish and invertebrates (**Figure 1.1**). However, evolutionary biologists continue to debate the extent to which ornamentation in females results from sexual selection on females through male mate choice and/or competition for mates (Clutton-Brock, 2009), versus other processes, such as within-sex resource competition (LeBas, 2006).

Figure 1.1 *Female ornamentation in a range of species: a) Barbary macaque (Macaca sylvanus), photographer: Cara Evans, b) striped plateau lizard (Sceloporus virgatus), reproduced from Weiss et al. (2011), c) Eclectus parrots (Eclectus roratus), accessed via flickr.com, under a Creative Commons license (photographer username: 'holidaypointau'), d) two-spotted gobies (Gobius flavescens), reproduced from Amundsen & Forsgren (2001), e) long-tailed dance fly (Rhamphomyia longicauda), reproduced from Funk & Tallamy (2000).*

Although comparative studies of sexual selection in primates have focused more on males than females, several comparative studies have investigated the evolution of 'exaggerated sexual swellings' exhibited by the females of some Catarrhine primates ('Old world' monkeys and apes) (Clutton-Brock & Harvey, 1976; Nunn et al., 2001; Nunn, 1999; Pagel & Meade, 2006; Sillen-Tullberg & Moller, 1993). Exaggerated sexual swellings are large, conspicuous, brightly coloured periodic swellings of the female ano-genital tissue, present in 30-40% of Catarrhine species (**Figure 1.2**). Existing comparative studies suggest that exaggerated swellings are a derived trait in the Catarrhines, having evolved at least three times independently, in the lineages leading to chimpanzees and bonobos, to red colobus monkeys and to the clade containing baboons and macaques (Nunn, 1999; Pagel & Meade, 2006; Sillen-Tullberg & Moller, 1993). Changes in swelling size are controlled by cyclic fluctuations in oestrogen and progesterone, where peak size tends to occur around the time of ovulation (e.g. Brauch et al., 2007; Deschner et al., 2004; Higham et al., 2008). Male primates are attracted to the size and colour of swellings (Bielert et al., 1989; Girolami & Bielert, 1987) and increase mating effort when females are maximally swollen (e.g. Gesquiere et al., 2007). Swellings are likely to be energetically costly traits due to their large size (Bielert & Busse, 1983), and the delicate tissues are vulnerable to injury (Matsumodo-Oda, 1998). Therefore, several features suggest that swellings function in mate attraction.

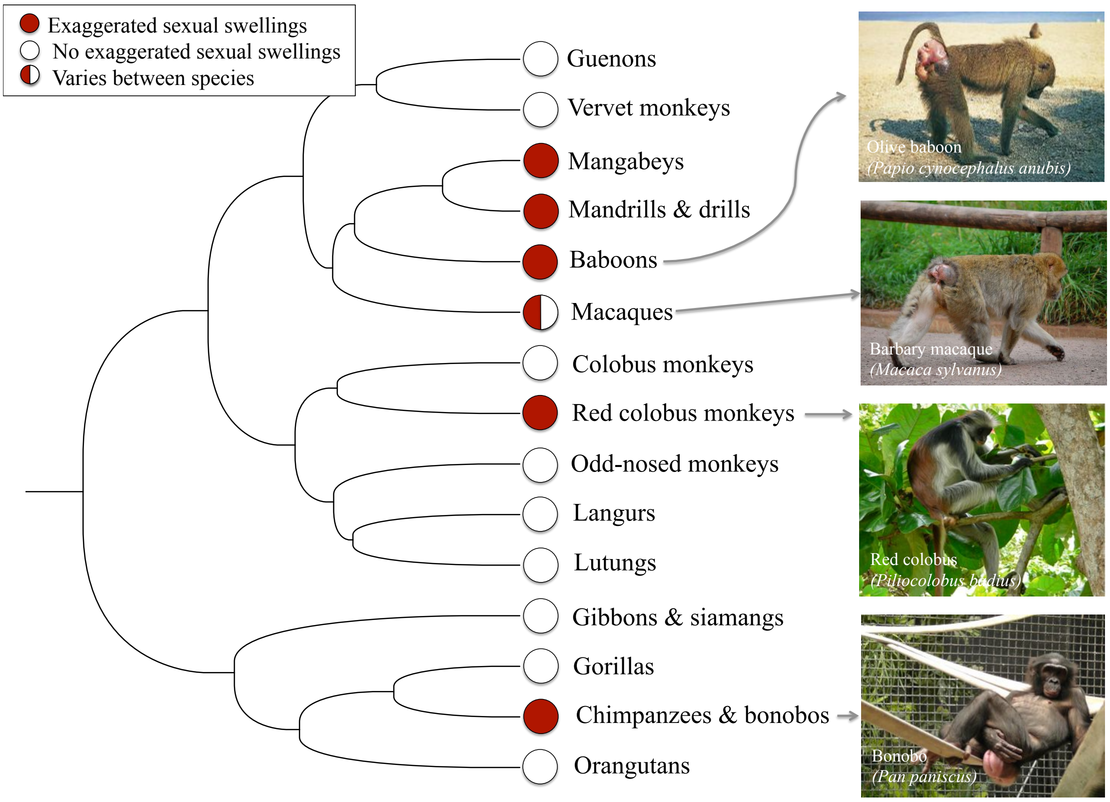


Figure 1.2: *simplified representation of the distribution of exaggerated sexual swellings across Catarrhine primate species. Data on the presence of swellings across species was compiled from primary and secondary published literature (see Chapter 4). A dated consensus phylogeny was obtained from 10kTrees (Arnold et al. 2010) and drawn in FigTree (Rambaut, 2007). Examples of species with exaggerated swellings include olive baboons, Barbary macaques, red colobus monkeys and bonobos (pictured). Photograph sources from top to bottom: olive baboon, reproduced from Domb & Pagel (2001), Barbary macaque, photographer: Cara Evans, red colobus monkey, accessed via flickr.com, under a Creative Commons license, photographer: Lori Newman, bonobo, photographer: Elisabeth Orr.*

Despite several existing comparative studies and reviews (e.g. Nunn et al., 2001; Nunn, 1999; Pagel, 1994; Stallmann & Froehlich, 2000), the evolution of exaggerated swellings remains challenging to explain. Investment in ornaments is generally less likely for females than males due to asymmetric costs of reproduction (Fitzpatrick et al., 1995), which are especially skewed in the Catarrhine primates due to slow life histories (Kaplan et al., 2000) and generally low paternal investment (Whitten, 1987). Further, species with swellings tend to be those where males are promiscuous and competitive in mating (e.g. Muller & Wrangham, 2004), so it is not immediately apparent why females should require a large, costly signal to attract males. Early explanations for the evolution of swellings argued that swellings enhance various benefits of mating for females, including either increased mating from preferred males (Clutton-Brock & Harvey, 1976; Hamilton, 1984) or from multiple males, protecting females against infanticide (Hrdy, 1979, 1981). More recently, Nunn (1999) argued that swellings perform both of these apparently contradictory functions, increasing both mating effort from preferred males and from multiple males, allowing females to balance the benefits of paternity concentration and confusion. Similarly, the ‘paternal care’ hypothesis has argued that swellings benefit females by manipulating paternal investment from single, preferred males versus multiple males (Alberts & Fitzpatrick, 2012).

Alternatively, Pagel's (1994) hypothesis proposed that swellings evolved due to female competition and male mate choice. Pagel (1994) presented theoretical evidence that where males compete for access to females, the costs of mating effort should favour male choosiness in mating. Therefore, where males are choosy, females should compete for access to males. Pagel (1994) argued that if swellings signalled only ovulation timing, there would be no fitness advantage for males preferring to mate with individual females with larger swellings, rather, males should prefer all females equally when fully swollen. Therefore, Pagel's hypothesis required that swellings signal some aspect of individual female quality. However, some researchers have argued that whereas the relationship between swelling size and fluctuations in ovarian hormones is well established, there is currently far less evidence to support swellings as signals of individual female quality (Zinner et al. 2002; Zinner et al., 2004). For example, although swelling size is positively associated with several measures of fecundity in a population of female wild baboons (Domb & Pagel, 2001), these relationships may be accounted for by confounding effects of body mass and food provisioning (Zinner et al., 2002). Further, comparative studies have not supported the predicted association between swellings and measures of female-female competition across species (Nunn et al., 2001).

Chapter 3: Are exaggerated sexual swellings in female Catarrhine primates honest signals of fertility and quality?

In Chapter 3, I investigated the honesty of sexual swellings as signals of fertility and mate quality, using meta-analyses and phylogenetic comparative methods. Currently, the extent to which swellings precisely signal ovulation is uncertain, with the reported onset of peak swelling ranging from the day of ovulation (e.g. Brauch et al., 2007) to two weeks prior to ovulation (Reichert et al., 2002). Evidence for an association between swelling size and individual female quality is also conflicting (e.g. Domb & Pagel, 2001; Setchell & Wickings, 2004). The two most prominent hypotheses for the evolution of swellings, the 'graded-signal' (Nunn, 1999) and 'reliable-indicator' (Pagel, 1994) argue that swellings signal either temporal fertility or individual female quality, respectively. In this chapter, I present the results of meta-analyses and comparative analyses of cross-species datasets compiled from primary literature, showing that while swellings are, on average, honest signals of ovulation timing, there is currently little evidence that swellings signal female quality. However, the apparent honesty of swellings is affected by study methodology, for example, studies using finer-scaled methods of measuring swelling size report that peak swelling size is closer to ovulation than studies using coarser estimations of swelling size. Therefore, swellings may be more precise signals of ovulation than previously thought. Further, there are currently too few studies of swellings and female quality to draw firm conclusions about the relationship between swellings and female quality.

Chapter 4: The evolution of exaggerated sexual swellings in Catarrhine primates

In Chapter 4, I used phylogenetic comparative statistical analyses to investigate the evolution of exaggerated swellings in female Catarrhine primates, which remains contentious despite many prior hypotheses, comparative analyses and reviews (e.g. Hrdy & Whitten, 1987; Nunn, 1999; Nunn et al., 2001; Pagel, 1994; Sillen-Tullberg & Moller, 1993; Stallmann & Froehlich, 2000; Zinner et al., 2004). Major hypotheses disagree primarily over whether exaggerated swellings evolved due to the benefits of manipulating paternity ('paternal care' hypothesis: Alberts & Fitzpatrick, 2012; 'graded-signal' hypothesis: Nunn, 1999) or due to sexual selection on females, via male mate choice and female-female competition ('reliable-indicator' hypothesis: Pagel, 1994). In this chapter, I use phylogenetic comparative analyses to test the predictions of the 'graded-signal', 'paternal care' and 'reliable-indicator' hypotheses, finding no evidence for predicted associations between swellings and infanticide risk, paternal care or aggressive female-female competition. However, I show that swellings have evolved in species characterised by conditions that should favour male mate choice, including costly mating due to sperm competition and male-male competition, and opportunity for mate choice due to large female group sizes. Additionally, I present evidence for co-evolution of swellings with elongated penises in males, supporting the hypothesis that swellings function in cryptic female choice (Dixson & Mundy, 1994; Dixson, 2002). I attempt to incorporate elements of preceding hypotheses into a novel 'female ornamentation' framework in order to present a comprehensive explanation for the evolution of exaggerated sexual swellings in Catarrhine primates.

1.2.2 Evolution of brain size, cognition and culture in primates

"No one, I presume, doubts that the large proportion which the size of man's brain bears to his body, compared to the same proportion in the gorilla or orang, is closely connected with his higher mental powers" – Darwin, *The Descent of Man and Selection in Relation to Sex,* (1871)

Extant primates exhibit striking variation in brain mass, from ~3g in dwarf lemurs to ~460g in gorillas (Navarrete, n.d.). The question of why brains vary in size across species is interesting in itself (Barton, 2006), but the more compelling question, of whether evolutionary increases in brain size correspond to increases in cognitive abilities such as learning ability, memory capacity and processing speed, has occupied biologists since the *Descent of Man* (Darwin, 1871) at least. The question of why brain size enlargement, driven primarily by expansion of the neocortex (Dunbar, 1998; Finlay & Darlington, 1995; Rilling & Insel, 1999), occurred in several primate lineages, including hominids (great apes), Anthropoids (monkeys and apes) and Catarrhines (Old World monkeys and apes) (Striedter, 2005), continues to be investigated despite many comparative studies of primate brain size over the past 20-30 years (e.g. Clutton-Brock & Harvey, 1980; Barton 2012). The general idea that selection over macro-evolutionary timescales shapes neuro-anatomical features, as it does other biological traits, is fairly uncontroversial, but in practice, the use of comparative analyses to investigate brain size evolution involves several controversies, including what brain 'size' means and how best to capture and analyse variation in brain size across species (Harvey & Krebs, 1990).

A primary source of controversy in comparative studies of brain size concerns assumptions about the relationship between enlarged brain size and cognitive traits (e.g. Healy & Rowe, 2007). Typically, comparative studies of brain size investigate co-variation of brain size with social, ecological or life-history variables, thought to correspond to selection pressures for increased cognitive abilities, using brain size is used as a proxy measure for certain cognitive traits (Deaner et al., 2007; Lefebvre et al., 2004). For example, the 'social intelligence' hypothesis has typically been investigated by comparative studies of the relationship between neocortex volume and sociality, assuming that increased neocortex volume is reflective of increased cognitive abilities such as "problem solving" or "reasoning" (Dunbar, 1998; Joffe & Dunbar, 1997). However, the volume of large, multi-functional brain regions seems, *a priori*, to be a crude measure of particular cognitive traits of interest in a given comparative study (Striedter, 2005). Currently, there is surprisingly little evidence that selection for increased brain size results in increased cognitive abilities (Striedter, 2005). To date, there is perhaps only a single published study demonstrating that artificial selection for increased brain size results in corresponding increases in apparent learning ability, in guppies (Kotrschal et al., 2013). Further, evidence of complex cognition in species with extremely small brains, such as learning of rules based on abstract concepts in honeybees (Giurfa et al., 2001), challenges simplistic ideas about the relationship between brain size and cognitive 'capacity' (Chittka & Niven, 2009).

The idea that brain size reflects increased 'intelligence' is especially controversial, perhaps attributable in part to a history of pseudo-science and prejudice in the study of human brain size and intelligence (Gould, 1984). Although not easily defined, there is some consensus that intelligence is *"…a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience"* (Gottfredson, 1997). Some researchers argue that a broader definition of intelligence, as a domain-general learning ability, including cognitive and behavioural flexibility, can usefully be applied to non-human species (e.g. Reader et al. 2011; Roth & Dicke, 2005b). Variation in intelligence across species is not viewed as a '*scala naturae'* in which intelligence decreases with phylogenetic distance from humans, rather, increased intelligence may have evolved multiple times independently, including in species of primates, cetaceans and corvids (Emery & Clayton, 2004; Marino, 2002). Conversely, other researchers argue that there is insufficient evidence that some species are more intelligent than others, and instead that where species differences in cognition exist, they are better understood as species-specific cognitive adaptations, which do not map onto a single, linear dimension of 'intelligence' (e.g. Macphail & Barlow, 1985).

Despite the apparent crudeness of brain size as a measure of cognition, and the difficulty inherent in defining and measuring intelligence, brain size appears to co-vary with measures of intelligence both within and across species. In humans, variation in performance on diverse cognitive tasks is largely explained by a single underlying statistical dimension, termed *'g'* for 'general factor' (Deary, 2001; Neisser, 1996), which correlates with whole brain size (Rushton & Ankney, 2009). Similarly, across primates, a meta-analysis of performance on laboratory-based cognitive tasks, such as reversal learning and detour problems, found that the ranked overall performance of each genus could be predicted with 85% accuracy by a single latent variable (Deaner et al., 2006). Further, a comparative analysis of estimated 'rates' of social learning, innovation, tool use, extractive foraging and tactical deception, based on a systematic literature search and correcting for research biases, found that a single component explained the majority of variation in all five behaviours, which was termed 'g_{s1}' where the 's' subscript denotes 'species' (Reader et al., 2011). Both Deaner's (2006) and Reader's (2011) measures of species *'g'* co-vary with brain size, and with each other (Deaner et al., 2007; Reader et al., 2011). Although the mechanism of these relationships remains largely unknown, increased overall brain size may reflect more specific neurological features (Barton, 2006; Barton, 2012), such as more neurons, more cortical areas and greater cross-modal connectivity (Changizi & Shimojo, 2005; Striedter, 2005), which underpin increased sensory acuity, processing speed, memory capacity and cross-modal integration, and therefore greater cognitive flexibility in general (Chittka & Niven, 2009; Roth & Dicke, 2005b).

If intelligence and brain size co-vary across species, and have co-evolved multiple times independently, common selection pressures may have favoured the evolution of increased brain size and intelligence in distantly related lineages (Emery & Clayton, 2004; Marino, 2002). Many hypotheses for the evolution of increased brain size and intelligence have been proposed, which make testable predictions about co-variates of brain size and intelligence across species. Such hypotheses have in common the assumption that increased brain size reflects selection for increased overall 'information-processing' capacity (Jerison, 1985), but emphasise different selection pressures in particular. Proponents of the 'social intelligence' hypothesis have argued that sociality is the most important selection pressure for increased brain size in primates (Dunbar & Shultz, 2007; Shultz & Dunbar, 2007). Broadly, the 'social intelligence' hypothesis argues that social complexity, particularly large, stable social groups, requires increased 'processing power' to mentally represent and manage social relationships (Dunbar, 1998), and to employ strategic or 'Machiavellian' behaviours such as 'tactical deception' (Whiten & Byrne, 1988). In support of the social intelligence hypothesis, comparative analyses have demonstrated associations between neocortex size and social group size (Dunbar, 1998), grooming clique size (Kudo & Dunbar, 2001) and tactical deception rate (Byrne & Corp, 2004). However, the cognitive mechanisms that account for cross-species relationships between social group size and brain size remain largely to be explored (Byrne & Bates, 2007), particularly as social group size does not predict Reader et al's (2011) measure of general cognitive abilities (g_{s1}) across primate species.

In addition to sociality, ecological and environmental selection pressures may help to explain the evolution of increased brain size in primates. 'Foraging intelligence' hypotheses propose that particular foraging strategies, such as extraction, reliance on resources that are patchily distributed in space and time, and dietary generalism, select for cognitive abilities such as visuo-motor skill, spatial memory, and behavioural flexibility (e.g. Barton, 2012; Gibson, 1986; Overington et al., 2011; Parker & Gibson, 1977). Accordingly, there is a very general association across vertebrates between brain size and reliance on 'hard-to-access' versus abundantly distributed food sources (Striedter, 2005) and in primates, comparative analyses have reported associations between measures of brain size and dietary reliance on fruits, which are typically patchily distributed and often require extraction (Barton, 1996; Clutton-Brock & Harvey, 1980). In addition to foraging ecology, some researchers have argued that climatic fluctuation on short time-scales selected for increased behavioural flexibility in the human lineage, allowing human ancestors to adapt quickly to environmental change through altering dietary or ranging habits, for example (Potts, 1998; Richerson et al. 2005; Richerson & Boyd, 2000). There has so far been little investigation of whether the 'environmental variation' hypothesis can explain enlarged brain size across primates, although one comparative study found no association between climatic variation and either neocortex size or innovation rate (Reader & MacDonald, 2003).

Finally, in addition to extrinsic, socio-ecological or environmental selection pressures, increased reliance on learning may itself select for increased brain size and intelligence, potentially resulting in positive feedback selection and runaway increases in learning ability (Boyd & Richerson, 1985; Reader et al., 2011; Wilson, 1985). In species already reliant on learning for survival and reproduction, due for example to complex sociality and foraging strategies, selection may favour increased life history, particularly a lengthened juvenile period, to enhance the acquisition of learned skills (Joffe, 1997; Kaplan et al., 2000). In support of this hypothesis, in human evolution, increased brain size and reliance on learned behaviour appear to have evolved in association with extended life history (Kaplan et al., 2000; Kaplan & Robson, 2002), Further, the 'cultural intelligence' hypothesis argues that reliance on learned behaviour, increased brain size and intelligence can become mutually reinforcing selection pressures (Reader et al., 2011; Whiten & van Schaik, 2007). Increased brain size and learning ability could enable greater reliance on learned, including socially transmitted, behaviour, due to increased learning ability and memory capacity. In turn, increased reliance on learned behaviour for survival could select for increased brain size and learning ability due to the survival advantages of more efficient learning (Reader et al., 2011; Whiten & van Schaik, 2007). In support of the 'cultural intelligence' hypothesis, existing comparative analyses have shown that brain size positively co-varies with estimated rates of social learning across primate species (Reader & Laland, 2002). Further, species of primates, cetaceans and corvids with enlarged brains, such as chimpanzees, killer whales and New Caledonian crows, all exhibit behavioural variation across populations suggestive of cultural traditions (Hunt & Gray, 2003; Rendell & Whitehead, 2001; Whiten et al., 1999).

The preceding hypotheses are not necessarily mutually exclusive, as multiple factors, including social, ecological, life history variables, may have contributed to the evolution of increased brain size and intelligence in primates (Barton, 2012; Dunbar & Shultz, 2007). However, the question of which variables best explain variation in brain size across species remains contentious, to the point that a recent critical review described the current state of comparative analyses of brain size as a "bewildering array of correlations", arguing that "continuing to add to this body of work will do relatively little to advance our understanding of either brain evolution or function" (Healy & Rowe, 2007). A large part of the controversy surrounding comparative analyses of brain size results from the practice of using brain size as a proxy measure for cognitive traits of interest (Deaner et al., 2000; Lefebvre et al., 2004). Accordingly, the analyses presented in Chapters 5 and 6 examine cross-species variation in estimated measures of behaviours such as social learning, innovation and tactical deception, obtained from Reader et al. (2011) and Byrne & Whiten (1990), rather than variation solely in measures of brain size. Data from Reader et al. (2011) are based on estimated 'rates' of behaviours from systematic literature surveys, corrected for research effort, and are therefore imperfect measures of species typical cognitive traits. However, advantages of this 'taxonomic counts' approach versus other methods of comparing cognition across species, such as comparison of performance on laboratory-based cognitive tasks, include the large, cross-species samples available, and the possibly more naturalistic estimates of behavioural variation between species (Lefebvre, 2011; Reader et al., 2011; Reader & Laland, 2002).

Chapter 5: Co-variation of intra-sexual competition and measures of cognitive abilities across primates

Amongst the various hypotheses for increased cognitive abilities in primates is the lesser-known idea, suggested originally by early proponents of the 'social intelligence' hypothesis (Chance & Mead, 1953), that intra-sexual competition could favour the ability to employ 'strategic' social behaviour in mating competition, such as 'sneak mating', for example. Existing comparative analyses have shown that relative brain size is greatest in the most promiscuous mating systems (Shultz & Dunbar, 2007) and may be positively associated with body size dimorphism (Sawaguchi, 1997). In some primate species, there are reports of deception (Byrne & Whiten, 1990) and innovation (Kummer & Goodall, 1985), used seemingly in order to gain mating opportunities. In Chapter 5, I investigated the hypothesis that intra-sexual competition has favoured cognitive abilities in primates by investigating cross-species associations of male-male competition and mating system with tactical deception rate, innovation rate and $g_{s1,}$ obtained from Reader et al. (2011) and (Byrne & Whiten, 1990). I found that relative testes mass predicted tactical deception, innovation and $g_{s1,}$ and that deception rate was greatest in multi-male, multi-female mating systems. Using sub-sets of data on deception and innovation, which included the sex of the individual, I show that relationships between deception, innovation and testes mass, and between deception and mating system, are primarily driven by deception and innovation in males. I therefore present evidence to support the co-evolution of cognitive traits, especially the ability to employ tactical deception, with male-male competition and promiscuous mating in primates.

Chapter 6: Evolution of brain size, general cognitive abilities and culture in primates

In Chapter 6, I attempted to address some remaining issues concerning the evolution of enlarged brain size and intelligence in primates. In particular, rather than assuming the brain size is a proxy measure of cognitive traits, first, I investigated relationships between brain size and $g_{s1,}$ using a broader range of brain size measures (absolute brain size, relative brain size, relative neocortex size and relative cerebellum size), and more appropriate, up-to-date phylogenetic statistical methods than previous analyses (Reader et al., 2011; Reader & Laland, 2002). Second, I investigated the extent to which socio-ecological, environmental and life history variables, corresponding to major hypotheses for increased brain size, predict not only measures of brain size but additionally $g_{s1.}$ Third, in order to incorporate predictions of the 'cultural intelligence' hypothesis, I investigated the relationships between measures of brain size and social learning and innovation rate, and the extent to which socio-ecological, environmental and life history variables predict not only brain size but also social learning and innovation rate. Finally, I used multi-variate analyses in order to investigate whether multiple predictors of brain size $g_{s1,}$ social learning and innovation could be identified. I found that all four measures of brain size predicted $g_{s1,}$ social learning and innovation, and that group size and extended life history, particularly an extended lifespan, were the primary predictors of increased brain size in primates. Additionally, social group size predicted not only brain size, but social learning and innovation, and extended life history predicted not only brain size but $g_{s1,}$ social learning and innovation. Relationships between $g_{s1,}$ social learning and innovation and their predictors were exponential rather than linear, suggesting possible support for 'runaway' evolutionary processes.

1.3 Conclusions: benefits and limitations of the comparative approach

Chapter 7: General discussion

In Chapter 7, I discuss the principal findings of the thesis and their contributions to the general issue of the utility of the comparative method for understanding macro-evolutionary processes. I argue that the comparative method, supported by modern phylogenetic statistical methods, is an indispensable tool for the study of macro-evolutionary phenomena, especially for testing co-evolutionary hypotheses. However, like all research methods, the comparative method involves trade-offs between benefits and limitations. The most pressing limitation is that the development of sophisticated statistical methods for dealing with phylogenetic signal in cross-species data appears to have overshadowed concerns about the quality of data used in comparative analyses (Nunn, 2011). The comparative analyses presented in this thesis attempted to use the best possible methodology, including the use of the most appropriate and up-to-date phylogenetic methods, investigating the effects of confounding variables and outliers, and addressing ambiguity in classification of biological variables. However, data-quality issues remain inherent in cross-species analyses of existing datasets, such as lack of accounting for within-species variation in traits, the use of small samples or single individuals to represent species-typical traits, difficulty in measuring hard-to-quantify traits such as ‘innovativeness’, and possibility of researcher bias in assembling datasets (Freckleton, 2009; Nunn & Barton, 2001). None of these issues should, however, preclude further comparative analyses of existing datasets (MacLean et al., 2011; Nunn, 2011). Rather, as with any other scientific approach, the results of comparative analyses should be interpreted in context, and their assumptions investigated further by external research. Comparative analyses, therefore, remain a fundamental tool in exploring the evolutionary processes responsible for extant biological diversity.

Chapter 2: General methods

2.1. Phylogenetic comparative statistical methods

Phylogenetic comparative statistical methods are specialised statistical methods designed for the analysis of cross-species datasets. When examining relationships between variables across species in order to test co-evolutionary hypotheses, phylogenetic, rather than conventional, statistical methods should typically be employed for two main reasons. Firstly, cross-species datasets may violate the assumption of conventional statistical methods that data are independent (Felsenstein, 1985). Phylogenetic non-independence arises when species data exhibit phylogenetic signal, i.e. where variation in phenotypic characters is partly determined by phylogenetic relationships, such that closely related species are more phenotypically similar than distantly related species (Harvey & Pagel, 1991; Nunn, 2011). Where phylogenetic signal is high, conventional statistical relationships may overestimate statistical confidence in apparent relationships between variables (Felsenstein, 1985) (**Figure 2.1**). For instance, a review of >500 comparative analyses from published articles reported that 27% of significant non-phylogenetic correlations were non-significant ($p>0.05$) in phylogenetically-controlled analyses (Carvalho et al. 2006). Secondly, phylogenetic statistical methods effectively make analyses of cross-species datasets explicitly evolutionary, such that historical, rather than extant, relationships between variables can be investigated (Nunn & Barton, 2001; Nunn, 2011). Crucially, phylogenetically-informed comparative analyses can identify multiple, independent evolutionary associations between traits, which are essential for testing co-evolutionary hypotheses (Harvey & Pagel, 1991).

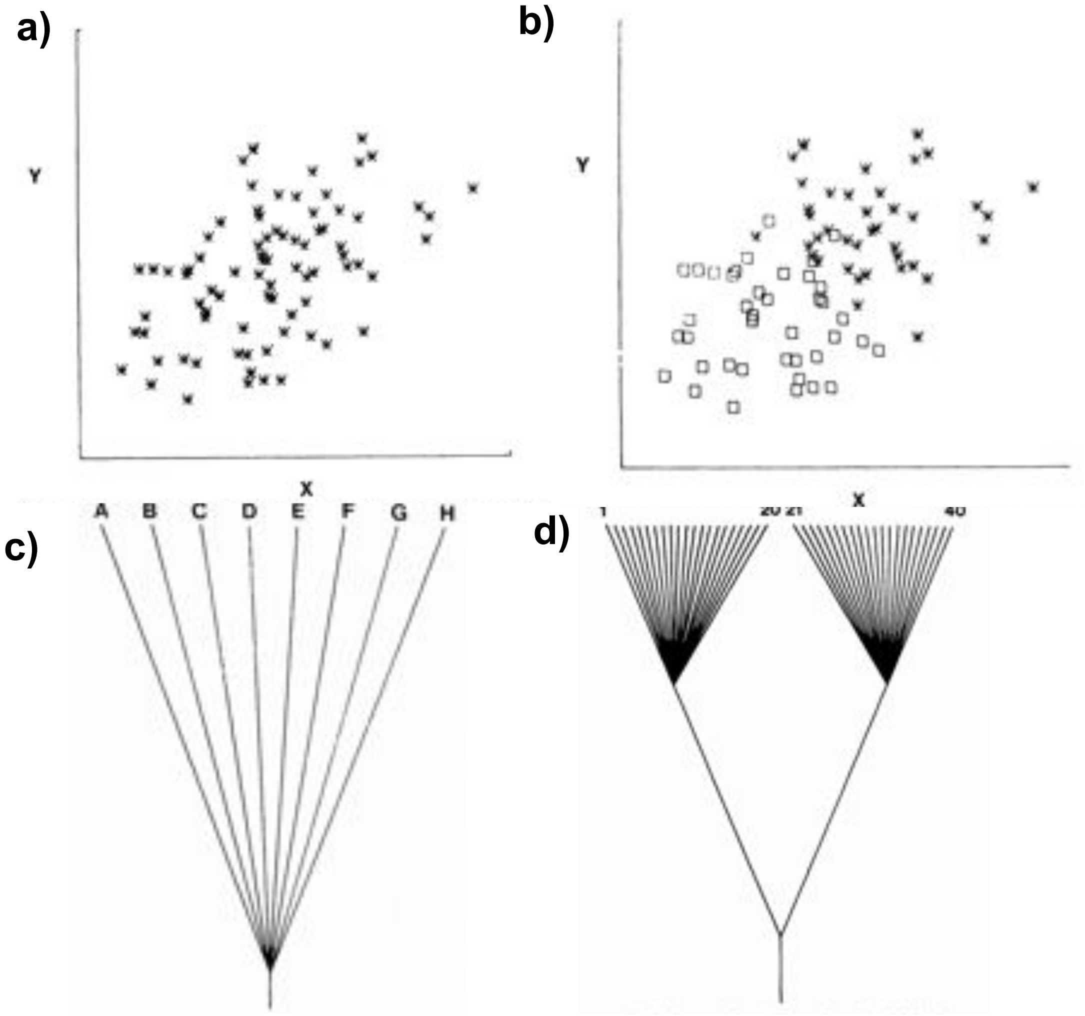


Figure 2.1 *This figure illustrates the danger of ignoring phylogenetic relationships in statistical analysis of cross-species correlations, adapted from Felsenstein (1985). Using conventional correlation, the variables Y and X appear to be correlated (2.1a), and we effectively assume that all species are independent data-points, with evolutionary change in Y and X having occurred in independent evolutionary lineages as represented by a 'star' phylogeny (2.1c). However, in a worst-case scenario, the distribution of data across species may be 'clumped' due to a small number of phylogenetic radiations (2.1d), representing only a small number of evolutionary events, and therefore there may be insufficient degrees of freedom to conclude that Y and X are correlated (2.1b).*

2.1.2 Primate phylogenies

Primatologists have conducted comparative research since at least the 1930s (e.g. Zuckerman, 1933), but because reliable molecular phylogenies have been available only since the 1980s (Pagel, 1999), primatologists have only recently been able to routinely incorporate reliable estimates of phylogenetic relatedness into comparative studies. Prior to the availability of primate phylogenies built from molecular data, comparative analyses of primates sometimes relied on phylogenies built from morphological data, often lacking branch lengths and with conflicting topologies (e.g. Plavcan et al., 1995; Sillen-Tullberg & Moller, 1993). The results of phylogenetic comparative analyses based on such approximate trees may be unreliable due to inaccurate estimates of evolutionary change in characters (Harvey & Pagel, 1991: 94) and are likely to result in variation in results between trees

(Huelsenbeck, 2000). ‘Supertrees’ – composite phylogenies built from multiple existing estimates – allowed for larger-scale phylogenetic comparative analyses across the primate order (Bininda-Emonds et al., 2007; Purvis, 1995). However, supertrees are still single phylogenetic hypotheses, and therefore do not address phylogenetic uncertainty (Bininda-Emonds, 2004). Additionally, supertrees become out-dated as new molecular data become available (Arnold et al., 2010). All comparative analyses in the following chapters were based on a recent Bayesian phylogeny reconstruction, which is regularly updated as additional genetic data become available (10ktrees.fas.harvard.edu, Arnold et al., 2010). Bayesian phylogenetic reconstructions provide posterior probability distributions for trees, rather than single ‘best’ estimates, and therefore incorporate remaining uncertainty into phylogeny reconstruction (Huelsenbeck et al., 2000).

10kTrees provides posterior probability distributions of phylogenies for up to 301 primate species, estimated using Bayesian Markov-Chain Monte Carlo (MCMC) analyses of 11 mitochondrial and 6 autosomal genes (Arnold et al., 2010). Bayesian phylogenetic reconstructions estimate the posterior probabilities of parameters, including trees and models of evolution, given the likelihood of the data and the prior probability of the tree (Huelsenbeck et al. 2001). MCMC is used to estimate parameter values, by starting with a random tree with arbitrary branch lengths and arbitrary values for models of evolutionary change. In subsequent iterations, a change in either the tree or the model values is proposed and accepted with a probability in proportion to the ratio of the likelihood of the current tree/model to the tree/model of the previous iteration. After a ‘burn-in’ period, MCMC chains should ‘settle’ on a range of most probable trees, where the time spent visiting each tree indicates its posterior probability (Arnold et al., 2010). 10kTrees phylogenies were estimated using general time reversible (GTR) and Hasegawa, Kishino and Yano (HKY) substitution models. 10kTrees phylogenies were dated using molecular branch lengths and six fossil calibration points (Arnold et al., 2012). Although comparative analyses can be conducted across ‘blocks’ of phylogenies in order to account for phylogenetic uncertainty in comparative analyses, 10ktrees phylogenies are well resolved, showing little remaining uncertainty. Therefore, single, 50% majority rule consensus trees from the posterior distributions were employed in all analyses. Such trees contain only clades supported by >50% of the trees in the posterior sample. Support for major clades was far higher than >50%, however (**Figure 2.2**).

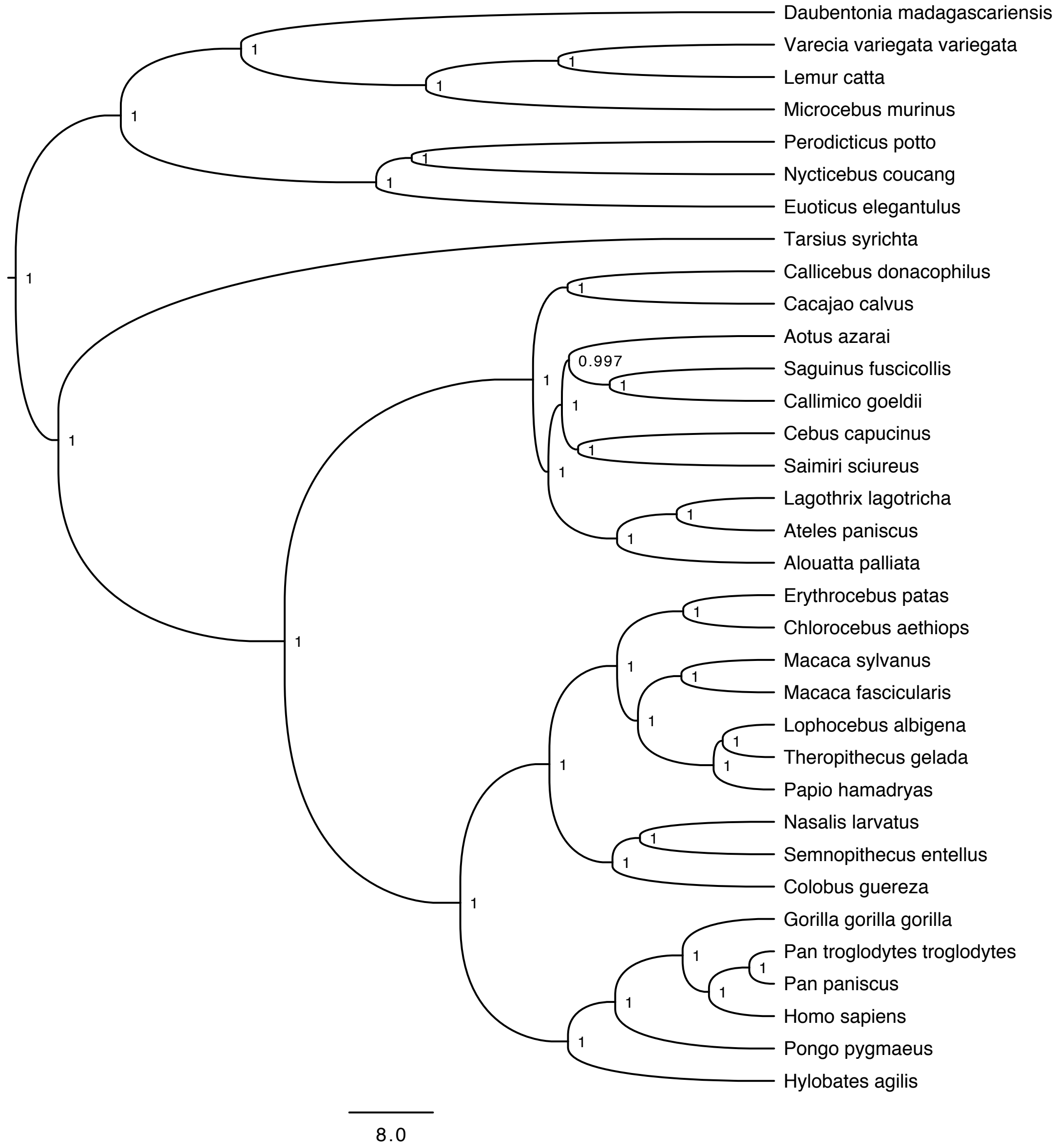


Figure 2.2: *dated maximum clade credibility tree for 34 primate species, for 1000 phylogenies downloaded from 10kTrees (Version 3, Arnold et al., 2012). Scale bar indicates millions of years. Node values indicate posterior support and are all over 99% for this sample, suggesting low phylogenetic uncertainty. The tree was estimated using TreeAnnotator (Drummond et al. 2012) and drawn using FigTree (Rambaut, 2007).*

2.1.3 Phylogenetic generalised least squares regression

For comparative statistical analyses involving a continuous dependent variable predicted by discrete and/or continuous independent variables, phylogenetic generalised least squares regression (PGLS) can be used to incorporate phylogenetic relatedness into statistical analyses of cross-species data (Grafen, 1989; Martins & Hansen, 1997; Pagel, 1997). In regression analysis, residual error is fitted using a variance-covariance matrix, where off-diagonals are the expected co-variance of observations (Field et al., 2012). In conventional regression, since observations are expected to be independent, model residuals are assumed to be normally distributed, with a mean of 0 (Grafen, 1989; Martins & Hansen, 1997).

However, in cross-species analyses, observations are not expected to be independent, rather, residual variation may be phylogenetically structured where closely related species co-vary more than distantly related species (Martins & Hansen, 1997). PGLS accounts for phylogenetic relatedness of species by inputting the shared ancestry between species – i.e. the length of time from the base of the tree to the node at which a pair of species diverge – as the expected co-variance of model residuals between species (Grafen, 1989; Pagel, 1997). A constant-variance (Brownian motion) model of phenotypic evolutionary change can be assumed, where expected co-variance between species is directly proportional to evolutionary divergence, and in which case, PGLS is equivalent to ordinary least squares regression using Felsenstein's (1985) phylogenetically independent contrasts approach (Blomberg et al., 2012; Grafen, 1989).

Evolutionary change may not always be realistically represented by a Brownian motion model, however (Martins & Hansen, 1997; Pagel, 1997). Phylogenetic signal varies between biological traits, with behavioural traits such as displays and daily movement distances tending to exhibit lower phylogenetic signal than morphological traits such as brain size and testes mass (Blomberg et al., 2003). In some cases, low phylogenetic signal may be an artefact of phylogenetic uncertainty, high measurement error for data or low sample size. Alternatively, low phylogenetic signal may reflect evolutionary processes such as frequent convergent evolution or rapid adaptive evolution (Blomberg et al. 2003). Where phylogenetic signal is low, assumption of high phylogenetic signal could result in type II errors (Carvalho et al., 2006). An advantage of PGLS over independent contrasts is that the assumed model of evolutionary change can be varied by transforming the phylogeny (Pagel, 1997). To account for variation in phylogenetic signal, phylogenies can be transformed using Pagel's λ, which multiples the expected co-variances between species by a value between 0 and 1, where 0 represents minimum and 1 maximum phylogenetic signal (Freckleton, et al., 2002). When $\lambda=0$, the tree is transformed to a 'star' phylogeny, in which all species are assumed to be equally related, whereas when $\lambda=1$, the tree is untransformed, such that a Brownian motion model of trait evolution is assumed. The value of λ is determined by the fit between the model of evolution and the observed co-variances between species, which can be estimated by maximum likelihood (Freckleton et al., 2002).

2.1.4 Co-evolution of discrete traits

PGLS is not suitable for datasets consisting only of discrete data. Rather, Pagel's (1994) method can be used to investigate possible co-evolution of two binary traits, by estimating continuous-time Markov models of evolutionary change. Models of evolutionary change consist of 'transition rates' between states of binary characters (i.e. from 0 to 1 and from 1 to 0). Transition rates cannot usually be determined analytically, but rather must be estimated using iterative search procedures. Transition rates are estimated as those that maximize the likelihood of the distribution of characters across species, given a phylogeny with known branch lengths (Harvey & Pagel, 1991). To test hypotheses that traits have co-evolved, the likelihood of a model of evolution in which traits evolve independently can be compared to the likelihood of a 'dependent' model of evolution in which traits are permitted to co-evolve, using a likelihood ratio test. In the independent model, separate transition rates are estimated for each trait, whereas in the dependent model, the probability of change in one trait is permitted to vary according to the state of the other trait, not permitting simultaneous transitions in traits (Pagel, 1994). Further, where the dependent model is favoured over the independent model, the directionality and temporal order of evolutionary change can be investigated in this framework (Pagel, 1997)

2.2 Methodological concerns about the use of phylogenetic comparative analyses

Prior to the development of statistical methods for estimating phylogenetic signal in PGLS regressions, researchers wishing to conduct comparative analyses faced uncertainty over whether phylogenetic or conventional methods should be employed, and often, in an attempt to 'cover all bases', would present results from both approaches (Freckleton, 2009). Therefore, this practice can lead to interpretation difficulties, as results often differ between phylogenetic and conventional statistical analyses of the same data (Carvalho et al., 2006). The use of PGLS negates this issue, however, as the influence of phylogeny is not assumed *a priori* but estimated from the data, and scaled accordingly, through transformation of branch lengths (Pagel, 1997). Therefore, PGLS is appropriate for the analysis of data that vary in phylogenetic signal, including data with zero phylogenetic signal. PGLS may be especially appropriate for analyses of behavioural variables such as those obtained from Reader et al. (2011), as cognitive and behavioural traits tend to exhibit low phylogenetic signal (Blomberg et al., 2003; MacLean et al., 2011). Some caution, however, should be employed when interpreting phylogenetic signal estimated by PGLS analyses. Phylogenetic signal is not known with certainty, and estimates for λ may be uncertain for lower (<30 species) sample sizes (Freckleton et al., 2002). Furthermore, low phylogenetic signal has multiple potential explanations, including not only biological processes, but methodological issues such as high measurement error (Blomberg et al., 2003).

Comparative studies of brain size have been criticised for a reliance on bi-variate statistical associations (Healy & Rowe, 2007). Multiple PGLS regression, however, can be used to incorporate multiple predictor variables into regression models, for example, to investigate independence and relative strength of multiple independent variables, and potentially disentangle multiple evolutionary hypotheses. Multiple PGLS can also be used to address confounding variables, a common issue in comparative analyses (Freckleton, 2009; Harvey & Pagel, 1991; Nunn, 2011). For example, body size scales with many biological traits including brain mass (Barton, 2006). Including confounding variables as predictors in multiple regression is preferable to using ratio measures, as many biological scaling relationships are not isometric. For example, brain-body slopes tend to be <1, and therefore brain/body ratio is not independent of body size (Striedter, 2005). A further alternative, in which residuals are extracted prior to analysis, and subsequently used as data in further analyses, has been shown in simulations to underestimate relationships between predictors and outcome variables where predictors are collinear, whereas the multiple regression approach is not affected by this issue (Freckleton, 2009; Freckleton, 2002). The multiple regression approach is limited in that multiple interactions between predictors may be difficult to interpret, and species sample sizes decrease as additional predictors are included. Overall, however, PGLS provides a flexible statistical framework in which many methodological concerns relating to comparative analyses can be addressed.

Chapter 3: Are exaggerated sexual swellings in female Catarrhine primates honest signals of fertility and female quality?

3.1. Introduction

Female primates exhibit large, brightly coloured anogenital swellings in around 30-40% of Catarrhine (Old World) species (Pagel & Meade, 2006; Sillen-Tullberg & Moller, 1993). Such swellings are found in baboons, mangabeys, mandrills, red and olive colobus monkeys, chimpanzees, bonobos and some species of macaques and guenons. The anogenital area swells and reddens periodically, due to hormonally controlled water retention and dilation of the capillaries in the tissue (Dixson, 2012). Experimental studies have demonstrated that swelling size increases and decreases in response to increases in oestrogen and progesterone respectively (e.g. Carlisle et al., 1981; Gillman & Stein, 1941; Gillman, 1940). The primate ovarian cycle is characterised by a mid-cycle peak in oestrogen just prior to ovulation, followed by an increase in progesterone (Martin, 2007). Therefore, ovulation tends to occur within the period of maximum swelling size, suggesting that swellings are honest signals of female fertility (Nunn, 1999). However, uncertainty remains regarding the precision of swellings as signals of female fertility, and regarding whether swellings signal only temporal fertility, or additionally, individual female quality such as fecundity, health or social rank.

Several aspects of primate mating behaviour further support swellings as honest signals of fertility. Copulations and mating consortships are more frequent when females are fully swollen (Gesquiere et al., 2007; Phillips & Wheaton, 2008), as are behaviours indicative of male and female mating interest such as anogenital inspections by males and solicitations of copulations by females (Clarke et al., 2009; Matsumodo-Oda, 1998). Experimental studies have demonstrated that male baboons respond to visual cues of size and red colouration in swellings, when controlling for behavioural and olfactory cues (Bielert & Anderson, 1985; Bielert et al., 1989; Girolami & Bielert, 1987). However, studies of swelling size changes and the timing of ovulation report considerable variation in the reliability of swellings as signals of the timing of ovulation. For example, although the day of peak swelling coincides with the day of ovulation in some studies (Brauch et al., 2007), others find that the peak swelling period begins fourteen days prior to ovulation and that swellings can remain fully swollen for long periods, in some cases for 50% of the ovarian cycle (Reichert et al., 2002). If swellings reach peak size several days prior to ovulation and remain large over extended periods, swelling size can only be at best approximate cues to the timing of ovulation (Nunn, 1999).

Swellings may function as signals of individual female 'quality' – i.e. genetic or phenotypic fitness – in addition to temporal fertility, such as fecundity, health or social rank (Pagel, 1994). In support of this idea, Domb & Pagel (2001) found that in a population of wild female baboons, swelling size was positively correlated with measures of female fecundity. For example, females with larger swellings began to reproduce earlier and produced greater numbers of surviving offspring than females with smaller swellings. However, the overall evidence for swellings as signals of female quality is currently equivocal and so far, only a handful of studies have investigated this issue. In contrast to Domb & Pagel (2001), Setchell & Wickings (2004) did not find that swelling size was positively correlated with measures of fecundity (age at first birth and inter-birth interval) in a study of semi-free ranging mandrills (*Mandrillus sphinx)*. Similarly, Huchard et al. (2009) found that wild female baboons (*Papio ursinus)* with larger swellings had higher body mass index than females with smaller swellings, whereas Setchell & Wickings (2004) found no significant correlations between body mass index and swelling size in the mandrill population.

The extent to which swellings are accurate signals of fertility, and whether they signal female quality, are issues relevant to current hypotheses for the function and evolution of exaggerated swellings. Nunn (1999) argued that exaggerated swellings are 'graded signals' of female fertility, meaning that swelling size fluctuations correspond to changes in the probability of ovulation across the ovarian cycle. Nunn (1999) and later Zinner et al. (2004) argued that exaggerated swellings are generally honest signals of female fertility, but do not signal the precise timing of ovulation with total reliability. Features of exaggerated swellings that were argued to obscure the timing of ovulation are first, variation in the timing of peak swelling in relation to ovulation, and second, the long, gradual period of increase up to peak size which results in a large swelling being present for several days at time. These properties of the swellings were argued to increase female fitness by allowing them to balance the benefits of mating preferentially with dominant males and with the benefits of mating with multiple males, the latter including paternity confusion. Similarly, a later 'paternal care' hypothesis argued that swellings both concentrate and spread paternity probability between males in order to manipulate paternal investment from single versus multiple males (Alberts & Fitzpatrick, 2012). Nunn's (1999) review suggested that exaggerated swellings are less accurate than smaller, labial swellings, which are presumably the ancestral state of larger swellings. Alternatively, Pagel's (1994) 'reliable indicator' hypothesis holds that swellings are signals of individual female quality, which evolved due to sexual selection on females through both male mate choice and female-female competition for mates. Nunn's graded-signal hypothesis, conversely, does not require that swellings signal individual female quality.

In order to investigate the extent to which swellings in the Old World primates are honest signals of fertility and quality, I used meta-analytic methods to examine first, the relationship of onset and duration of peak swelling to the timing of ovulation, and second, the relationship between swelling size and individual female quality, across a sample of articles from published scientific literature. Although there have been several prior reviews of the signalling properties and evolutionary function of swellings (e.g. Nunn, 1999; Stallmann & Froehlich, 2000; Zinner et al., 2004) these two issues remain unresolved. Furthermore, in the last decade or so, many studies on the timing and duration of swellings in relation to ovulation, and several studies on the relationship between swellings and individual female characteristics have been published. These studies have increasingly employed non-invasive measures of hormonal parameters and fine-scaled measures of swelling size using photographs and video methods. I predicted that if swellings are honest signals of the timing of ovulation, the onset of peak swelling should fall, on average, within the peri-ovulatory period (defined as -3 to +2 days relative to ovulation) in which conception is most probable (Restall, 1967; Royston, 1982; Wilcox et al., 1995), and the duration of peak swelling should not extend outside of the peri-ovulatory period. I predicted that if swellings are signals of individual female quality, the summary effect size for the relationship between female quality and swelling size should be positive and significantly different from zero.

Additional predictions were made about the effects of article methodology on the reported results. Studies varied in how swelling size was measured – either estimated using a categorical scale (often 3, 4, or 5 point), or directly measured on a continuous scale, using for example, callipers, or by measurement from photographs or video using digital methods. It was predicted that studies using direct measurement would report that peak swelling was closer to ovulation, with a shorter duration than studies using categorical estimates of swelling size, because finer scaled changes during the period of peak swelling may be obscured by categorical estimates of swelling size (Deschner et al., 2004). I also predicted that studies of wild, non food-provisioned populations would report that swellings were more accurate as signals of both fertility and quality than food-provisioned populations (either captive or free-ranging). As swellings are produced by ovarian hormones, food provisioning may increase swelling size (Mori et al, 1997) creating a ceiling effect and reducing variation, obscuring potential relationships between swelling size and ovulation timing or quality (Huchard et al., 2009). I investigated the idea that exaggerated swellings are less accurate as signals of the timing of ovulation than small, labial swellings (i.e. the onset of peak swelling is further from ovulation and peak swelling is longer than in small swellings), as proposed by the graded signal hypothesis (Nunn 1999). Finally, because the datasets comprised of multiple species, phylogenetic signal in data on peak swelling onset and duration was estimated. For the data on swelling size and female quality, genus was used as a moderator variable to investigate potential taxonomic differences.

3.2 Methods

3.2.1 Literature search and inclusion criteria

Articles were sourced primarily by keyword searches of the Web of Knowledge and Google Scholar ("primate swelling ovulation", "primate swelling (o)estrogen" and "primate swelling quality"). Titles were read for all articles returned by the Web of Knowledge, and for the first 20 results pages returned by Google Scholar searches. Relevant articles (i.e. those that referred to both swelling size and either ovulation, hormonal parameters or female quality) were read in full and checked against inclusion criteria. Articles included in the data on swelling size and ovulation were those that presented sufficient information to determine the mean day of peak swelling onset and/or peak swelling duration, relative to ovulation. Articles included in the data on swelling size and female quality were those that reported analyses of between-individual swelling size and any continuous measure of female quality, including, for example, age, social rank and body condition (not including body size). Articles unavailable online or in print via the University library were excluded. The datasets included species of Old World primates with large, exaggerated swellings (e.g. baboons), intermediate sized swellings (e.g. red colobus monkeys) and small, labial swellings (e.g. gorillas), whereas species with only genital colour changes (e.g. rhesus macaques) were excluded. Keyword searches identified 28 studies for the ovulation data, and 7 studies for the female quality data, that matched the inclusion criteria. An additional 7 articles on swelling size and ovulation were located by following up references in an existing review (Nunn 1999) and from references cited in studies identified by the literature searches. In total, the swelling size and ovulation dataset consisted of 35 articles across 16 species, and the swelling size and female quality dataset consisted of 7 articles, across 6 species.

3.2.2 Swelling size and ovulation

Data on the timing of peak swelling onset and duration in relation to ovulation were split into two datasets. The first contained the mean onset and/or duration of peak swelling relative to ovulation for each article (the ‘ovulation meta-dataset’). For all articles included in the ovulation meta-dataset, I recorded the mean timing of the onset of peak swelling (defined as 100% size, except in Mohle et al. (2005) where peak swelling was defined as 80% size) in relation to ovulation, in days. For example, if peak swelling occurred 3 days before ovulation, -3 was recorded. This value was extracted either from summary diagrams, summary tables or reported figures in the text of the article (see **Table 3.1** for details of specific sources). Where the author did not estimate the timing of ovulation, ovulation was estimated to occur two days after the mid-cycle oestrogen peak, or one day after the mid-cycle luteinising hormone (LH) peak, where provided (McArthur, 1981; Nadler et al., 1985; Shaikh et al., 1982; Thomson et al., 1992; Wildt et al., 1977). Oestrogen or LH peaks were usually visibly clear and identifiable from summary diagrams. I also recorded the duration of peak swelling, as the number of days from the onset of peak (100%) swelling to the beginning of post-ovulatory detumescence. Again, this value was extracted either from summary diagrams, summary tables or figures in the text of the article. The ‘ovulation meta-dataset’ is included in Appendix A.i. In order to investigate the proportion of the ovarian cycle for which females are fully swollen, onset and duration of peak swelling were averaged and combined with data on average cycle lengths per species that were sourced from Harvey & Clutton-Brock (1985) and van Schaik et al., (1999). The dataset used for analyses of the proportion of the ovarian cycle for which females are fully swollen is included in Appendix A.ii.

For some articles, summary tables or graphs presented raw data, rather than means, for the onset and/or duration of peak swelling in relation to ovulation for each ovarian cycle included in the study. These data were collated into a second dataset consisting of 205 cycles, from 21 articles, across 12 species (the ‘ovulation raw dataset’). The timing of ovulation was identified in the same manner as for the ovulation meta-dataset. In some cases, additional information was required from authors whose papers were identified as relevant and met inclusion criteria but did not contain sufficient information to be included in the ovulation raw dataset. Data on the onset of peak swelling per cycle was requested for Mohle (2005) and Higham et al. (2008) and provided by the corresponding authors, however data from Higham (2008) were not included in the analyses as the onset of peak swelling specifically could not be determined from this data. The ‘ovulation raw dataset’ is included in Appendix A.iii.

Species	**Swelling type**	**Population**	**Swelling measure**	**Onset of peak (100%) swelling & source**	**Duration of peak (100%) swelling & source**	**Sample size (n=cycles)**	**Ovulation estimation**	**Study**
Cercocebus atys lunulatus	Exaggerated	Captive	Volume (ruler)	-1 (Fig. 1)	1 (Fig 1)	6	Oestrogen peak +2 days	Aidara et al. 1981
Macaca tonkeana	Exaggerated	Free-ranging (provisioned)	Categorical (3 level)	-3 (Fig. 1)	2 (Fig. 1)	9	Oestrogen peak +2 days	Aujard et al. 1998
Hylobates lar	Small	Wild	Categorical (3 level)	-5.3 (Fig. 3)	8.4 (Fig. 3)	15	Author's method	Barelli et al. 2007
Macaca nemestrina	Exaggerated	Captive	Categorical (3 level)	-5.5 (Results section)	5 (Fig.1)	21	Author's method	Blakley et al. 1981
Macaca sylvanus	Exaggerated	Free-ranging (provisioned)	Composite size (digital method)	0 (Fig. 3)	1 (Fig. 3)	19	Author's method	Brauch et al. 2007
Gorilla beringei	Small	Free-ranging (non-provisioned)	Categorical (4 level)	0 (Fig. 2)	1 (Fig. 2)	1	Oestrogen peak +2 days	Czekala & Sicotte 2000
Pan paniscus	Exaggerated	Captive	Categorical (5 level)	NA	14.5 (Fig. 2)	2	NA	Dahl et al. 1991
Pan troglodytes	Exaggerated	Captive	Categorical (5 level)	NA	3 (Fig. 2)	2	NA	Dahl et al. 1991
Papio hamadryas anubus	Exaggerated	Captive	Categorical (3 level)	-10 (Fig. 2)	10 (Fig. 2)	9	Author's method	Daspre et al. 2009
Pan troglodytes verus	Exaggerated	Wild	Categorical (3 level)	-7.3 (Fig. 5)	9.894 (Fig. 5)	33	Author's method	Deschner et al. 2003
Pan troglodytes verus	Exaggerated	Wild	Area (digital method)	0 (Fig. 3)	1 (Fig. 3)	29	Author's method	Deschner et al. 2004
Pan troglodytes	Exaggerated	Captive	Categorical (5 level)	-4 (Fig. 2)	4 (Fig. 2)	14	Author's method	Emery & Whitten 2003
Pan troglodytes schweinfurthii	Exaggerated	Wild	Categorical (3 level)	1.5 (Fig. 1)	3 (Fig. 1)	57	Oestrogen peak +2 days	Emery Thompson 2005
Macaca fascicularis	Small (subcaudal)	Wild	Categorical (5 level)	-9.944 (Fig. 3)	15 (Fig. 3)	9	Author's method*	Engelhardt et al. 2005
Papio cynocephalus	Exaggerated	Wild	Categorical (10 level)	-2 (Fig. 1)	3 (Fig. 1)	422	Oestrogen peak +2 days	Gesquiere et al. 2007
Pan troglodytes	Exaggerated	Captive	Categorical (5 point)	-9.334 (Figs 2-4)	9 (Figs 2-4)	3	Oestrogen peak +2 days	Graham et al. 1972
Pan troglodytes	Exaggerated	Captive	Categorical (5 point)	-8 (Fig. 2)	7.333 (Fig. 2)	3	Oestrogen peak +2 days	Graham et al. 1977
Cercocebus torquatus atys	Exaggerated	Captive	Categorical (9 point)	-2 (Fig. 1)	NA	4	Oestrogen peak +2 days	Gust 1994
Pan paniscus	Exaggerated	Captive	Categorical (3 level)	-11.222 (Table 3)	12.778 (Table 3)	9	Oestrogen peak +2 days	Heistermann et al. 1996
Papio hamadryas anubis	Exaggerated	Wild	Composite size (digital method)	-3 (Fig. 2)	1 (Fig. 2)	13	Author's method	Higham 2008 (*Horm. Behav.)*
Macaca nigra	Exaggerated	Wild	Width & height (digital method)	-0.5 (Fig. 3a)	2 (Fig. 3a)	31	Author's method***	Higham et al. 2012
Pan troglodytes	Exaggerated	Wild	Categorical (3 level)	-7.5 (Fig. 1)	12.5 (Fig. 1)	4	LH peak +1 day	Howland et al. 1971
Pan paniscus	Exaggerated	Captive	Categorical (4 level)	-3 (Fig. 1)	8.5 (Fig. 1)	2	Oestrogen peak +2 days	Jurke et al. 2000
Pan troglodytes	Exaggerated	Captive	Categorical (5 level)	-12 (Fig. 1)	16 (Fig. 1)	1	Oestrogen peak +2 days	McArthur et al. 1981
Macaca sylvanus	Exaggerated	Free-ranging (provisioned)	Composite size (digital method)	3 (Fig. 4)	1 (Fig. 4)	5	Author's method	Mohle et al. 2005
Gorilla gorilla gorilla	Small	Captive	Categorical (3 level)	NA	1.8 (median, results text)	7	NA	Nadler 1975
Gorilla gorilla gorilla	Small	Captive	Categorical (4 level)	-2 (Fig. 1)	2 (Fig. 1)	3	LH peak +1 day	Nadler et al. 1979

Pan troglodytes	Exaggerated	Captive	Categorical (5 level)	-10 (Fig. 4)	12 (Fig. 4)	11	LH peak +1 day	Nadler et al. 1985
Hylobates lar	Small	Captive	Categorical (8 level)	-2.334 (Fig. 1&2)	2.334 (Fig. 1&2)	6	LH peak +1 day	Nadler et al. 1993
Mandrillus sphinx	Exaggerated	Captive	Categorical (3 level)	0 (Fig. 3)	1 (Fig. 3)	40	Oestrogen peak +2 days	Phillips & Wheaton 2008
Pan paniscus	Exaggerated	Captive	Categorical (3 level)	-14.304 (Fig. 2)	15.217 (Fig. 2)	23	Author's method	Reichert et al. 2002
Macaca tonkeana	Exaggerated	Free-ranging (provisioned)	Categorical (3 level)	-1.143 (Table 3)	2.143 (Table 3)	8	Author's method****	Thierry et al. 1996
Cercocebus torquatus atys	Exaggerated	Captive	Categorical (6 level)	-3.286 (Table 5)	7 (Table 5)	7	Author's method	Whitten & Russell 1996
Mixed Papio cynocephalus & anubis	Exaggerated	Captive	Categorical (5 level)	-2.096 (Results text & Fig.1)*****	2 (Results text)	52 (onset), 40 (duration)	Author's method	Wildt et al. 1977
Macaca sylvanus	Exaggerated	Wild	Categorical (3 point)	-5.167 (Fig. 1)	6.083 (Fig. 1)	12	Author's method	Young et al. 2012

***Table 3.1** Articles included in the 'ovulation meta-dataset', consisting of mean onset and duration of peak swelling relative to ovulation, as reported in article results, figures or summary tables. Articles arranged in alphabetical order according to lead author.*

*Author estimated ovulation as 'window' from -2 to -3 days prior to faecal progesterone rise. Ovulation assumed to occur on day -2.5 to estimate onset and duration.

** Complete figure obtained from study authors.

*** Author estimated ovulation as two day 'window' – ovulation assumed to occur in centre of window

**** Day of progesterone rise

***** Weighted average from results text. Author presents timing of ovulation relative to detumescence in results text, but shows that peak onset is 2 days prior to detumescence (Fig.1) so results text can be used to infer timing of ovulation relative to peak onset.

Citations for articles included in ovulation datasets

Aidara, D., et al. (1981), *J. Reprod. Fertil.*, 62: 475–481; Aujard, F., et al. (1998), *Am. J. Primatol.*, 46: 285–309; Barelli, C., et al. (2007), *Horm. Behav.*, 51: 221–230; Blakley, G. B., et al.. (1981), *Laboratory Animals*, 15:351–353; Brauch, K., et al.. (2007). Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (Macaca sylvanus) of Gibraltar. *Horm. Behav.*, 52:375–383; Czekala, N., & Sicotte, P. (2000), *Am. J. of Primatol.*, 51:209–215; Dahl, J. F. et al. (1991,. *Am. J. Primatol.*, 24:195–209; Daspre, A., et al. (2009), *Am. J. Primatol*, 71:529–538; Deschner, T., et al. (2003), *Anim. Behav.*, 66:551–560; Deschner, T., et al. (2004), *Horm. Behav.* 46:204–215; Emery, M. A., & Whitten, P. L. (2003), *Behav. Ecol. Sociobiol.*, 54:340–351; Emery Thompson, M. (2005), *Am. J. Primatol.*, 67:137–158; Engelhardt, et al. (2005), *Horm. Behav.*, 47:195–204; Gesquiere, L. R., et al. (2007), *Horm. Behav.*, 51:114–125; Graham, C. E. et al. (1977), *J. Reprod. Ferti* 50:23–28; Graham, C. E., et al. (1972), *Endocrinology*, 91: 13; Gust, D. A. (1994), *Int. J. Primatol*, 15:289–301; Higham, J. P., et al. (2012), *BMC Ev. Biol.*, 12:89; Howland, B. E., et al. (1971), *Biol. Reprod.*, 4:101–105; Jurke, M., et al. (2000), *Primates*, 41: 311–319; McArthur, J. W. et al. (1981), *Am. J. Primatol.*, 1:265–270; Mohle, U., et al. (2005), *Am. J. Primatol.*, 66:351–368, Nadler, R. D. (1975), *Science*, 189:813–814; Nadler, R. D. et al. (1993), *J. Endocrinol.*, 136:447–455; Nadler, R. D. et al. (1979). *Endocrinology*, 105:290–296. Nadler, R. D., et al. (1985), *Am. J. Primatol*, 9:273–284; Phillips, R. S., & Wheaton, C. J. (2008), *Zoo Biol.*, 27:320–330; Reichert, K. E., et al. (2002), *Ethology*, 108: 583–600; Thierry, B., et al. (1996). *Am. J. Primatol.*, 39:, 47–62; Whitten, P. L., & Russell, E. (1996), *Am. J. Primatol.*, 40(1), 67–82; Wildt, D. E., et al. (1977), *Primates*, 18, 261–270: Young, C. et al. (2013), *Horm. Behav.* 63:32–39.

3.2.3 Swelling size and female quality

For all articles included in the female quality meta-dataset, I recorded correlation coefficients (Pearson's R or Spearman's Rho) and sample sizes for all between-female analyses that correlated swelling size with continuous measures of female quality (see **Table 3.2**). The dataset included various measures of swelling size, including area, length, depth and width, and various measures of female quality, including age, body condition, parasite load, social rank, fecundity and genetic diversity. Partial correlation coefficients were not included. Effect sizes were transformed to reflect the direction of predictions, so that, for example, a negative relationship between rank and swelling size would be transformed to positive as this is in the predicted direction (low numbers = high ranks). In two cases, correlation coefficients were not reported for analyses of swelling size and female quality, and were acquired by requests to the corresponding authors who provided either R-values (Emery & Whitten, 2003) or original data (Mohle 2005), which were then re-analysed using Spearman's rank tests. In two further cases, analyses of swelling size and female quality used cycles as the unit of analysis rather than individual females (Gesquiere et al., 2007 and Huchard et al., 2009). The corresponding authors either provided original data (Huchard 2009) or referred us to alternative unpublished data (Fitzpatrick et al., n.d.; Gesquiere et al., 2007). These data were then re-analysed by Spearman's rank tests on averaged measures of swelling size for each individual. The dataset consisting of between-female correlation coefficients for relationships of swelling size to measures of female quality is included in Appendix A.iv.

Species	**Population**	**Swelling size measure**	**Quality measure**	**N**	**Effect size**	**Study**
Papio c. anubis	Wild	Length	Age	22	-0.61	Domb & Pagel 2001
Papio c. anubis	Wild	Depth	Age at first conception	20	-0.52	Domb & Pagel 2001
Papio c. anubis	Wild	Length	Age at first conception	22	-0.67	Domb & Pagel 2001
Papio c. anubis	Wild	Width	Age at first conception	21	-0.29	Domb & Pagel 2001
Papio c. anubis	Wild	Depth	No. offspring per year	20	0.3	Domb & Pagel 2001
Papio c. anubis	Wild	Length	No. offspring per year	22	0.55	Domb & Pagel 2001
Papio c. anubis	Wild	Width	No. offspring per year	21	0.1	Domb & Pagel 2001
Papio c. anubis	Wild	Depth	No. surviving offspring per year	20	0.38	Domb & Pagel 2001
Papio c. anubis	Wild	Length	No. surviving offspring per year	22	0.53	Domb & Pagel 2001
Papio c. anubis	Wild	Width	No. surviving offspring per year	21	0.27	Domb & Pagel 2001
Papio c. anubis	Wild	Depth	Proportion of surviving offspring	20	0.29	Domb & Pagel 2001
Papio c. anubis	Wild	Length	Proportion of surviving offspring	22	0.4	Domb & Pagel 2001
Papio c. anubis	Wild	Width	Proportion of surviving offspring	21	0.36	Domb & Pagel 2001
Papio c. anubis	Wild	Length	Social rank	18	0.087	Domb & Pagel 2001
Pan troglodytes	Captive	Anal width	Age	14	-0.547	Emery & Whitten 2003
Pan troglodytes	Captive	Height	Age	14	-0.448	Emery & Whitten 2003
Pan troglodytes	Captive	Area	Age	14	-0.428	Emery & Whitten 2003
Pan troglodytes	Captive	Labial width	Age	14	-0.619	Emery & Whitten 2003
Pan troglodytes	Captive	Area	Body condition	14	0.39	Emery & Whitten 2003
Pan troglodytes	Captive	Area	Parity	14	-0.593	Emery & Whitten 2003
Pan troglodytes	Captive	Height	Parity	14	-0.536	Emery & Whitten 2003
Papio cynocephalus	Wild	Width	Age	46	0.398	Fitzpatrick (n.d.)
Papio cynocephalus	Wild	Width	Parity	46	0.345	Fitzpatrick (n.d.)
Papio cynocephalus	Wild	Width	Rank	46	0.183	Fitzpatrick (n.d.)
Papio ursinus	Wild	Area	Age	11	-0.166	Huchard et al. 2009
Papio ursinus	Wild	Area	Body condition	11	-0.091	Huchard et al. 2009
Papio ursinus	Wild	Area	Rank	11	-0.415	Huchard et al. 2009
Macaca sylvanus	Free-ranging (provisioned)	Area	Age	12	0.077	Mohle et al. 2005
Macaca sylvanus	Free-ranging (provisioned)	Area	Rank	12	-0.287	Mohle et al. 2005
Macaca sylvanus	Free-ranging (provisioned)	Area	Waist/hip ratio	9	-0.092	Mohle et al. 2005
Mandrillus sphinx	Captive	Depth	Age	26	-0.219	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Length	Age	29	0.049	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Age	29	0.101	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Depth	Age at first birth	22	0.244	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Length	Age at first birth	22	0.073	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Age at first birth	19	0.105	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Depth	Body mass index	26	0.338	Setchell & Wickings 2004

Mandrillus sphinx	Captive	Length	Body mass index	29	0.195	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Body mass index	29	0.311	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Depth	Inter birth interval	16	0.351	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Length	Inter birth interval	16	-0.221	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Inter birth interval	15	0.021	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Depth	Mean no. cycles to conception	24	0.039	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Length	Mean no. cycles to conception	24	0.061	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Mean no. cycles to conception	21	0.187	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Depth	Rank	26	0.369	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Length	Rank	29	0.195	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Width	Rank	29	0.081	Setchell & Wickings 2004
Mandrillus sphinx	Captive	Height	B. coli % abundance	10	-0.047	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	B. coli % abundance	10	-0.022	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	B. coli abundance	10	-0.261	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	B. coli abundance	10	-0.343	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	E. histolyca/dispar abundance	10	-0.084	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	E. histolyca/dispar abundance	10	0.063	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	Nematode abundance	10	0.14	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	Nematode abundance	10	-0.051	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	Nematode % presence	10	-0.049	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	Nematode % presence	10	-0.227	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	Neutrophil/lymphocyte ratio	10	-0.007	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	Neutrophil/lymphocyte ratio	10	0.167	Setchell et al. 2006
Mandrillus sphinx	Captive	Height	Genetic diversity	32	0.023	Setchell et al. 2006
Mandrillus sphinx	Captive	Width	Genetic diversity	32	0.019	Setchell et al. 2006

Table 3.2 *Articles and unpublished data included in the meta-dataset on female quality and swelling size.*

Citations for articles included in the female quality meta-dataset

Domb, L. G., & Pagel, M. (2001), *Nature*, 410: 204–206; Emery, M. A., & Whitten, P. L. (2003), *Behav. Ecol. Sociobiol*., 54:340–351.Fitzpatrick, C. L., et al. (n.d.). Unpublished data; Huchard, E., et al. (2009), *Proc. R. Soc. B. Lond,* 276:1889–97; Mohle, U., et al.. (2005), *Am. J. Primatol.*, 66:351–368; Setchell, J. M. et al. (2006), *Behav. Ecol. Sociobiol.*, 61: 305–315. Setchell, J. M., & Wickings, E. J. (2004). *Behav. Ecol*, 15:438–445.

3.2.4 Moderator variables: article methodology and swelling types

Several methodological features of the studies were recorded for all datasets. Swelling size had been either estimated visually, using a categorical scale (usually 3, 4 or 5 point), or measured on a continuous scale, by physical measuring devices such as callipers or by measurement from photographs or video using digital methods. Studies using categorical estimated measured were coded as 'visual' and those using continuous, direct meaurement as 'direct'. I recorded whether the population was 'non-provisioned', i.e. natural feeding or 'provisioned', i.e. captive or free-ranging, food-provisioned groups. The study sample size was recorded as number of cycles for the ovulation meta-datasets, and the number of individuals for the quality dataset. The type of swelling was coded either as 'exaggerated' (large size, encompassing anogenital tissue, which included all *Pan* and *Papio* species), 'medium' (labial tissues plus some anogenital or subcaudal tissues, to a lesser extent than large swellings, which included all *Cercocebus, Mandrillus and Macaca* species), or 'small' (labial tissues only, which included all *Gorilla* and *Hylobates* species). For the female quality dataset, I additionally coded measures of female quality into 8 categories (age, parity, social rank, fecundity, body condition, immune status, parasitism and genetic diversity).

3.2.5 Statistical methods

For the ovulation meta-dataset, statistical methods for weighted data were used to analyse the data in order to take into account differences in sample sizes between studies. Weighted statistical methods were used to estimate the mean, standard deviation and effects of moderator variables on peak swelling onset and duration. Data were weighted by article sample size, as the number of ovarian cycles. Weighted statistical analyses were run in R (R Core Team, 2013) using the package 'Weights' (Pasek, 2012). For the ovulation raw dataset, ordinary summary statistics were used to find the mean and standard deviation for the onset and duration of peak swelling. Linear models and linear mixed models were used to investigate the effects of the moderator variables. Article identity was used as a random factor to account for possible non-independence of data from within the same study. Linear models and linear mixed models were run in R (R Core Team, 2013*)* using the package 'nlme' (Pinheiro et al., 2013). In order to investigate differences in the duration of peak swelling as a proportion of ovarian cycle length between swelling types, data on duration of peak swelling from both the ovulation meta-dataset and the ovulation raw-dataset were averaged per species. Phylogenetic generalised least squares regression (PGLS) was then used to investigate the effect of swelling type peak on swelling duration, using species-level average ovarian cycle lengths, obtained from Harvey & Clutton-Brock (1985) and Van Schaik (1999) as a co-variate.

For the female quality dataset, random-effects meta-analyses were used to estimate summary effect sizes. Effect sizes were Fisher's Z transformed. Each article contained multiple effect sizes from same study population, but effect sizes were not used as the unit of analysis to avoid pseudo-replication (Borenstein et al., 2009). Rather, the data were first split into three categories of measures of female qualities: 1) measures of body condition/fecundity, 2) measures of age/parity, and 3) social rank. Data were grouped together where different measures were thought to reflect the same underlying aspect of female quality, and because there were very few studies for some categories of female quality. Within each sub-set, where there were multiple effect sizes per study, effect sizes and sample sizes were averaged per article such that each article contributed a single effect size and sample size. Meta-regression was then used to investigate the effect of article-level moderator variables on effect sizes. Not all moderator variables could be investigated due to small sample sizes and insufficient variation in the samples. Measures of parasitism, genetic diversity or immune system function were not included in meta-analyses as these all came from a single study (Setchell et al. 2006). Meta-analyses and meta-regressions were run in R (R Core Team, 2013) using the package 'metafor' (Viechtbauer, 2010).

3.2.6 Phylogenetic signal

In datasets containing multiple species, datapoints may not be independent but rather contain phylogenetic signal, whereby closely related species are more phenotypically similar than distantly related species (Harvey & Pagel, 1991). To address phylogenetic non-independence, data on onset of peak swelling and duration of maximum swelling were averaged per species and phylogenetic signal estimated using Pagel's λ. Pagel's λ is a measure of the extent to which the error structure in a model is predicted by the phylogenetic relationships between species, estimated from the data and phylogeny, assuming a Brownian motion model of evolutionary change (Pagel, 1999; Pagel, 1997). λ varies from 0 to 1, where 0 indicates minimal and 1 maximal influence of phylogenetic structure on the data. Analyses involving Pagel's λ were run in R, using the Caper package (Orme et al., 2011). Single, dated consensus phylogenies were downloaded from 10ktrees (Arnold et al., 2010, version 3, http://10ktrees.fas.harvard.edu/).

3.3 Results

3.3.1 Onset & duration of peak swelling relative to ovulation (ovulation meta-dataset)

In the ovulation meta-dataset (comprising mean onset and duration of swelling size per article) the weighted mean for peak swelling onset was -2.67 days relative to ovulation (*SD*=3.12, *n*=32, **Figure 3.1**). The weighted mean for peak swelling duration was 3.89 days (*SD*=3.34, *n*=34, **Figure 3.1**). One article contributed a large amount of cycles (Gesquiere 2007: *n*=422 cycles) relative to other articles, however, removing data for this article did not strongly affect the results (without the Gesquire article, onset: -3.30 days, duration: 4.72 days). A weighted T-test showed that studies using 'direct' methods of measuring swelling size reported that peak swelling onset was significantly closer to ovulation than studies using 'visual' methods (direct: -0.59 days, visual: -2.95 days, *p*=0.008, *n*=33, **Figure 3.2a**). 'Direct' studies reported a significantly shorter duration of peak swelling than 'visual' studies (direct: 1.30 days, visual: 4.23 days, *p*<0.001, *n*=35, **Figure 3.2b**). Studies of non-provisioned populations reported that peak swelling onset was marginally closer to ovulation than studies of food-provisioned populations (non-provisioned: -2.09 days, provisioned: -4.09 days, *p*=0.10, *n*=33). There was no significant difference in peak swelling duration between food-provisioned and non-provisioned populations (p=0.34, n=35). There were no significant differences in either onset or duration between small, medium or large swellings, in weighted T-tests (*ps*>0.3). Using averaged onset and duration of peak swelling per species, Pagel's λ was estimated as 0 using maximum likelihood for both onset of peak swelling (and duration (*ns*=16), suggesting that there was no phylogenetic signal in this dataset (**Figure 3.3**).

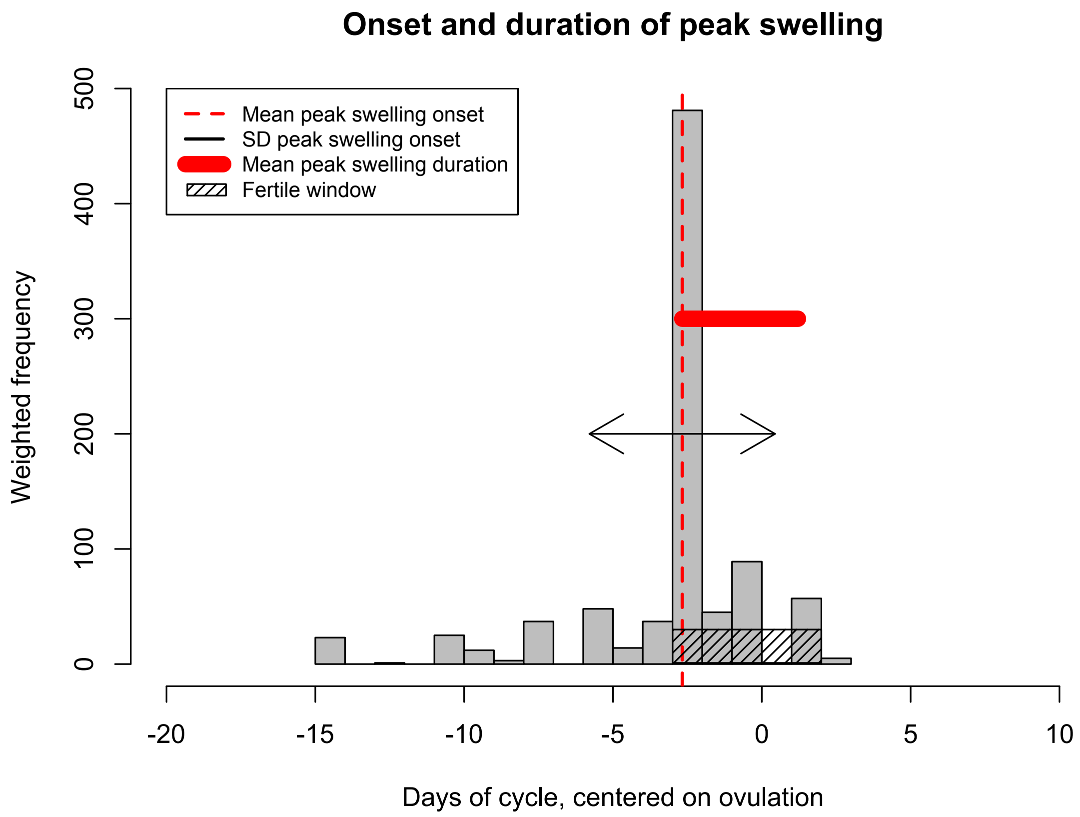


Figure 3.1 *Mean onset and duration of peak swelling for the ovulation meta-dataset, plotted onto a weighted histogram.*

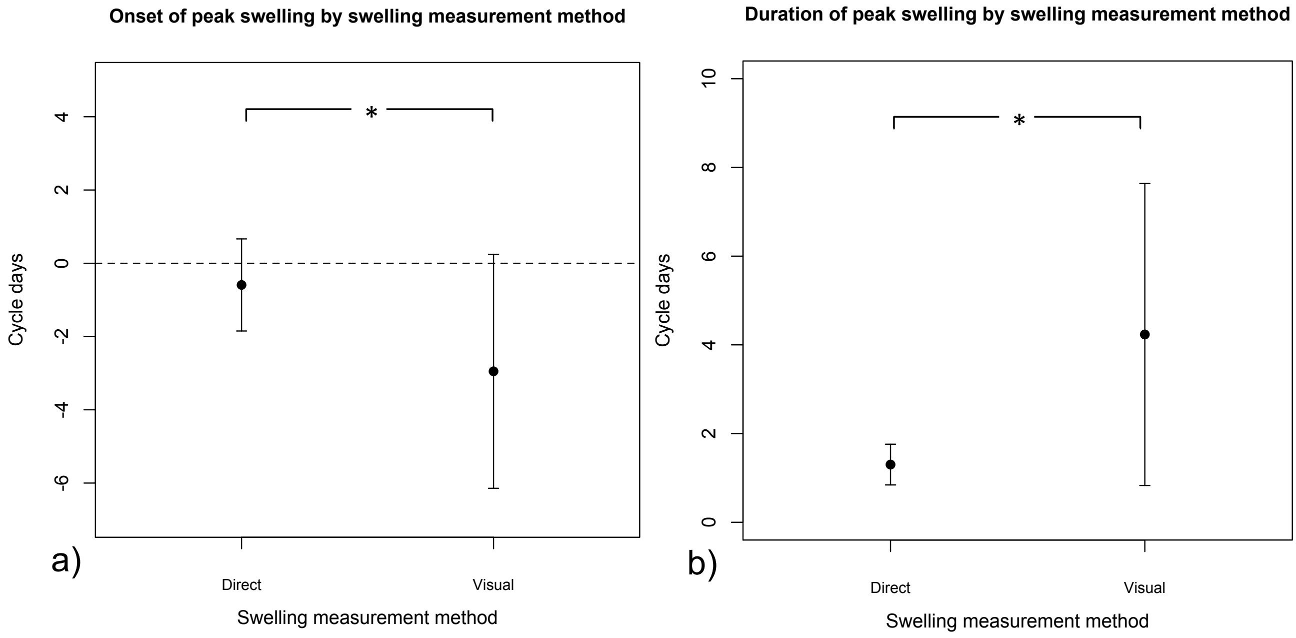
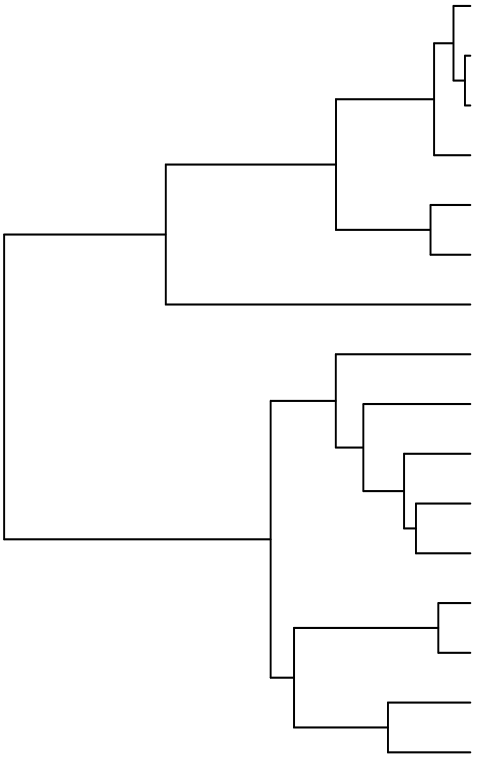


Figure 3.2 *Differences in a) weighted mean onset and b) weighted mean duration of peak swelling between studies measuring swellings using 'direct' (e.g. callipers or from photos or video) versus 'visual' methods (estimation using a categorical scale). Bars indicate weighted standard deviations, * = p<0.05.*



Onset	Duration	
-3.89	5.73	*Pan troglodytes verus*
-7.06	7.92	*Pan troglodytes troglodytes*
1.5	3	*Pan troglodytes schweinfurthii*
-12.70	14.28	*Pan paniscus*
-2	1.86	*Gorilla gorilla gorilla*
0	1	*Gorilla beringei*
-4.67	6.52	*Hylobates lar*
-1.31	2.69	*Macaca sylvanus*
-9.94	15	*Macaca fascicularis*
-5.5	5	*Macaca nemestrina*
-1	2	*Macaca nigra*
-2.13	2.07	*Macaca tonkeana*
-2	3	*Papio cynocephalus*
-5.86	4.68	*Papio anubis*
0	1	*Mandrillus sphinx*
-2.18	1	*Cercocebus torquatus atys*

Figure 3.3 *Average onset and duration of peak swelling in relation to ovulation per species, using data from the ovulation meta-dataset, alongside a consensus phylogenetic tree obtained from 10kTrees (Arnold et al. 2010). Variation across species did not correspond to phylogenetic distance as indicated by the lack of phylogenetic signal in the data (Pagel's λ=0).*

3.3.2 Onset & duration of peak swelling relative to ovulation (ovulation raw-dataset)

In the ovulation raw dataset (comprising onset and duration of peak swelling per cycle), the mean day of onset of peak swelling was -7.61 days relative to ovulation (*n*=165, *SD*=5.80). The mean duration of peak swelling was 9.73 days (*n*=190, *SD*=5.75). Linear mixed models, using the article identity as a random factor (which in all cases significantly improved the model fit as assessed by AIC value), reported no significant differences in either onset or duration of peak swelling size between swelling size measurements ('direct' or 'visual') or population types (provisioned or non-provisioned) (*p*s>0.7). However, the raw dataset only included data from one study that used the 'direct' method of measuring swellings. Linear mixed models showed that there were some significant differences in onset and duration between swelling size categories (**Figure 3.4a, b**) The peak onset for large swellings was significantly further from ovulation than for small (*p*=0.002) and medium swellings (*p*=0.005). Peak onset was not significantly different between small and medium swellings (*p*=0.36). Duration of peak swelling was significantly longer in large than small swellings (*p*=0.003) and marginally longer than in medium swellings (*p*=0.06). Duration of peak swelling was marginally longer in medium than in small swellings (*p*=0.08). Using averaged onset and duration of peak swelling per species, Pagel's λ was estimated as 0 for both onset of peak swelling and duration (*ns*=11), suggesting that there was no phylogenetic signal in this dataset.

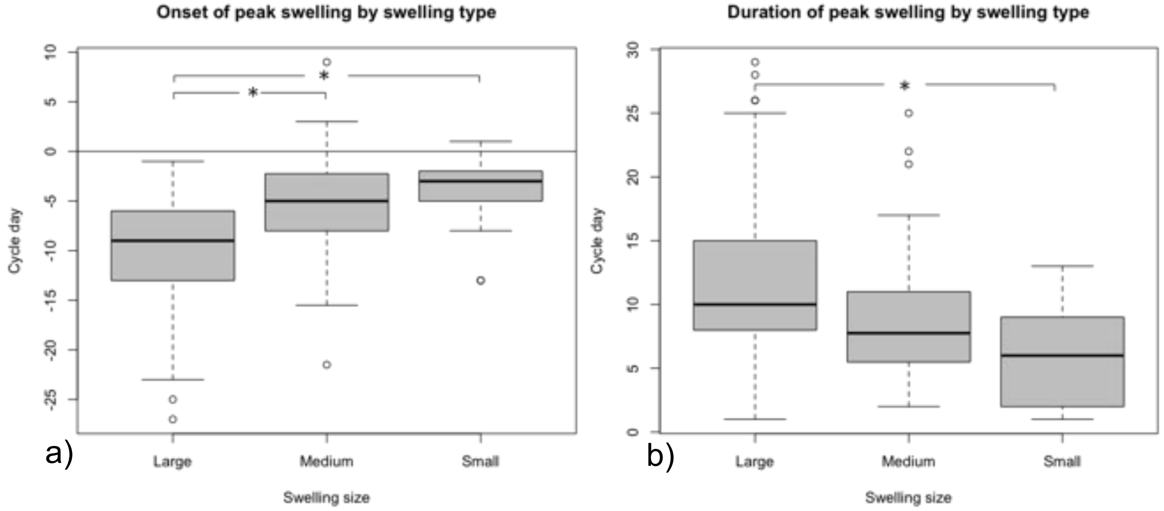


Figure 3.4 *Differences in onset (a) and duration (b) between swelling size categories, using data from the ovulation raw dataset. *=p<0.5.*

3.3.3 Duration of peak swelling as a proportion of cycle length

I investigated differences between swelling types (exaggerated, intermediate and small) in the proportion of the ovarian cycle where females were fully swollen by using average cycle lengths per species, and data on duration of peak swelling averaged per species from both the ovulation datasets. A PGLS regression demonstrated that the proportion of the cycle where females were fully swollen did not differ between swelling types using per species weighted mean peak swelling duration from the 'ovulation meta-dataset' (*ps*>0.5, *n*=12, **Figure 3.5,** see Appendix E.i for full model results). This analysis suggests that although species with larger swellings have longer peak swelling periods, they also have longer ovarian cycles so that the proportion of days at peak swelling does not increase with swelling size. The relationship between swelling size categories and peak swelling duration as a proportion of cycle length was not investigated using peak swelling duration from the 'ovulation raw-dataset' due to smaller sample size and over-parameterization (*n*=8 species, estimating 4 parameters). Differences between article-level moderator variables could not be investigated as this dataset contained average values per species across multiple articles.

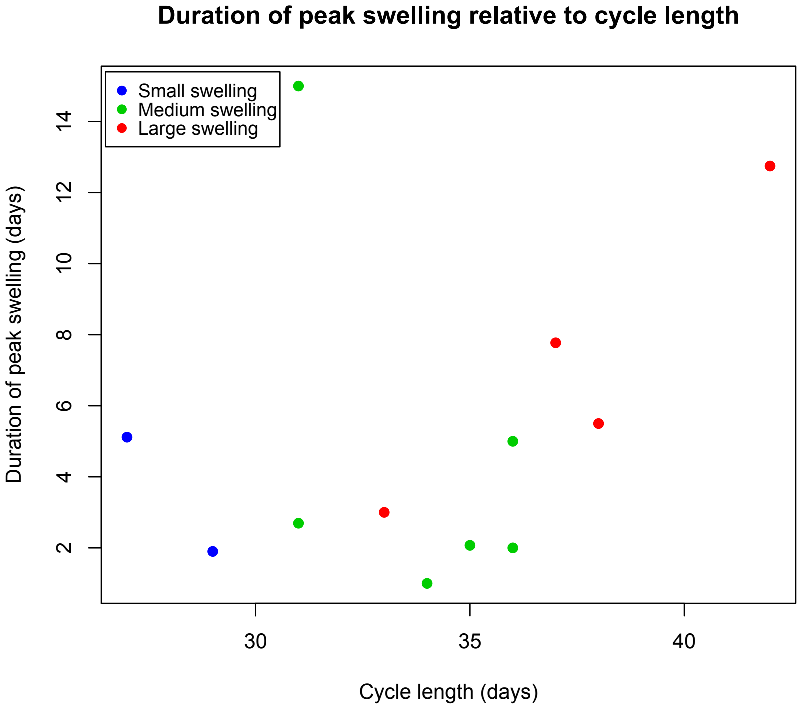


Figure 3.5 Duration of peak swelling in days plotted against cycle length, for the three size categories of swellings, using data from the ovulation meta-datasets, averaged per species.

3.3.4 Swelling size and female quality: summary effects and effects of moderators

The summary effect sizes for the random-effects meta-analyses on sub-sets of the female quality data were weak and not significantly different from zero. The strongest positive summary effect was for swelling size and body condition/fecundity (0.17, *p*=0.18, *n*=5, **Figure 3.6**). The summary effect for the age/parity subset was negative and non-significant (-0.15, *p*=0.43, *n*=6, **Figure 3.7**), and the summary effect for social rank was positive and non-significant (0.09, *p*=0.38, *n*=5, **Figure 3.7**). There were no significant effects of moderator variables (population type and swelling size category) in meta-regression analyses, for any subsets (*ps*>0.1).

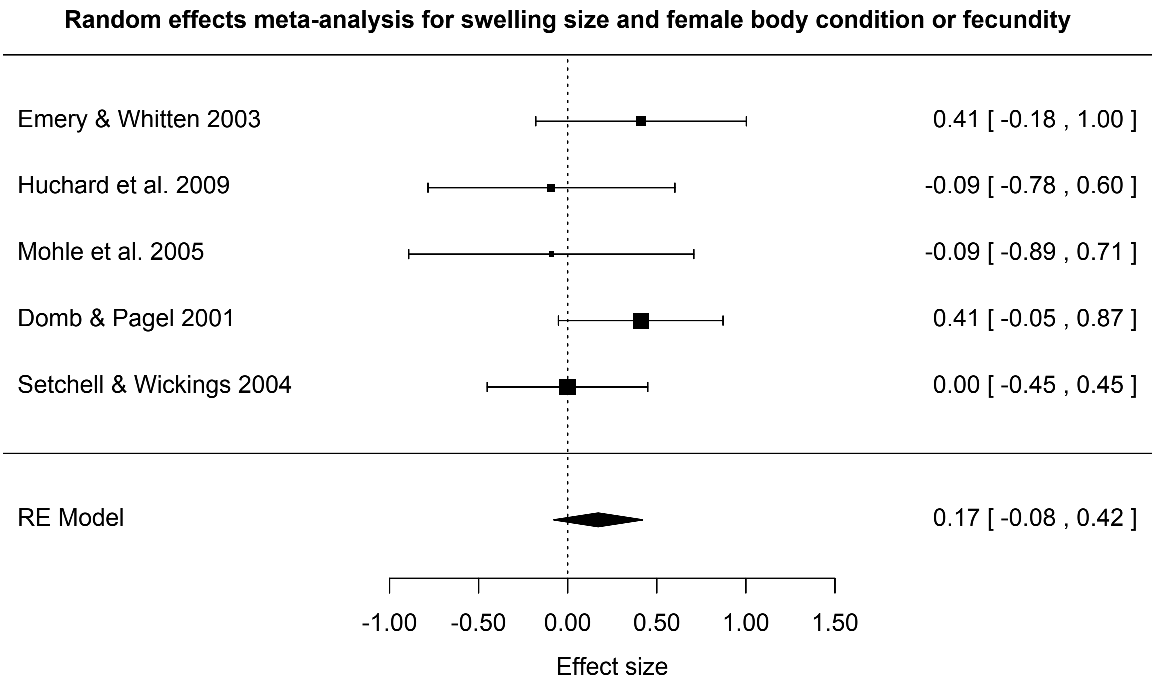


Figure 3.6: *Forest plot for random effects meta-analysis of studies of swelling size and female body condition or fecundity. Error bars represent 95% confidence intervals, points represent effect sizes, box size represents article weighting. Right column lists effect sizes and confidence intervals.*

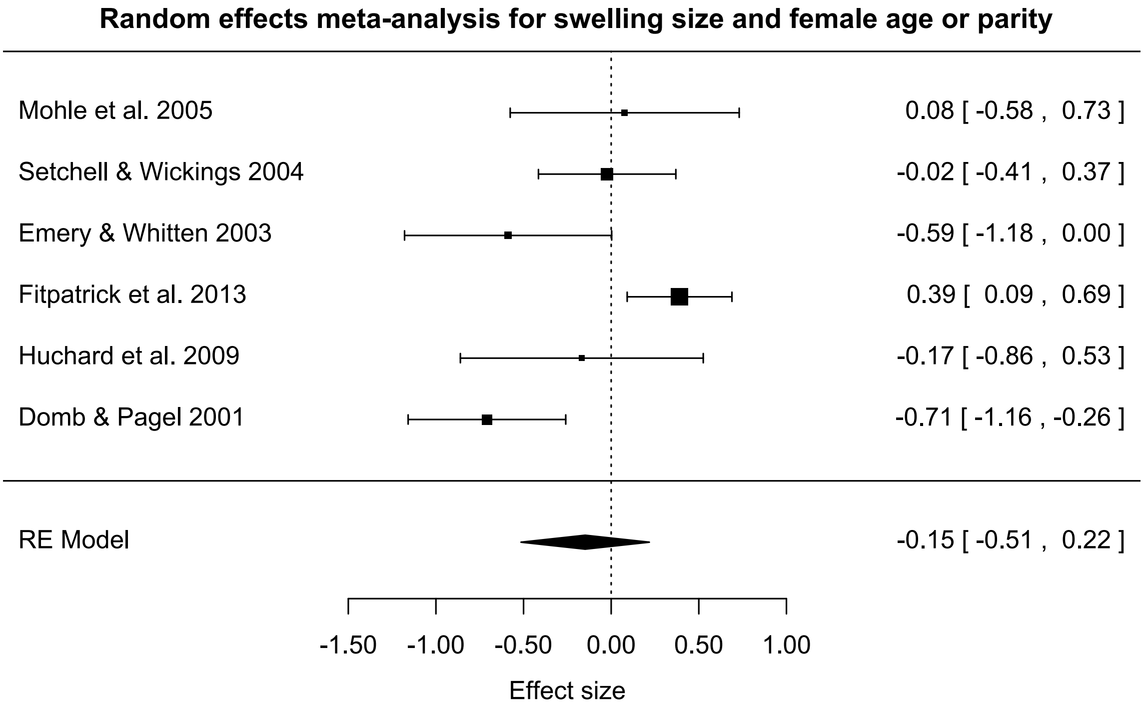


Figure 3.7 Forest plot for random effects meta-analysis of studies of swelling size and female age or parity. Error bars represent 95% confidence intervals, points represent effect sizes, box size represents article weighting. Right column lists effect sizes and confidence intervals.

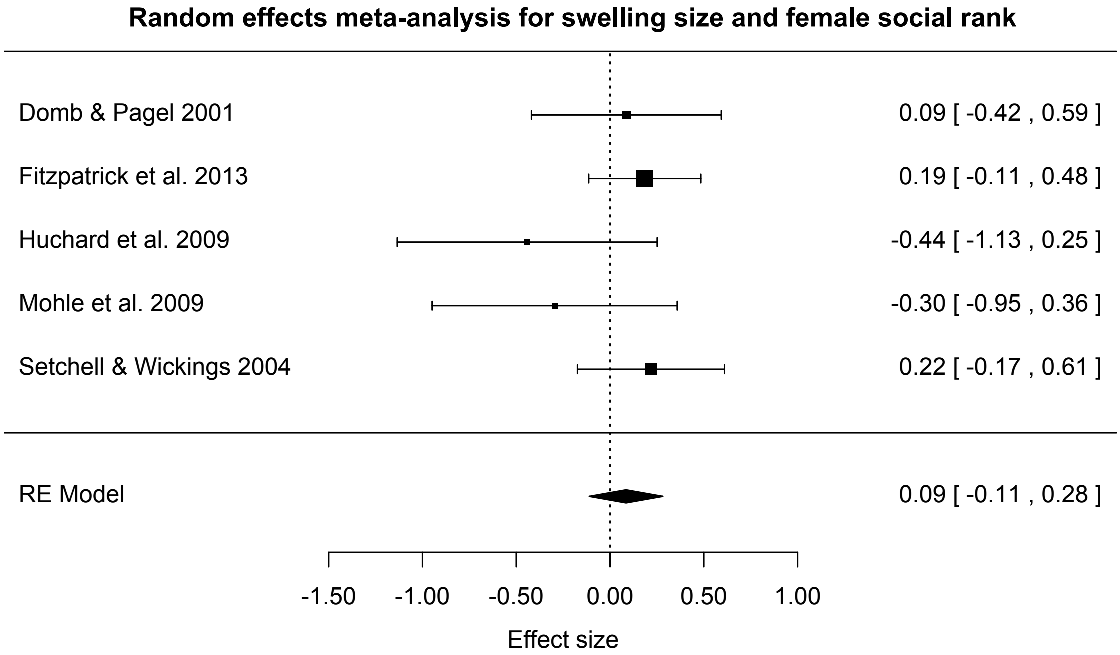


Figure 3.8: *Forest plot for random effects meta-analysis of studies of swelling size and female social rank. Error bars represent 95% confidence intervals, points represent effect sizes, box size represents article weighting. Right column lists effect sizes and confidence intervals.*

3.4 Discussion

The results addressed two issues regarding Catarrhine primate sexual swellings, using meta-analytic methods: the honesty of swelling size as a signal of ovulation timing, and the relationship between swelling size and female quality. Analyses of meta-data from published articles suggested that the peak swelling period is confined to within the peri-ovulatory period. In contrast, analyses of raw data from articles reported that peak swelling begins several days before the peri-ovulatory period, lasting for around 10 days. Analyses of article meta-data found that articles in which swelling size was measured by either callipers or from photographic images (‘direct’ methods) reported that peak swelling was closer to ovulation and had a shorter duration than articles where swelling size was estimated using categorical scales. There were non-significant differences in the predicted direction for onset and duration of peak swelling between provisioned and non-provisioned populations. Analyses of raw data from articles reported that peak size for large, exaggerated swellings was further from ovulation, with a longer duration, than for smaller swellings. However, analyses of peak swelling duration relative to ovarian cycle length suggested that the longer duration of larger swellings is not an increase in the proportion of the cycle where the swelling is at peak size. Phylogenetic signal was found to be minimal for both peak swelling onset and duration. Meta-analyses of the relationship between swelling size and female quality found weak, non-significant summary effects. Therefore, current evidence supports swellings as signals of temporal fertility rather than individual female quality, but the apparent precision of swellings as signals of temporal fertility depends on methodological factors.

According to the results of analyses of the ovulation meta-data, swelling size is an accurate cue to the timing of ovulation, as the peak swelling period size falls within the peri-ovulatory period. Conversely, the results from the ovulation raw data would suggest that swellings are a poor cue to the timing of ovulation. Differences in variance between the datasets are expected, because the raw dataset probably better reflects between-cycle variation in the onset and duration of peak swelling than the ovulation meta-dataset. However, the directionality of the difference between the results would not be expected from differences in variance alone. This disparity can possibly be explained, rather, by the effect of swelling measurement method on onset and duration of peak swelling. The finding that studies using estimation on categorical scales report that swellings are less reliable cues of ovulation timing than studies using 'direct' measurement methods suggests that the apparently deceptive properties of swellings can partly be accounted for by methodological factors. 'Visual' methods seem to obscure fine scale changes in swelling size, and seemingly long periods of peak swelling may in fact comprise of gradual size changes which accurately reflect changes in ovulation probability within the peak swelling period. The ovulation meta-dataset contained 6 articles where 'direct' methods were used to measure swelling size, whereas the ovulation raw-dataset only contained one such article. The minimal phylogenetic signal for peak swelling onset and duration supports this interpretation, as low phylogenetic signal may result where variation across species is due largely to methodological factors (Blomberg et al. 2003).

3.4.1 The graded signal and reliable indicator hypotheses

The results concerning swelling size and ovulation are generally compatible with the graded-signal hypothesis (Nunn, 1999) and the paternal-care hypothesis (Alberts & Fitzpatrick, 2012), which argue that swellings are approximately honest signals of the timing of ovulation. The results of analyses of the article raw data additionally supported the predictions of the graded signal hypothesis that swelling size partly obscures the timing of ovulation by remaining at peak size for several days, and that larger swellings have longer duration at peak size than smaller swellings, suggesting that evolutionary enlargements in swelling size were accompanied by decreased accuracy of swellings as signals of ovulation timing (Nunn 1999). However, the results from the ovulation meta-dataset suggest that swellings could be more accurate than previously thought (Nunn, 1999), which may be explained by the lack of studies in which swellings were directly measured on fine scales at the time of Nunn's review. Of the studies using finer-scaled methods to measure swelling size, all but one were conducted after 1999. Analyses of the ovulation meta-dataset did not support the idea that large swellings were less accurate cues to ovulation than small swellings, which again may be due to the inclusion of more studies using fine-scaled measures of swelling size in the meta-dataset than the raw-dataset. Categorical estimation of swelling size probably tends to report that large swellings are less accurate than smaller swellings because the differences in absolute size between points on a categorical scale are greater for large swellings than for smaller swellings, therefore, categorical scales could obscure more fine scale variation in swelling size for large than small swellings.

The results of the meta-analyses of swelling size and female quality do not support the prediction of the reliable indicator hypothesis (Pagel, 1994) that swelling size is a signal of female quality, as no effect sizes were significantly different from zero. The summary effect size for measures of age and parity was negative in direction, suggesting that swelling size decreases over female lifetimes, whereas typically, older females are more fecund and preferred by male primates (Anderson, 1986; Muller et al., 2006). The results suggest that future research may be most likely to find positive correlations between swelling size and female quality in terms of body condition (such as body mass index) or fecundity. However, there are so few studies so far that have investigated the relationship between swelling size and female quality that it would be premature to draw strong conclusions at the present time. It remains possible that swellings are signals of individual female quality indirectly, via their relationship with reproductive hormones. Given that large swellings are probably costly traits, given their large size and weight (Bielert & Busse, 1983), and that they are produced by ovarian cycling hormones, large swellings may be condition-dependent signals (Andersson, 1994; Zahavi, 1975) which cannot be produced by females with amenorrhoea induced by poor health or malnutrition.

3.4.2 Further issues

The analyses presented here do not address the possible effect of variation in peak swelling size in relation to ovulation on the honesty of swelling size as a signal of ovulation timing. For example, even if peak swelling size coincides with ovulation on average, there could be such large variation in peak swelling onset in relation to ovulation between cycles that peak swelling size is unlikely to be a reliable signal of ovulation in any one given cycle. The results of the analyses of the article raw data suggested that peak swelling onset varied considerably in relation to ovulation, with a standard deviation of +/- 6 days, whereas the mean peak swelling onset from the article meta-data reported a standard deviation of +/- 3 days. Some error is expected in any biological signal (Maynard Smith, 1991; Searcy & Nowicki, 2005), but the potential adaptive significance of signalling error is not easy to determine. Further, the honesty of swelling size as a signal of ovulation timing depends not only on the properties of the swelling, but also on the perceptual abilities of male primates. So far, there is some evidence that male primates are able to detect fine-scaled changes in swelling size and adjust their mating investment accordingly (e.g. Deschner et al., 2004; Higham et al., 2009). Multi-modal cues might be used by male primates, such that even if swelling size alone is only an approximate cue, swelling size in combination with vocal, olfactory and behavioural cues (e.g. Clarke et al., 2009) may allow male primates to determine the probable day of ovulation or the peri-ovulatory period. A meta-analysis of swelling size and male mating interest might be useful in shedding light on the extent to which male primates are aware of the timing of ovulation.

Although swellings may be honest signals of the timing of ovulation within typical ovarian cycles, occurrences of apparently deceptive swellings have been recorded in pregnant, adolescent, lactating or reproductively abnormal females (Anderson & Bielert, 1994; Engelhardt et al., 2007; Gordon et al., 1991; Nunn et al., 2001; Wallis, 1983; Zinner et al., 2002). Some authors have concluded that such swellings could be a specific adaptation in females for paternity confusion, protective against infanticide by males (Engelhardt et al., 2005; Zinner & Deschner, 2000). Currently, it is uncertain whether such swellings are deceptive or whether they reflect by-products of hormonal fluctuations. For instance, pregnancy swellings coincide with a rise in oestrogen levels in pregnancy, which is common across primate species with and without swellings (e.g. Engelhardt et al., 2007; Gordon et al., 1991) and may be involved in maintaining pregnancy (Albrecht et al., 2000; Czekala et al., 1983). Similarly, the extremely large swellings often seen in adolescent primates may be the result of hormonal irregularities typical of the adolescent period (Anderson & Bielert, 1994). There is currently mixed evidence as to whether males are able to distinguish between 'deceptive' and normal swellings (Anderson & Bielert, 1994; Engelhardt et al., 2007; Gesquiere et al., 2007; Gordon et al., 1991; Gust, 1994; Mohle et al., 2005; Phillips & Wheaton, 2008). A comparative study of possible relationships between the presence of apparently deceptive swellings, such as pregnancy swellings, and infanticide risk could be useful in investigating the hypothesis that swellings enhance paternity confusion.

3.4.3 Conclusions

Genital swelling size in female Catarrhine primates is at least an approximately honest cue to the timing of ovulation. The extent to which swelling size is a precise signal of the timing of ovulation depends on how the swelling size is measured and which statistical methods are used to analyse data from published articles. Analyses of article meta-data using weighted statistical methods, including several studies where swellings are measured on a fine scale, suggest that swellings are an accurate signal of the timing of ovulation. Conversely, analyses of raw data from articles, using ordinary statistical methods, including almost solely studies where swellings are measured using visual estimation on categorical scales, suggest that swellings are only approximate signals of the timing of ovulation. Additional raw data from articles using ‘direct’ measurement of swelling size are therefore needed to draw firmer conclusions on the honesty of swellings as a signal of ovulation timing. Additionally, meta-analyses of male primates responses to swelling size changes and comparative studies of the purportedly deceptive aspects of swelling size could shed further light on the honesty of swelling size as a signal of ovulation. Although there is currently little evidence to support the idea that swelling size is a signal of female quality, there have been few studies so far, and these studies have used a diverse range of measures of female quality. Therefore, there may not be sufficient data at present to rule out a relationship between swelling size and female quality. Primate sexual swellings therefore, are an example of a large, conspicuous, visual signal of female fertility, unusual in mammalian species with conventional sex roles.

Chapter 4: the evolution of exaggerated sexual swellings in Catarrhine primates

4.1 Introduction

The large, brightly coloured anogenital swellings exhibited by the females of some species of Catarrhine primates may be an example of female ornamentation, when defined broadly as a conspicuous and decorative trait with no obvious survival function (Amundsen, 2000). Sexual selection has been used to explain the evolution of a variety of ornamental traits in males by their function in mate attraction and/or mate competition, such as the lion's mane (West & Packer, 2002). In the *Descent of Man* (1871), Darwin argued that female ornaments were merely 'anomalous cases' explained by correlated inheritance with male traits, and until recently, female ornaments have received little research attention in comparison to male ornaments (Amundsen, 2000b). Many examples of putative female ornamentation have now been documented across a broad taxonomic range (**Figure 4.1**), but debate amongst evolutionary biologists remains regarding the extent to which female ornaments are the result of sexual selection on females via mate competition and/or mate choice (e.g. Clutton-Brock, 2009), versus other processes such as competition for resources, rather than mating opportunities (e.g. LeBas, 2006). Recent sexual selection research suggests that female ornamentation may result from male mate choice and/or female-female competition even in species with conventional 'sex roles', such that males are the more competitive, lower-investing sex. For example, in two-spotted gobies *(Gobiusculus flavescens),* males compete for access to females, but prefer to mate with females with brighter orange belly colouration (Amundsen & Forsgren, 2001).

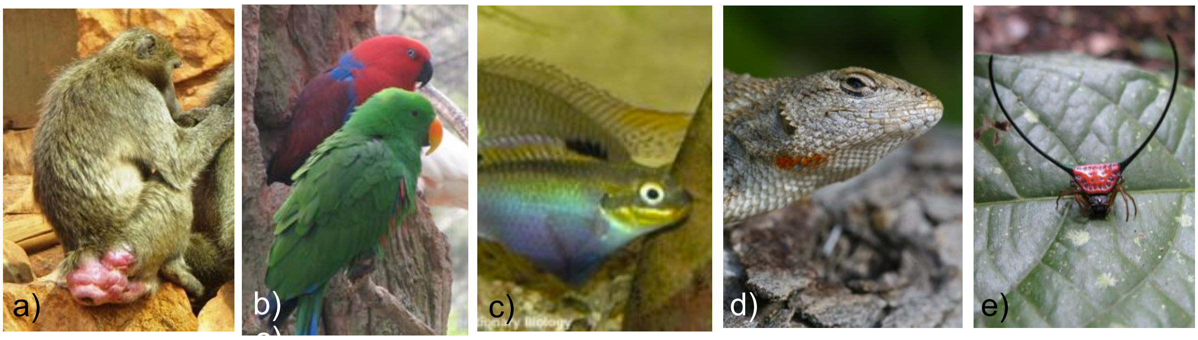


Figure 4.1 *Putative examples of female ornamentation:a) Chacma baboon (Papio ursinus) (Creative commons licensed, accessed via Wikimedia Commons), b) Eclectus parrots (Eclectus roratus), accessed via flickr.com, under a Creative Commons license (photographer username: 'holidaypointau'),, c) cichlid (Pelcivachromis taeniatus), reproduced from (Baldauf et a., 2010), d) striped plateau lizard (Sceloporus virgatus), reproduced from (Weiss, et al., 2011), e) horned spider (Gasteracantha arcuata) (Creative commons licensed, accessed via Flickr.com, user 'rothbaum'.*

Sexual swellings show several hallmarks of sexually selected ornaments. Swellings may function as honest fertility signals, as they typically reach peak size around the time of ovulation (e.g. Brauch et al., 2007; Deschner et al. 2004, see previous chapter). Whilst non-visual signals of reproductive status are fairly common in female mammals, including in primates, such as copulation calls in Barbary macaques (Semple & McComb, 2000) and odour cues in ring-tailed lemurs (Scordato & Drea, 2007) conspicuous, visual signals are unusual in female mammals (Stockley & Bro-Jørgensen, 2011). Swellings appear to exert additional costs over olfactory, vocal or behavioural cues to reproductive status as they comprise up to 10% of female body weight at peak size (Bielert & Busse, 1983) and are vulnerable to injury (Matsumodo-Oda, 1998). Male primates show a strong attraction to swellings. For example, in experiments using artificial swellings, captive male baboons (*Papio ursinus*) respond to swelling size and red colouration, controlling for behavioural and olfactory cues (Bielert et al. 1989; Girolami & Bielert, 1987). In wild populations, male mating effort tracks changes in swelling size across the ovarian cycle (e.g. *Papio cynocephalus,* Gesquiere et al. 2007). Female ornamentation can sometimes be explained by 'sex role reversal', where males provide the majority of paternal care and females are the more competitive sex, as in pipefishes, for example (Berglund et al. 1997). However, in the Catarrhine primates, substantial paternal investment is rare (Whitten, 1987), and in species with swellings, males are typically promiscuous and competitive in mating (e.g. chimpanzees, Muller & Wrangham, 2004).

Male mate choice may have favoured the evolution of exaggerated swellings, even without sex-role reversal. Mate choice and mate competition are not mutually exclusive, rather, males may be both choosy and competitive in mating (Bonduriansky, 2001). Theoretical evidence suggests that choosiness is determined primarily by a) mating investment, b) mate quality variance, and c) constraints on choosiness (Kokko & Johnstone, 2002; Kokko & Monaghan, 2001). Firstly, mate choice is favoured when mating is costly. In primates, mating may be costly for males due to time and energy costs of competing for mates (Pagel, 1994), including producing large ejaculates (Dewsbury, 1982; Small, 1988; Wedell et al., 2002) and mate-guarding (Alberts et al. 1996), or due to increased injury risk from aggressive competition (Drews, 1996). Risk of disease transmission may pose an additional cost of mating (Sheldon, 1993). Secondly, mate choice is favoured where there is high variation in mate quality (Bonduriansky, 2001; Parker, 1983). Female primates vary widely in their fecundity and fertility, in relation to demographic factors such as age and social rank (Pusey, 1997), and infertility may be as high as 10% in wild populations (Anderson, 1986). Finally, choosiness is determined by the costs of mate choice – i.e. investment in locating and assessing mates (Barry & Kokko, 2010; Parker, 1983). In primates, the costs of mate choice for males may be low in species with large, stable social groups containing multiple females, relative to species with small or dispersed social groups where females are encountered infrequently.

In addition to male mate choice, female-female competition for mates may have favoured the evolution of sexual swellings. The ‘reliable-indicator’ hypothesis argues that exaggerated swellings evolved due to female-female competition for mating investment from choosy males (Pagel, 1994). Female primates may compete for various benefits of mating, such as access to preferred dominant males, protection from harassment, and sperm (Pagel, 1994). The reliable-indicator hypothesis should predict that across primate species, swellings are associated with measures of female-female competition for mates. However, an existing comparative study (Nunn et al. 2001) did not find that swellings were associated with elongated female canines, female-biased adult sex ratio and high reproductive synchrony, used as measures of female-female competition. Large female canine length is associated with categorical measures of intensity of intra-sexual competition amongst females (Plavcan et al. 1995) and female-female competition for mates may be most intense under a female-biased adult sex ratio and when females are highly synchronised in their sexual receptivity, i.e. a female-biased operational sex ratio (Nunn et al., 2001). Further, although females may compete most intensely for access to males in single-male breeding systems (Nunn et al., 2001), comparative studies suggest that swellings have co-evolved with multi-male, multi-female mating systems (e.g. Pagel & Meade, 2006).

Signals of temporal fertility, such as swellings (Nunn, 1999; Zinner et al., 2004, see previous chapter) may be less likely than signals of individual female quality to be strongly selected by male mate choice between females, rather, all females may be equally preferred when maximally fertile (Bonduriansky, 2001: 311; Pagel, 1994). However, where females with larger ornaments accrue increased direct benefits of mating relative to females with smaller ornaments, male mate choice may select for enlargement of temporal fertility cues (Bonduriansky, 2001: 311). In primates, females with larger swellings could receive various increased direct benefits of mating relative to females with smaller swellings. Both the graded signal hypothesis (Nunn, 1999) and the paternal care hypothesis (Alberts & Fitzpatrick, 2012) for the evolution of exaggerated swellings argue that swellings signal temporal fertility due to the benefits of manipulating paternity probability between males. The graded signal hypothesis argues that swellings simultaneously confuse and concentrate paternity probability, balancing the benefits of multi-male mating, such as infanticide avoidance, versus the benefits of mating with high quality males, such as ‘good genes’ (Nunn, 1999). The paternal care hypothesis argues that swellings provide probabilistic paternity information to males, benefitting females by balancing paternal investment between multiple and single, preferred males (Alberts & Fitzpatrick, 2012).

In species with swellings, pre-copulatory mate choice may be compromised in both sexes and sexual conflict may arise. Male primates are limited in their ability to monopolise females in large social groups (Cords, 2000) which are typical of many Catarrhine species, and may therefore employ cryptic mate choice, via the selective allocation of sperm towards fertile females (Wedell et al. 2002). Swellings appear to elicit sperm production in males (Girolami & Bielert, 1987), and may therefore function in attracting increased sperm investment from males. Female pre-copulatory choice is also likely to be compromised in species with large social groups comprising of multiple males, due to the costs of rejecting mates. In Catarrhine primates, males are often able to constrain female mate choice through aggression due to greater body strength and social dominance (Smuts & Smuts, 1993). Limits on female pre-copulatory mate choice may result in ‘convenience polyandry’ where females accept multiple copulations in order to avoid harassment from males (Rivera & Andrés, 2002), and cryptic, post-copulatory mechanisms of female mate choice (Thiel & Hinojosa, 2003). Although swellings attract mates, they may make deposition of sperm physically difficult for males due to the lengthening of the reproductive tract, by as much as 50% at peak size in some chimpanzee females (Dixson & Mundy, 1994; Dixson, 2002). Therefore, swellings may allow females to accept copulations from multiple males, whilst maintaining mate choice through cryptic mechanisms.

Here, I tested several predictions in relation to the evolution of sexual swellings in Catarrhine primates, using phylogenetic comparative analyses. First, I tested the prediction that swellings evolved in association with male mate choice, due to high costs of mating for males, high variation in female quality and low search costs for males. As measures of the costs of mating competition for males, I used testes mass, male group size, adult sex ratio and body size dimorphism. As a measure of the cost of mating due to disease risk, I used sexually transmitted disease (STD) prevalence. As a measure of both variation in female quality and low search costs for males, I used female group size. Second, I re-examined the prediction of the reliable-indicator hypothesis that swellings are associated with female-female competition for mates (Pagel, 1994), using female canine length as a measure of female-female competition (Plavcan et al. 1995). Third, as the graded signal hypothesis argues that swellings partly function to protect against infanticide (Nunn, 1999), I tested the prediction that species with swellings are associated with high infanticide risk. Infanticide risk was estimated as the length of the lactational period relative to gestation, where a long period of lactational amenorrhoea indicates a high infanticide risk (van Schaik & Kappeler, 1997). Fourth, I tested the prediction of the paternal care hypothesis that swellings have co-evolved with male care-taking, using a categorical measure of male care (Alberts & Fitzpatrick, 2012). Finally, I tested the prediction that swellings are associated with cryptic female choice by investigating the association of swellings with penile length (Dixson & Mundy, 1994; Dixson, 2002). All analyses investigated potential confounds with mating system by running additional analyses restricted to include species with multi-male mating systems only.

4.2 Methods

4.2.1 Comparative datasets

Data on the presence of exaggerated sexual swellings in the Catarrhine primates were obtained from primary scientific literature using keyword searches of the Web of Knowledge (e.g. 'primate swellings'). Relevant articles, i.e. those mentioning sexual anatomy or behaviour in female Catarrhine primates, were identified by reading abstracts of all returned search results. Articles identified as relevant were then examined for descriptions of presence or absence of swellings. Swellings were coded as a factor on two levels: 'exaggerated' and 'none'. Swellings were coded as 'exaggerated' if they were described in the primary literature as typically present in a species, and sufficiently large that they encompassed tissue outside of the vulva, such as the anogenital area. Therefore, small vulval swellings, as in *Hylobates lar,* for example, were not regarded as exaggerated swellings. Subcaudal swellings, as in *Macaca assamensis* and *Macaca fascicularis*, were considered ambiguous and as a result all analyses were run with these species coded as either with or without exaggerated swellings (referred to as 'up-coded' and 'down-coded' respectively). Sample size was increased by including additional data from several secondary sources Dixson, (1998); Fashing, (2006); Hrdy & Whitten, (1987); Nunn, (1999); Rowe, (1996); Sillen-Tullberg & Moller, (1993); Thierry et al. (2000), and personal communications from A. Korstjens. Classifications were generally in agreement between secondary sources, but conflicts were resolved by majority vote. Taxonomic ambiguities were resolved with reference to the International Union for the Conservation of Nature (IUCN) 'red list' (2013) and Rowe (1996). All other variables were obtained from secondary datasets. Data on testes mass were sourced primarily from Harcourt et al. (1995), with additional data from Dixson (1998), Dunham & Rudolf, (2009) and Lemaitre et al. (2009). Data on the prevalence of sexually transmitted diseases were obtained from the Global Mammal Parasite Database (Nunn & Alitzer 2005), averaged per species, and including only reports listed as ‘rechecked’ by the lead author. Data on male and female group sizes were obtained primarily from Mitani et al. (1996), with additional data from: Ostner et al. (2008), Fashing (2006), Kutsukake & Nunn (2006), Plavcan (2004), van Noordwijk & van Schaik (2004), Paul (2000), Struhsaker (1975), Lehmann & Dunbar (2009), Cords (2000), Dunbar (2000) and Sterck & van Hooff (2000). Group sizes refer to the number of adults typically present in the social group. Where multiple data sources were available for group size, values were preferentially taken from sources from wild populations and/or where primary sources were cited, or averaged across sources where sources were equally preferred. Data on female upper canine lengths were obtained from Plavcan & Ruff (2008), and male and female body masses from Smith & Jungers (1997).

Data on paternal care were obtained from Smuts & Gubernick (1992) and Whitten (1987). Paternal care was coded as a factor on two levels (‘tolerant or occasional’ and ‘intensive or affiliative’), based on the original four level coding system used in Whitten (1987). Conflict between sources in classification of paternal care were resolved with reference to primary sources cited by Smuts & Gubernick (1992) and Whitten (1987). Data on weaning period length and gestation length were obtained from the PanTheria database (Jones et al., 2009). Infanticide risk was estimated by lactational period length/(lactational period length + gestation length), as in Van Schaik & Kappeler (1997). Data on approximate (ranked) penile length were obtained from Dixson (1987). Mating system data were obtained from Anderson et al. (2004); Dixson (1987); Dixson (1998); Dunham & Rudolf (2009); Harcourt et al. (1995); Hrdy & Whitten (1987); Lindenfors & Tullberg (1998); Schillaci (2008); Weckerly (1998); Wlasiuk & Nachman (2010). Conflicts between mating system sources were resolved by majority vote. Species with both multi-male and single-male mating systems, depending on the population (e.g. Hanuman langurs, *Semnopithecus entellus*), were addressed by running analyses using two alternative coding schemes for mating systems, one where ambiguous species were coded as either multi-male (‘up-coded’) and single-male (‘down-coded’). See Table 4.1 , for complete dataset used for analyses in the current chapter, also included in Appendix B.

Species	Exaggerated swelling?	Mating system	Male group size	Female group size	Penile length (ranked)	Testes mass (g)	M. body mass (kg)	Gestation length (days)	Weaning length (days)	F. canine length (mm)	F. body mass (kg)	STD prev.	Primary sources for swellings
Allenopithecus nigroviridis	Y	MMMF	NA	NA	NA	16.96	6.12	NA	106.15	8.33	3.18	NA	NA
Cercocebus agilis	Y	NA	NA	NA	NA	NA	9.5	NA	NA	8.65	5.66	NA	Walker et al. (2004)
Cercocebus galeritus	Y	MMMF	2	6	NA	NA	9.61	174.43	NA	NA	5.26	0.27	Kinnaird (1990)
Cercocebus torquatus	Y	MMMF	NA	NA	NA	NA	9.47	168.98	NA	NA	5.5	0.33	NA
Cercocebus torquatus atys	Y	MMMF	NA	NA	NA	25.1	11	165.08	NA	9.53	6.2	NA	Whitten & Russell (1996)
Cercopithecus ascanius	N	PG	1	9.5	3	3	3.7	148.5	146.54	10.3	2.92	0.00	NA
Cercopithecus cephus	N	PG	NA	3.4	3	NA	4.29	169.51	362.93	9.59	2.88	0.10	NA
Cercopithecus diana	N	PG	NA	7	3	NA	5.2	NA	362.93	12.32	3.9	NA	NA
Cercopithecus hamlyni	N	NA	NA	NA	3	NA	5.49	NA	NA	NA	3.36	NA	NA
Cercopithecus lhoesti	N	PG	NA	NA	NA	NA	5.97	NA	NA	10.82	3.45	0.00	NA
Cercopithecus mitis	N	PG	1	18	3	NA	7.93	138.39	688.08	10.135	4.25	NA	Rowell (1970)
Cercopithecus neglectus	N	PG	1	3	3	NA	7.35	172.07	417.62	11.64	4.13	0.19	NA
Cercopithecus nictitans	N	PG	NA	4.1	3	NA	6.67	169.51	NA	11.22	4.26	0.12	NA
Cercopithecus solatus	N	PG	NA	NA	NA	NA	6.89	NA	NA	NA	3.92	NA	Charpentier et al. (2005), Peinot et al. (1999)
Chlorocebus aethiops	N	MMMF	3	4.25	NA	13	4.26	NA	217.76	11.91	2.98	0.40	Andelman (1987)
Colobus angolensis	N	NA	1.3	1.6	NA	NA	9.68	NA	NA	9.57	7.57	NA	Korstjens, pers. comm.
Colobus guereza	N	MMMF	1	3	2	2.98	13.5	169.02	387.79	14.34	9.2	0.24	Korstjens, pers. comm., Harris & Monfort (2006)
Colobus polykomos	N	MMMF	5.5	4.35	2	10.7	9.9	172.69	213.78	10.81	8.3	NA	Korstjens, pers. comm.
Colobus satanas	N	NA	1.666667	5.5	NA	NA	10.4	192.76	NA	NA	7.42	0.00	Sabater Pi (1973)
Colobus vellerosus	N	NA	3	6.5	NA	NA	8.5	NA	NA	NA	6.9	NA	NA
Erythrocebus patas	N	PG	3	12.5	3	7.2	12.4	167.2	211.79	12.43	6.5	0.15	Dixson (1983)
Gorilla beringei	N	NA	1	3	NA	28.96	162.5	NA	NA	NA	97.5	NA	Czekala & Sicotte (2000), Watts (1991)
Gorilla gorilla gorilla	N	PG	1	2.25	1	15.01	170.4	257	920.35	17.4	71.5	0.07	Nadler et al. (1979), Nadler (1975)
Hylobates agilis	N	MG	NA	NA	1	6.32	5.88	NA	NA	NA	5.82	NA	Mootnick (2006)
Hylobates lar	N	MG	1	1	NA	5.5	5.9	212.91	725.86	15.79	5.34	NA	Barelli et al. (2007), Mootnick (2006)
Hylobates moloch	N	MG	NA	NA	NA	6.1	6.58	241.2	NA	NA	6.25	NA	Hodgkiss et al (2010), Maheshwari et al (2010), Mootnick (2006)
Hylobates muelleri	N	MG	NA	NA	NA	NA	5.71	206.7	NA	NA	5.35	NA	Mootnick (2006)
Hylobates pileatus	N	MG	NA	NA	NA	NA	5.5	200.16	635.13	16.87	5.44	NA	Mootnick (2006)
Lophocebus albigena	Y	MMMF	3.75	6	NA	NA	8.25	182.64	211.71	8.75	6.02	0.18	Arlet et al. (2008), Deputte (1991), Rowell & Chalmers (1970)
Lophocebus aterrimus	Y	MMMF	3.8	NA	NA	13.78	7.84	NA	NA	8.82	5.76	NA	NA
Macaca arctoides	N	MMMF	NA	NA	5	48.2	12.2	176.6	377.66	NA	8.4	0.01	Murray et al. (1985)
Macaca assamensis	Y/N	MMMF	NA	NA	NA	NA	11.3	NA	NA	NA	6.9	NA	Furtbauer et al. (2010), Fooden (1971), Hill (1966)
Macaca cyclopis	Y	PG/MMMF	3.3	NA	NA	NA	6	161.06	205.24	NA	4.94	NA	Wu & Lin (1992)
Macaca fascicularis	Y/N	MMMF	4	6.75	3	35.2	5.36	164.69	283.53	10.67	3.59	0.05	Malaivijitnond et al (2007), Gumert (2007), Engelhardt et al. (2007), (2005), Nawar & Hafez (1972)
Macaca fuscata	N	MMMF	3	9	NA	72.3	11	172.99	265.04	9.59	8.03	0.24	Hanby & Brown (1974), Mori et al (1997), Okayasu (2001), Takahata (1980), Fujita et al (2004)
Macaca maura	Y	MMMF	4.25	NA	NA	NA	9.72	167.19	497.16	NA	6.05	0.17	Okamoto et al (2000), Matsumara (1993)
Macaca mulatta	N	MMMF	2.5	9	NA	46.2	7.7	166.07	304.16	8.19	5.37	0.73	Dubuc et al. (2009), Small (1990), Chapais (1983), Loy (1971), Hill (1966) Kaufman (1965)
Macaca nemestrina	Y	MMMF	3	22	4	66.7	11.2	171	292.6	12.24	6.5	0.09	Hadidain & Bernstein (1979), Bullock et al (1972), Caldecott (1986), Hill (1966)
Macaca nigra	Y	MMMF	6	30	5	NA	9.89	172.43	365	11.38	5.47	0.16	Engelhardt et al (2008), Bernstein & Baker (1988), Bernstein et al (1982)
Macaca ochreata	Y	NA	NA	NA	NA	NA	5.3	NA	NA	NA	2.6	0.18	Hill (1966)
Macaca radiata	N	MMMF	7	9	NA	48.2	6.67	161.56	332.25	NA	3.85	NA	McArthur et al (1972), Hill (1966), Simonds (1965)
Macaca silenus	Y	PG/MMMF	1.75	7	NA	42	NA	172	362.93	10.12	NA	NA	Singh et al (2006), Clarke et al (1993)
Macaca sinica	N	MMMF	5	9.5	3	NA	5.68	180.9	NA	9.96	3.2	0.17	Hill (1966)
Macaca sylvanus	Y	MMMF	9	10.5	NA	NA	11.1	164.84	210.25	11.29	NA	0.12	Pfefferle et al (2008), Brauch et al (2007), Mohle et al (2005)
Macaca thibetana	N	NA	4.5	9.5	NA	NA	15.2	169.02	451.79	NA	9.5	NA	Zhao (1993)
Macaca tonkeana	Y	NA	1	NA	NA	NA	14.9	NA	NA	10.12	9	0.12	Aujard et al (1998), Thierry et al (1996), (1994)
Mandrillus leucophaeus	Y	PG	NA	NA	5	41.05	17.5	179.22	486.66	11.7	12.5	0.50	Marty et al. (2009), Hill (1966)
Mandrillus sphinx	Y	PG	3	14	5	68	31.6	173.99	348.01	9.42	12.9	0.59	Huchard et al. (2009), Phillips & Wheaton (2008), Setchell & Wickings (2004), Setchell et al (2006)
Miopithecus talapoin	Y	MMMF	13	27	NA	5.2	2.5	164.38	178.98	6.7	2	0.22	Gautier-Hion (1974), Rowell (1977), Rowell (1972), Scruton & Herbert (1970)
Nasalis larvatus	N	PG/MMMF	NA	5	2	13.8	20.4	165.04	211.75	10.42	9.82	NA	Murai (2006), (2004) , Yeager (1990)
Pan paniscus	Y	MMMF	8	8	5	135.2	45	235.24	1081.31	11.24	33.2	NA	Paoli et al. (2006), Reichert et al. (2002), Hohmann & Fruth (2000), Jurke et al (2000)
Pan troglodytes schweinfurthii	Y	MMMF	12.3	NA	NA	NA	42.7	NA	NA	15.6	33.7	NA	Deschner & Boesch (2007), Thompson (2005), Tutin (1979)
Pan troglodytes troglodytes	Y	MMMF	10	35	5	157.9	59.7	231.49	1260.81	NA	NA	0.42	NA
Pan troglodytes verus	Y	MMMF	5.2	NA	NA	NA	46.3	NA	NA	NA	41.6	NA	Deschner et al. (2004)
Papio anubis	Y	MMMF	14	34	NA	93.5	25.1	178.96	596.6	15.95	13.3	0.07	Garcia et al (2008), Scott (1984)
Papio cynocephalus	Y	MMMF	8	13	NA	52	21.8	172.99	450.42	9.12	12.3	0.25	Nguyen et al (2009), Gequiere et al (2007), Beehner et al (2006), Rasmussen (1985)
Papio hamadryas	Y	PG	1	2	5	27.1	16.9	180	363.96	11.17	9.9	0.10	Higham et al. (2009), Guy et al (2008), Zinner et al. (1994)
Papio papio	Y	MMMF	NA	8	NA	88.9	NA	184.42	NA	NA	12.1	0.22	Gauthier (1999)
Papio ursinus	Y	MMMF	7	14.5	NA	72	29.8	185.92	877.09	12.12	14.8	0.29	Huchard et al. (2010), (2009a), (2009b)

Piliocolobus badius	Y	PG/MMMF	3.5	9.5	NA	NA	12.3	151.41	783.93	8.55	8.25	0.53	Korstjens pers comm. Struhsaker (1975)
Piliocolobus kirkii	Y	NA	4.3	13.45	NA	NA	5.8	165	NA	7.62	5.46	NA	Korstjens, pers comm.
Piliocolobus preussi	Y	NA	NA	NA	NA	NA	NA	195	NA	NA	NA	NA	NA
Piliocolobus tephrosceles	Y	NA	4	12	NA	NA	NA	NA	NA	NA	NA	NA	Korstjens et al. (2009), Struhsaker (1975)
Pongo pygmaeus	N	PG	1	1	NA	34.2	78.5	259.42	1088.8	15.95	35.8	0.07	Galdikas (1981)
Procolobus verus	Y	NA	1.25	2	NA	NA	4.7	167.84	NA	7.43	4.2	0.00	Korstjens, pers comm. Korstjens & Noe (2004), Korstkens & Schippers (2003), Kuhn (1972)
Rhinopithecus bieti	N	NA	NA	NA	NA	NA	15	170	NA	NA	9.96	NA	He et al. (2001)
Rhinopithecus roxellana	N	MMMF	NA	NA	NA	NA	17.9	199.34	NA	8	11.6	NA	Ren et al (1995)
Semnopithecus entellus	N	PG/MMMF	1	12	NA	NA	13	197.7	402.1	10.83	9.89	0.00	Ostner et al (2006)
Symphalangus syndactylus	N	MG	1	1	1	NA	11.9	230.66	635.38	18.04	10.7	NA	NA
Theropithecus gelada	N	PG	1	4	3	NA	19	178.64	494.95	12.27	11.7	0.00	Dunbar (1987), Dunbar & Dunbar (1974)
Trachypithecus cristatus	N	PG	1	9.3	NA	6.2	6.61	NA	362.93	10.94	5.76	NA	NA
Trachypithecus johnii	N	PG	1	5.1	NA	NA	12	NA	NA	NA	11.2	NA	NA
Trachypithecus obscurus	N	PG/MMMF	1	5	2	4.8	7.9	146.63	362.93	8.51	6.26	NA	NA
Trachypithecus vetulus	N	NA	1	3.9	NA	NA	8.17	204.72	245.78	NA	5.9	0.00	NA

Table 4.1 *Comparative dataset used for all analyses in the current chapter. Mating system abbreviations: MG = monogamous, PG = polygynous, MMMF = multi-male, multi-female*

Citations: primary sources for swelling data

Andelman,(1987), *Am. Nat.*, 129:785–799; Arlet et al. (2008), *Ethology*, 114:851–862; Aujard, et al. (1998). *Am. J. Primatol.*, 46:285–309; Barelli et al. (2007), *Horm. Behav*., 51:221–230; Beehner et al. (2006), *Behav. Ecol.*, 17:741–750; Bernstein et al. (1982), *Primates*, 23: 587–591; Bernstein & Baker (1988), *Fol. Primatol.*, 51:61–75. Brauch, K., et al. (2007). *Horm. Behav.*, 52:375–383; Bullock et al. (1972), *J. Reprod. Fertil*., 31:225–236; Caldecott, (1984). *Anim. Behav.*, 34:208–220; Chapais (1983), *Behav. Ecol. and Sociobiol.*, 12:215–228;Charpentier et al. (2005), *Int. J. Primatol.*, 26:697–710; Clarke (1993), *Am. J. Primatol*, 31:275; Czekala & Sicotte (2000), *Am. J. Primatol*, 51:209–215; Deputte, B. (1991). *Fol. Primatol.*, 57:57–69; Deschner, & Boesch (2007), *Int. J. Primatol.*, 28: 389–406; Deschner et al. (2004), *Horm. Behav.,* 46:204–215; Dixson (1983). *Adv. Study Behav.*, 13:63–106; Dubuc et al. (2009), *Int. J. Primatol.*, 30:777–789; Dunbar (1977), *J. Human. Evol.*, 6:667–668; Dunbar & Dunbar (1974), *Anim. Behav.*, 22:203–204; Emery Thompson (2005), *Am. J. Primatol.*, 67:137–158; Engelhardt (2008), *Fol. Primatol.*, 79:326; Engelhardt et al (2007), *Horm. Behav.*, 51:3–10; Engelhardt et al. (2005), *Horm. Behav.*, 47:195–204; Fooden (1971), *Primates,* 12:63–73; Fujita et al. (2004), *Am. J. Primatol.*, 64:367–375; Fürtbauer et al. (2010), *Int. J. Primatol.*, 31:501–517; Galdikas, B. (1981). In C. Graham (Ed.), *Reproductive biology of the great apes: comparative and biomedical perspectives* (pp. 281–300). New York: Academic Press; Garcia et al. (2008), *Reproduction*, 135:89–97; Gauthier (1999), *Am. J. Primatol*, 47:67–74; Gautier-Hion, & Gauter (1974), *Fol. Primatol.*, 22:134–177; Gesquiere et al (2007), *Horm. Behav.*, 51:114–125; Gumert (2007), *Anim. Behav.*,, 74:1655–1667; Guy et al. (2008), *Anim. Reprod. Sci.*, 108: 412–424; Hadidian & Bernstein (1979). *Primates*, 20:429–442; Hanby & Brown (1974), *Behaviour*, 49:152–196; Harris et al. (2006), *Am. J. Primatol*, 68:383–396; He et al. (2001), *Am. J. Primatol*, 55:223–232; Higham et al. (2009), *Horm. Behav.*, 55:, 60–67; Hill (1966). *Primates: comparative anatomy and taxonomy 6. Catarhini, Cercopithecoidea, Ceropithecinae.* Edinburgh: Ed. University Press; Hodgkiss et al. (2010), *Zoo Biol.,* 29:449–456;
Hohmann & Fruth (2000), *Anim. Behav.*, 60:107–120; Huchard et al. (2009), *Behav. Ecol. Sociobiol.,* 63:1231–1242; Huchard et al. (2009), *Proc. R. Soc. B. Lond.,* 276:1889–97; Huchard et al., (2010), *BMC Evol. Biol.,* 10; Jurke et al. (2000), *Primates,* 41: 311–319; Kaufmann & Kaufman (1965), *Ecology*, 46:500–512; Kinnaird (1990), *Am. J. Primatol.*, 22:285–289; Korstjens & Noe (2004), *Am. J. Primatol.*, 62:261–273; Korstjens & Schippers (2003), *Int. J. Primatol.*, 24:515–539; Loy (1971), *Primates,* 12:1–31; Maheshwari et al. (2010), *HAYATI J. Biosciences*, 17:43–49; Malaivijitnond et al. (2007), *Am. J. Primatol.*, 735:721–735; Marty et al.. (2009), *Int. J. Primatol.*, 30:807–823; Matsumara (1993), *Primates*, 34:99–103; McArthur et al. (1972), *Fol. Primatol.*, 17:107; Mohle et al. (2005),. *Am. J. Primatol.*, 66:351–368; Mootnick (2006), *Prim. Conserv.*, 21:103–138; Mori et al. (1997), *Int. J. Primatol.*, 18:553–579; Murai (2004). *Ecol. Research*, 19:451–454; Murai (2006), *Am. J. Primatol.*, 68:832–837; Murray et al. (1985), *Int. J. Primatol.*, 6:101–113; Nadler (1975), *Science*, 189:813–814;Nadler et al. (1979), *Endocrinol.,* 105:290–296; Nawar & Hafez (1972) Primates, 13: 43–56; Nguyen et al. (2009), *Behav. Ecol. Sociobiol.,* 63:1331–1344; Okamoto et al. (2000), *Am. J. Primatol.*, 52:1–11; Okayasu, (2001), *Anth. Sci.,* 109: 121–140; Ostner et al. (2006); *Am. J. Primatol.*, 68: 701–712; Paoli et al. (2006), *Am. J. Primatol.*, 68:333–347; Peignot et al. (1999), *Fol. Primatol*., 70, 29–36; Petit & Thierry (1994), *Anim. Behav.*, 48:1427–1436; Pfefferle et al. (2008), *Proc. Roy. Soc. B. Lond*., 275:571–578; Phillips & Wheaton (2008), *Zoo Biol.*, 27:320–330; Rasmussen (1985), *Behav. Ecol. Sociobiol.,* 17:161–170; Reichert, et al. (2002), *Ethology*, 108:583–600; Ren et al. (1995), *Primates,* 36:135–143; Rowell (1970), *J Reprod Fertil,* 22:321–338; Rowell (1972), *Adv. Study Behav.,* 4: 69–105; Rowell (1977), *Fol. Primatol.*, 28:188–202; Rowell & Chalmers (1970), *Fol. Primaol.*, 12: 264–272; Sabater Pi (1973), *Fol. Primatol.*,19:193–207; Scott (1984), In *Female primates: studies by women primatologists*. AR Liss; Scruton & Herbert (1970). *J. Zool.*, 162:419–436; Setchell et al. (2006), Behav. Ecol. and Sociobiol., 61:305–315; Setchell & Wickings (2004), *Behav. Ecol.*, 15:438–445; Simonds (1965) In I. DeVore (Ed.), *Field Studies of Monkeys and Apes* (pp. 175–176). NY: Holt, Rinehart and Winston; Singh et al. (2006), *Current Science*, 90; Small (1990), *Primates*, 31: 339–350; Struhsaker (1975), *The red colobus monkey.* Chicago: Univ. of Chicago Press; Takahata (1980), *Primates,* 21:303–329; Thierry et al. (1996), *Am. J. Primatol.*, 39:47–62; Tutin (1979), *Behav. Ecol. Sociobiol.* 6:29–38; Walker et al. (2004), *Am. J. Primatol.*, 64:123–131; Watts (1991). *Am. J. Primatol.*, 24:211–225; Whitten & Russell (1996), *Am. J. Primatol.*, 40:67–82, Wu & Lin (1992), *Primates*, 33:85–97; Yeager (1990), *Am. J. Primatol.*, 20: 95–106; Zhao (1993), *Primates*, 34:431; Zinner et al. (1994), Behav. Ecol. and Sociobiol. 35:175–183.

4.2.2. Phylogenetic comparative methods

In order to control for phylogenetic non-independence and to incorporate phylogenetic relatedness into statistical analyses of cross-species data, phylogenetic comparative statistical methods were used to analyse the data (Harvey & Pagel, 1991; Nunn, 2011). All phylogenies were single dated consensus trees, downloaded from 10kTrees (Arnold et al. 2010). Phylogenetic generalized least squares (PGLS) regression was used for analyses involving continuous variables (Grafen, 1989; Pagel, 1997), estimating phylogenetic signal (λ, where 0=minimum and 1=maximum) by maximum likelihood. To investigate the relationship between swellings and paternal care, Pagel's (1994) 'Discrete' method was used, which estimates parameters for models of evolution of binary traits, from given phylogenies and distributions of traits across species. The 'Discrete' method was used to compare a model of independent evolution, in which transition rates between states of traits are estimated separately for each trait, with a model of dependent evolution, in which transition rates for each trait are allowed to depend the state of the other trait. Models were compared using a likelihood ratio test, where the model with the higher log likelihood was determined to fit the data significantly better if twice the difference in log-likelihoods was >2 (Pagel & Meade, 2007). PGLS analyses were run in the 'caper' R package (Orme et al., 2011; R Core Team, 2013), and 'Discrete' analyses were run in BayesTraits (version 1, Pagel & Meade, 2007).

4.2.2 Regression models

Swellings were coded as a factor on two levels ('exaggerated' or 'none') and used as an independent variable in all analyses. Mating system was coded as a factor on three levels ('multi-male, multi-female', 'polygynous' or 'monogamous'). All continuous variables were ln-transformed prior to analyses to normalise distributions. All analyses where testes mass or canine length were dependent variables controlled for body size by including body mass as a co-variate. Body mass was not included as a co-variate where penile length was the outcome variable as body mass was unrelated to penile length (p=0.6, n=26). The relationship between swellings and body mass dimorphism was investigated by using swellings to predict male body mass, with female body mass as an additional co-variate. The relationship between swellings and adult sex ratio was investigated by using swellings to predict male group size, with female group size as an additional co-variate. Model performance was checked by visual inspection of the distribution of model residuals. All models were checked for outliers, where outliers were determined *a priori* as those with standardised residuals of >3 (+/-). Where outliers were discovered, models were run both with and without the outlier species included.

Where slopes appeared to differ between species with and without exaggerated swellings, models with and without interaction terms between swellings and predictor variables were compared. Models were compared using Akaike Information Criterion (AIC) values, following the convention where the better fitting model was determined to be favoured where its AIC value was >2 units lower than alternative models. Where models with interaction terms were favoured according to AIC comparison, results are reported from models with differing slopes for species with and without exaggerated swellings. See Appendix E for full model results for all multi-variate models included in Chapter 4.

4.3 Results

4.3.1 Costs of mating for males: swellings and testes mass

Slopes for the effect of male body mass on testes mass appeared to differ between species with and without exaggerated sexual swellings. A model estimating separate slopes for species with and without swellings by including an interaction term between swellings and male body mass fit the data significantly better than a model without the interaction term included (>9 AIC units lower). The slope for male body mass and testes mass was significantly steeper for species with and without swellings (with swellings: $\beta=1.12$, $p<0.001$ without swellings: $\beta=0.29$, $p<0.13$, *ps* for slope difference=0.002, $n=31$), regardless of coding scheme used for swellings, suggesting that in swelling species, there is a greater increase in testes mass with increasing male body mass than in non-swelling species (**Figure 4.2)** In species with multi-male, multi-female mating systems only, model fit was also improved by including an interaction term for swellings and male body mass, although significance varied across coding schemes (1.7-2.6 AIC units lower). Similarly, within multi-male, multi-female species only, there was a marginally steeper slope between testes mass and male body mass in swelling species than non swelling species (*ps*<0.1, *n* mating system 'upcoded'=20, *n* mating system 'downcoded'=18). See Appendix E.ii for full model results.

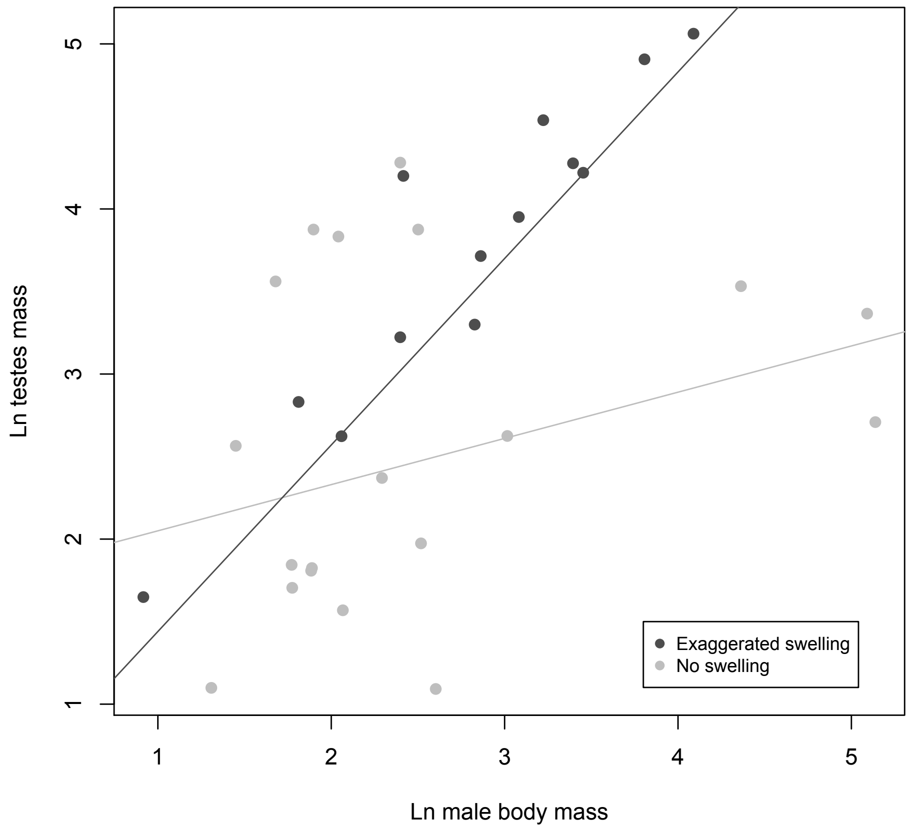


Figure 4.2: *In species with exaggerated swellings, testes mass scales significantly more steeply with body mass than in species without swellings. Slopes are presented using the 'down-coded' version of swelling data but results did not differ between coding schemes.*

4.3.2 Costs of mating for males: swellings and body mass dimorphism

Body mass dimorphism did not significantly differ between species with and without exaggerated swellings, either across all species (*ps*>0.4, *n*=68), or amongst species with multi-male, multi-female mating systems only (*ps*>0.2, *n* mating system 'upcoded'=32, *n* mating system 'downcoded'=27). See Appendix E.iii for full model results.

4.3.3 Costs of mating for males: swellings and male group size

Male group size was significantly larger in species with than without exaggerated swellings, regardless of coding scheme used for swellings (*ps*<0.001, R^2=0.29, λ=0, *n*=51). Amongst species with multi-male, multi-female mating systems ('down-coded') only, male group size was either significantly or marginally larger in species with than without exaggerated swellings, depending on the coding scheme used for mating system ('down-coded': *ps*≤0.03, R^2=0.17, λ=0, *n*=23, **Figure 4.3**, 'up-coded': *ps*≤0.1, *n*=28).

4.3.4 Costs of mating for males: swellings and adult sex ratio

Slopes for the effect of female group size on male group size appeared to differ between species with and without exaggerated sexual swellings. A model estimating separate slopes for species with and without swellings by including an interaction term between swellings and male body mass fit the data significantly better than a model without the interaction term included (>4 AIC units lower). The slope for female group size on male group size was significantly steeper for species with and without swellings (*ps*=0.02, *n*=45), regardless of coding scheme used for swellings, suggesting that in swelling species, there is a greater increase in male group size with increasing female group size than in non-swelling species (**Figure 4.4)** In species with multi-male, multi-female mating systems only, model fit was not significantly improved by including the interaction term between female group size and swellings (<2 AIC units lower). Without the interaction term, amongst species with multi-male, multi-female mating systems only, adult sex ratio did not differ between species with and without exaggerated swellings (*ps*>0.2, *n* mating system 'up-coded'=23, *n* mating system 'down-coded'=19). See Appendix E.iv for full model results.

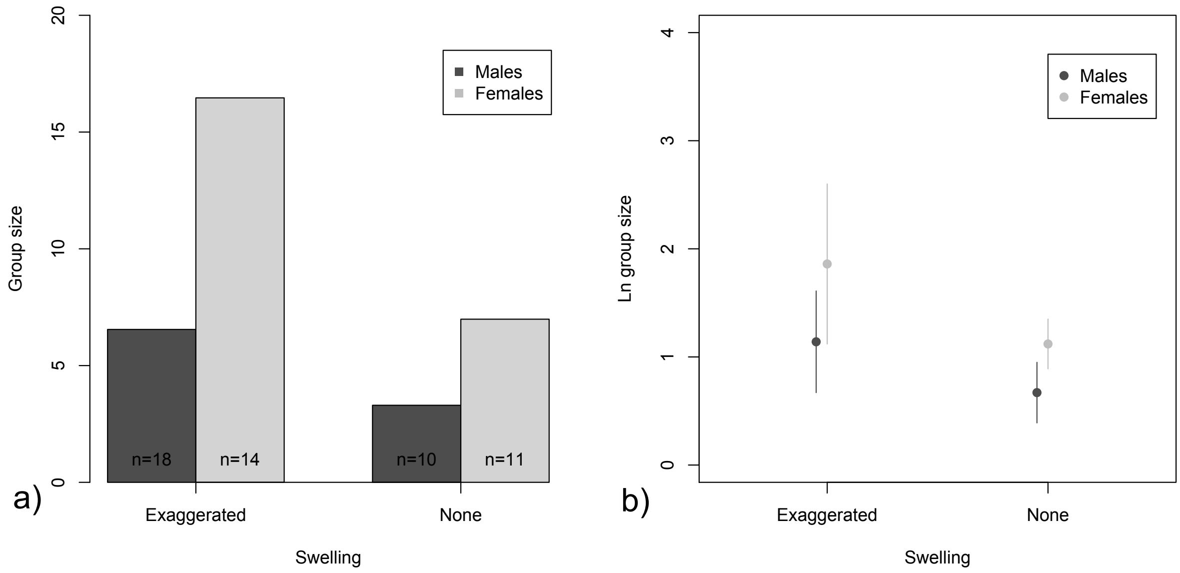


***Figure 4.3** a) mean number of males and females in social groups for species with and without exaggerated swellings ('down-coded'), from raw data, including only species with multi-male, multi-female mating systems ('up-coded'), b), estimated mean ln-group size from the PGLS model where swelling ('down-coded') predicted group size, in multi-male mating species only (results presented using the 'up-coded' classification scheme for mating system). Bars represent standard error. Within species with multi-male, multi-female mating systems, male group size is marginally larger, and female group size significantly larger, in species with exaggerated swellings than species without exaggerated swellings.*

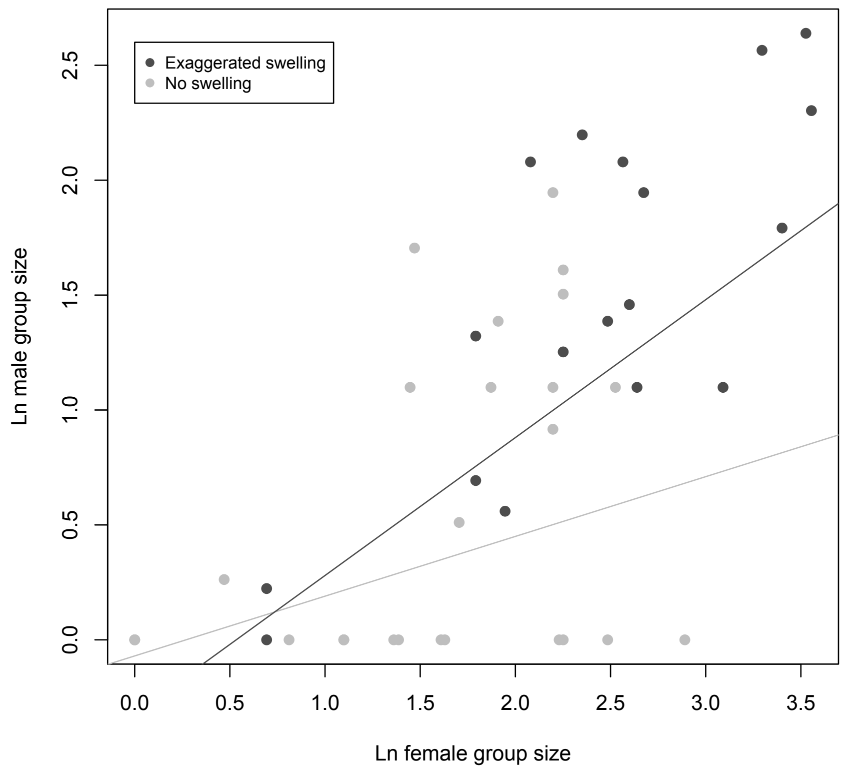


Figure 4.4: *In species with exaggerated swellings, male group size scales significantly more steeply with female group size than in species without swellings, depending on the coding scheme used for swellings. Slopes are presented using the 'down-coded' version of swelling data.*

4.3.5 Costs of mating for males: swellings and STD prevalence

STD prevalence was greater than in species with than without exaggerated swellings, although this difference was only significant for the 'down-coded' classification scheme for swellings (p=0.04, R^2=0.09, λ=0, n=39), and marginal for the 'up-coded' classification scheme (p=0.07). Rhesus macaques (*Macaca mulatta*) were identified as an outlier and when removed, the difference in STD prevalence between species with and without exaggerated swellings became significant for both classification schemes for swellings (*ps*<0.01, R^2=0.18, λ=0, n=38, **Figure 4.5**). There was no difference in STD prevalence between species with and without exaggerated swellings amongst species with multi-male, multi-female mating systems only (*ps* ≥0.2, *n* 'upcoded'=22, *n* 'downcoded'=20).

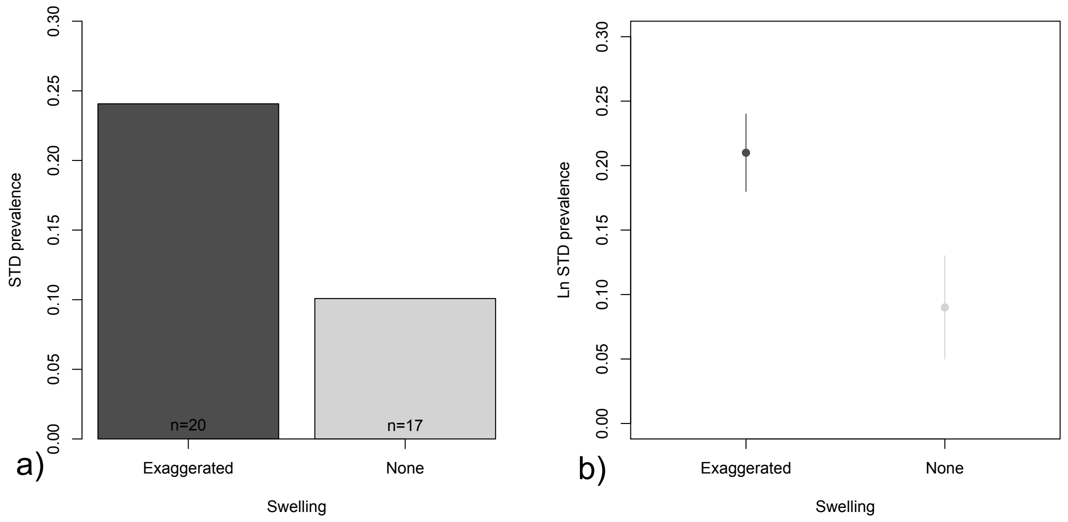


***Figure 4.5** a) mean STD prevalence for species with and without exaggerated swellings ('down-coded'), from raw data, excluding a statistical outlier (Macaca mulatta), b) estimated mean ln STD prevalence from the PGLS model where swelling ('down-coded') predicted STD prevalence, excluding a statistical outlier (Macaca mulatta). Bars represent standard error.*

4.3.6 Variation in female quality/costs of mate choice for males: swellings and female group size

Female group size was significantly larger in species with than without swellings, regardless of coding scheme used for swellings (*ps*≤0.002, R^2=0.17, λ=0.32, *n*=50). Female group size was also significantly larger in species with than without swellings amongst species with multi-male mating systems only, regardless of coding scheme used for either swellings or mating system (*ps*≤0.02, R^2=0.27, λ=0, *n* 'down-coded'=20, *n* 'up-coded'=25, **Figure 4.3**). However, female group size is not independent of male group size but rather is strongly predicted by male group size (*p*<0.001, R^2=0.47, λ=0, *n*=45), and when including male group size as an additional co-variate, there was no significant difference in female group size between swelling and non-swelling species, either across all species or within multi-male, multi-female species only (*ps*>0.07).

4.3.7 Female-female competition: swellings and female canine length

Species with swellings had significantly smaller canine lengths for their body mass than species without swellings (*ps*≤0.01, R^2=0.23, λ=0.52, *n*=47, **Figure 4.6**), regardless of coding scheme used for swellings. Amongst species with multi-male, multi-female mating systems only, female canine length did not differ between species with and without exaggerated swellings, regardless of coding scheme for either swellings or mating system (*ps*≥0.6, *n* 'up-coded'=24, *n* 'down-coded'=20). There was no significant interaction between female body mass and swellings, either across all species or within multi-male, multi-female species only, as model fit was not significantly improved by including an interaction term between female body mass and swellings (≤2 AIC units lower). See Appendix E.iv for full model results.

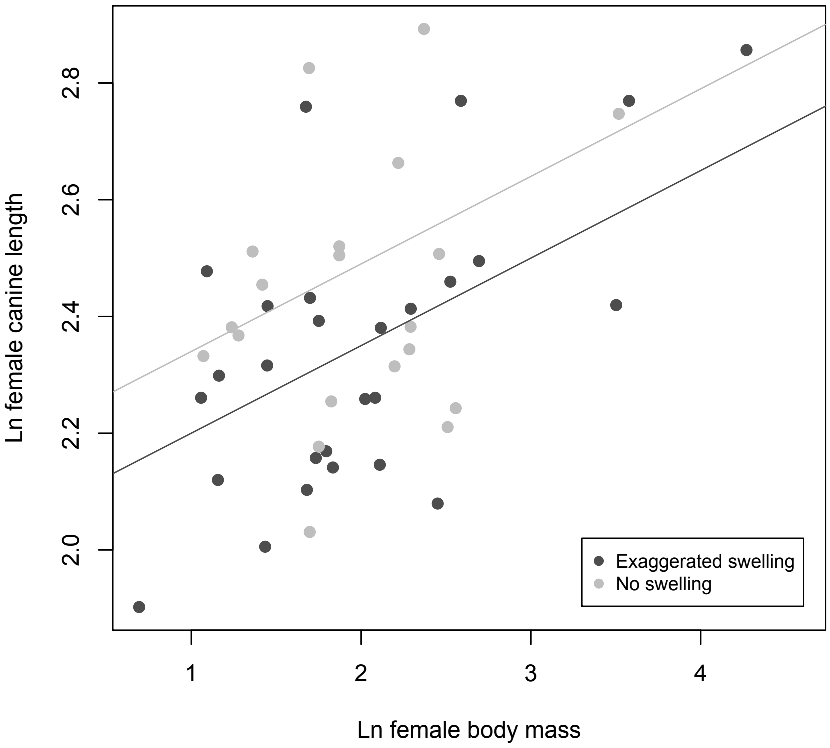


Figure 4.6: *females in species with exaggerated swellings have significantly smaller canines for their body size than females in species without swellings. Results are presented using the 'up-coded' classification scheme for swellings, but coding scheme did not affect the results.*

4.3.8 Direct benefits of mating for females: swellings and infanticide risk

There was no significant difference in infanticide risk between species with and without exaggerated swellings, for either coding scheme for swellings, either across all species (*ps*>0.6, *n*=40) or amongst species with multi-male, multi-female mating systems only (*ps*>0.4, *n* mating system 'up-coded'=24, *n* mating system 'down-coded'=18).

4.3.9 Direct benefits of mating for females: swellings and paternal care

The dependent model did not fit the data significantly better than the independent model (log likelihood ratio <2), suggesting no evidence for correlated evolution of swellings and paternal care, regardless of coding scheme used for swellings, either across all species or amongst species with multi-male, multi-female mating systems only.

4.3.10 Cryptic female choice: swellings and penis length

Males in species with exaggerated swellings had significantly longer penises for their body size than males in species without exaggerated swellings (*ps*<0.001, R^2=0.53, λ=0.59, *n*=26), regardless of coding scheme used for swellings and whether or not an outlier was included (*Macaca arctoides*). Within species with multi-male, multi-female mating systems only, there remained significant or marginal differences in penis length between species with exaggerated swellings and species without exaggerated swellings, (*ps*≤0.1, *n* 'up-coded'=11, *n* 'down-coded'=9).

4.4 Discussion

In species with exaggerated sexual swellings, absolute number of males and STD prevalence were greater than in species without swellings, consistent with the hypothesis that in species with swellings, males experience high mating costs. In swelling species, testes mass increased with body size with a significant slope of >1, whereas in non-swelling species, testes mass increased with body size with a shallow, non-significant slope. Therefore, in swelling species, the costs of sperm production may increase more rapidly with body size than in non-swelling species, consistent with the prediction that in species with swellings, males experience high costs of sperm production. Female group size was significantly larger in species with than without exaggerated swellings, both across all species and amongst species with multi-male, multi-female mating systems only. Therefore, in swelling species, males are likely to experience high variation in female quality and low costs of choice, conditions favourable to male mate choice in combination with costly mating. Female group size, however, was not independent of male group size, rather, both male and female group sizes seem to be larger in absolute terms in species with than without swellings, with a more even sex ratio. Female canine length was significantly shorter in species with than without exaggerated swellings, contradicting the prediction of the 'reliable-indicator' hypothesis that swellings are associated with high female-female competition. Exaggerated swellings were not associated with either high infanticide risk or male care-taking, in contrast to the predictions of the 'graded-signal' and 'paternal-care' hypotheses. In swelling species, males had significantly longer penises than in species without swellings, supporting the hypothesis that swellings may function in cryptic female choice. The evolution of exaggerated sexual swellings may therefore be partly explained by both male mate choice and cryptic female choice, as an unusual example of visual female ornamentation in a non sex-role reversed mammal species.

4.4.1 Costs of mating for males: sperm competition

The finding that males have testes mass scales more steeply with body mass in species with than without exaggerated swellings is consistent with the hypothesis that costly sperm production can favour the evolution of female ornamentation through male mate choice. Larger-bodied species with swellings have increasingly large testes mass, compared to larger-bodied species without swellings. Species with large testes produce high volumes of ejaculate (Moller, 1989) in response to high sperm competition (Harcourt et al., 1995). Despite the lower costs and greater potential benefits of multiple mating for males relative to females (Bateman, 1948; Trivers, 1972), the historical assumption of negligible limits on male mating rate (Bateman, 1948; Darwin, 1871) has been challenged by the recognition that sperm is physiologically costly to produce and can become depleted (Dewsbury, 1982; Small et al., 1988; Wedell et al., 2002). For example, male Japanese macaques (*Macaca fuscata*) expend up to 6% of their daily basal metabolic rate on ejaculate production (Thomsen et al., 2006), and both Rhesus macaques (*Macaca mulatta*) and bonnet macaques (*Macaca radiata*) decrease sperm production outside of the breeding season (Gupta et al. 2000). If sperm is costly, males are predicted to bias sperm allocation towards highly ornamented females where ornamentation is related to female fertility (Wedell et al., 2002, Reinhold et al. 2002). Accordingly, experimental studies in both primates and non-primates have demonstrated that males produce more sperm in response to females with larger ornaments, where ornaments signal female fertility or fecundity (*Papio ursinus,* Girolami & Bielert, 1987, *Gallus gallus*, Cornwallis & Birkhead, 2007).

4.4.2 Costs of mating for males: male-male competition

Adult male group size and adult sex ratio is greater (more male-biased) in species with than without exaggerated swellings, suggesting that there is strong pre-copulatory competition between males in species with swellings. However, size dimorphism did not differ between species with and without swellings. In primates, male-male competition may be costly either in terms of risk of injury from fights, or time and energy required for mate-guarding. As the results demonstrated associations between swellings and male group size, but not body size dimorphism, mating costs for males in species with swellings may arise from mate-guarding rather than physical aggression. Mate-guarding may be especially costly in species with year-round breeding (Alberts et al., 1996) and where non-synchronous receptivity causes a strongly male-biased operational sex ratio (Emlen & Oring, 1977), both of which are characteristic of species with exaggerated swellings (Nunn et al., 2001; van Schaik et al.

1999). Although competitiveness and choosiness in mating were once considered as alternative behavioural strategies or ‘sex roles’, typical to males and females respectively (Darwin, 1871), theoretical evidence suggests that high male-male competition should favour the selective allocation of mating effort towards high quality females (Pagel, 1994). In primates, males appear to exhibit mate choice even where males are promiscuous and competitive in mating (e.g. *Papio cynocephalus,* Gesquiere et al., 2007; *Macaca sylvanus*, Kuester & Paul, 2011; *Pan troglodytes,* Muller et al., 2006; *Macaca thibetana,* Zhang et al., 2010). However, empirical evidence in support of the assumption that increased male-male competition favours discriminate mating is currently limited to a study of spiders (*Zygiella x-notata,* Bel-Venner et al. 2008), and therefore the prediction that male-male competition favours choosy mating in male primates remains to be investigated.

4.4.3 Costs of mating for males: STD risk

The prevalence of sexually transmitted diseases (STDs) was significantly greater in species with than without exaggerated swellings (after removal of a statistical outlier, *Macaca mulatta*). Although STDs tend to be associated with low mortality risk, STDs often cause sterility and therefore pose a significant cost to mating (Knell, 1999; Lockhart et al., 1996; Nunn & Alitzer, 2004, Daly, 1978; Freeland, 1976). STD risk may be especially costly for male primates as STDs are more prevalent in females than males (Nunn & Alitzer, 2004). As swellings are largest around the time of ovulation (e.g. Brauch et al., 2007), males should benefit from preferring to mate when females are fully swollen due to the trade off between risk of STD transmission and increased conception probability. The association of STD prevalence with exaggerated swellings across species may explain the short duration of copulations (Nunn & Alitzer, 2006; Tutin & McGinnis, 1981), and ano-genital inspections by males (e.g. *Papio hamadryas* ursinus, Clarke et al. 2009) typical to species with exaggerated swellings, as behavioural defences against disease transmission (Hamilton, 1990; Sheldon, 1993). However, the effect of STD risk on male mate choice in primates remains to be investigated empirically. Further, if individual females with larger swellings are associated with higher copulation rates and therefore increased STD risk, males may, in fact, not benefit from between-female mate choice based on swelling size.

4.4.4 Variation in female quality

Adult female group size, in absolute terms, was larger in species with than without exaggerated swellings. Female group size was larger in swelling species even amongst species with multi-male, multi-female mating systems, suggesting that the relationship between female group size and swellings is not simply due to larger overall group sizes in multi-male, multi-female mating systems. Theoretical evidence suggests that costly mating is insufficient to favour the evolution of mate choice alone, rather, there must also be variation in mate quality. If all potential mates were of equal quality, there would be no benefit of choosing between mates, even if mating was costly (Bonduriansky, 2001; Parker, 1983). Where female group sizes are large, male primates may experience larger variation in the quality of potential mates, in terms of current fertility, age and fecundity, for example, and therefore males in swelling species may experience greater opportunity for mate choice than males in species without swellings. Currently, the direct effect of female quality variation on male mate choice in primates is unknown and therefore requires additional empirical investigation, but experimentally increased female quality variation in bush-crickets (*Kawanaphila nartee*) results in a higher proportion of mate rejections by males, under a male-biased OSR (Kvarnemo & Simmons, 1999).

Female group size however, is not larger in swelling species when accounting for male group size. Rather, analyses of the relative number of males and females demonstrated that in swelling species, male group size scales more steeply with female group size than in non-swelling species, although this effect did not remain within multi-male, multi-female species only. Together, the analyses of swellings and male and female group sizes suggest that in swelling species, there are both more males and more females in absolute terms than in non-swelling species. For a given increase in female group size, there is a greater increase in male group size in swelling than non-swelling species. However, female group size does not increase independently of male group size. Further, there were no differences in adult sex ratio between swelling and non-swelling species within multi-male, multi-female species only. Therefore, swelling species appear to be characterised by sex ratios typical of multi-male, multi-female mating systems – larger overall group sizes, with more even sex ratios, than non-swelling species.

4.4.5 Costs of mate choice for males

In addition to high variation in female quality, low costs of mate choice for males are required for selection to favour male mate choice. Costs of choice are important because even very poor mating opportunities should be accepted where there is little chance of obtaining alternative mates (Barry & Kokko, 2010). In swelling species, due to associations with large numbers of females, males may have greater opportunity to reject potential mates in favour of alternatives than in non-swelling species. In species with exaggerated swellings, not only are female group sizes large, but females are often year-round breeders, receptive to mating throughout the ovarian cycle (Hrdy & Whitten, 1987; van Schaik et al., 1999), further increasing the opportunity for mate choice in contrast to species where males typically encounter few females at a time and receptivity to mating is limited to a short window. Mating systems in which males and females live in year-round, stable associations, with extended receptivity in females are not common in mammals, where more typically, receptivity is confined to a few hours or days per breeding cycle (Hrdy & Whitten, 1987). Therefore, constraints on male mate choice may be help to explain the rarity of female ornamentation in mammals outside of Catarrhine primates. Although currently empirical evidence for the relationship between search costs and choosiness in male primates is lacking, experimental variation in female encounter rate is positively associated with mate-rejection in male katydids (Shelly & Bailey, 1992).

4.4.6 Female-female competition

In contrast to the prediction of the 'reliable indicator' hypothesis that females in species with swellings compete strongly for access to mates, female canine length was not greater in species with than without swellings, replicating the results of previous comparative analyses (Nunn et al., 2001). Rather, female canine length was significantly smaller in species with swellings than without swellings. Therefore, there is currently little evidence that swellings evolved due to direct, physical competition between females in primates. However, aggressive competition between individuals is not necessarily required for the evolution of ornamentation. For example, decorative plumage in birds, such as elongated tails in male widowbirds, may have evolved due to female mate choice rather than male-male contest competition (Andersson, 1994: 335). Competition between female mammals takes both aggressive and more subtle forms, including displays, threats and harassment (Stockley & Bro-Jørgensen, 2011). Competition may also occur via the properties of swellings themselves, to the extent that swellings attract the mating effort of males at the expense of other females' fitness (Pagel, 1994; Stockley & Bro-Jørgensen, 2011). Due to greater reproductive investment, investment in aggressive competition may be more constrained in females than males (Stockley, & Campbell, 2013). Further, the costs of swellings themselves (Bielert & Busse, 1983; Matsumodo-Oda, 1998) may trade-off with investment in additional exaggerated traits, which could explain the negative association between swellings and female canine length.

4.4.7 Direct benefits of mating for females

Previous evidence suggests that swellings signal temporal fertility rather than individual female quality (Nunn, 1999; Zinner et al., 2004, previous chapter), yet between-female co-variation of ornament size and fitness is required for male mate choice to exert strong selection pressure on female fertility cues. However, male mate choice can favour enlarged fertility cues in females where direct benefits of mating for females scale with both ornament size and male mating effort (Bonduriansky, 2001). For example, exaggeration of fertility cues in dance flies (*Rhamphomyia longicauda*) appears to have evolved due to male provision of nutrients to females, which increases with ornament size (Funk & Tallamy, 2000). In Catarrhine primates, females with larger swellings could plausibly receive increased direct benefits of mating through infanticide avoidance or paternal investment, as argued by the graded signal (Nunn, 1999) and paternal care hypotheses (Alberts & Fitzpatrick, 2012). However, the current analyses showed no associations between swellings and either infanticide risk or paternal care across species, and therefore the potential increased benefits of mating due to enlarged swellings remain to be explored. Another possibility, also suggested by the graded-signal hypothesis, is that exaggerated swellings increase protection from harassment received by females (Nunn, 1999). Alternatively, where sperm is limited, females with enlarged swellings would benefit from increased conception probability due to increased mating opportunities. In some primate species, extremely high copulation rates (Watts, 2007) and low fertility (Drea, 2005) are suggestive of sperm limitation. Additionally, preferred, dominant males may be especially sperm limited in promiscuous species (Preston et al. 2001).

4.4.8 Cryptic female choice

The results demonstrated that males in species with exaggerated swellings had elongated penises relative to males in species without swellings. The association of exaggerated swellings and longer penis length is consistent with the prediction that swellings function in cryptic female choice (Dixson & Mundy, 1994; Dixson, 2002). Elongated female reproductive tracts may enhance sperm competition and, where there is heritable variation between males in sperm quality, biasing of paternity towards preferred males (Keller & Reeve, 1995). Cryptic female choice is likely to be favoured where pre-copulatory female choice is constrained, as is likely in the Catarrhine primates due to the larger body size and social dominance of males (Smuts & Smuts, 1993). Penis elongation in males therefore may have evolved in response to enhanced cryptic female choice, as an example of genital co-evolution (Brennan et al., 2007). Younger or subordinate males are often less preferred by females relative to dominant males in primates, but females often receive harassment from juvenile, subordinate males (Niemeyer & Anderson, 1983). If older, dominant males have longer penises relative to younger males, swellings could allow females to accept copulations from less preferred males whilst biasing paternity towards preferred males, as an example of an adaptation to ‘convenience polyandry’ (Rivera & Andrés, 2002; Thiel & Hinojosa, 2003). Therefore in addition to increasing conception probability, by increasing sperm allocation, swellings could enhance cryptic female choice.

4.4.9 Limitations of the present analyses

The effect of confounding variables and data quality are common limitations of comparative analyses (Nunn, 2011). Some of the current analyses were limited in that effects of mating system and swellings could not be distinguished. For example, the relationships between exaggerated swellings and testes mass, STD prevalence and male group size either weakened or did not remain when including only species with multi-male, multi-female mating systems. Since swellings and multi-male, multi-female mating systems are closely associated in Catarrhine primates (Pagel & Meade, 2006), effects of swellings and mating system may not always be statistically distinguishable. Further, the quality of currently available comparative datasets limits the confidence in some results. For example, further comparative analyses are required to ensure that relative lactation length is a good measure of infanticide risk. Penis length data were based on ranking rather than actual measurements, and data on male care-taking were rough, categorical estimations, which may not adequately reflect variation in male investment in offspring across primates. Therefore, both the paternal care and the cryptic female choice hypotheses warrant further investigation. In addition, swellings were treated as a binary variable, whereas there may be more subtle variations in swelling size across species. The question of the evolution of exaggerated sexual swellings would benefit from novel cross-species datasets, comprising of more accurate measures of variables of interest.

4.4.10 Conclusions

The current analyses suggest that exaggerated swellings may be an unusual example of a female visual ornament, resulting from male mate choice and cryptic female choice, in a non sex-role reversed mammal species. Exaggerated swellings seem to have evolved where conditions favour male mate choice due to costly mating, variation in female quality and low costs of mate choice. Additionally, swellings may have been favoured due to the benefits of cryptic female mate choice and increasing conception probability where sperm is limited. Although predictions of the graded-signal and paternal care hypotheses were not supported, these hypotheses warrant investigation by further comparative analyses using more sophisticated measures of infanticide risk or paternal care. The idea that swellings evolved due to fitness benefits for females, including paternity manipulation, is not incompatible with the idea that swellings evolved due to male mate choice, and therefore the current project suggests a framework in which previously opposing hypotheses may be reconciled (Nunn et al., 2001; Nunn, 1999; Pagel, 1994; Zinner et al., 2004). Furthermore, the current framework may help to explain the evolution of female ornaments in diverse taxa. For example, female Alpine accentors (*Prunella* collaris) have bright red cloacal swellings during the breeding season, which are used in female courtship displays (Nakamura, 1990). Similarly to some Catarrhine primate species, Alpine accentors are characterised by high sperm competition and large male and female social groups, and males commonly reject solicitations from females suggesting that they are choosy in mating (Davies et al. 1996). The current findings may therefore generalise beyond primates and help to explain female ornamentation in non-primates due to convergent selection pressures.

Chapter 5: *co-variation of intra-sexual competition and measures of cognitive abilities across primate species*

5.1 Introduction

The process of sexual selection explains the evolution of a variety of exaggerated physical traits in animals, including weapons such as horns, and ornaments such as decorative colours (Andersson, 1994; Darwin, 1871). Darwin proposed that in addition to physical traits, cognitive ability could be sexually selected, controversially citing “the higher powers of the imagination and reason” in human males, present in females too due to “the law of equal transmission”, as an example (1871: 463). However, researchers have only recently begun to investigate evidence for sexual selection acting on cognitive traits (Boogert et al. 2011; Jacobs, 1996; Miller, 2000; Van Bergen, 2004). In a variety of animal species, a growing number of studies suggest that cognitive ability can be favoured in mate choice. For example, female guppies and meadow voles prefer males that perform better on maze learning tasks (Shohet & Watt, 2009; Spritzer et al. 2005), female crossbills prefer males observed to perform better on an extractive foraging task (Snowberg & Benkman, 2009), and female songbirds often prefer males with large song repertoires (e.g. Searcy, 1992). In male bowerbirds, performance on cognitive tasks is positively correlated with mating success (Keagy et al. 2009, 2011), and high cognitive ability may function as a cue to general phenotypic quality across a range of species (Boogert et al., 2011). The extent to which cognitive abilities are related to intra-sexual competition, however, largely remains to be investigated.

In some primate species, intra-sexual competition may have favoured cognitive traits that underpin the ability to employ ‘strategic’ mating behaviour, i.e. behaviour supported by cognitive abilities such as forward planning, perspective taking and behavioural flexibility, used to gain mating opportunities. For example, ‘sneak mating’, in which mating takes place out of sight and hearing of dominant individuals, may require individuals to be able to plan behaviour, understand the perspective of dominant individuals and adjust behaviour to specific social circumstances (le Roux et al., 2013). Similarly, the ‘social intelligence’ hypothesis has argued that increased brain size and cognitive abilities co-evolved with complex sociality (e.g. Dunbar, 1998) due to selection for cognitive abilities used in ‘Machiavellian’ social behaviour (Whiten & Byrne, 1997), including in competition for mates (Chance & Mead, 1953; Dunbar, 1998; Lindenfors et al., 2007; Pawlowski et al., 1998; Sawaguchi, 1997). However, proponents of the ‘social intelligence’ hypothesis have argued that intra-sexual competition has played a relatively minor role in the evolution of increased brain size and cognitive abilities in primates compared to that of multiple, stable social bonds (Shultz & Dunbar, 2007; Whiten & Byrne, 1997). If intra-sexual competition has favoured such 'strategic' behaviour in primates, measures of the intensity of intra-sexual competition should be positively associated with measures of relevant cognitive abilities across primate species.

'Strategic' mating behaviour could be particularly advantageous where individuals' ability to physically monopolise mates is limited, favouring alternative mating strategies, as is likely in species with large social groups (Cords, 2000) and promiscuous mating systems (Dunham & Rudolf, 2009). For example, in promiscuous mating species such as chimpanzees, long-tailed macaques and spider monkeys, mating competition occurs not only through aggression but also through alternative strategies including 'sneak' mating and opportunism, especially in subordinate individuals (Engelhardt et al. 2006; Gibson, 2010; Wroblewski et al., 2009). Further, sperm competition may select for the ability to estimate competition intensity through cognitive mechanisms in order to optimally invest mating effort (Shifferman, 2012). 'Strategic' mating behaviour may not be limited to males, rather, females may also employ such behaviour in competition for mates or as a counter-strategy to male monopolisation (Drea, 2005).

Alternatively, selection may favour 'strategic' mating behaviour in species with polygynous rather than promiscuous mating systems, typically characterised by intense competition between males for monopolisation of females, such as gorillas (Plavcan, 2001; Watts, 2000). For example, in gorillas, 'sneak mating' has been reported in females and subordinate or extra-group males (Byrne & Whiten, 1990), possibly functioning as a counter-strategy to male monopolisation. However, because males are typically able to monopolise the majority of matings in polygynous species, there may be less opportunity for selection for alternative reproductive tactics in polygynous than in promiscuous mating species. In contrast to promiscuous or polygynous species, in monogamous species, 'strategic' social behaviour is unlikely to be advantageous in mate competition. For example, in some monogamous gibbons, intra-sexual competition primarily involves aggressive defence of mates and territory from extra-group individuals (Palombit, 1993). In such species, social groups are small, often consisting only of monogamous pairs and juveniles (Kleiman, 1977). Therefore, there may be little opportunity for individuals to use 'strategic' social behaviour to compete for mates in monogamous species, rather, aggressive behaviour and displays directed at extra-group individuals may be sufficient.

‘Strategic’ mating behaviour may involve three cognitive abilities in particular. First, ‘tactical deception’ – defined as ‘acts deployed such than another individual is likely to misinterpret what the acts signify, to the advantage of the agent’ (Byrne & Whiten, 1990: 3). For example, ‘sneak’ matings reported in some primate species, which take place out of sight and hearing of dominant individuals, apparently allow individuals to gain matings that would not otherwise be possible (Byrne & Whiten, 1990; le Roux et al., 2013). Second, the ability to innovate, defined as ‘the tendency to discover novel solutions to environmental or social problems’ (Reader & Laland, 2002), could help individuals compete for mates through the use of novel behaviour in mating attempts. For example, chimpanzees have been reported to gain mating success through novel courtship gestures and by incorporating novel objects into dominance displays, resulting in rises in dominance rank (Goodall, 1986; Kummer & Goodall, 1985). At least 10% of recorded primate innovations occurred in the contexts of courtship, display or aggression (Reader & Laland, 2001). Finally, general intelligence, defined as a domain-general cognitive ability involving planning, reasoning and problem-solving (Reader et al., 2011) might be favoured by intra-sexual competition if, for instance, enhanced learning ability or memory improved the ability of individuals to create or exploit mating opportunities, undermine competitors or mentally monitor mating interactions with conspecifics.

Here, I tested the hypothesis that intra-sexual competition is positively associated with cognitive abilities across primate species. First, I tested the prediction that cognitive abilities are positively associated with intra-sexual competition where monopolisation of mates is limited, as in species with promiscuous mating systems. I therefore tested the prediction that measures of species-typical cognitive abilities are positively associated with testes mass (as a proxy measure of sperm competition, Harcourt et al. 1995) and greater in multi-male, multi-female mating systems than other mating systems. Second, I tested the alternative hypothesis that measures of cognitive abilities are positively associated with intra-sexual competition where males monopolise groups of females. I therefore tested the prediction that measures of cognitive abilities are positively associated with male-biased size dimorphism (as a proxy measure of male-male competition for monopolisation of females) (Leutenegger & Kelly, 1977) and greater in polygynous mating systems than other mating systems. As measures of cognitive abilities, I used tactical deception rate, innovation rate and g_{s1} (a composite measure of general intelligence) from Reader et al. (2011) and Byrne & Whiten (1990). Additionally, using a sub-set of data on deception and innovation where the sex of the individual was available, I investigated whether mating system and measures of intra-sexual competition predicted rates of tactical deception and innovation in males and females specifically.

5.2 Methods

5.2.1 *Phylogeny-based comparative statistical methods*

Due to phylogenetic non-independence in cross-species datasets, phylogenetic comparative statistical methods were used to analyse the data (Harvey & Pagel, 1991; Nunn, 2011). Specifically, phylogenetic generalized least squares regression (PGLS) was used to incorporate phylogenetic relatedness into statistical analyses (Grafen, 1989; Pagel & Meade, 2006; Pagel, 1997). Phylogenetic signal (λ) was estimated by maximum likelihood, where 0=minimum and 1=maximum (Pagel, 1999). All analyses were run in R, using the 'caper' package (Orme et al., 2011; R Core Team, 2013). All analyses were run using single consensus dated phylogenies, downloaded from 10kTrees (version 3, Arnold et al. 2010, 10ktrees.fas.harvard.edu).

5.2.2. *Data sources*

Data on tactical deception, based on a survey of primatologists' observations, were obtained from Byrne & Whiten (1990). Data on innovation, based on a survey of primate literature, were obtained from Reader et al. (2011). Both data on tactical deception and innovation included zero values, which indicate that no reports of tactical deception or innovation were recorded for that species, despite its inclusion in the search methods employed by Byrne & Whiten (1990) and Reader et al. (2011). A measure of research effort - the number of articles published per species in *The Zoological Record* from 1993 to 2001 – was obtained from Reader et al. (2011). For a sub-set of the data on tactical deception and innovation, the sex of the focal individual had been recorded by the authors, allowing for the estimation of rates of tactical deception and innovation in males and females specifically. A species was coded as zero for one sex if there were no reports of deception or innovation for that sex, despite there being reports of deception or innovation for the other sex. For the tactical deception data, I coded the sex of the focal individual from the reports in the original database (Byrne & Whiten 1990). In some reports, pairs of individuals were involved in deceptive behaviour, for example in the case of 'sneak' mating. In this case, the report was coded according to the sex of the individual who was reported to have initiated the interaction. In a few cases where both parties were implicated equally, one report of deception was counted for each sex. For the innovation data, I obtained the sex of the focal individual from additional data provided by the lead author (Reader et al. 2011).

g_{s1} – a composite measure of general intelligence estimated from the rates of social learning, innovation, tool use, extractive foraging and tactical deception across primate species – was not taken directly from Reader et al. (2011) but was estimated using data from Reader et al. (2011) using a phylogenetic principal components analysis (PPCA) in the R package *PhyTools* (Revell, 2011). The same method for estimating g_{s1} was employed as by the original authors, except that phylogeny was incorporated into analyses using phylogenetic signal (λ) estimated by maximum likelihood, rather than by using independent contrasts. 'Reduced' versions of the counts of the behaviours from the Reader et al. (2011) dataset were used for the PPCA, where the authors had excluded reports coded as more than one behaviour type, such as 'innovative tool use', to reduce autocorrelation between the variables. Prior to the PPCA, I corrected each of the behavioural variables for research effort by extracting standardised residuals from a phylogenetic generalised least squares (PGLS) regression, where research effort was the predictor variable. The PPCA extracted a single component, which explained 69% of the variance in the data, onto which all variables loaded, with loadings ranging from 0.78 to 0.86. Species loadings on the first principal component were then taken as g_{s1} (n=190).

Data on measures of intra-sexual competition and species-typical mating systems were obtained from secondary datasets. Data on testes mass were sourced primarily from Harcourt, et al., (1995), with additional data from Dixson (1998), Dunham & Rudolf (2009) and Lemaitre et al., (2009). Male and female body masses were sourced primarily from Smith & Jungers (1997), with additional data from Plavcan & Ruff (2008). Body mass dimorphism was estimated by taking standardised residuals from a PGLS regression of female body mass on male body mass (Ranta et al. 1994). Data on species-typical mating systems were sourced primarily from Lindenfors & Tullberg (1998), with additional data from Dixson (1987), Dixson (1998), Harcourt, et al. (1995), Hrdy & Whitten (1987) and Weckerly (1998). Data on social group size were obtained from the PanTheria online database (Jones et al., 2009, http://esapubs.org/archive/ecol/e090/184/).

Data on species-typical mating systems were coded as a three level factor as follows: monogamous (MG), polygynous (PG) and multi-male, multi-female (MMMF). Polyandrous species were excluded from analyses as predictions were not made regarding tactical deception, innovation and g_{s1} in these species. Disagreements between sources on the typical mating system for a given species were resolved by 'majority vote'. Intra-species variation in mating systems (e.g. as in Hanuman langurs, *Semnopithecus entellus*) was addressed by running analyses involving mating system using two alternative classification systems – one where such species were coded as the more promiscuous mating system ('up-coded' e.g. MMMF rather than PG), and one where mixed species were coded as the less promiscuous mating system ('down-coded' e.g. PG rather than MMMF). Two species were so varied in their classification that they could not be resolved into a single classification (*Avahi laniger* and *Variecia variegata variegata),* and were excluded from the analyses. See Appendix C for the complete dataset used for analyses included in the current chapter.

5.2.3 *Regression models, diagnostics and model comparison*

All continuous variables were ln-transformed to correct for right skew. See Appendix F.vii for comparison of distributions of ln-transformed versus untransformed data. Mating system was coded as a dummy variable. Multiple regression models were used to examine the effect of the measures of intra-sexual competition or mating system on the measures of cognitive abilities, controlling for research effort and body mass (where appropriate) by including them as co-variates. For analyses involving $g_{s1,}$ research effort was not included as a co-variate as g_{s1} was already corrected for research effort. All analyses involving testes mass as the independent variable controlled for body mass by including body mass as a co-variate. In order to investigate whether social group size confounded any associations between variables, models were compared with and without the inclusion of group size as an additional predictor. All analyses were checked for outliers, where outliers were determined *a priori* to be those with standardised residuals of >3 (+/-). Where outliers were discovered, analyses were repeated without the outlying species. Main effects were investigated by comparing models with and without the inclusion of a variable of interest. Model fit was compared using Akaike's Information Criterion (AIC), using the convention that a difference of >2 AIC units is taken as significant support for the model with the lower AIC value. Where relationships between predictors appeared to be exponential, models fitting exponential regression curves were compared to models fitting linear regression coefficients, and exponential regression coefficients used where model fit was improved. For analyses involving mating system, parameters were averaged across results using alternative classification schemes for mating system. Model parameters for analyses included in the current chapter are reported in full in Appendix F.

5.3 Results

5.3.1 *Testes mass and tactical deception rate*

Using an exponential curve for testes mass, testes mass was a significant predictor of both deception rate overall (β=0.02, p<0.001, model R^2=0.73, λ=0, n=31, **Figure 5.1a**) and deception rate in males only (β=0.02, p=0.009, model R^2=0.73, λ=0, n=19, **Figure 5.1b**). Models where testes mass was fitted as an exponential predictor fitted the data significantly better than models in which testes mass was fitted as a linear predictor (>8 AIC units lower). No outliers were identified. Testes mass did not predict deception in females only (p=0.7, n=19).

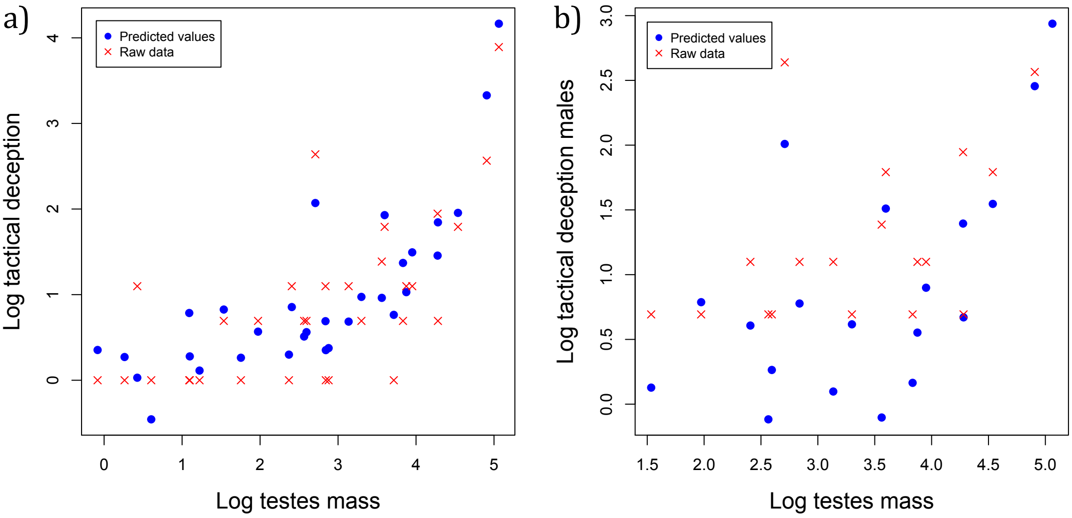


Figure. 5.1 *predicted values and raw data for a) log tactical deception rate overall and b) log tactical deception rate in males only, from the PGLS model including log testes mass, log body mass and log research effort as predictors. When fitted as an exponential curve, testes mass significantly predicted tactical deception rate both overall and in males only.*

When social group size and testes mass were both entered as exponential predictors of tactical deception in the same model, only testes mass was a significant predictor of tactical deception rate overall (β=0.02, p=0.003, model R^2=0.72, λ=0, n=29). No outliers were identified. Removing group size as a predictor of tactical deception improved model fit (3.4 AIC units lower). See Appendix F.i for full model parameters.

5.3.2 *Testes mass and innovation rate*

Using an exponential curve for testes mass, testes mass was a significant predictor of innovation rate overall (β=0.02, p<0.001, model R^2=0.60, λ=0, n=68, **Figure 5.2a**) and innovation in males only (β=0.02, p<0.001, model R^2=0.75, λ=0, n=24, **Figure 5.2b**). Models where testes mass was fitted as an exponential predictor fitted the data significantly better than models in which testes mass was fitted as a linear predictor (>10 AIC units lower). No outliers were identified. Testes mass did not predict innovation in females only (p=0.4).

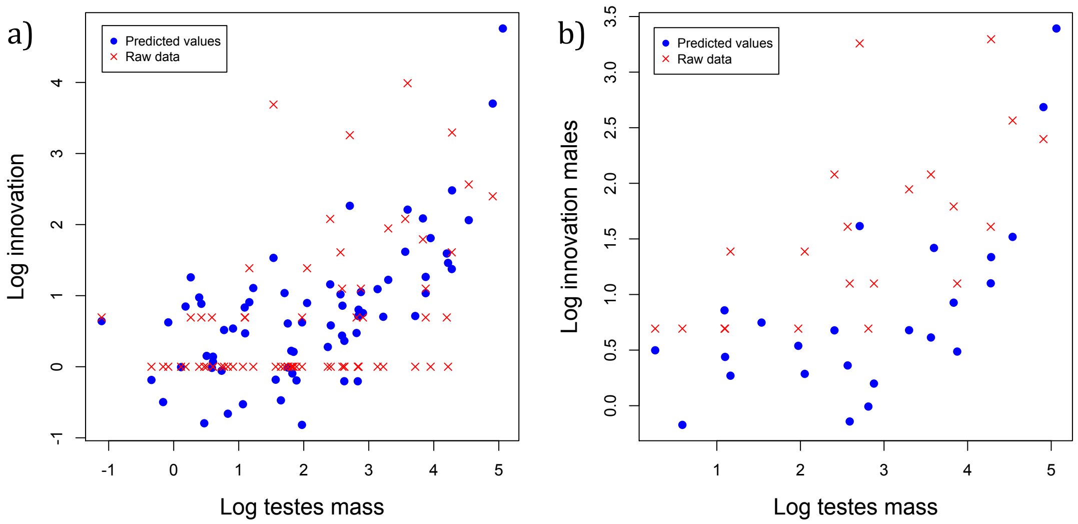


Figure. 5.2 *predicted values and raw data for a) log innovation rate overall and b) log innovation rate in males only, from the PGLS model including log testes mass, log body mass and log research effort as predictors. When fitted as an exponential curve, testes mass significantly predicted innovation rate both overall and in males only.*

When social group size and testes mass were both entered as exponential predictors of innovation in the same model, only testes mass was a significant predictor of innovation rate overall (β=0.02, p=0.003, model R^2=0.60, λ=0, n=66). Results were not affected by removal of an outlier (*Cebus apella*). Removing group size as a predictor of innovation improved model fit (2.7 AIC units lower). The effects of both testes mass and group size on tactical deception and innovation in males and females only were not investigated due to small sample sizes and over-parameterization. See Appendix F.ii for full model parameters.

5.3.3 *Testes mass and g_{s1}*

Using an exponential curve for testes mass, testes mass was a significant predictor of g_{s1} (β=0.09, p<0.001, model R^2=0.57, λ=0, n=68, **Figure 5.3**). Models where testes mass was fitted as an exponential predictor fitted the data significantly better than models in which testes mass was fitted as a linear predictor (>30 AIC units lower). Results were not affected by removal of outliers (*Pongo pygmaeus* and *Cebus apella*). When social group size and testes mass were both entered as exponential predictors of g_{s1} in the same model, only testes mass was a significant predictor of innovation rate overall (β=0.09, p<0.001, model R^2=0.66, λ=0, n=64). Results were not affected by removal of an outlier (*Pan troglodytes*). Removing group size as a predictor of innovation did not significantly affect model fit (<2 AIC units greater). See Appendix F.iii for full model parameters.

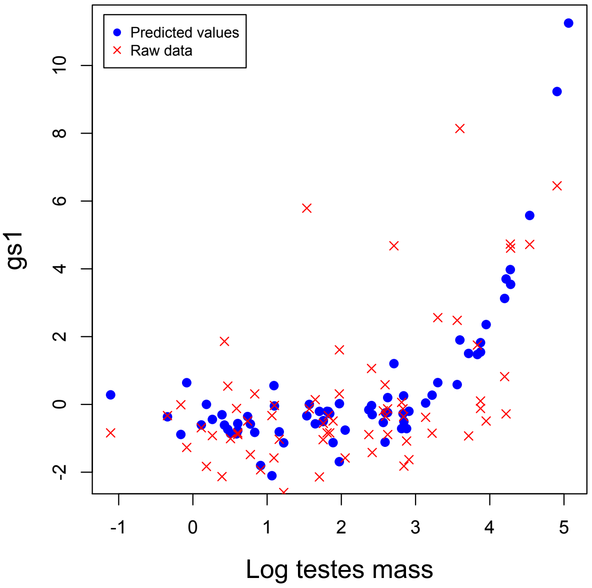


***Figure.* 5.3** *predicted values and raw data for g_{s1} from the PGLS model, including log testes mass and log body mass as predictors. When fitted as an exponential curve, testes mass significantly predicted g_{s1}*

5.3.4 *Body mass dimorphism*

Body mass dimorphism did not predict tactical deception, innovation or g_{s1} when fitted as a linear predictor (*ps*>0.1). Fitting body mass as an exponential predictor did not significantly improve model fit in any analysis (<2 AIC units difference). See Appendix F.iv for full model parameters.

5.3.5 *Mating system and tactical deception rate*

There was a main effect of mating system on tactical deception rate overall – i.e. a model predicting tactical deception rate from mating system and research effort fit the data significantly better than a model predicting tactical deception rate from research effort only (>2 AIC units lower), regardless of coding scheme used for mating system and whether or not chimpanzees (identified as an outlier) were removed from the analysis. Tactical deception rate was significantly greater in multi-male, multi-female than both monogamous species (p=0.02, n=41) and polygynous species (p=0.02) regardless of coding scheme used for mating system and whether or not chimpanzees were removed from the analysis (**Figure 5.4,** model R^2=0.16, λ=0.87, *n*=41). Tactical deception rate was not significantly greater in polygynous than monogamous species (*ps*>0.15).

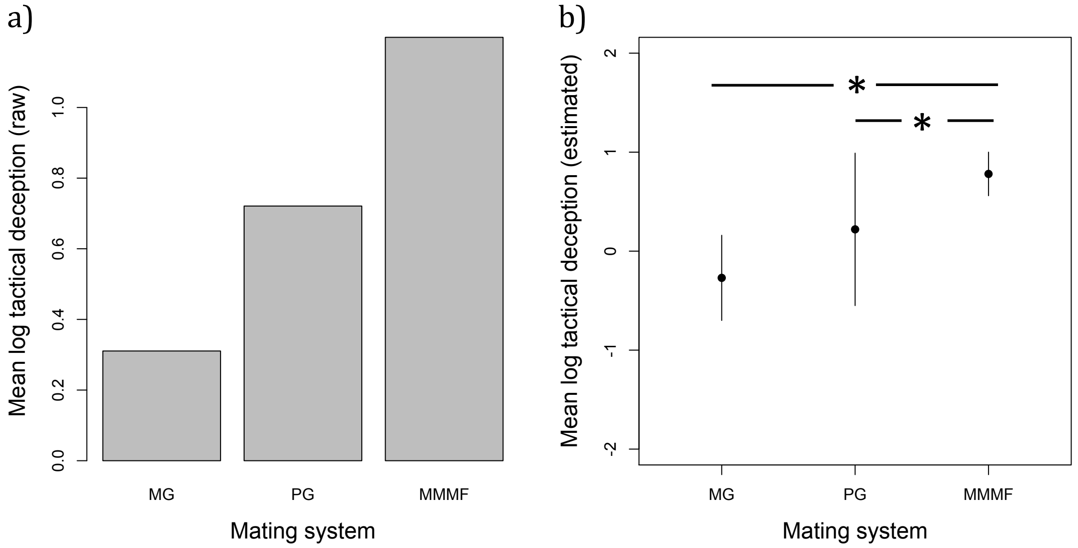


Figure. 5.4 *a) mean tactical deception rate from raw data and b) estimated mean tactical deception rate from the PGLS model, including mating system and research effort as predictors. Bars represent standard error, asterisks indicate p<0.05. Results are presented using the 'down-coded' version of mating system but did not differ between classification schemes.*

Although it appeared that the effect of mating system on tactical deception rate was due to variation in tactical deception rate in males rather than females **(Figure 5.5b)**, there was no main effect of mating system on tactical deception rate in either males or females only, i.e. a model using mating system and research effort to predict tactical deception rate in males or females only did not fit the data better than a model using only research effort to predict tactical deception rate in males or females only (<2 AIC units difference).

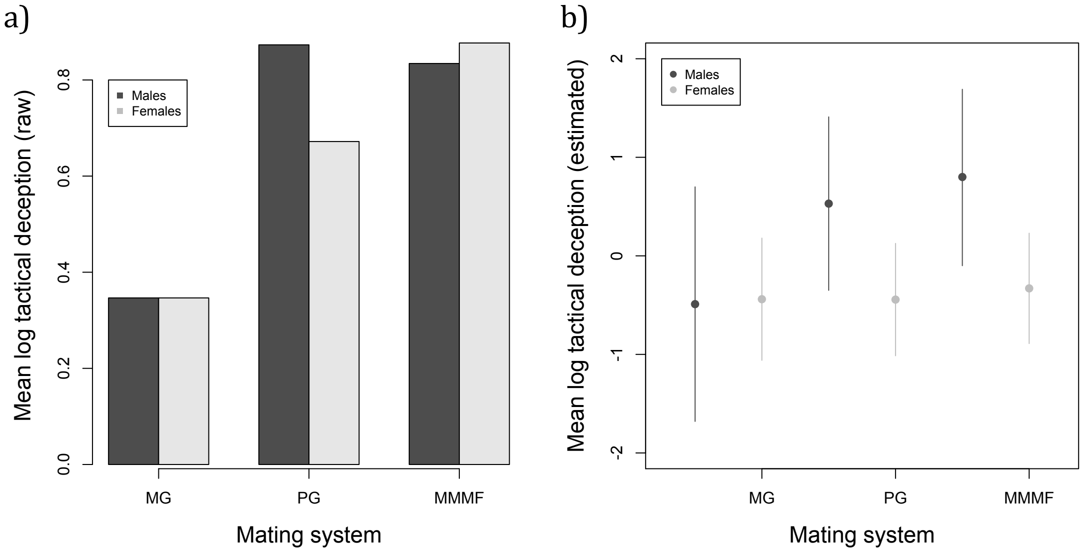


Figure. 5.5 *a) mean tactical deception rate for males and females from raw data and b) estimated mean tactical deception rate for males and females from the PGLS model, including mating system and research effort as predictors of tactical deception rate in males and females. Bars represent standard error. Results are presented using the 'down-coded' version of mating system.*

When both mating system and social group size were entered as predictors of tactical deception rate in the same model, no significant differences in tactical deception rate between mating system types remained (*ps*>0.09). However, group size itself was not a significant predictor of tactical deception rate in this model (*ps*>0.7). Group size and mating system co-varied, where group sizes were significantly larger in multi-male, multi-female than either polygynous or monogamous species (*ps*<0.001), and therefore independent effects of mating system and group size on tactical deception were not detectable. See Appendix F.v for full model parameters.

5.3.6 *Mating system and innovation rate*

There was no significant main effect of mating system on innovation rate overall, innovation rate in males only or innovation rate in females only, for either classifications of mating system i.e. a model using mating system and research effort to predict innovation rate did not differ significantly better than a model using only research effort to predict innovation rate (<2 AIC units difference).

5.3.7 *Mating system and* g_{s1}

There was no main effect of mating system on g_{s1}, i.e. a model including mating system as a predictor of g_{s1} did not fit the data better than a model including only the intercept as a predictor of g_{s1}. (<2 AIC units difference).

5.4 Discussion

Across primates, tactical deception rate, innovation rate and g_{s1} are positively associated with relative testes mass, a measure of sperm competition. Testes mass also predicted rates of tactical deception and innovation in males only, but not in females only. The associations between tactical deception rate, innovation rate and g_{s1} were robust to removal of outliers and were not confounded by social group size. Tactical deception rates differed between mating systems, such that species with multi-male, multi-female mating systems had higher rates of tactical deception than species with either polygynous or monogamous mating systems. The difference in tactical deception rate between mating systems appeared to be driven by differences in male rather than female deception rate, although the effect of mating system was not significant when data were analysed for each sex separately. Together, the results support the hypothesis that intra-sexual competition between males, where the ability of males to monopolise females is limited, has favoured the evolution of 'strategic' mating behaviour such as ‘sneak mating’, underpinned by increases in general cognitive abilities in some primate lineages, including the ability to employ deception and innovation. The results also support the idea that sperm competition may select for increased cognitive abilities due to the advantages of the ability to estimate competition intensity accurately and optimally invest mating effort (Shifferman, 2012). Furthermore, the results are consistent with the previous finding that relative brain size is largest in primate species with the most promiscuous mating systems (Shultz & Dunbar, 2007), and may help to explain why brain size has increased in primate lineages with an evolutionary history of promiscuous mating systems, such as chimpanzees and baboons.

Body mass dimorphism failed to predict tactical deception rate, innovation rate and g_{s1}. Therefore, there is little evidence that increased cognitive abilities in primates co-evolved with intra-sexual competition in the form of male-male competition for monopolisation of groups of females, as in gorillas, for example. Although tactical deception rates were greater in polygynous than monogamous species, this difference was not significant. Together, these results suggest that where males are able to monopolise females, there may be less opportunity for selection for alternative mating strategies such as ‘sneak’ mating. Rather, males in polygynous species instead may be primarily selected for traits that increase their competitive ability in aggressive interactions, such as enlarged body size, canine size and aggressive display behaviour. The lack of associations between body size dimorphism and tactical deception rate, innovation rate and g_{s1} contrast with a previous comparative analysis which suggested that relative neocortex volume was positively associated with body mass dimorphism (Sawaguchi, 1997). The discrepancy between the current results and the previous analysis may be accounted for by differences in study methodology, particularly the lack of control for phylogenetic non-independence in the prior study, which can result in increased risk of type I error (Carvalho et al., 2006).

Testes mass did not predict tactical deception rate and innovation rate in females, and tactical deception rate in females did not appear to differ between mating systems. Therefore, intra-sexual competition between males seems to account largely for increases in the ability to employ tactical deception and innovation in some primate lineages. Consistent with this result, there are more reports of innovation in male primates, and fewer in females primates, than expected from typical group compositions (Reader & Laland, 2001). However, the effect of intra-sexual competition on cognitive abilities in primates is unlikely to be limited to males. Testes mass was associated with g_{s1}, and overall rates of tactical deception and innovation, which are based on reports of the behaviour of both males and females, including many reports of females engaging in 'sneak mating' (Byrne & Whiten, 1990). Further, female mating behaviour in primates may be less well reported than male mating behaviour, due to the use of more subtle mating strategies than males, or historical assumptions of female passivity in mating behaviour (Drea, 2005; Hrdy, 1997). Although the analyses account for broad differences in research effort between species by including a measures of research effort as a co-variate, there may remain more subtle biases in the interpretation of behaviour of male and female animals (Karlsson Green & Madjidian, 2011) that are harder to account for in comparative analyses.

The results are broadly supportive of the 'social intelligence' hypothesis, which holds that increased brain size and cognitive abilities in primates co-evolved with social complexity, including the use of 'Machiavellian' behaviours such as tactical deception (Dunbar, 1998; Whiten & Byrne, 1988). However, the finding that testes mass appeared to be a stronger predictor of tactical deception rate, innovation rate and g_{s1} than group size demonstrates that mating strategies may be a more important component of 'social intelligence' in primates than previously thought, as proponents of the social intelligence hypothesis have typically argued that the complexity of multiple stable social relationships is the primary driver of increased primate brain size and intelligence (Shultz & Dunbar, 2007; Whiten & Byrne, 1997). Primates are distinctive not only for their large, stable social groups involving complex social bonds between multiple individuals, but also for the occurrence in some species of intense intra-sexual competition within stable social groups, rather than within temporary aggregations such as leks, which are common in other taxonomic groups (e.g. birds, ungulates: Shultz & Dunbar, 2007). The rarity of the combination of stable social groups and intense competition for mates in vertebrates outside of primates may help to explain why previous comparative analyses of non-primate taxa have typically reported little evidence for the hypothesis that intra-sexual competition favours increased brain size (e.g. bats: Pitnick et al., 2006, birds: Emery et al. 2007; carnivores and ungulates: Shultz & Dunbar, 2007). However, the results of a previous comparative analysis, which found no relationship between overall brain size and testes mass across primate species (Lemaitre et al., 2009), suggests that further analyses are required to investigate whether sexual selection pressures are related to neurological in addition to behavioural measures of cognitive traits in primates.

The current analyses are affected by two common limitations of comparative analyses: confounding variables and data quality (Nunn, 2011). First, although testes mass predicted tactical deception rate, innovation rate and g_{s1} independently of social group size, the effect of mating systems on tactical deception rate was confounded by social group size. Where predictors co-vary, as is the case for social group size and mating systems in primates, comparative analyses may not be able to detect independent effects of predictors. Second, the current analyses used measures of cognitive ability derived from the frequency of reports of behaviours in academic literature, known as the 'taxonomic count' approach (Lefebvre, 2011). Although general biases in research effort can be statistically controlled, more subtle biases such as anthropocentrism in interpretation of primate behaviour may persist (Healy & Rowe, 2007). However, the compensatory advantages of the 'taxonomic count' approach over alternatives, such as comparison of species on laboratory based cognitive tasks, include larger sample sizes, and potentially more naturalistic behavioural measures (Reader & Laland, 2002). In future, the 'taxonomic counts' approach could be applied to taxonomic groups for whom anthropomorphic research biases are less likely to affect measures of cognitive traits. For example, fishes could be a suitable group to further investigate the hypothesis that intra-sexual competition may favour increased cognitive abilities, particularly as some species exhibit strategic responses to sperm competition, such switching mate preferences in the presence of dominant rivals (e.g. Bierbach et al., 2011).

The current results suggest that the evolution of increased cognitive abilities in some primate lineages can partly be explained by selection for strategic mating behaviour, underpinned by general cognitive abilities including the ability to employ tactical deception and innovation. As an illustration, within the apes, chimpanzees, characterised by high sperm competition and promiscuous mating, have higher scores for tactical deception, innovation and g_{s1} than gorillas, characterised by competition between males for monopolisation of females, who in turn have higher scores than monogamous gibbons (Reader et al., 2011). The results contribute to a growing body of work showing that sexual selection affects cognitive as well as physical traits (reviewed in Boogert et al., 2011). These analyses, however, are the first demonstration that intra-sexual competition is positively related to measures of cognitive ability across primate species, without using brain size as a proxy measure of cognitive traits. The results add to many existing socio-ecological correlates of primate cognitive abilities (Healy & Rowe, 2007), but many authors now recognise that a plurality of selection pressures is likely to have lead to enhanced cognitive abilities and enlarged brain size in primates rather than any single definitive variable (Barton, 2012; Shultz & Dunbar, 2007).

Chapter 6: Evolution of brain size, general cognitive abilities and culture in primates

6.1 Introduction

Despite a great deal of research interest into the evolutionary explanations for variation in brain size, cognitive abilities and reliance on culturally transmitted behaviour across primate species, fundamental issues remain unresolved. In particular, questions remain concerning first, the relationships between brain size, cognitive abilities and reliance on culture across species; and second, the evolutionary explanations for variation in brain size, cognitive abilities and culture across species. Until recently, comparative studies have typically used measures of brain size as proxy measures for cognitive traits. However, Reader et al.'s (2011) cross-species dataset, consisting of estimated rates of behaviour such as social learning, innovation and tool use, allows for comparative analyses of more direct estimates of cognitive and behavioural traits, including measures of general cognitive abilities and reliance on culturally transmitted behaviour (Reader & Laland, 2002; Reader et al., 2011). In this chapter, I investigate, first, relationships between measures of brain size and a measure of general cognitive abilities (g_{s1}), social learning rate and innovation rate, from Reader et al. (2011). Second, I evaluate hypotheses for increased brain size, general cognitive abilities and reliance on culture in primates, by investigating multiple predictors of brain size, g_{s1}, social learning rate and innovation rate across species.

6.1.1 Enlarged brain size in primates

Brain size in extant non-human primates ranges from ~3g in fat-tailed dwarf lemurs to ~460g in gorillas (Navarrete, n.d.). Overall brain size has increased in several primate lineages (Striedter, 2005), largely due to disproportionate increases in neocortex size, which comprises ~50-80% of total brain volume (Dunbar, 1998; Finlay & Darlington, 1995; Rilling & Insel, 1999). Most simply, brain size can be measured in absolute terms, but because brain size is strongly correlated with body size across species (Barton, 2006), comparative analyses more often investigate variation in brain size relative to body size (e.g. Fish & Lockwood, 2003; Shultz & Dunbar, 2007). Alternatively, many comparative studies of primates address the large expansion of the neocortex, either in absolute terms, relative to brain volume or relative to both brain volume and body mass (e.g. Barton, 1996; Byrne & Corp, 2004). More recently, comparative analyses have also investigated variation in cerebellum size, which has expanded in primate evolution in concert with the neocortex (Barton, 2012). Divergent measures of brain size may capture variation in a common underlying dimension of size

(Finlay & Darlington, 1995), or, where there have been mosaic increases in brain regions, the results and interpretation of comparative analyses may differ according to the specific measure of brain size employed (Barton & Harvey, 2000; Deaner et al., 2000; Dunbar & Shultz, 2007b).

6.1.2 Co-variation of brain size and cognitive abilities

Typically, comparative analyses of brain evolution have used brain size as a proxy for cognitive abilities (Deaner et al., 2007; Lefebvre et al., 2004). For example, neocortex size has been assumed to reflect “problem solving” and “reasoning” abilities (e.g. Dunbar, 1998; Joffe & Dunbar, 1997). While the cognitive abilities of insects, such as abstract concept formation in honeybees, challenge simplistic assumptions about the relationship between brain size and cognition (Giurfa et al., 2001, Chittka & Niven, 2009), enlarged brain size may reflect neuro-anatomical features that more meaningfully correspond to increased cognitive abilities, such as absolute increases in number of neurons (Barton, 2006; Barton, 2012). Increases in overall brain size may reflect increased general ‘intelligence’, defined as domain-general learning ability, including mental abstraction and behavioural flexibility (Reader et al., 2011; Roth & Dicke, 2005b). In primates, whole brain volume and neocortex volume co-vary with a composite measure of performance on laboratory-based cognitive tasks (Deaner et al., 2007), and neocortex volume co-varies with a composite estimate of general intelligence derived from the rates of behaviours such as tool use and innovation (g_{s1}, Reader et al., 2011). However, some researchers argue that cross-species variation in cognition is better understood as species-specific cognitive adaptations, rather than variation in a one-dimensional measure of ‘intelligence’ (e.g. Barton, 2012; Shettleworth, 1998).

6.1.3 Co-variation of brain size, cognitive abilities and culture

Enlarged brain size, increased cognitive abilities and reliance on culture, defined as behaviour acquired through social learning and social transmission (Laland & Hoppitt, 2003), appear to have co-evolved in multiple independent vertebrate lineages, including species of primates, cetaceans and birds (Emery & Clayton, 2004; Marino, 2002). Within primates, social learning and innovation rates co-vary with each other, with tool use rate, and with measures of ‘executive brain’ (neocortex and striatum) volume, further suggestive of a single component underlying brain size, general cognitive abilities and culture (Reader et al., 2011; Reader & Laland, 2002). Such associations suggest that enlarged brains and increased cognitive abilities allow for an increased ability to acquire and retain socially transmitted behaviour (Reader et al., 2011; Whiten & van Schaik, 2007). Although smaller-brained species, including insects, are capable of social learning (e.g. Mery et al., 2009, Leadbeater & Chittka, 2007), and innovation has been observed in smaller-brained primates such as ring-tailed lemurs (Hosey et al., 1997), larger-brained species may be capable of more complex, efficient and higher fidelity methods of social learning, supporting the spread of innovations (Reader & Laland, 2002; Whiten & van Schaik, 2007).

6.1.4 Hypotheses for increased brain size and cognitive abilities

Several hypotheses have been proposed for the evolution of enlarged brain size and increased cognitive abilities in primates, which make distinct predictions regarding correlations between brain size and cognitive traits across species (**Table 6.1**). The most prominent hypotheses can be briefly summarised as follows. The 'social intelligence' hypothesis argues that increased brain size and cognitive abilities in primates is related to social complexity (Dunbar, 1998; Whiten & Byrne, 1988). The 'foraging intelligence' hypothesis proposes that foraging behaviours such as extraction, reliance on patchily distributed foods, and dietary generalism select for increased brain size and cognitive abilities (Clutton-Brock & Harvey, 1980; Gibson, 1986; Parker & Gibson, 1977). The 'environmental variation' hypothesis argues that climatic fluctuations select for increased brain size and behavioural flexibility (Potts, 1998; Richerson et al. 2005; Richerson & Boyd, 2000). The 'life history length' hypothesis argues that extended life history co-evolved with increased brain size and cognitive abilities due to selection for an increased learning period (Joffe, 1997; Kaplan et al. 2000). Alternatively, however, extended life history and large adult brain size may have co-evolved due to developmental constraints rather than the need for an extended learning period, in that producing offspring with larger, energetically costly brains requires a longer gestation (Barton & Capellini, 2011) and spreading reproduction more widely over the lifespan (Isler & van Schaik, 2009), resulting in a slower life history overall. Finally, the related 'cultural intelligence' hypothesis argues that reliance on culturally transmitted behaviour is both a cause and a consequence of enlarged brain size and general cognitive abilities (Boyd & Richerson, 1985; Reader & Laland, 2002; Whiten & van Schaik, 2007; Wilson, 1985). The preceding hypotheses are not necessarily mutually exclusive, rather, multiple selection pressures may have favoured the evolution of enlarged brains and increased cognitive abilities in primates (Barton, 2012).

Hypothesis	Corresponding predictor variable	Example of associated reference
Social intelligence	Group size	Dunbar & Shultz (2007)
Foraging intelligence	% fruit & seeds, diet breadth	Parker & Gibson (1977)
Environmental variation	Latitude range	Richerson & Boyd (2000)
Life history length	Life history length, juvenile period, longevity	Kaplan et al. (2000)
Cultural intelligence	Social learning, innovation	Boyd & Richerson (1985)

***Table 6.1**: summary of hypotheses for increased brain size and cognitive abilities in primates, with associated predictions and references. All predicted associations are positive.*

6.1.5 Hypotheses for increased reliance on culture

Currently, the reasons that certain primate species, such as chimpanzees and capuchins, appear to rely on culture more than others are largely unknown (Reader et al., 2011). However, several social, environmental and life-history variables have been proposed to predict reliance on culture, which overlap with predictors of enlarged brain size and enhanced cognitive abilities, including sociality (Boyd & Richerson, 1985; Derex et al., 2013; Henrich, 2004; Whiten & van Schaik, 2007) complex foraging, including reliance on patchily distributed foods, extraction and dietary generalism (Galef & Giraldeau, 2001; Jaeggi et al., 2010, Overington et al., 2011), environmental variation (Henrich & McElreath, 2003; Potts, 1998; Richerson et al., 2005; Richerson & Boyd, 2000) and slower life histories, including extended juvenile period and/or longevity (Joffe, 1997; Kaplan et al., 2000; Kummer & Goodall, 1985; Reader & Laland, 2001; Whiten & van Schaik, 2007). The ‘cultural intelligence’ hypothesis argues that increased reliance on culture, once established, may become self-reinforcing (Henrich & McElreath, 2003; Reader et al., 2011; Whiten & van Schaik, 2007). Existing comparative analyses, however, report limited evidence for predictors of increased reliance on culture in primates. Group size does not appear to predict social learning or innovation (Reader & Laland, 2002; Reader et al., 2011), measures of foraging complexity predict social learning, but not innovation (Reader et al., 2011), and climatic variation is not associated with innovation rate (Reader & MacDonald, 2003). No associations between life history speed and social learning or innovation rate have yet been published.

6.1.6 Current project

Many predictors of brain size across primates have been identified, including social (e.g. Dunbar, 1998), ecological (e.g. Barton, 1996) and life history (e.g. Joffe, 1997) variables. However, despite existing attempts to provide single, coherent framework for the evolution of brain size in primates (e.g. Barton, 2006; Dunbar & Shultz, 2007b; Reader et al., 2011), important issues remain to be resolved. For example, researchers disagree over the importance of social group size as a driver of the evolution of brain size and intelligence (Dunbar & Shultz, 2007b; Reader et al., 2011). The current chapter attempts to review evidence for current hypotheses and provide a coherent framework for the evolution of enlarged brain size, cognitive abilities and reliance on culture in primates. First, I examine relationships between four measures of brain size (absolute whole brain size, relative whole brain size, relative neocortex size and relative cerebellum size) with (g_{s1}), social learning rate and innovation rate, obtained from Reader et al., (2011). The four brain measurements were chosen in order to investigate whether predictors of brain size applied to variation in a single underlying dimension of brain size, versus increases in specific measures of brain size or specific brain regions. Second, I investigate socio-ecological, environmental and life history predictors of both brain size and g_{s1}, social learning rate and innovation. Further, I use multi-variate analyses to examine relative importance of predictors and whether multiple independent predictors of brain size and cognitive abilities could be identified.

Furthermore, the current analyses attempt to address some methodological concerns typical of comparative analyses of brain size and cognition. Previous comparative analyses of brain size have often used the independent contrasts method to account for phylogenetic non-independence (e.g. Reader & Laland, 2002; Reader et al., 2011). However, cognitive and behavioural traits may exhibit low phylogenetic signal relative to morphological traits (Blomberg et al., 2003; MacLean et al., 2011). The current analyses therefore use the phylogenetic generalised least squares (PGLS) method to estimate phylogenetic signal (Pagel's λ) and scale the influence of phylogeny accordingly. To address concerns about data quality, the current analyses use the largest available species datasets, with social, ecological and life history traits obtained from sources compiled independently of the current project (Jones et al., 2009). Finally, the current analyses explored the possibility of non-linear relationships between variables, not yet investigated by existing comparative analyses (e.g. Reader et al., 2011).

6.2 Methods

6.2.1 Phylogenetic comparative methods

Phylogenetic comparative statistical methods, specifically phylogenetic generalized least squares regressions (PGLS), were used to analyse the data in order to account for phylogenetic non-independence and to incorporate phylogenetic relatedness into statistical analyses (Harvey & Pagel, 1991; Nunn, 2011). Phylogenetic signal (Pagel's λ, where

1=maximum and 0=minimum) was estimated by maximum likelihood for all analyses. Phylogenies were single dated consensus trees, downloaded from the 10kTrees online resource (Arnold et al. 2010). All analyses were run in R (R Core Team, 2013) in the packages “caper” (Orme et al. 2011) and “phytools” (Revell, 2011). All right-skewed variables were natural log-transformed prior to statistical analyses. Species names were matched between phylogenies and datasets using primate taxonomic references (IUCN, 2013; Rowe, 1996).

6.2.2. Brain size

Four measures of brain size were used in statistical analyses: absolute whole brain volume, relative brain volume, relative neocortex size and relative cerebellum size. Relative whole brain volume was estimated by using body size as a co-variate in statistical analyses. Relative neocortex and cerebellum size were estimated by including remaining brain volume (brain volume minus neocortex, or brain volume minus cerebellum, respectively) and body size as co-variates in statistical analyses. Brain volume data were obtained from an unpublished dataset, currently under development within the Laland lab (Navarrete, n.d.). This dataset contains brain specimens obtained from the Primate Brain Bank (PBB) (http://www.primatebrainbank.org), supplemented by specimens from other authors, including Stephan et al. (1981). PBB specimens come from captive animals, preserved post-mortem using sucrose fixation. Magnetic Resonance Images (MRIs) of the specimens were taken at the Utrecht Neuroimaging Centre, Universty of Utrecht, from 2009-2013. Dr Ana Navarrete measured volumes of interest from the MRIs for intact specimens (n=36 species). Each structure was sampled using a minimum of 20 slices. The dataset also includes average body mass from wild species, originally compiled by Isler et al. (2008). There were 1-6 specimens available per species. Where multiple specimens were available for a species, mean values were taken across specimens. All brain structure measures should be taken as approximate measurements of volume, as without stereological cuts, structures cannot be delineated with complete certainty. Data for *Saimiri boliviensis* were excluded due to specimen damage.

6.2.3 g_{s1}, social learning and innovation

A composite measure of general cognitive abilities (g_{s1}), and rates of social learning and innovation were obtained from Reader et al. (2011). A measure of research effort - the number of articles published per species in *The Zoological Record* from 1993 to 2001 – was also obtained from Reader et al. (2011). g_{s1} was not taken directly from Reader et al. (2011) but was estimated from rates of social learning, innovation, tool use, extractive foraging and tactical deception from Reader et al. 2011 using a phylogenetic principal components analysis (PPCA) in the R package "Phytools" (Revell, 2011). The same methods for estimating g_{s1} were used as by the original authors, except that phylogenetic relatedness was accounted for by the PGLS rather than independent contrasts approach. Reader et al.'s (2011) 'reduced' versions of the rates of the behaviours from the Reader dataset were used for the PPCA, where the authors had excluded reports coded as more than one behaviour type, such as 'innovative tool use', to reduce autocorrelation between the variables. Prior to the PPCA, all variables were corrected for research effort by extracting standardised residuals from a phylogenetic generalised least squares (PGLS) regression, where research effort was the predictor variable. Phylogenetic signal (λ) was estimated using maximum likelihood for a single consensus phylogeny. The PPCA extracted a single component, which explained 69% of the variance in the data, onto which all variables loaded in the same direction, with loadings ranging from 0.78 to 0.86. Scores for the first principal component were then taken as g_{s1} (n=190).

6.2.4 Socio-ecological, environmental and life history variables

Data on social group size, latitude range and life history were obtained from the PanTheria online dataset (Jones et al., 2009). Social group size refers to the typical number of individuals forming stable social associations, in non-captive populations. Latitude range was estimated as maximum latitude minus minimum latitude reported for wild populations. Life history length is a composite measure, estimated from a phylogenetic principal components analysis (PPCA) of six life history variables: gestation length, inter-birth interval, weaning age, age of sexual maturity, age at first birth and maximum longevity. In pairwise PGLS analyses, all life history variables were found to be significantly positively associated ($Ps<0.01$). The PPCA extracted a single component, which explained 64% of the variance, onto which all variables loaded (loadings 0.58-0.90, $\lambda=0.84$). Scores of this component were taken as a composite measure of life history length. Additionally, age of sexual maturity was used as a measure of juvenile period length and maximum longevity as a measure of longevity. Diet breadth data were obtained by request from the lead author of Reader et al. (2011). Diet breadth is the number of food types typically eaten, out of a maximum of 13 different categories (e.g. invertebrates, seeds/nuts, flowers). Percentage of fruit and seeds in the diet was taken from Walker et al. (2006). See Appendix D for the complete dataset used for analyses included in the current chapter.

6.2.5 Regression models

To investigate whether brain size positively co-varied with g_{s1}, social learning and innovation, g_{s1}, social learning and innovation were used as outcome variables, predicted by measures of brain size. To investigate predictors of brain size, measures of brain size were used as outcome variables predicted by socio-ecological, environmental and life history variables. To test the 'cultural intelligence' hypothesis, g_{s1}, social learning and innovation were used as predictors of measures of brain size. To investigate predictors of g_{s1}, social learning and innovation, g_{s1}, social learning and innovation were used as outcome variables predicted by socio-ecological, environmental and life history variables. Where social learning or innovation were outcome variables, research effort was included as a co-variate. Analyses where g_{s1} was the outcome variable did not include research effort as a co-variate, as research effort is already taken into account in the estimation of g_{s1}. Body mass and/or remaining brain volume were included as additional co-variates where appropriate. Results from PGLS models are reported in full in Appendices G and H.

6.2.6 Multi-variate analyses

Where multiple predictors of measures of brain size, g_{s1}, social learning or innovation were identified, multiple predictors were entered into the same statistical model to investigate whether predictors remained significant in multi-variate models and to investigate independence of predictor variables. Composite life history length could not be included as a predictor in models where either juvenile period or maximum longevity were also predictors due to auto-correlation, since composite life history was estimated from the PPCA including both juvenile period and maximum longevity. Similarly, g_{s1} could not be entered as a predictor where social learning or innovation were also predictors, since g_{s1}, is composite measure of variables including social learning and innovation.

6.2.7 Model performance and diagnostics

For all analyses, model performance was checked by visual examination of model residuals and checking for outliers. Outliers in the model residuals were determined *a priori* to be those with standardised residuals of >3 (+/-). Where outliers were discovered, analyses were repeated without the outlying species. Models were compared using Akaike's Information

Criterion (AIC), using the convention that a difference of >2 AIC units is taken as significant support for the model with the lower AIC value. Where relationships between predictors appeared to be exponential, models fitting exponential regression curves were compared to models fitting linear regression slopes. Where exponential regression curves improved model fit, results using exponential regression curves are reported, otherwise, results for linear slopes are reported.

6.3 Results

6.3.1 Brain size and g_{s1}, social learning and innovation

Using exponential curves for measures of brain size, which fit the data significantly better than linear slopes (>5 AIC units lower), absolute brain volume, relative brain volume, relative neocortex volume and relative cerebellum volume all significantly predicted g_{s1}, social learning and innovation (*ps*<0.01, *ns*=61-62, model R^2s=0.56-0.65, λ=0, **Table 6.2, Figure 6.1**). Relationships were not affected by removal of species identified as outliers. See Appendix G.i for full model parameters.

	Absolute brain	**Relative brain**	**Neocortex**	**Cerebellum**
g_{s1}	***	***	***	***
Social learning	***	***	***	**
Innovation	***	***	***	**

***Table 6.2**: Summary table of p-values for exponential relationships between four measures of brain size (absolute whole brain size, relative whole brain size, relative neocortex size and relative cerebellum size) and g_{s1}, social learning and innovation. *** = $p<0.001$, ** = $p<0.01$ and * = $p<0.05$.*

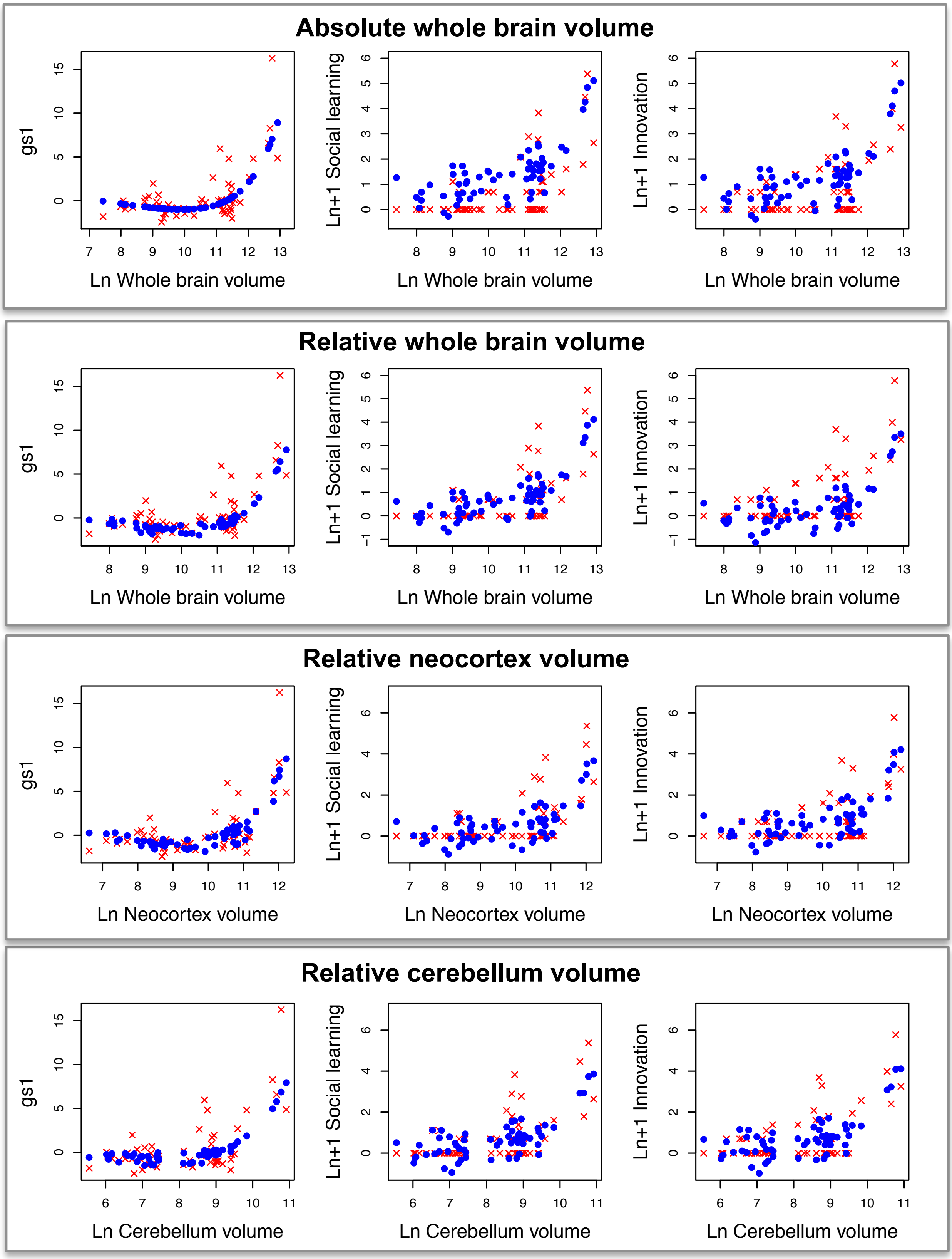


Figure 6.1 *relationships between measures of brain size and* g_{s1}*, social learning and innovation, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01).*

6.3.2 Predictors of brain size, g_{s1}, social learning and innovation

6.3.2.1 Social intelligence

Social group size did not signficantly predict absolute whole brain volume (p=0.13, n=58). Social group size significantly predicted relative brain volume (p=0.002, R^2=0.89, λ=0.93, n=58) and relative neocortex volume (p=0.02, R^2=0.93, λ=0.2, n=58, **Figure 6.2**). Social group size did not predict relative cerebellum volume (p=0.80, n=58) or g_{s1} (p=0.2, n=166). Using exponential curves for group size, which fitted the data significantly better (>3 AIC units) than linear slopes, group size significantly predicted social learning and innovation (ps<0.001, R^2s=0.40-0.42, λ=0, n=168, **Figure 6.2**). Relationships were not affected by removal of outliers. See Appendix G.ii for full model parameters.

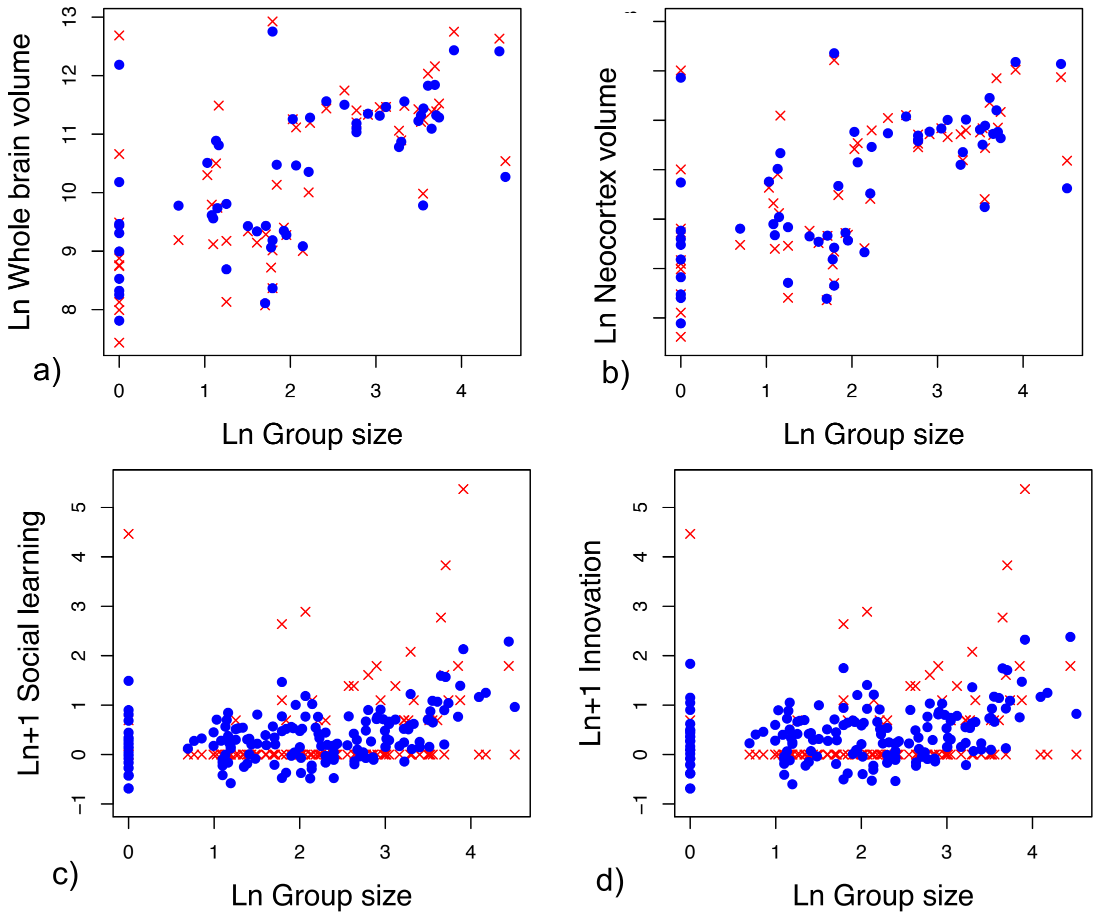


Figure 6.2 *Relationships between social group size and a) relative brain size, b) relative neocortex size, c) social learning and d) innovation, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01).*

6.3.2.2 Foraging intelligence

Percentage of fruit and seeds in the diet did not predict any measure of brain volume, or any measure of cognitive abilities (ps>0.20). Diet breadth did not predict any measure of brain size (ps>0.2). Diet breadth was a weak but significant predictor of g_{s1} (p=0.03, R^2=0.02,

λ=0.85, *n*=165) and a significant predictor of social learning (*p*=0.02, R^2=0.33, λ=0.62, *n*=167) (**Figure 6.3**). Diet breadth did not predict innovation (*p*=0.56, R^2=0.32, λ=0.61, *n*=167). Relationships were not affected by removal of outliers. See Appendix G.iii for full model parameters.

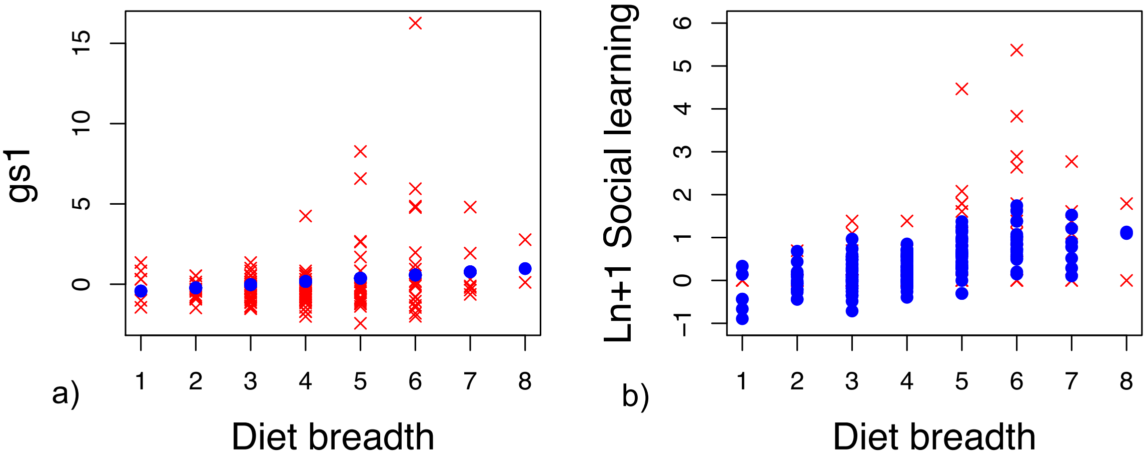


Figure 6.3 *Relationships between diet breadth and* g_{s1} *and social learning, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01).*

6.3.2.3 Environmental variation

Latitude range did not predict any measure of brain volume (*ps*>0.2). Using exponential curves for latitude range, which fitted the data significantly better (>2 AIC units) than linear slopes, latitude range weakly but significantly predicted g_{s1} (*p*=0.02, R^2=0.03, λ=0.85, *n*=174) and social learning (*p*=0.05, R^2=0.29, λ=0.64, *n*=184) and marginally predicted innovation (*p*=0.06, R^2=0.30, λ=0.64, *n*=184) (**Figure 6.4**). Relationships between latitude range and g_{s1} and social learning were not affected by removal of outliers. The relationship between latitude range and innovation became significant with removal of outliers (*p*=0.001, R^2=0.37, λ=0, *n*=180) (**Figure 6.4**). See Appendix G.iv for full model parameters.

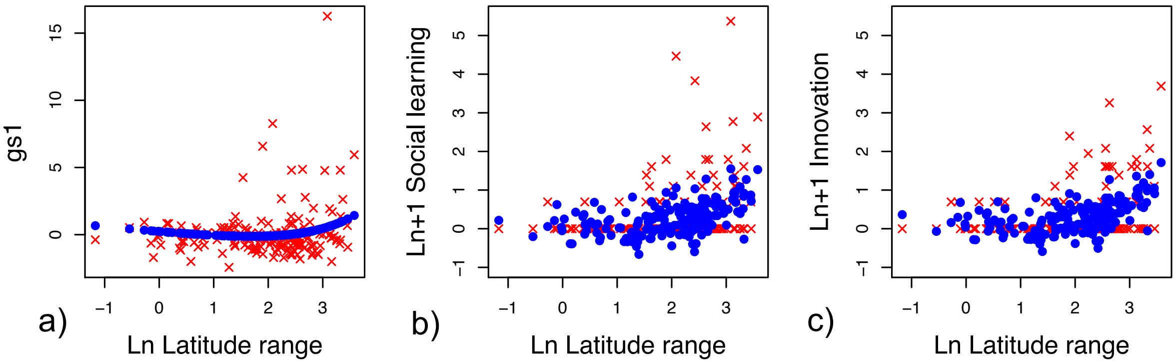


Figure 6.4 *Relationships between latitude range and a)* g_{s1}*, b) social learning and c) innovation, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01). For the association between latitude range and innovation, the relationship was significant only after the removal of four species identified as statistical outliers.*

6.3.2.4 Life history length

Composite life history length significantly predicted absolute brain size ($p<0.001$, $R^2=0.73$, $\lambda=0.58$, $n=47$), relative brain size ($p<0.001$, $R^2=0.94$ $\lambda=0.67$, $n=47$), relative neocortex volume ($p=0.006$, $R^2=0.93$, $\lambda=0.32$, $n=47$) and relative cerebellum volume ($p=0.008$, $R^2=0.96$, $\lambda=0.93$, $n=47$) (**Figure 6.5**).

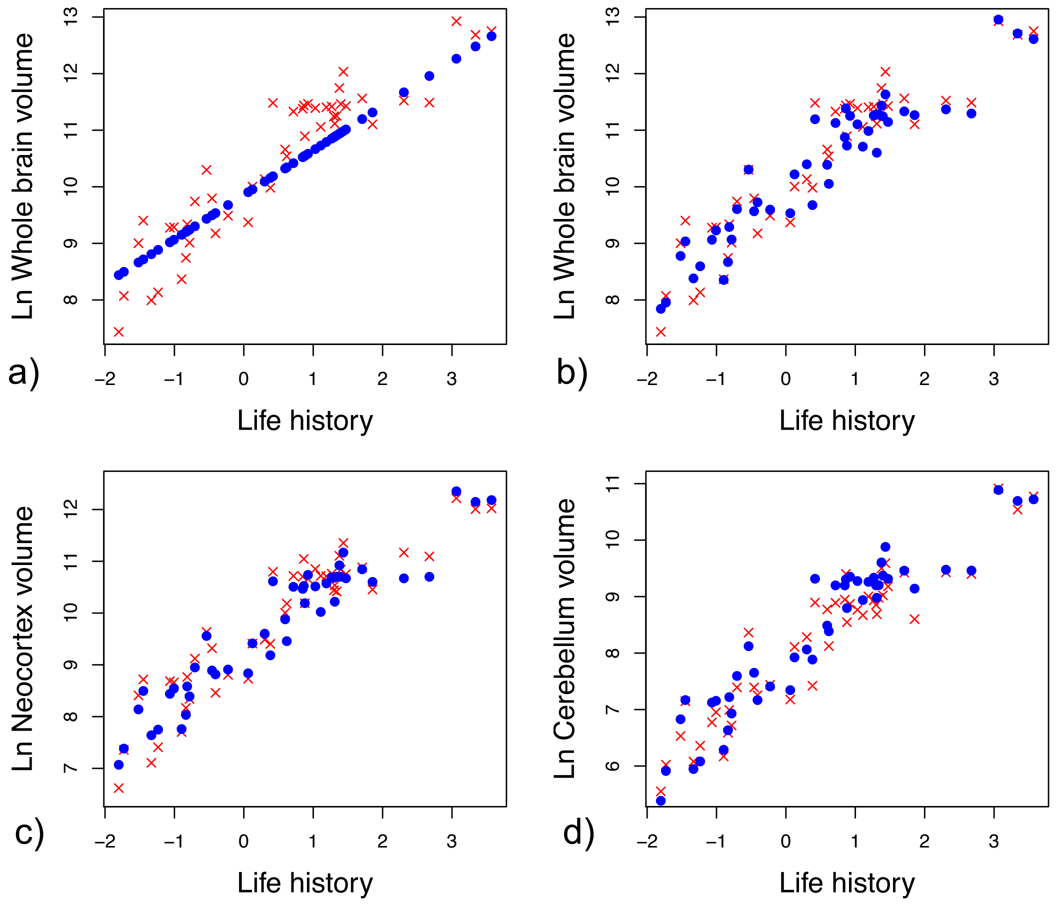


Figure 6.5 *Relationships between the composite measure of life history speed and a) absolute brain volume, b) relative brain volume, c) relative neocortex volume and d) relative cerebellum volume, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01).*

Using exponential curves for composite life history length, which fitted the data significantly better (>10 AIC units) than linear slopes, composite life history length significantly predicted g_{s1}, social learning and innovation *(ps*<0.001, $R^2s=0.51$-0.57, $\lambda=0$, n=74) (**Figure 6.6**). Relationships were robust to removal of outliers and inclusion of body mass, a potentially confounding variable. See Appendix G.v for full model parameters.

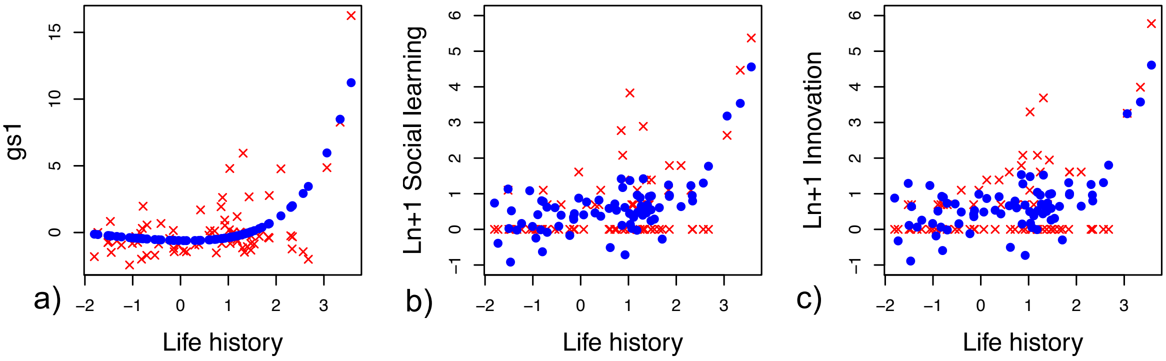


Figure 6.6 *Relationships between the composite measure of life history speed and a)* g_{s1}*, b) social learning and c) innovation, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (*$p<0.01$*).*

Juvenile period length significantly predicted absolute brain volume ($p<0.001$, $R^2=0.84$, $\lambda=0$, $n=53$), relative brain volume ($p=0.003$, $R^2=0.91$, $\lambda=0.87$, $n=53$), relative neocortex volume ($p<0.001$, $R^2=0.95$, $\lambda=0.16$, $n=53$), but did not significantly predict cerebellum volume ($p=0.14$, $n=53$) (**Figure 6.7**). Juvenile period did not predict g_{s1}, ($p=0.7$, n=103) (**Figure 6.8**). Using exponential curves for juvenile period, which fitted the data significantly better (>2 AIC units) than linear slopes, juvenile period significantly predicted social learning (p=0.04, $R^2=0.42$, $\lambda=0$, n=103), and innovation (p=0.02, $R^2=0.43$, $\lambda=0$, n=103) (**Figure 6.8**), but relationships between juvenile period and social learning and innovation were not robust to the removal of outliers, or inclusion of body mass as a co-variate (*ps*>0.1). See Appendix G.v for full model parameters.

Maximum longevity significantly predicted absolute brain volume ($p=0.009$, $R^2=0.12$, $\lambda=1$, $n=56$) and relative whole brain volume ($p=0.002$, $R^2=0.90$, $\lambda=0.93$, $n=56$). Maximum longevity did not predict relative neocortex or cerebellum volume (*ps*>0.15) (**Figure 6.7**). Using an exponential curve for maximum longevity, which fitted the data significantly better (>30 AIC units) than a linear slope maximum longevity significantly predicted g_{s1}, social learning and innovation (*ps*<0.001, $R^2s=0.44\text{-}0.63$, $\lambda=0\text{-}0.08$, $n=117$) (**Figure 6.8**). These relationships were robust to the removal of outliers and the inclusion of body mass as a co-variate. See Appendix G.v for full model parameters.

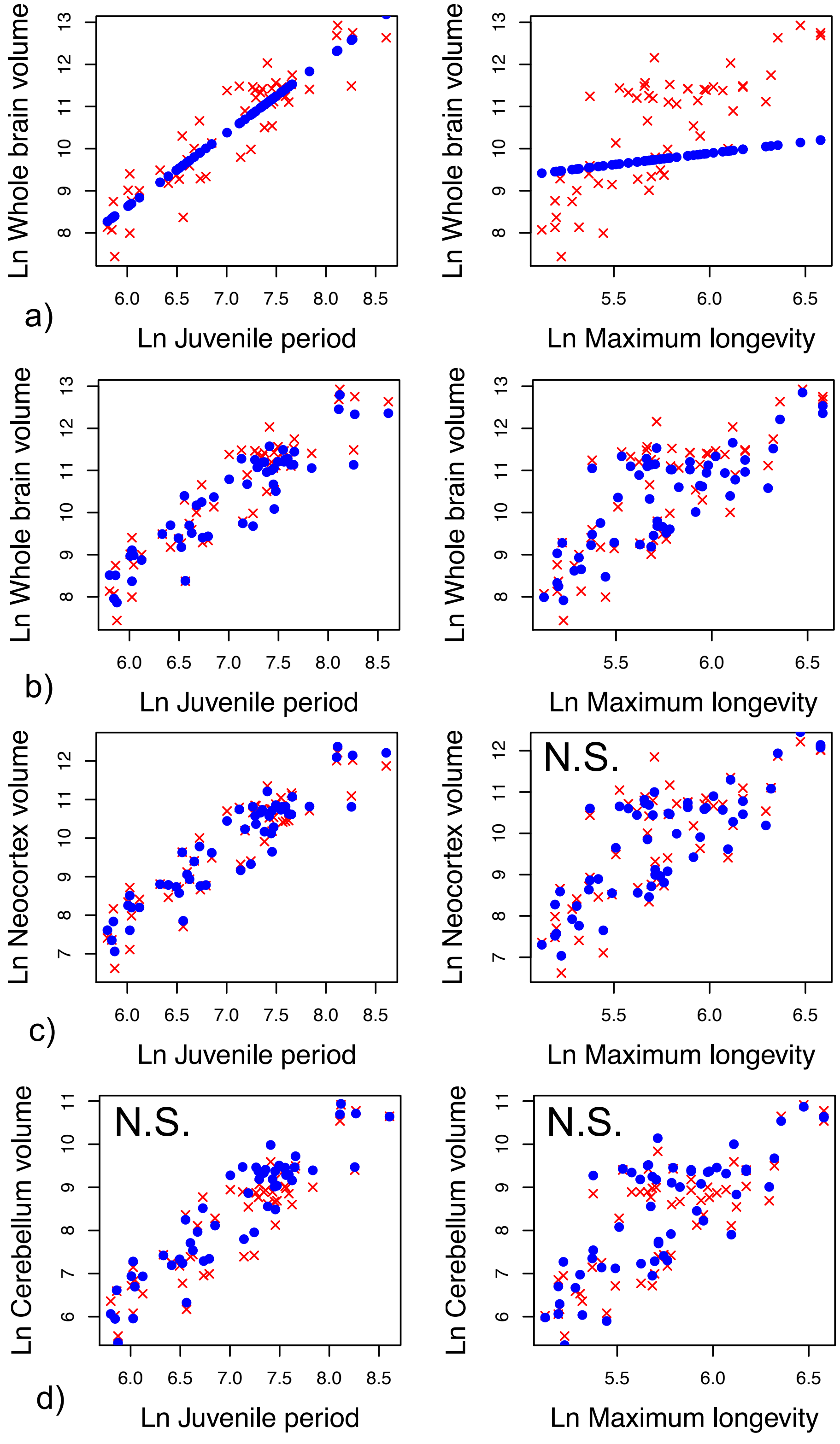


Figure 6.7 *Relationships between juvenile period and maximum longevity and a) absolute brain volume, b) relative brain volume (i.e. body mass included as co-variate), c) relative neocortex volume and d) relative cerebellum volume, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01) unless indicated ('N.S.' =p>0.05).*

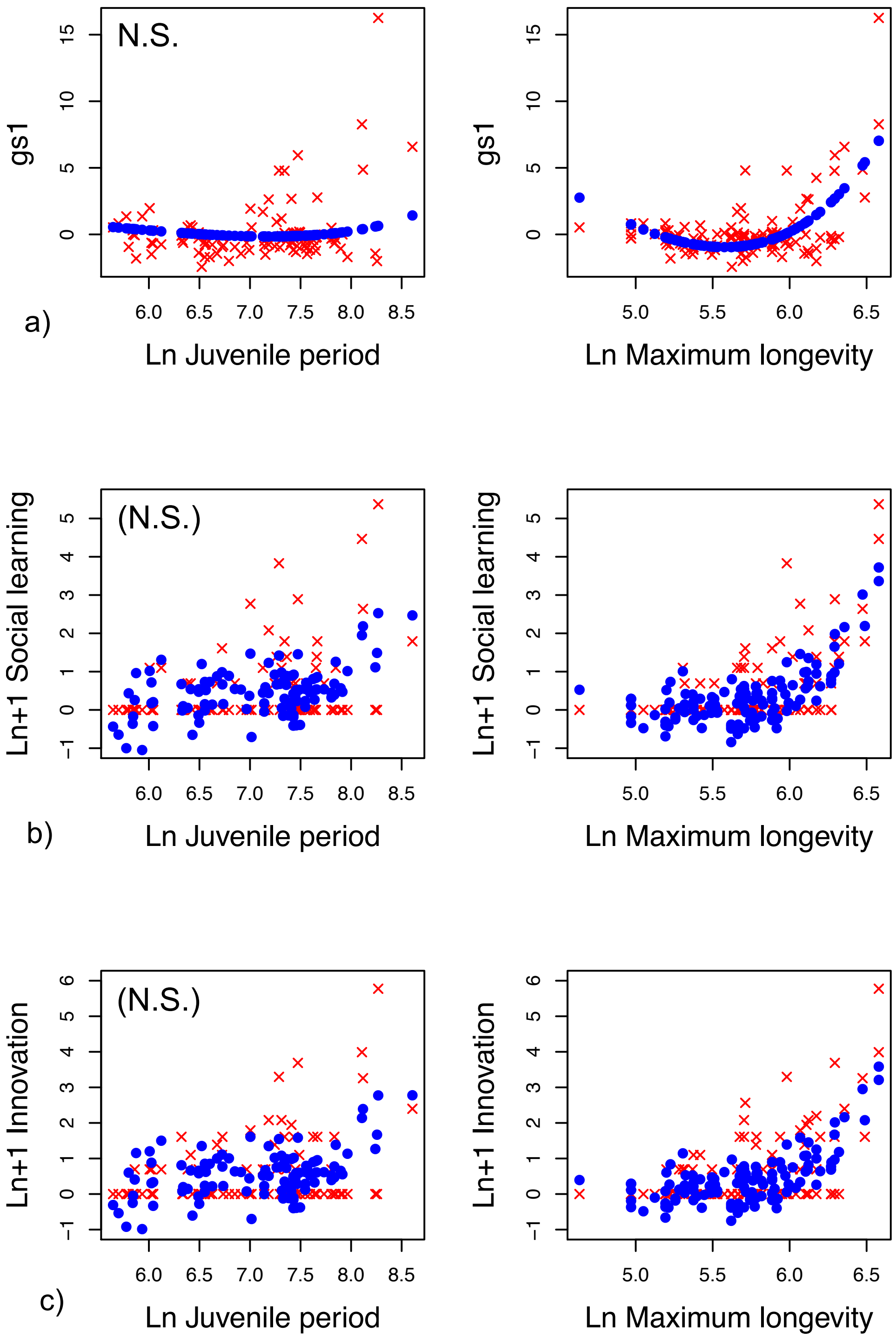


Figure 6.8 *relationships between juvenile period and maximum longevity and a)* g_{s1}*, b) social learning and c) innovation, represented by raw data (red crosses) and predicted values from PGLS models (blue circles). All relationships shown were significant (p<0.01) unless indicated ('N.S.' =p>0.05, (N.S.)=p>0.05 after removal of outliers or inclusion of body mass).*

6.3.2.5 Cultural intelligence

To investigate the predictions of the 'cultural intelligence' hypothesis, the relationships between brain size and g_{s1}, social learning and innovation were investigated both by using g_{s1}, social learning and innovation as outcome variables predicted by brain size (see section 6.3.1), and using brain size as the outcome variable, predicted by g_{s1}, social learning and innovation. Absolute whole brain size was not significantly predicted by g_{s1}, social learning and innovation (ps=0.08-0.13, n=62). Relative brain size was significantly predicted by g_{s1} (p=0.04, R^2=0.87, λ=1, n=62) and social learning (p=0.006, R^2=0.87, λ=1, n=62) (**Figure 6.9**), and marginally by innovation (p=0.08, R^2=0.87, λ=0.99, n=62). Relative neocortex and cerebellum sizes were not predicted by g_{s1}, social learning or innovation (ps>0.5). See Appendix G.vi for full model parameters.

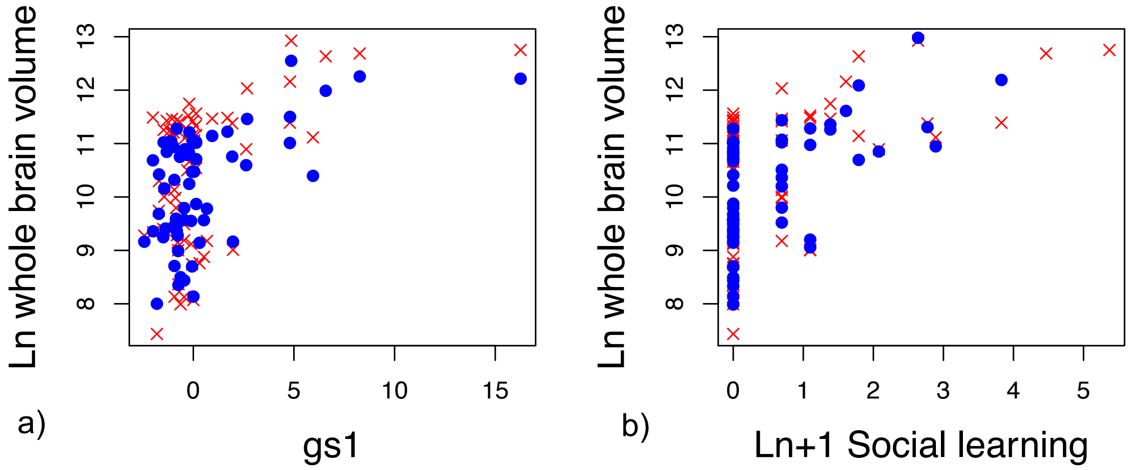


Figure 6.9 relationships between a) g_{s1} and b) social learning and relative brain volume, represented by raw data (red crosses) and predicted values from PGLS models (blue circles).

6.3.3 Multi-variate analyses

Multiple predictors of absolute brain size, relative brain size, neocortex size, g_{s1}, social learning and innovation were identified by the preceding analyses (summarised below in **Table 6.3**). In multi-variate models, I used absolute brain size, relative brain size, neocortex size, g_{s1}, social learning and innovation as outcome variables, predicted by all significant or marginal predictors identified from the preceding analyses, with additional co-variates such as body mass and research effort where appropriate. Exponential curves were fit for group size, latitude range and life history measures. Cerebellum size was only predicted by a single variable, composite life history speed and so was not included in multi-variate analyses.

	G.S.	%F.S.	D.B.	L.R.	L.H.	J.P.	M.L.	g_{s1}	S.L.	Inn.
Absolute brain	N.S.	N.S.	N.S.	N.S.	***	***	**	.	N.S.	N.S.
Relative brain	**	N.S.	N.S.	N.S.	***	**	**	*	**	.
Neocortex	*	N.S.	N.S.	N.S.	**	***	N.S.	N.S.	N.S.	N.S.
g_{s1}	N.S.	N.S.	*	*	***	N.S.	***	N.A.	N.A.	N.A.
Social learning	***	N.S.	*	*	***	(N.S.)	***	N.A.	N.A.	N.A.
Innovation	***	N.S.	N.S.	(**)	***	(N.S.)	***	N.A.	N.A.	N.A.

***Table 6.3**: Summary table of p-values for relationships between socio-ecological, environmental and life history variables (G.S. = group size, %F.S. = % fruit and seeds in diet, D.B. = diet breadth, L.R. = latitude range, L.H. = composite life history speed, J.P. = juvenile period, M.L. = maximum longevity, S.L. = social learning, Inn. = innovation) as predictors of the four measures of brain size and g_{s1}, social learning and innovation. *** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$, . = $p<0.1$, N.S. = non-significant ($p>0.1$), (**) = significant after removal of outlier, (N.S.) = non-significant after removal of outlier.*

For each outcome variable, I first ran full models containing all significant or marginal predictors identified from the preceding analyses. I then compared these full models with reduced models, containing only the predictors that were significant in the full multi-variate models. Finally, I compared multi-variate models to single-variate models. A summary table for multi-variate models is presented below (**Table 6.4**), and models discussed in turn in the following sections. See Appendix H for model parameters reported in full.

Outcome var.	**Model**	**Predictors**	**A.I.C.**	**R^2**	**n**
Absolute brain	Full	Juv. period*** Max. longevity* g_{s1}	76.61	0.67	51
	Reduced	Juv. period*** Max. longevity**	**76.55**	0.87	51
	Single var.	Juv. period**	83.16	0.85	51
	Single var.	Max. longevity**	87.98	0.18	51
Relative brain	Full	Group size** Juv. period, Max. longevity** Social learning, Innovation	**-16.78**	0.92	48
	Reduced	Group size** Max. longevity***	-15.59	0.92	48
	Single var.	Group size*	-2.35	0.89	48
	Single var.	Max. longevity***	-8.17	0.90	48
Neocortex	Full	Group size, Juv. period**	**8.72**	0.97	50
	Single var.	Group size*	17.81	0.96	50
	Single var.	Juv. period**	10.57	0.96	50
g_{s1}	Full	Diet breadth, Latitude range, Max. longevity***	**445.94**	0.46	113
	Single var.	Max. longevity***	449.08	0.44	113
Social learning	Full	Group size, Diet breadth, Latitude range, Juv. period, Max. longevity***	**158.22**	0.71	88
	Single var.	Max. longevity***	164.20	0.66	88
Innovation	Full	Group size, Latitude range, Juv. period, Max. longevity***	191.93	0.60	89
	Single var.	Max. longevity***	**186.48**	0.60	89

***Table 6.4** Summary table for results of analyses using multiple socio-ecological, environmental and life history variables to predict measures of brain size, g_{s1}, social learning and innovation. ***=$p<0.001$, **=$p<0.01$, *=$p<0.05$. Best fitting models according to AIC values are highlighted in bold.*

6.3.3.1 Absolute brain size

In the full model, only juvenile period and maximum longevity were significant predictors of absolute brain size (*ps*<0.05, R^2=0.67, *n*=51). In a reduced model containing only juvenile period and maximum longevity as predictors of absolute brain size, both remained significant (*ps*<0.01, R^2=0.87), but model fit was not significantly improved relative to the full model. Removing either juvenile period or maximum longevity from the reduced model significantly decreased model fit, but removing juvenile period worsened the model fit more than removing maximum longevity, suggesting that while both predicted brain size, juvenile period was a stronger predictor than maximum longevity. No outliers were identified. See Appendix H.i for model parameters reported in full.

6.3.3.2 Relative brain size

In the full model, only group size and maximum longevity were significant predictors of relative brain size (*ps*<0.01, R^2=0.92, λ=1, *n*=48). Both group size and maximum longevity remained significant predictors of relative brain size in a reduced model (*ps*<0.01, R^2=0.92, λ=0.97, *n*=48). Group size and maximum longevity were not associated with each other (*ps*>0.7), and removing either group size or maximum longevity significantly worsened model fit. Removing maximum longevity worsened model fit more than removing group size, suggesting that while group size and maximum longevity are independent predictors of relative brain size, maximum longevity is a stronger predictor than group size. No outliers were identified. See Appendix H.ii for model parameters reported in full.

6.3.3.3 Neocortex size

In the full model, only juvenile period significantly predicted relative neocortex volume (*p*=0.002, R^2=0.97, λ=0, *n*=50). Removing juvenile period, but not group size, from the full model significantly worsened model fit, suggesting that juvenile period was a stronger predictor of relative neocortex volume than social group size. No outliers were identified. See Appendix H.iii for model parameters reported in full.

6.3.3.4 g_{s1}

In the full model, only maximum longevity significantly predicted g_{s1} (*p*<0.001, R^2=0.46, λ=0.05, *n*=113). However, a reduced model using only maximum longevity to predict g_{s1} was a significantly poorer fit to the data than the full model. Results were not affected by removal of an outlier. See Appendix H.iv for model parameters reported in full.

6.3.3.5 Social learning

In the full model, only maximum longevity significantly predicted social learning (*p*<0.001, R^2=0.71, λ=0, *n*=88). However, a reduced model using only maximum longevity to predict social learning was a significantly poorer fit to the data than the full model. Results were not affected by removal of an outlier. See Appendix H.v for model parameters reported in full.

6.3.3.6 Innovation

In the full model, only maximum longevity significantly predicted innovation ($p<0.001$, $R^2=0.60$, $\lambda=0$, $n=89$). A reduced model using only maximum longevity to predict social learning fit the data significantly better than the full model. However after removal of an outlier (*Papio cynocephalus*), group size, juvenile period and maximum longevity were all significant predictors of innovation in the full model ($ps<0.05$, $R^2=0.66$, $\lambda=0$, $n=88$). See Appendix H.vi for model parameters reported in full.

6.4 Discussion

6.4.1 Brain size, general intelligence and culture

6.4.1.1 Brain size and general intelligence

Across primate species, all four measures of brain size – absolute brain size, relative brain size, neocortex size and cerebellum size – predicted the composite measure of general cognitive abilities (g_{s1}). Therefore, despite the apparent crudeness of brain size as a measure of cognitive abilities (Healy & Rowe, 2007), brain size and general intelligence appear to be positively associated in primates. The co-variation of g_{s1} and neocortex volume across primates has been previously identified (Reader et al., 2011), but the current analyses show that in addition to neocortex volume, g_{s1} is predicted by both absolute and relative whole brain volume, and cerebellum volume, supporting the idea that a single, underlying measure of brain 'size' predicts general cognitive abilities in primates (Reader et al., 2011). Further, the association of g_{s1} with both neocortex and cerebellum size supports the idea that primate cognitive evolution is underpinned by concerted evolution of these structures (Barton, 2012), and that technical skill is an important component of primate intelligence (Byrne, 1997). Although the mechanism of the relationship between overall increases in brain size and g_{s1} is not revealed by the current analyses, brain enlargement results in more neurons, more cortical areas and greater cross-modal connectivity (Barton, 2006; Changizi & Shimojo, 2005; Striedter, 2005). Such increases may underpin increased sensory acuity, processing speed, memory capacity and cross-modal integration, supporting increased general cognitive flexibility or 'intelligence' (Chittka & Niven, 2009; Roth & Dicke, 2005a).

6.4.1.2 Brain size and social learning

All measures of brain size significantly predicted social learning rate, extending previous comparative analyses which showed a correlation between social learning rate and ‘executive brain’ (neocortex + striatum) and neocortex volumes (Reader et al., 2011; Reader & Laland, 2002). The current analyses therefore add further support to the idea that enlarged overall brain size supports increased reliance on culture (Reader et al., 2011; Whiten & van Schaik, 2007). The mechanism of the relationship between brain size and social learning across species is currently unknown (Reader & Laland, 2002), and evidence of social learning in insects (e.g. Leadbeater & Chittka, 2007; Mery et al., 2009) demonstrates that large brains are not a pre-requisite for social learning. However, enlarged brain size may support more efficient, high-fidelity forms of social learning (Reader & Laland, 2002; Whiten & van Schaik, 2007). For example, increased perceptual ability, processing speed and memory capacity could increase the ability to acquire and retain socially learned behaviour. Greater cross-modal integration of perceptual, motor and abstract cognition could facilitate more efficient translation of observed behaviour into replicated actions (Byrne, 1997). The storage of learned motor skills as ‘internal models’, supported by the cerebellum (Glickstein & Doron 2008, Wolpert et al. 1998), may underpin the ability to socially learn action sequences requiring fine motor coordination, such as nut-cracking in chimpanzees (Marshall-Pescini & Whiten 2008) and nettle processing in gorillas (Byrne et al. 2011), that seems to be limited to only the largest-brained primates (Byrne, 1997).

6.4.1.3 Brain size and innovation

All measures of brain size significantly predicted innovation rate, extending previous comparative analyses demonstrating a correlation between innovation and ‘executive brain’ (neocortex + striatum) and neocortex volumes (Reader et al., 2011; Reader & Laland, 2002). As measures of brain size additionally predicted g_{s1}, and innovation rate is a component of g_{s1} (Reader et al., 2011), the results support the idea that innovation is a manifestation of behavioural flexibility, i.e. the ability to employ flexible cognitive and behavioural responses to novel problems (Lefebvre et al., 2004; Reader et al., 2011). Innovation rate is positively associated with relative forebrain volume in birds, suggesting that innovation, brain size and behavioural flexibility have co-evolved in multiple, distantly related taxa (Lefebvre et al., 2004; Lefebvre et al., 1997). The current findings that not only neocortex but also cerebellum volume predicted innovation suggests that multiple cognitive traits, including not only behavioural flexibility, but visuo-motor skills, supported together by the neocortex and cerebellum (Barton, 2012; Sanes, 2003; Sultan & Glickstein, 2007) could account for the relationship between brain size and innovation in primates. As measures of brain size predicted both innovation and social learning, and previous comparative analyses found that social learning and innovation co-varied across primates (Reader & Laland, 2002), innovation appears to be a component of reliance on culturally transmitted behaviour as well as behavioural flexibility (Reader et al., 2011; Whiten & van Schaik, 2007). Both social transmission and innovation are required to support the evolution of cultural traditions (Hoppitt & Laland, 2013; Whiten & van Schaik, 2007).

6.4.1.4 Summary: brain size, general intelligence and culture

Together, the relationships between measures of brain size and, g_{s1}, social learning and innovation support the idea that enlarged brain size, general intelligence and reliance on culture have co-evolved in primates (Reader et al., 2011; Reader & Laland, 2002; Whiten & van Schaik, 2007). The current analyses are novel in that the possibility of non-linear relationships between brain size, g_{s1}, social learning and innovation were explored, and found to be were exponential rather than linear in function, suggesting that while evolutionary increases in brain size are initially accompanied by small increases in general cognitive abilities and reliance on culture, increases in g_{s1}, social learning and innovation accelerate with increases in brain size. These exponential relationships are suggestive of a runaway process in which after a certain threshold, brain size, cognitive abilities and reliance on culturally transmitted behaviour become mutually re-enforcing (Reader et al., 2011; Whiten & van Schaik, 2007; Wilson, 1985). Consistently with this interpretation, variation in brain size is fairly widely spread across primate taxa, and tended to be associated with moderate-high phylogenetic signal (λ) in the current analyses, whereas analyses involving g_{s1}, social learning and innovation exhibited zero phylogenetic signal, with increased g_{s1}, social learning and innovation concentrated in just a few large-brained lineages (**Figure 6.10**). The contrast in the distribution and phylogenetic signal between brain size and g_{s1}, social learning and innovation suggests that increases in g_{s1}, social learning and innovation occurred rapidly, late in primate evolution, following a longer period of more gradualistic evolution of brain size.

6.4.2 Predictors of brain size, intelligence and culture

6.4.2.1 Social intelligence

In support of the 'social intelligence' hypothesis and several previous comparative analyses (e.g. Dunbar & Shultz, 2007), social group size predicted relative brain size and neocortex size. Social group size did not predict g_{s1}, suggesting that group size is not directly related to increased general cognitive abilities (Reader et al., 2011). However, these analyses provide the first demonstration that social group size predicts social learning and innovation rate across primates, consistent with the prediction that sociality increases the opportunity for social learning and the spread of innovations at the macro-evolutionary scale (Boyd & Richerson, 1985; Henrich, 2004; Powell et al., 2009; Whiten & van Schaik, 2007). Larger social groups support increased culture due to increased number of demonstrators, greater likelihood of high-fidelity copying, more opportunity to preferentially copy skilled individuals and therefore greater opportunity for the social transmission of innovations (Henrich, 2004, Derex et al., 2013; Muthukrishna et al., 2014). Previous comparative analyses did not find associations between group size and social learning or innovation (Reader & Laland, 2002a; Reader et al., 2011). This discrepancy may be accounted for by the novel use of non-linear regression coefficients by the current analyses, and/or the use of PGLS rather than independent contrasts, which is more suitable for traits with low phylogenetic signal such as social learning and innovation rate. Although group size predicted measures of brain size and social learning and innovation, measures of life history were stronger predictors than group size in multi-variate analyses, suggesting that group size is not necessarily the most important driver of the evolution of primate brain size, cognition and culture.

6.4.2.2 Foraging intelligence

In contrast to predictions of the 'foraging intelligence' hypothesis, the current analyses found no associations between percentage of fruit and seeds in the diet and brain size, or g_{s1}, social learning and innovation. Diet breadth did not predict any measure of brain size, or innovation. Diet breadth predicted g_{s1} and social learning, but these associations were relatively weak and did not remain in multi-variate analyses. Therefore, the current analyses find little evidence to support the role of 'foraging intelligence' in the increased size of large brain structures, general cognitive abilities and reliance on social learning and innovation in primates. Reader et al. (2011) reported a positive correlation between both dietary percentage of fruit and diet breadth with social learning rate, a discrepancy which could be accounted for by the use of more appropriate phylogenetic statistical methods in the current project.

Possibly, foraging ecology selects for change in size of smaller brain structures, such as the hippocampus, as suggested by comparative studies of food-storing in birds (Krebs et al., 1989), rather than larger-scale brain size increases, which do not affect overall brain size. Alternatively, foraging behaviours may predict the size of larger brain structures within certain primate radiations, rather than across primates as a whole. For example, frugivory predicts neocortex size within diurnal haplorhine species (Barton, 1996).

6.4.2.3 Environmental variation

In contrast to the prediction of the 'environmental variation' hypothesis, latitude range did not predict any measure of brain size. Latitude range did predict g_{s1}, social learning and innovation, but curves fitted for these relationships were shallow and statistically relatively weak, and latitude range did not predict g_{s1}, social learning and innovation in multi-variate analyses. The 'environmental variation' hypothesis proposes that climatic fluctuations over timescales of decades or centuries favoured evolutionary increases in brain size and cultural repertoire in human evolution (Henrich & McElreath, 2003; Potts, 1998; Richerson et al., 2005). Species latitude range may be a poor measure of the climatic variation actually experienced by individuals. However, a previous comparative analysis found no relationship between a more direct measure of climactic variation and either innovation rate or brain size in primates (Reader & MacDonald, 2003). Therefore, whilst climatic variation may help to explain the expansion of brain size and cultural capacity in human evolution, it appears not to have been an important factor in the evolution of primate brain size, cognitive abilities and culture.

6.4.2.4 Life history length

In support of the 'life history length' hypothesis, the composite measure of life history speed strongly predicted not only all four measures of brain size, but additionally g_{s1}, social learning and innovation. Although positive associations between brain size and life history length have been demonstrated by previous comparative analyses (Joffe, 1997), these analyses are the first to demonstrate that primates with slower life histories score higher on measures of intelligence and increased reliance on culture than those with faster life histories, as predicted by proponents of the 'life history length' hypothesis (Kaplan et al., 2000). However, in contrast to idea that juvenile period is critical period for learning skills for survival and reproduction (Joffe, 1997; Kummer & Goodall, 1985), this relationship appeared to be driven primarily by increased longevity. Longevity strongly predicted not only measures of brain size but also g_{s1}, social learning and innovation. While juvenile period predicted measures of brain size, relationships between juvenile period with g_{s1}, social learning and innovation were either non-significant or weak, and were not robust to removal of outliers or inclusion of confounding variables. The closer relationship of g_{s1}, social learning and innovation to longevity rather than juvenile period length is consistent with the greater frequency of primate innovations in adults than juveniles than expected by chance (Reader & Laland, 2001).

In multi-variate models, life history measures were generally better predictors of brain size, g_{s1}, social learning and innovation than other variables, including social group size. Both juvenile period and longevity remained significant predictors of absolute brain size in multi-variate models, suggesting that increases in both juvenile period length and overall lifespan are related to increases in absolute brain size in primates. However, multi-variate analyses suggested that longevity primarily predicted relative brain size, whereas juvenile period was related to neocortex size. Therefore, extensions of specific life history phases may relate to specific brain enlargements.

Further analyses, however, are required in order to disentangle the hypothesis that extended life history is selected due to the benefits of a longer learning period, from the alternative possibility that relationships between measures of life history speed and brain size, g_{s1}, social learning and innovation are explained through developmental rather than cognitive mechanisms. In particular, the relationships between the measures of life history speed with brain size, g_{s1}, social learning and innovation could be confounded by a longer period of maternal investment required for larger brain size at birth (Barton & Capellini, 2011). Therefore, further analyses are required in order to investigate these results, in which effects of specific measures of life history traits are compared. For instance, if increased lifespan and g_{s1}, social learning and innovation are related due to the benefits of an increased learning period, relationships should remain when taking measures of maternal investment such as gestation and lactation periods into account. Moreover, the use of a composite measure of 'life history speed' may be limited given recent evidence of two independent life history dimensions in mammalian evolution, corresponding to 'output' (investment per reproductive event) and 'timing' (the distribution of reproduction across the lifespan) (Bielby et al., 2007). The possibility of additional dimensions in life history speed may explain why the principal components analysis of life history left 36% of variation unexplained.

6.4.3 Summary: the evolution of brain size, cognition and 'cultural intelligence'

The current results, together with the 'cultural intelligence' hypothesis, propose an evolutionary scenario by which enlarged brain size, increased general intelligence and reliance on culture may have evolved in primates. In support of the 'cultural intelligence' hypothesis, relative brain size was not only a predictor of g_{s1} and social learning, but was predicted by g_{s1} and social learning in turn, suggestive of a feedback loop between reliance on culture and increased brain size and intelligence (Boyd & Richerson, 1985; Reader et al., 2011; Wilson, 1985). Where g_{s1}, social learning or innovation were predicted by brain size, group size or life history, relationships were exponential rather than linear. These exponential relationships are suggestive of a positive feedback loop between selection pressures for increased brain size and learning ability in some primate lineages (Reader et al., 2011; Whiten & van Schaik, 2007; Wilson, 1985). Therefore, whilst brain size enlargement may have been initially driven by increased social group size and life history length, in certain lineages, reliance on culture may have passed a critical threshold after which rapid increase in g_{s1}, social learning and innovation occurred, late in primate evolution (**Figure 6.10**). Further, the rarity of increased g_{s1}, social learning and innovation across primate species is consistent with theoretical evidence that reliance on culturally transmitted behaviour is unlikely to spread initially, but becomes self-reinforcing once established (Henrich & McElreath, 2003).

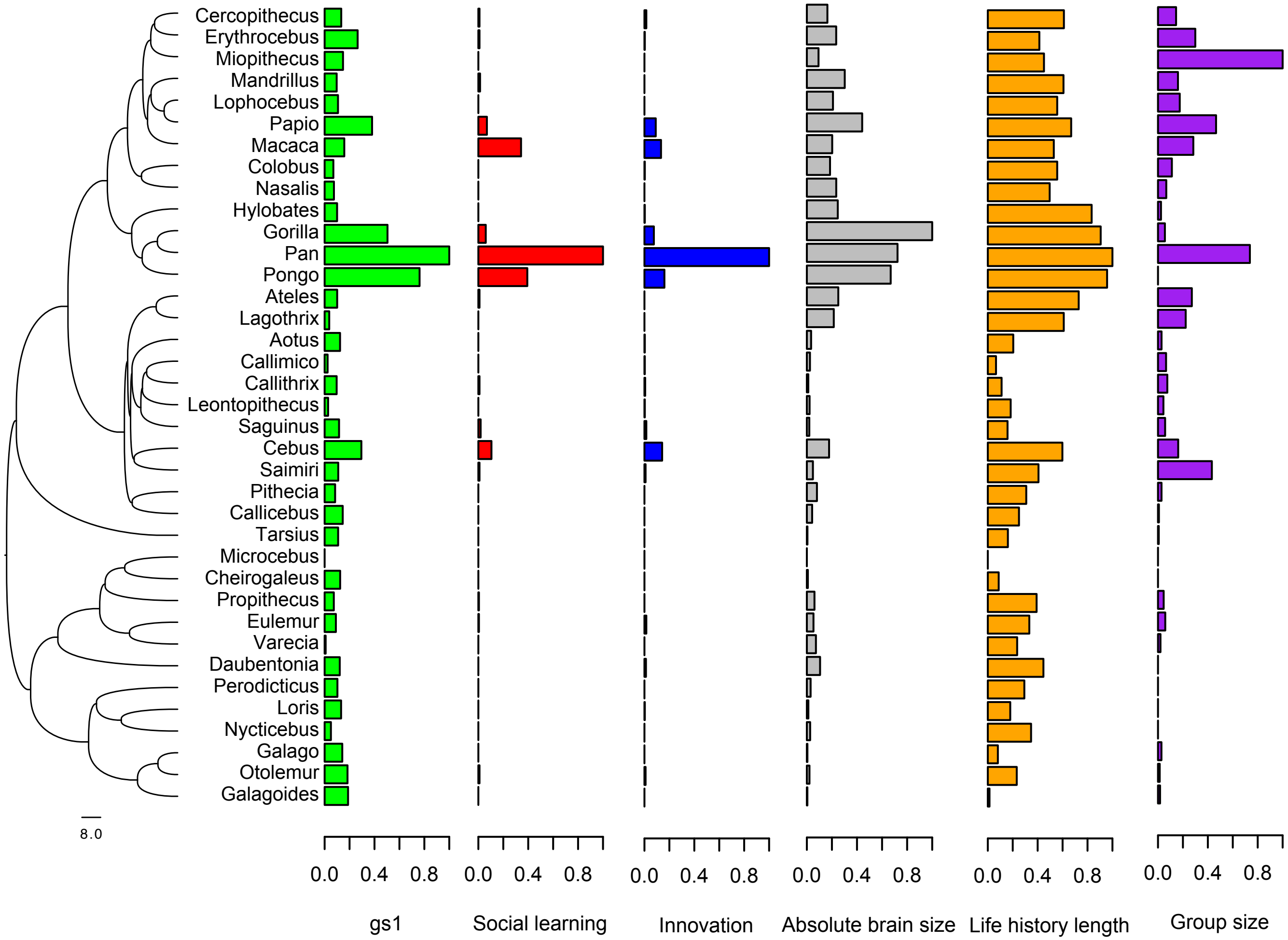


Figure 6.10 *Distribution of* g_{s1}*,social learning, innovation, absolute brain size, composite life history length and group size across primate genera.* g_s*, brain size, life history length and group size are averaged per genus. Social learning and innovation were summed for each genus and divided by sum research effort per genus.. All variables are normalised with minimum 0 and maximum 1 for ease of visual comparison. Scale bar for the phylogeny represents millions of years.*

6.4.4. Limitations of current analyses

Although the current findings show cross-species statistical associations between brain size, cognitive abilities and socio-ecological variables consistent with co-evolutionary hypotheses; the causality, directionality and underlying macro-evolutionary processes are not explicitly addressed by PGLS analyses (Nunn, 2011). For example, the relationship between life history speed and brain size is not necessarily accounted for by life history speed selecting for increased brain size, but rather, extended life history could be a by-product of selection for increased brain size. Determination of causality in phylogenetic analyses is additionally complicated due to the possibility of reciprocal causation in macro-evolutionary processes (Laland et al. 2011). A further limitation of the current analyses is the use of behavioural measures, such as ‘innovation rate’, estimated from the frequency of reported behaviours in primate literature (Reader & Laland, 2002; Reader et al., 2011). The extent to which ‘rates’ of behaviours such as social learning and innovation accurately reflect underlying, species-typical ‘abilities’ remains to be explored by further comparative analyses. Additionally, it is possible that the apparently sparse, phylogenetically labile distribution of g_{s1}, social learning and innovation across species results from remaining research biases, unaccounted for by the current analyses, rather than from true variation in behaviour across species. However, at the present time, Reader et al’s (2011) behavioural measures are the best available data for addressing primate cognitive and behavioural evolution on the broad evolutionary scale.

6.4.5 Conclusions

Together, the current findings suggest that enlarged brain size, increased general cognitive abilities and increased reliance on social learning and innovation have co-evolved as a single adaptive complex in some primate lineages, favoured by common selection pressures including increased sociality and extended life history. Although enlarged brain size, cognitive abilities and reliance on social learning and innovation may have been initially favoured by increased sociality and extended life history, in a small number of primate linages, possibly representing only four independent evolutionary events in the lineages leading to great apes, baboons, macaques and capuchin monkeys, a critical threshold in reliance on learned behaviour may have been reached, leading to mutually reinforcing selection for increased brain size, cognitive abilities and reliance on social learning and innovation. The results support the idea that enlarged brain size, general cognitive abilities and reliance on culture have co-evolved at the broader evolutionary scale, in species of corvids, cetaceans and primates (Hunt & Gray, 2003; Rendell & Whitehead, 2001; Whiten et al., 1999). Although humans were not included in comparative analyses, the combination of complex sociality, extended lifespan, enlarged brain size, increased general cognitive abilities and reliance on culturally transmitted behaviour for survival appears to have reached a zenith in our own species (Pagel, 2012). The exponential relationships between brain size and g_{s1}, social learning and innovation across non-human primates appear to mimic the cumulative growth of cultural capacity in association with increasing brain size throughout human evolution.

Chapter 7: General Discussion

The preceding chapters comprise applications of the comparative method, supported by modern phylogenetic and meta-analytic statistical methods, to two major questions in primate evolution. First, Chapters 3 and 4 investigated the evolution of exaggerated sexual swellings in female Catarrhine primates, and second, Chapters 5 and 6 investigated the evolution of enlarged brain size and increased cognitive abilities in the primate order. The following discussion summarises the principal findings of the thesis and explains their broader implications for the value of the comparative method in understanding sexual selection and cognition at the macro-evolutionary level.

Chapter 3: Are exaggerated sexual swellings in female Catarrhine primates honest signals of fertility and quality?

In Chapter 3, I used both meta-analytic and phylogenetic statistical methods to investigate the honesty of exaggerated sexual swellings as signals of ovulation timing, and whether swellings signal female quality, as well as temporal fertility. Meta-data from published articles confirmed the within-cycle relationship between peak swelling size and the peri-ovulatory period. In contrast, there was at best only weak evidence for between-female correlations between swelling size and measures of female quality, such as fecundity and social rank. Therefore, while there is good evidence for swellings as signals of temporal fertility, in support of the assumptions of the graded signal (Nunn, 1999) and paternal care (Alberts & Fitzpatrick, 2012) hypotheses, there is currently relatively little evidence for swellings as signals of female quality (Domb & Pagel, 2001; Pagel, 1994). However, the apparent accuracy of swellings as signals of temporal fertility was affected by variation across articles in how swelling size was measured. Studies that measured swelling size directly, on a continuous scale, reported that the onset of peak swelling coincided almost exactly with the day of ovulation, lasting for less than two days. However, studies measuring swellings using coarser, categorical scales to estimate swelling size reported that peak swelling size began around 3 days prior to ovulation, lasting for around 4 days. Further, using a second dataset comprising of raw, per-cycle data on the timing and duration of peak swelling, in which all but one study had measured swellings using categorical estimation, peak swelling onset occurred, on average, over 7 days prior to ovulation, lasting for 10 days.

The principal findings of Chapter 3 suggest two broader conclusions. Firstly, the results demonstrate that comparative analyses can be complemented by investigation of the current function of a trait. Although comparative analyses can explore one of Tinbergen's four questions, concerning the macro-evolutionary processes responsible for cross-species variation in extant traits, such analyses do not address the remaining three questions, concerning development, mechanism and function of traits within a species (Bateson & Laland, 2013). Therefore, such questions require external justification and investigation. By confirming that swelling size is related to temporal fertility, the results of these analyses helped to frame a novel hypothesis for the evolution of sexual swellings, which was subsequently explored in comparative analyses in the following chapter. In the case of swellings, the signalling properties of swellings are especially important because fertility versus quality signals require distinct evolutionary explanations. In particular, whilst male mate choice based on individual fecundity cues is likely to favour the evolution of enlarged signals in females, male mate choice based on temporal fertility cues may be less likely to favour enlarged signals as all females may be equally preferable when maximally fertile, therefore generating little between female variation in fitness in relation to signal size (Bonduriansky, 2001; Pagel, 1994). However, male mate choice may favour exaggerated fertility cues where, individual females receive benefits of mating which scale with ornament size and male mating effort (Russell Bonduriansky, 2001; Funk & Tallamy, 2000), such as increased fertilisation probability or provisioning by males, for example.

The second broader conclusion drawn from the analyses presented in Chapter 3 is the importance of methodological factors in comparing traits across species. Analyses of the timing and duration of peak swelling size attempted to investigate the 'honesty' of sexual swellings as signals of fertility, as measured by the temporal fit of the period of peak swelling to the peri-ovulatory period. However, depending on a) the way that swelling size was measured by articles, and b) whether analyses were based on a dataset comprised of the mean onset and duration of peak swelling per article, versus a smaller dataset containing per-cycle data on the onset and duration of peak swelling, the average temporal distance between peak swelling and ovulation varied by as much as 7 days. Such variation is not trivial but would correspond to very different interpretations of the function of swellings. Where peak swellings coincide with ovulation, highly accurate information on the timing of ovulation is potentially signalled to males, whereas if peak swellings begin 7 days prior to ovulation, there will be many days on which, despite maximum swelling size, ovulation is very unlikely to occur (**Figure 7.1**). Further caution in interpreting cross-species variation in swelling properties is urged by the low phylogenetic signal exhibited by both onset and duration of peak swelling, which can be caused by high measurement error (Blomberg et al., 2003). The findings presented in chapter 3, further, highlight the need for greater understanding of the perception of swellings by male primates in understanding their signalling properties. The function of swellings as probabilistic signals of ovulation timing challenges a dichotomous view of biological signals as either 'honest' or 'deceptive'. Rather, the 'honesty' of probabilistic signals can be better described as varying on a continuum from high to low signalling accuracy. Similarly, the fertility signals of female long-tailed dance flies (Funk & Tallamy, 2000), in which enlarged abdomen size is correlated with egg maturation, but less reliably than for closely related species with smaller abdomens, appear to be neither completely honest nor deceptive. However, the possibility that such signals of temporal fertility may additionally function as honest, condition-dependent signals of female health due to their relationship with ovarian cycling hormones warrants further investigation.

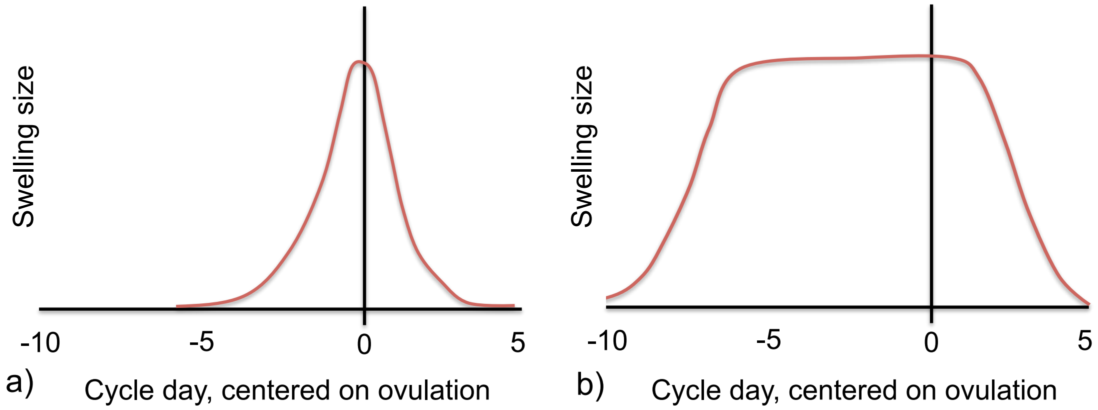


Figure 7.1 *Schematic representations of swelling size changes across the ovarian cycle, based on the a) most 'honest' and b) most 'deceptive' extremes of the range of reported onset and duration of peak swelling across different methods of measuring swelling size, and different methods of summarising variation in onset and duration of peak swelling across existing datasets, identified by the analyses presented in chapter 3.*

Chapter 4: The evolution of exaggerated sexual swellings in Catarrhine primates

In Chapter 4, I used phylogenetic comparative analyses to investigate hypotheses for the evolution of exaggerated sexual swellings in female Catarrhine primates. In contrast to previous hypotheses, which have argued that swellings function in manipulating paternity probability either partly to avoid infanticide (Nunn, 1999) or to solicit paternal investment (Alberts & Fitzpatrick, 2012), swellings were not found to be associated with infanticide risk or paternal care-taking. Further, in contrast to Pagel's (1994) 'reliable-indicator' hypothesis, which argued that swellings evolved due to sexual selection on females, female canine length (used as a measure of aggressive female-female competition) was not greater in swelling species than non-swelling species, replicating the results of a previous analysis (Nunn et al. 2001). However, the role of male mate choice in the evolution of swellings, also proposed by

Pagel (1994), had not, until now, been investigated by comparative analyses. I developed a novel ‘female ornamentation’ framework, drawing together elements of previous hypotheses in addition to predictions derived from recent developments in sexual selection research (e.g. Barry & Kokko, 2010; Kokko & Monaghan, 2001), which proposed that male mate choice and cryptic female choice favoured the evolution of swellings. In support of this hypothesis, swellings were found to be associated with conditions favourable to male mate choice due to a) costly mating from ejaculate production and male-male competition, indicated by large relative testes mass and large male group sizes in swelling species, and b) opportunity for male mate choice due to larger female group sizes (in absolute terms) in swelling species. Further, I found evidence that swellings have co-evolved with elongated penises in males, as proposed originally by Dixson & Mundy (1994) but not until now tested by phylogenetic comparative analyses, suggesting antagonistic genital co-evolution due to sexual conflict, and that swellings may function in cryptic female choice, similarly to examples of co-evolution of length of male and female reproductive organs in other species, such as stalk-eyed flies (Kotrb et al. , 2013)

The current findings help to shed light on the general conditions that favour the evolution of female ornamentation, and concur with broader developments in contemporary sexual selection theory. Swellings are one of an increasing number of examples of female ornamentation now documented across a broad taxonomic range (e.g. Amundsen & Forsgren, 2001; Weiss, 2006) that cannot be explained simply by a reversal of the ‘sex roles’ of classical sexual selection theory (Darwin, 1871). Mate ‘choice’ and ‘competition’ are no longer viewed as distinct, mutually-exclusive, sex-typical processes (Shuker, 2010), and males may be both choosy and competitive in mating (Clutton-Brock, 2007). The extent to which choosiness is advantageous in either sex has been shown by theoretical models to depend on the cost and benefits of mate choice, rather than simply by patterns of parental investment (Kokko & Monaghan, 2001). Although such developments in sexual selection theory are increasingly widely recognised, the analyses here are perhaps the first application of such ideas to comparative analyses of primate anatomy and behaviour. The findings may, further, help to explain the evolution of female ornamentation in non-primate taxa. For example, similarly to Catarrhine primates, bright ornamentation occurs alongside strong male-male competition and large, polygynadrous-mating social groups, without full ‘sex-role’ reversal in at least two bird species (Eclectus parrots: Heinsohn & Legge, 2003; Alpine accentors: Nakamura, 1990). Further investigations of hypotheses for the evolution of female ornamentation would be ideally directed towards birds, as there is far more variation in female ornamentation than across the Catarrhine primates, where swellings may have evolved only three times independently (Nunn, 1999; Pagel & Meade, 2006).

A common limitation of comparative analyses concerns the use of proxy variables in place of variables that are harder to quantify (Nunn, 2011). Male 'choosiness', for example, was not directly measured, rather, analyses examined the conditions thought to favour mate choice in males. The use of such 'proxy' variables is not ideal as the extent to which proxy measures truly reflect variation in the variable of interest may be questioned, and therefore, there may be multiple possible interpretations of the results of comparative analyses. For example, the relationship between swellings and male group size can either be interpreted as support for the prediction of the 'graded-signal' hypothesis that swellings balance benefits of single versus multiple mating (Nunn, 1999), or the idea that male competition favours male choosiness in mating (Pagel, 1994). The assumptions made regarding proxy variables were justified with reference to existing theoretical models and empirical work from non-primate taxa. However, several assumptions remain to be further justified by empirical investigation in primates, such as the relationship between sperm competition and male mate choice, for example. Ideally, more direct measures of variables of interest would have been employed by the current analyses; for example, male choosiness could have been estimated by a percentage of mating opportunities typically rejected by males. Comparative analyses typically trade-off the limitations of relying on readily available secondary datasets, often comprising coarse behavioural measures, with the benefits of large-scale analyses that can suggest broad evolutionary trends, the assumptions of which can stimulate further, finer-scaled investigations. Observational studies of primates would be especially valuable in investigating the assumptions made by the current analyses regarding the conditions favourable to mate choice in male primates.

Chapter 5: ***co-variation of intra-sexual competition and measures of cognitive abilities across primate species***

In Chapter 5, I used phylogenetic comparative analyses to investigate the hypothesis that increased cognitive abilities co-evolved with the intense intra-sexual competition in primates, based on data obtained from Byrne & Whiten (1990) and Reader et al. (2011). Specifically, I investigated the hypothesis that intra-sexual competition favours the ability to employ 'strategic' social behaviour, presumably involving cognitive abilities such as forward planning and behavioural flexibility, in competition for mates, such as ‘sneak mating’. In support of this hypothesis, across primate species, sperm competition (as measured by relative testes mass) was positively associated with tactical deception rate, innovation rate and g_{s1}. Body mass dimorphism, however, did not predict tactical deception rate, innovation rate or g_{s1}, suggesting that cognitive abilities are positively associated with non-aggressive forms of mating competition. Associations of testes mass with deception and innovation appeared to be driven by deception and innovation in males rather than females. Deception rate was greatest in species with multi-male, multi-female mating systems, which also appeared to be driven by increased deception rate in males specifically. Together, the results suggest that intra-sexual competition within large, promiscuous-mating social groups has favoured the evolution of the ability to employ ‘strategic’ behaviour, such as deception, in primates.

The results presented in chapter 5 concur with wider evidence that sexual selection shapes not only physical but cognitive traits at the within-species level (Boogert et al., 2011; Jacobs, 1996). Although existing comparative studies of primates had suggested positive relationships between brain size and either male-male competition (Sawaguchi, 1997) or mating promiscuity (Shultz & Dunbar, 2007), the current analyses further suggest the particular cognitive and behavioural traits that may be favoured by intra-sexual competition at the macro-evolutionary scale. The results are broadly supportive of the ‘social intelligence’ hypothesis, but suggest that intra-sexual competition is a more important driver of primate cognitive abilities than previously thought, especially as testes mass was a better predictor of tactical deception rate, innovation rate and g_{s1}, than was social group size. Future comparative analyses may wish to investigate the extent to which the current results are specific to primates, due to the unusual co-association of large, stable social groups with intense mate competition in many primate species, versus suggestive of a more general evolutionary association. Although it may be tempting to apply the current findings to the evolution of increased brain size and cognitive abilities in humans, as proposed originally by Darwin (1871), archaeological and comparative evidence suggests a trend towards decreased promiscuity and intra-sexual competition in the *Homo* lineage (Dixson, 2009). Therefore, if sexual selection did contribute to cognition and brain size evolution in humans (amongst many other possible factors), it is more likely to have acted through mutual mate choice than intense intra-sexual competition (Miller, 2000).

The current analyses used existing datasets on the 'rates' of behaviours, such as tactical deception, derived from literature searches as measures of cognitive traits, instead of the more common approach in comparative analyses of using brain size as a proxy measure for cognition. A potential advantage of this 'taxonomic counts' approach is that analyses are based on behavioural measures, rather than the more common approach of using volumetric brain measures as proxy measures of behavioural measures (Lefebvre, 2011). However, the assumptions of this approach require additional empirical investigation, particularly the extent to which 'rates' of behaviours, derived from frequency of reports in literature, truly reflect propensity or ability of species towards particular behaviours. Further, the cognitive mechanisms underpinning such behaviours as 'innovation' are generally unknown. The possibility remains that results such as those presented in Chapter 5 are in fact accounted for by 'situational' rather than cognitive mechanisms. For example, it is possible that all primate species are potentially capable of such abilities as tactical deception, but only exhibit such behaviours under certain environmental conditions. In general, variation in cognitive traits is notoriously difficult to quantify across species, and alternative approaches, such as experimental tests of cognitive abilities, have their own disadvantages, including lack of ecological validity and typically smaller sample sizes (Reader et al., 2011). Therefore, datasets on 'rates' of behaviour derived from literature such as those collated by Reader et al., (2011) and Lefebvre et al. (1997) are currently the most useful data available for testing cognitive evolutionary hypotheses at the broad, macro-evolutionary scale, despite the need for further investigation of their assumptions.

Chapter 6: Evolution of brain size, general cognitive abilities and culture in primates

In Chapter 6, I attempted to address some remaining issues concerning the evolution of enlarged brain size, increased general cognitive abilities, and reliance on culture in primates, using phylogenetic comparative analyses of a large cross-species dataset including brain volume measures, behavioural measures from Reader et al. (2011), and socio-ecological, environmental and life history variables. I investigated first, relationships between four measures of brain size (absolute brain size, relative brain size, relative neocortex size and cerebellum size) and g_{s1}, social learning rate and innovation rate, finding that all four measures of brain size were strongly related to g_{s1}, social learning and innovation. Second, I investigated socio-ecological, environmental and life history predictors of brain size, g_{s1}, social learning and innovation, using multi-variate models where multiple predictors of brain size, g_{s1}, social learning and innovation were identified. Overall, social group size and life history measures were the strongest predictors of brain size, g_{s1}, social learning and innovation. Social group size, however, predicted social learning and innovation, but not g_{s1}. The relationship between brain size, g_{s1}, social learning and innovation and life history seemed to be driven by extended longevity rather than specific extension of the juvenile period, as longevity predicted both measures of brain size and g_{s1}, social learning and innovation, whereas juvenile period only predicted measures of brain size. Where brain size, group size or life history were predictors of g_{s1}, social learning or innovation, statistical assocations were exponential rather than linear, consistent with a 'runaway' process in primate cognitive evolution by which increased brain size, cognitive abilities and reliance on culture became mutually reinforcing selection pressures. However, the PGLS analyses presented do not directly test the idea that 'runaway' processes explain the evolution of behaviours such as innovation in primates. Rather, additional analyses of the rates of evolution of traits such as innovation, for example, using the 'delta' parameter in the PGLS framework (Pagel, 1999), are required in order for runaway hypotheses to be tested directly.

The results presented in Chapter 6 support the idea that enlarged brain size, increased general cognitive abilities and greater reliance on culture have co-evolved in multiple independent primate lineages, driven by common selection pressures, particularly increased sociality and longevity. Further, the results suggest an evolutionary process by which increased sociality and extended life history initially favoured gradualistic increases in brain size, cognitive abilities, social learning and innovation, followed by a 'runaway' process in a certain few lineages, such as great apes and capuchin monkeys. The proposed scenario for the evolution of increased brain size, cognitive abilities and reliance on culture amongst primate species supports the idea that these traits have co-evolved independently in other taxa, such as cetaceans and corvids, for example (Hunt & Gray, 2003; Rendell & Whitehead, 2001), in response to convergent selection pressures, as cetaceans and corvids too are characterised by complex sociality and slow life history (Emery & Clayton, 2004; Emery et al., 2007; Marino, 2002). A limitation, however of these analyses is that PGLS regressions do not explicitly address the causal directionality of statistical associations (Harvey & Pagel, 1991; Nunn, 2011). Additional comparative analyses, using more sophisticated phylogenetic statistical methods, such as phylogenetically controlled path analysis, may be helpful in resolving such issues (von Hardenberg & Gonzalez-Voyer, 2013). However, statistical investigations can only indirectly infer causation (Shipley, 2000), and phylogenetic causal methods face additional complexities in that macro-evolutionary processes may involve reciprocal causation (Laland et al., 2011).

Conclusion

The power of the comparative method is the potential for discovery of the evolutionary processes that account for current biological diversity (Pagel, 1999), which has been a central aim of evolutionary biology since *The Origin of Species* (Darwin, 1859). The preceding chapters presented the results of four projects that used phylogenetic comparative statistical methods to investigate a) the evolution of exaggerated sexual swellings in primates and b) the evolution of enlarged brain size, cognitive abilities and culture in primates, two of the most compelling questions in primate evolution. The principal findings in terms of the first question were that exaggerated swellings are signals of temporal fertility, which appear to have evolved in species with conditions favouring male mate choice and cryptic female choice, suggesting that sexual swellings are an unusual example of a sexually selected visual ornament in a mammal species. The principal findings in relation to the second question are first, that sexual selection may shape the evolution of cognitive as well as physical traits at the macro-evolutionary level, and second, that enlarged overall brain size, general cognitive abilities and reliance on culture have co-evolved in primate species, driven primarily by increased sociality and extended life history. The preceding analyses employed up-to-date phylogenetic statistical methods and primate phylogeny estimates, characteristic of the modern comparative method, in order to best incorporate available knowledge on primate phylogenies into statistical analyses (Arnold et al., 2010; Nunn, 2011). Throughout the thesis, however, conclusions were drawn with some remaining caution due to concerns about the quality of existing cross-species datasets. Therefore, in future, greater investment in comparative analyses should be directed towards improving the quality of comparative datasets, to catch up with the tremendous potential of phylogenetic comparative methods to use the present to reconstruct the past.

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Appendix A: datasets for analyses presented in chapter 3

A.i) onset and duration of peak swelling relative to ovulation, per article

Reference	Species	Swelling size category	Population	Swelling measure	Day peak onset	Days peak duration	N cycles onset	N cycles duration
Aidara et al. 1981	*Cercocebus atys lunulatus*	Intermediate	Provisioned	Direct	-1	1	6	6
Aujard et al. 1998	*Macaca tonkeana*	Intermediate	Provisioned	Visual	-3	2	9	9
Barelli et al. 2007	*Hylobates lar*	Small	Non-provisioned	Visual	-5.333	8.4	15	15
Blakley et al. 1981	*Macaca nemestrina*	Intermediate	Provisioned	Visual	-5.5	5	21	21
Brauch et al. 2007	*Macaca sylvanus*	Intermediate	Provisioned	Direct	0	1	19	19
Czekala & Sicotte 2000	*Gorilla beringei*	Small	Non-provisioned	Visual	0	1	1	1
Dahl et al. 1991	*Pan paniscus*	Large	Provisioned	Visual	NA	14.5	NA	2
Dahl et al. 1991	*Pan troglodytes*	Large	Provisioned	Visual	NA	3	NA	2
Daspre et al. 2009	*Papio hamadryas anubis*	Large	Provisioned	Visual	-10	10	9	9
Deschner et al. 2003	*Pan troglodytes verus*	Large	Non-provisioned	Visual	-7.3	9.894	33	33
Deschner et al. 2004	*Pan troglodytes verus*	Large	Non-provisioned	Direct	0	1	29	29
Emery & Whitten 2003	*Pan troglodytes*	Large	Provisioned	Visual	-4	4	14	14
Emery Thompson 2005	*Pan troglodytes schweinfurthii*	Large	Non-provisioned	Visual	1.5	3	65	65
Engelhardt et al. 2005	*Macaca fascicularis*	Intermediate	Non-provisioned	Visual	-9.94	15	9	9
Gesquiere et al. 2007	*Papio cynocephalus*	Large	Non-provisioned	Visual	-2	3	422	422
Graham et al 1972	*Pan troglodytes*	Large	Provisioned	Visual	-9.334	9	3	3
Graham et al. 1977	*Pan troglodytes*	Large	Provisioned	Visual	-8	7.333	3	3
Gust 1994	*Cercocebus torquatus atys*	Intermediate	Provisioned	Visual	-2	NA	4	NA
Heistermann et al. 1996	*Pan paniscus*	Large	Provisioned	Visual	-10.222	12.778	7	7
Higham et al. 2008	*Papio hamadryas anubis*	Large	Non-provisioned	Direct	-3	1	13	13
Higham et al. 2012	*Macaca nigra*	Intermediate	Non-provisioned	Direct	-1	2	31	31
Howland et al. 1971	*Pan troglodytes*	Large	Provisioned	Visual	-7.5	12.5	4	4
Jurke et al 2000	*Pan paniscus*	Large	Provisioned	Visual	-3	8.5	2	2
McArthur et al. 1981	*Pan troglodytes*	Large	Provisioned	Visual	-12	16	1	1
Mohle et al. 2005	*Macaca sylvanus*	Intermediate	Provisioned	Direct	3	1	5	5
Nadler 1975	*Gorilla gorilla gorilla*	Small	Provisioned	Visual	NA	1.8	NA	25
Nadler et al. 1979	*Gorilla gorilla gorilla*	Small	Provisioned	Visual	-2	2	3	3
Nadler et al. 1985	*Pan troglodytes*	Large	Provisioned	Visual	-10	12	11	11
Nadler et al. 1993	*Hylobates lar*	Small	Provisioned	Visual	-3	1.833	6	6
Phillips & Wheaton 2008	*Mandrillus sphinx*	Intermediate	Provisioned	Visual	0	1	40	40
Reichert et al. 2002	*Pan paniscus*	Large	Provisioned	Visual	-14.304	15.217	23	23
Thierry et al. 1996	*Macaca tonkeana*	Intermediate	Provisioned	Visual	-1.143	2.143	8	8
Whitten & Russell 1996	*Cercocebus torquatus atys*	Intermediate	Provisioned	Visual	-3.286	1	7	7
Wildt et al. 1977	*Papio anubis/cynocephalus*	Large	Provisioned	Visual	-2.096	2	52	40
Young et al. 2013	*Macaca sylvanus*	Intermediate	Non-provisioned	Visual	-5.167	6.083	12	12

A.ii) onset and duration of peak swelling relative to ovulation, per cycle

Reference	Species	Day peak onset	Days peak duration	Individual ID	Swelling measure	Population	Swelling size category
Aujard et al. 1998	*Macaca tonkeana*	-7	11	Eri	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-5	10	Eri	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-9	11	Els	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-8	10	Els	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-5	6	Dai	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-6	9	Dai	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-6	7	Mar	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	NA	6	Veo	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-5	7	Jul	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	-4	6	Jul	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	NA	11	Ver	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	NA	12	Ver	Visual	Provisioned	Intermediate
Aujard et al. 1998	*Macaca tonkeana*	NA	15	Ver	Visual	Provisioned	Intermediate
Barelli et al. 2007	*Hylobates lar*	-4	10	Daow	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-8	12	Daow	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-6	8	Hannah	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-4	6	Hannah	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-4	9	Nasima	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-3	6	Natasha	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-13	5	Natasha	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-13	7	Andromeda	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-3	5	Andromeda	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-7	10	Jenna	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-7	10	Jenna	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	1	8	Cassandra	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-3	8	Cassandra	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-3	9	Brit	Visual	Non-provisioned	Small
Barelli et al. 2007	*Hylobates lar*	-3	13	Brit	Visual	Non-provisioned	Small
Czekala & Sicotte 2000	*Gorilla beringei*	0	1	Mw	Visual	Non-provisioned	Small
Dahl et al. 1991	*Pan troglodytes*	NA	5	NA	Visual	Provisioned	Exaggerated
Dahl et al. 1991	*Pan troglodytes*	NA	1	NA	Visual	Provisioned	Exaggerated
Dahl et al. 1991	*Pan paniscus*	NA	4	NA	Visual	Provisioned	Exaggerated
Dahl et al. 1991	*Pan paniscus*	NA	25	NA	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-9	10	"66"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-3	4	"407"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-14	14	"64"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-9	10	"61"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-9	8	"41"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-18	19	"70"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-10	11	"40"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-9	5	"328"	Visual	Provisioned	Exaggerated
Daspre et al. 2009	*Papio hamadryas anubis*	-9	8	"48"	Visual	Provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	9	Atra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-8	10	Atra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-4	8	Atra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	9	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-5	6	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-7	8	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-5	7	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	6	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	7	Duna	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-7.5	8.5	Eva	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-7.5	8.5	Eva	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-7	9	Isha	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-9	10.5	Isha	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-13	15	Kabisha	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-12	17	Kabisha	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-13	16	Kabisha	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-12	15	Mandy	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-11	14	Mandy	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-8	10	Margot	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	8	Margot	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	7	Margot	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-10	13	Olivia	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-3	16	Sumatra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-11	17	Sumatra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	10	Sumatra	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-8	11	Tita	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	7	Tita	Visual	Non-provisioned	Exaggerated

Deschner et al. 2003	*Pan troglodytes verus*	-7	11	Tita	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	10	Yucca	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-1	5	Zora	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-9	10	Zora	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	8	Zora	Visual	Non-provisioned	Exaggerated
Deschner et al. 2003	*Pan troglodytes verus*	-6	10	Zora	Visual	Non-provisioned	Exaggerated
Engelhardt et al. 2005	*Macaca fascicularis*	-9.5	11	SA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-0.5	5	SA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-21.5	25	FA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-15.5	21	KA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-2.5	9	KA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-13.5	22	AA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-13.5	17	LA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-2.5	8	CA	Visual	Non-provisioned	Intermediate
Engelhardt et al. 2005	*Macaca fascicularis*	-10.5	17	MA	Visual	Non-provisioned	Intermediate
Graham et al. 1972	*Pan troglodytes*	-14	15	ChimpA	Visual	Provisioned	Exaggerated
Graham et al. 1972	*Pan troglodytes*	-3	1	ChimpB	Visual	Provisioned	Exaggerated
Graham et al. 1972	*Pan troglodytes*	-11	12	ChimpC	Visual	Provisioned	Exaggerated
Graham et al. 1977	*Pan troglodytes*	-10	11	NA	Visual	Provisioned	Exaggerated
Graham et al. 1977	*Pan troglodytes*	-10	9	NA	Visual	Provisioned	Exaggerated
Graham et al. 1977	*Pan troglodytes*	-4	5	NA	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-4	4	KO	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-11	14	HE	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-14	14	DZ	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-18	16	DZ	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-3	7	DZ	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-18	23	HO	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-6	7	KO	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-23	26	CC	Visual	Provisioned	Exaggerated
Heistermann et al. 1996	*Pan paniscus*	-2	4	CC	Visual	Provisioned	Exaggerated
Howland et al. 1971	*Pan troglodytes*	-5	7	Chimp1	Visual	Provisioned	Exaggerated
Howland et al. 1971	*Pan troglodytes*	-1	5	Chimp2	Visual	Provisioned	Exaggerated
Howland et al. 1971	*Pan troglodytes*	-16	21	Chimp3	Visual	Provisioned	Exaggerated
Howland et al. 1971	*Pan troglodytes*	-8	17	Chimp4	Visual	Provisioned	Exaggerated
Jurke et al. 2000	*Pan paniscus*	-3	6	NA	Visual	Provisioned	Exaggerated
Jurke et al. 2000	*Pan paniscus*	-3	11	NA	Visual	Provisioned	Exaggerated
McArthur et al. 1981	*Pan troglodytes*	-12	16	ChimpX	Visual	Provisioned	Exaggerated
Mohle et al. 2005	*Macaca sylvanus*	-4	NA	Pix	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-5	NA	Pix	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-1.5	NA	Qu	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-9	NA	Lei	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-8	NA	Ga	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-5.5	NA	Val	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	-4.5	NA	Sa	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	15.5	Pix	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	8.5	Pix	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	8	Pix	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	11.5	Q	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	5.5	Q	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	9.5	Q	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	12	Le	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	8	Le	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	6.5	Sun	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	5.5	Sun	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	9.5	Ga	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	5.5	Ga	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	6	Re	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	7.5	Re	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	NA	Cr	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	16	Cr	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	6	Val	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	11.5	Val	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	6.5	Sa	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	NA	Sa	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	9	Es	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	6	Es	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	14	Lei	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	7.5	Lei	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	15	Fr	Direct	Provisioned	Intermediate
Mohle et al. 2005	*Macaca sylvanus*	NA	11	Fr	Direct	Provisioned	Intermediate
Nadler et al. 1979	*Gorilla gorilla gorilla*	-2	2	GorillaA	Visual	Provisioned	Small
Nadler et al. 1979	*Gorilla gorilla gorilla*	-2	3	GorillaB	Visual	Provisioned	Small
Nadler et al. 1979	*Gorilla gorilla gorilla*	-2	1	GorillaC	Visual	Provisioned	Small
Nadler et al. 1985	*Pan troglodytes*	-13	14	ChimpAA	Visual	Provisioned	Exaggerated
Nadler et al. 1985	*Pan troglodytes*	-14	16	ChimpBB	Visual	Provisioned	Exaggerated
Nadler et al. 1993	*Hylobates lar*	-1	1	7391	Visual	Provisioned	Small
Nadler et al. 1993	*Hylobates lar*	-4	3	B8242	Visual	Provisioned	Small
Nadler et al. 1993	*Hylobates lar*	-1	1	7391	Visual	Provisioned	Small

Nadler et al. 1993	*Hylobates lar*	-3	4	B8242	Visual	Provisioned	Small
Nadler et al. 1993	*Hylobates lar*	0	1	B8080	Visual	Provisioned	Small
Nadler et al. 1993	*Hylobates lar*	-5	1	101083	Visual	Provisioned	Small
Reichert et al. 2002	*Pan paniscus*	-8	11	Kom	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-6	10	Kic	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-13	16	Kic	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-18	7	Kam	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-9	11	Kam	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-3	2	Bon	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-16	13	Sal	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-17	23	Sal	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-20	26	Sal	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-22	28	Sal	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-27	29	Uke	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-12	17	Uke	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-25	9	Uke	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-12	14	Uke	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-23	21	Nat	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-11	10	Nat	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-18	20	Nat	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-18	21	Nat	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-16	17	Mar	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-8	9	Mar	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-9	13	Mar	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-11	14	Mar	Visual	Provisioned	Exaggerated
Reichert et al. 2002	*Pan paniscus*	-7	9	Mar	Visual	Provisioned	Exaggerated
Thierry et al. 1996	*Macaca tonkeana*	-1	2	CAT	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	-2	2	CAT	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	-1	2	BEA	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	0	2	BEA	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	-1	2	BEA	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	1	3	VEO	Visual	Provisioned	Intermediate
Thierry et al. 1996	*Macaca tonkeana*	-4	2	BOU	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-2.5	8	FW	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-1	5	FW	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	9	7	FQ	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-10	8	FQ	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-3	7	FD	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-2.5	6	FD	Visual	Provisioned	Intermediate
Whitten & Russell 1996	*Cercocebus torquatus atys*	-4	8	FV	Visual	Provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-9	6	Ne	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-3	4	Na	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-2	5	Mo	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-4	3	Ke	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	0	3	Ke	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-12	14	Ho	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-13	10	He	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-5	4	GI	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-7	10	Jo	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-5	4	Fe	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	3	3	Da	Visual	Non-provisioned	Intermediate
Young et al. 2013	*Macaca sylvanus*	-5	6	Da	Visual	Non-provisioned	Intermediate

Table A.i) and ii) article citations: *Aidara, D., et al. (1981), J. Reprod. Fertil., 62: 475–481; Aujard, F., et al. (1998), Am. J. Primatol., 46: 285–309; Barelli, C., et al. (2007), Horm. Behav., 51: 221–230; Blakley, G. B., et al.. (1981), Laboratory Animals, 15:351–353; Brauch, K., et al.. (2007). Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (Macaca sylvanus) of Gibraltar. Horm. Behav., 52:375–383; Czekala, N., & Sicotte, P. (2000), Am. J. of Primatol., 51:209–215; Dahl, J. F. et al. (1991,. Am. J. Primatol., 24:195–209; Daspre, A., et al. (2009), Am. J. Primatol, 71:529–538; Deschner, T., et al. (2003), Anim. Behav., 66:551–560; Deschner, T., et al. (2004), Horm. Behav. 46:204–215; Emery, M. A., & Whitten, P. L. (2003), Behav. Ecol. Sociobiol., 54:340–351; Emery Thompson, M. (2005), Am. J. Primatol,, 67:137–158; Engelhardt, et al. (2005), Horm. Behav., 47:195–204; Gesquiere, L. R., et al. (2007), Horm. Behav., 51:114–125; Graham, C. E. et al. (1977), J. Reprod. Ferti 50:23–28; Graham, C. E., et al. (1972), Endocrinology, 91: 13; Gust, D. A. (1994), Int. J. Primatol, 15:289–301; Higham, J. P., et al. (2012), BMC Ev. Biol., 12:89; Howland, B. E., et al. (1971), Biol. Reprod., 4:101–105; Jurke, M., et al. (2000), Primates, 41: 311–319; McArthur, J. W. et al. (1981), Am. J. Primatol., 1:265–270; Mohle, U., et al.. (2005), Am. J. Primatol., 66:351–368, Nadler, R. D. (1975), Science, 189:813–814; Nadler, R. D. et al. (1993), J. Endocrinol., 136:447–455; Nadler, R. D. et al. (1979). Endocrinology, 105:290–296. Nadler, R. D., et al. (1985), Am. J. Primatol, 9:273–284; Phillips, R. S., & Wheaton, C. J. (2008), Zoo Biol., 27:320–330; Reichert, K. E., et al. (2002), Ethology, 108: 583–600; Thierry, B., et al. (1996). Am. J. Primatol.,, 39:, 47–62; Whitten, P. L., & Russell, E. (1996), Am. J. Primatol.,, 40(1), 67–82; Wildt, D. E., et al. (1977), Primates, 18, 261–270: Young, C. et al. (2013), Horm. Behav. 63:32–39.*

A.iii) peak swelling duration relative to ovarian cycle length, per species

Species	Cycle length (days)	Duration peak swelling (per article data)	Duration peak swelling (per cycle data)	Swelling size category
Gorilla gorilla gorilla	28.5	1.90	2.00	Small
Hylobates lar	27	5.12	6.52	Small
Macaca fascicularis	29.5	15.00	15.00	Intermediate
Macaca nemestrina	36	5.00	NA	Intermediate
Macaca nigra	36	2.00	NA	Intermediate
Macaca sylvanus	31	2.69	8.13	Intermediate
Macaca tonkeana	35	2.07	6.80	Intermediate
Mandrillus sphinx	34.5	1.00	NA	Intermediate
Pan paniscus	42	12.75	14.19	Large
Pan troglodytes	36.5	7.77	10.24	Large
Papio anubis	34.5	5.50	9.89	Large
Papio cynocephalus	32	3.00	NA	Large

Table A.iii) *duration of peak swelling, summarised for each species by taking a mean weighted by sample size (N ovarian cycles) from both the per article and per cycle datasets (see tables A.i and A.ii). Cycle lengths were obtained from Harvey & Clutton-Brock (1985) and van Schaik (1999) (see Chapter 3 for full citations). Where cycle lengths differed between sources, means were taken across both sources.*

A.iv) Effect sizes for between-female correlations of swelling size and female quality

Author	Species	Swelling size dimension	Female quality measure	Population	R	N
Domb & Pagel 2001	*Papio cynocephalus anubis*	Depth	Fecundity	Non-provisioned	0.52	20
Domb & Pagel 2001	*Papio cynocephalus anubis*	Depth	Fecundity	Non-provisioned	0.3	20
Domb & Pagel 2001	*Papio cynocephalus anubis*	Depth	Fecundity	Non-provisioned	0.38	20
Domb & Pagel 2001	*Papio cynocephalus anubis*	Depth	Fecundity	Non-provisioned	0.29	20
Domb & Pagel 2001	*Papio cynocephalus anubis*	Width	Fecundity	Non-provisioned	0.29	21
Domb & Pagel 2001	*Papio cynocephalus anubis*	Width	Fecundity	Non-provisioned	0.1	21
Domb & Pagel 2001	*Papio cynocephalus anubis*	Width	Fecundity	Non-provisioned	0.27	21
Domb & Pagel 2001	*Papio cynocephalus anubis*	Width	Fecundity	Non-provisioned	0.36	21
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Age	Non-provisioned	-0.61	22
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Fecundity	Non-provisioned	0.67	22
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Fecundity	Non-provisioned	0.55	22
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Fecundity	Non-provisioned	0.53	22
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Fecundity	Non-provisioned	0.4	22
Domb & Pagel 2001	*Papio cynocephalus anubis*	Length	Rank	Non-provisioned	0.087	18
Emery & Whitten 2003	*Pan troglodytes*	Anal width	Age	Provisioned	0.547	14
Emery & Whitten 2003	*Pan troglodytes*	Labial width	Age	Provisioned	0.619	14
Emery & Whitten 2003	*Pan troglodytes*	Area	Age	Provisioned	-0.428	14
Emery & Whitten 2003	*Pan troglodytes*	Height	Age	Provisioned	-0.448	14
Emery & Whitten 2003	*Pan troglodytes*	Area	Body condition	Provisioned	0.39	14
Emery & Whitten 2003	*Pan troglodytes*	Area	Parity	Provisioned	-0.593	14
Emery & Whitten 2003	*Pan troglodytes*	Height	Parity	Provisioned	-0.536	14
Fitzpatrick unpub	*Papio cynocephalus*	Width	Age	Non-provisioned	0.398	46
Fitzpatrick unpub	*Papio cynocephalus*	Width	Parity	Non-provisioned	0.345	46
Fitzpatrick unpub	*Papio cynocephalus*	Width	Rank	Non-provisioned	-0.183	46
Huchard et al. 2009	*Papio ursinus*	Area	Age	Non-provisioned	-0.16591	11
Huchard et al. 2009	*Papio ursinus*	Area	Body condition	Non-provisioned	-0.09091	11
Huchard et al. 2009	*Papio ursinus*	Area	Rank	Non-provisioned	0.41458	11
Mohle 2005	*Macaca sylvanus*	Area	Age	Provisioned	0.077	12
Mohle 2005	*Macaca sylvanus*	Area	Body condition	Provisioned	-0.092	9
Mohle 2005	*Macaca sylvanus*	Area	Rank	Provisioned	0.287	12
Mohle 2005	*Macaca sylvanus*	Area	Rank	Provisioned	0.135	12
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Age	Provisioned	-0.219	26
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Parity	Provisioned	0.445	26
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Rank	Provisioned	-0.369	26
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Body condition	Provisioned	0.338	26
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Fecundity	Provisioned	0.244	22
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Fecundity	Provisioned	-0.351	16
Setchell & Wickings 2004	*Mandrillus sphinx*	Depth	Fecundity	Provisioned	-0.027	24
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Age	Provisioned	0.101	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Parity	Provisioned	0.452	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Rank	Provisioned	-0.081	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Body condition	Provisioned	0.311	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Fecundity	Provisioned	-0.105	19
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Fecundity	Provisioned	0.021	15
Setchell & Wickings 2004	*Mandrillus sphinx*	Width	Fecundity	Provisioned	-0.187	21
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Age	Provisioned	0.049	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Body condition	Provisioned	0.195	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Fecundity	Provisioned	-0.073	22
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Fecundity	Provisioned	0.221	16
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Fecundity	Provisioned	-0.061	24
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Parity	Provisioned	0.373	29
Setchell & Wickings 2004	*Mandrillus sphinx*	Length	Rank	Provisioned	-0.195	29
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	0.101	10
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	0.154	10
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	0.324	10
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	0.25	10
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	0.18	10
Setchell et al. 2006	*Mandrillus sphinx*	Width	Parasites	Provisioned	-0.167	29
Setchell et al. 2006	*Mandrillus sphinx*	Width	Genetic diversity	Provisioned	0.019	30
Setchell et al. 2006	*Mandrillus sphinx*	Height	Genetic diversity	Provisioned	0.023	32
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	-0.14	10
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	0.261	10
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	0.084	10
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	0.049	10
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	0.047	10
Setchell et al. 2006	*Mandrillus sphinx*	Height	Parasites	Provisioned	0.007	31

Table A.iiii) article citations: Domb, L. G., & Pagel, M. (2001), *Nature*, 410: 204–206; Emery, M. A., & Whitten, P. L. (2003), *Behav. Ecol. Sociobiol*., 54:340–351.Fitzpatrick, C. L., et al. (n.d.). Unpublished data; Huchard, E., et al. (2009), *Proc. R. Soc. B. Lond,* 276:1889–97; Mohle, U., et al.. (2005), *Am. J. Primatol.*, 66:351–368; Setchell, J. M. et al. (2006), *Behav. Ecol. Sociobiol.*, 61: 305–315. Setchell, J. M., & Wickings, E. J. (2004). *Behav. Ecol*, 15:438–445.

Appendix B: dataset for analyses presented in chapter 4

Species	Swelling downcoded	Swelling upcoded	Mating system downcoded	Mating system upcoded	Male group size	Female group size	STD prevalence	Penile length	Testes mass	Male body mass	Gestation length days	Weaning age	Adult body mass	Female canine length	Female body mass
Allenopithecus nigroviridis	Y	Y	MMMF	MMMF	NA	NA	NA	NA	16.96	6.12	NA	106.15	4749.96	8.33	3.18
Cercocebus agilis	Y	Y	NA	NA	NA	NA	NA	NA	NA	9.50	NA	NA	7105.62	8.65	5.66
Cercocebus galeritus	Y	Y	MMMF	MMMF	2.00	6.00	0.27	NA	NA	9.61	174.43	NA	7077.66	NA	5.26
Cercocebus torquatus	Y	Y	MMMF	MMMF	NA	NA	0.33	NA	NA	9.47	168.98	NA	7293.07	NA	5.50
Cercocebus torquatus atys	Y	Y	MMMF	MMMF	NA	NA	NA	NA	25.10	11.00	165.08	NA	6941.24	9.53	6.20
Cercopithecus ascanius	N	N	PG	PG	1.00	9.50	0.00	3.00	3.00	3.70	148.50	146.54	3540.24	10.30	2.92
Cercopithecus cephus	N	N	PG	PG	NA	3.40	0.10	3.00	NA	4.29	169.51	362.93	3444.88	9.59	2.88
Cercopithecus diana	N	N	PG	PG	NA	7.00	NA	3.00	NA	5.20	NA	362.93	4358.91	12.32	3.90
Cercopithecus hamlyni	N	N	NA	NA	NA	NA	NA	3.00	NA	5.49	NA	NA	NA	NA	3.36
Cercopithecus lhoesti	N	N	PG	PG	NA	NA	0.00	NA	NA	5.97	NA	NA	5307.47	10.82	3.45
Cercopithecus mitis	N	N	PG	PG	1.00	18.00	NA	3.00	NA	7.93	138.39	688.08	5041.29	10.14	4.25
Cercopithecus neglectus	N	N	PG	PG	1.00	3.00	0.19	3.00	NA	7.35	172.07	417.62	5324.52	11.64	4.13
Cercopithecus nictitans	N	N	PG	PG	NA	4.10	0.12	3.00	NA	6.67	169.51	NA	5256.91	11.22	4.26
Cercopithecus solatus	N	N	PG	PG	NA	NA	NA	NA	NA	6.89	NA	NA	5256.91	NA	3.92
Chlorocebus aethiops	N	N	MMMF	MMMF	3.00	4.25	0.40	NA	13.00	4.26	NA	217.76	3695.99	11.91	2.98
Colobus angolensis	N	N	NA	NA	1.30	1.60	NA	NA	NA	9.68	NA	NA	8990.31	9.57	7.57
Colobus guereza	N	N	MMMF	MMMF	1.00	3.00	0.24	2.00	2.98	13.50	169.02	387.79	9925.88	14.34	9.20
Colobus polykomos	N	N	MMMF	MMMF	5.50	4.35	NA	2.00	10.70	9.90	172.69	213.78	8797.29	10.81	8.30
Colobus satanas	N	N	NA	NA	1.67	5.50	0.00	NA	NA	10.40	192.76	NA	9055.32	NA	7.42
Colobus vellerosus	N	N	NA	NA	3.00	6.50	NA	NA	NA	8.50	NA	NA	7700.18	NA	6.90
Erythrocebus patas	N	N	PG	PG	3.00	12.50	0.15	3.00	7.20	12.40	167.20	211.79	7966.30	12.43	6.50
Gorilla beringei	N	N	NA	NA	1.00	3.00	NA	NA	28.96	162.50	NA	NA	149325.19	NA	97.50
Gorilla gorilla gorilla	N	N	PG	PG	1.00	2.25	0.07	1.00	15.01	170.40	257.00	920.35	112588.99	17.40	71.50
Hylobates agilis	N	N	MG	MG	NA	NA	NA	1.00	6.32	5.88	NA	NA	5829.08	NA	5.82
Hylobates lar	N	N	MG	MG	1.00	1.00	NA	NA	5.50	5.90	212.91	725.86	5578.61	15.79	5.34
Hylobates moloch	N	N	MG	MG	NA	NA	NA	NA	6.10	6.58	241.20	NA	5860.81	NA	6.25
Hylobates muelleri	N	N	MG	MG	NA	NA	NA	NA	NA	5.71	206.70	NA	5909.81	NA	5.35
Hylobates pileatus	N	N	MG	MG	NA	NA	NA	NA	NA	5.50	200.16	635.13	5542.37	16.87	5.44
Lophocebus albigena	Y	Y	MMMF	MMMF	3.75	6.00	0.18	NA	NA	8.25	182.64	211.71	7418.71	8.75	6.02
Lophocebus aterrimus	Y	Y	MMMF	MMMF	3.80	NA	NA	NA	13.78	7.84	NA	NA	6510.37	8.82	5.76
Macaca arctoides	N	N	MMMF	MMMF	NA	NA	0.01	5.00	48.20	12.20	176.60	377.66	9358.04	NA	8.40
Macaca assamensis	N	Y	MMMF	MMMF	NA	NA	NA	NA	NA	11.30	NA	NA	8546.89	NA	6.90
Macaca cyclopis	Y	Y	PG	MMMF	3.30	NA	NA	NA	NA	6.00	161.06	205.24	5748.94	NA	4.94
Macaca fascicularis	N	Y	MMMF	MMMF	4.00	6.75	0.05	3.00	35.20	5.36	164.69	283.53	4569.32	10.67	3.59
Macaca fuscata	N	N	MMMF	MMMF	3.00	9.00	0.24	NA	72.30	11.00	172.99	265.04	10114.76	9.59	8.03
Macaca maura	Y	Y	MMMF	MMMF	4.25	NA	0.17	NA	NA	9.72	167.19	497.16	7290.30	NA	6.05
Macaca mulatta	N	N	MMMF	MMMF	2.50	9.00	0.73	NA	46.20	7.70	166.07	304.16	6455.19	8.19	5.37
Macaca nemestrina	Y	Y	MMMF	MMMF	3.00	22.00	0.09	4.00	66.70	11.20	171.00	292.60	7820.78	12.24	6.50
Macaca nigra	Y	Y	MMMF	MMMF	6.00	30.00	0.16	5.00	NA	9.89	172.43	365.00	7359.39	11.38	5.47
Macaca ochreata	Y	Y	NA	NA	NA	NA	0.18	NA	NA	5.30	NA	NA	2745.50	NA	2.60
Macaca radiata	N	N	MMMF	MMMF	7.00	9.00	NA	NA	48.20	6.67	161.56	332.25	4999.99	NA	3.85
Macaca silenus	Y	Y	PG	MMMF	1.75	7.00	NA	NA	42.00	NA	172.00	362.93	5995.25	10.12	NA
Macaca sinica	N	N	MMMF	MMMF	5.00	9.50	0.17	3.00	NA	5.68	180.90	NA	4655.99	9.96	3.20
Macaca sylvanus	Y	Y	MMMF	MMMF	9.00	10.50	0.12	NA	NA	11.10	164.84	210.25	11471.53	11.29	NA
Macaca thibetana	N	N	NA	NA	4.50	9.50	NA	NA	NA	15.20	169.02	451.79	10593.06	NA	9.50
Macaca tonkeana	Y	Y	NA	NA	1.00	NA	0.12	NA	NA	14.90	NA	NA	10035.53	10.12	9.00
Mandrillus leucophaeus	Y	Y	PG	PG	NA	NA	0.50	5.00	41.05	17.50	179.22	486.66	14253.30	11.70	12.50
Mandrillus sphinx	Y	Y	PG	PG	3.00	14.00	0.59	5.00	68.00	31.60	173.99	348.01	16685.06	9.42	12.90
Miopithecus talapoin	Y	Y	MMMF	MMMF	13.00	27.00	0.22	NA	5.20	2.50	164.38	178.98	1248.86	6.70	2.00
Nasalis larvatus	N	N	PG	MMMF	NA	5.00	NA	2.00	13.80	20.40	165.04	211.75	12265.65	10.42	9.82
Pan paniscus	Y	Y	MMMF	MMMF	8.00	8.00	NA	5.00	135.20	45.00	235.24	1081.31	35119.95	11.24	33.20
Pan troglodytes schweinfurthii	Y	Y	MMMF	MMMF	12.30	NA	NA	NA	NA	42.70	NA	NA	NA	15.60	33.70
Pan troglodytes troglodytes	Y	Y	MMMF	MMMF	10.00	35.00	0.42	5.00	157.90	59.70	231.49	1260.81	45000.00	NA	NA
Pan troglodytes verus	Y	Y	MMMF	MMMF	5.20	NA	NA	NA	NA	46.30	NA	NA	NA	NA	41.60
Papio anubis	Y	Y	MMMF	MMMF	14.00	34.00	0.07	NA	93.50	25.10	178.96	596.60	17728.56	15.95	13.30
Papio cynocephalus	Y	Y	MMMF	MMMF	8.00	13.00	0.25	NA	52.00	21.80	172.99	450.42	15822.15	9.12	12.30
Papio hamadryas	Y	Y	PG	PG	1.00	2.00	0.10	5.00	27.10	16.90	180.00	363.96	14007.08	11.17	9.90

Papio papio	Y	Y	MMMF	MMMF	NA	8.00	0.22	NA	88.90	NA	184.42	NA	18026.05	NA	12.10
Papio ursinus	Y	Y	MMMF	MMMF	7.00	14.50	0.29	NA	72.00	29.80	185.92	877.09	17729.44	12.12	14.80
Piliocolobus badius	Y	Y	PG	MMMF	3.50	9.50	0.53	NA	NA	12.30	151.41	783.93	8430.40	8.55	8.25
Piliocolobus kirkii	Y	Y	NA	NA	4.30	13.45	NA	NA	NA	5.80	165.00	NA	7158.29	7.62	5.46
Piliocolobus preussi	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	195.00	NA	8865.71	NA	NA
Piliocolobus tephrosceles	Y	Y	NA	NA	4.00	12.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Pongo pygmaeus	N	N	PG	PG	1.00	1.00	0.07	NA	34.20	78.50	259.42	1088.80	53408.29	15.95	35.80
Procolobus verus	Y	Y	NA	NA	1.25	2.00	0.00	NA	NA	4.70	167.84	NA	3977.86	7.43	4.20
Rhinopithecus bieti	N	N	NA	NA	NA	NA	NA	NA	NA	15.00	170.00	NA	11000.54	NA	9.96
Rhinopithecus roxellana	N	N	MMMF	MMMF	NA	NA	NA	NA	NA	17.90	199.34	NA	13456.80	8.00	11.60
Semnopithecus entellus	N	N	PG	MMMF	1.00	12.00	0.00	NA	NA	13.00	197.70	402.10	12679.29	10.83	9.89
Symphalangus syndactylus	N	N	MG	MG	1.00	1.00	NA	1.00	NA	11.90	230.66	635.38	10839.00	18.04	10.70
Theropithecus gelada	N	N	PG	PG	1.00	4.00	0.00	3.00	NA	19.00	178.64	494.95	15964.11	12.27	11.70
Trachypithecus cristatus	N	N	PG	PG	1.00	9.30	NA	NA	6.20	6.61	NA	362.93	7176.81	10.94	5.76
Trachypithecus johnii	N	N	PG	PG	1.00	5.10	NA	NA	NA	12.00	NA	NA	10595.08	NA	11.20
Trachypithecus obscurus	N	N	PG	MMMF	1.00	5.00	NA	2.00	4.80	7.90	146.63	362.93	7247.88	8.51	6.26
Trachypithecus vetulus	N	N	NA	NA	1.00	3.90	0.00	NA	NA	8.17	204.72	245.78	7205.08	NA	5.90

Table B: *Presence of exaggerated swellings, mating system, male group size (N male adults typically present in social group), female group size (N female adults typically present in social group), STD prevalence (proportion), penile length (ranked measure), testes mass (g), male body mass (kg), gestation length (days), weaning age (days), adult body mass (kg), female canine length (mm), female body mass (kg)*

Appendix C: dataset for analyses presented in chapter 5

Species	Gs1	Deception count	Deception count (males)	Deception count (females)	Innovation count	Innovation count (males)	Innovation count (females)	Research effort	Testes mass	Male body mass	Size dimorphism	Mating system downcoded	Mating system upcoded	Group size
Allenopithecus nigroviridis	-0.13	NA	NA	NA	0	NA	NA	6	16.96	6.12	1.97	MMMF	MMMF	40
Allocebus trichotis	-0.13	NA	NA	NA	0	NA	NA	6	NA	NA	NA	NA	NA	1
Alouatta belzebul	-0.79	NA	NA	NA	0	NA	NA	15	NA	7.27	0.22	NA	NA	7.4
Alouatta caraya	-1.63	NA	NA	NA	1	NA	NA	45	18.37	6.42	0.78	PG	MMMF	8.9
Alouatta guariba	NA	NA	NA	NA	1	1	0	37	NA	6.73	NA	MMMF	MMMF	7.4
Alouatta palliata	-0.38	2	2	0	0	NA	NA	79	23	7.15	0.29	MMMF	MMMF	13.1
Alouatta pigra	-1.18	NA	NA	NA	0	NA	NA	25	NA	11.4	1.52	NA	NA	5.5
Alouatta sara	0.14	NA	NA	NA	0	NA	NA	4	NA	NA	NA	NA	NA	NA
Alouatta seniculus	-0.11	NA	NA	NA	4	NA	NA	82	NA	6.69	0.11	PG	PG	7.9
Aotus azarai	-1.08	NA	NA	NA	0	NA	NA	22	NA	1.18	-1.01	MG	MG	4.1
Aotus brumbacki	1.42	NA	NA	NA	0	NA	NA	0	NA	NA	NA	NA	NA	NA
Aotus infulatus	-0.13	NA	NA	NA	0	NA	NA	6	NA	1.19	-1.01	NA	NA	NA
Aotus lemurinus	-0.84	NA	NA	NA	0	NA	NA	16	NA	0.92	-0.57	MMMF	MMMF	NA
Aotus nancymaae	-0.01	NA	NA	NA	0	NA	NA	5	NA	0.79	-0.69	NA	NA	4
Aotus nigriceps	0.87	NA	NA	NA	0	NA	NA	1	NA	0.88	-1.58	NA	NA	3.3
Aotus trivirgatus	-1.83	NA	NA	NA	0	NA	NA	58	1.2	0.81	-0.32	MG	MG	3.15
Aotus vociferans	-0.01	NA	NA	NA	1	NA	NA	12	NA	0.71	-0.7	NA	NA	3.3
Arctocebus calabarensis	0.87	NA	NA	NA	0	NA	NA	1	NA	0.31	-0.58	PG	MMMF	1
Ateles belzebuth	-0.63	NA	NA	NA	0	NA	NA	12	NA	8.29	-0.8	MMMF	MMMF	14.5
Ateles fusciceps	0.14	NA	NA	NA	0	NA	NA	4	NA	8.89	-1.2	MMMF	MMMF	NA
Ateles geoffroyi	-0.35	1	0	1	0	NA	NA	58	13.4	7.78	-0.75	MMMF	MMMF	42
Ateles paniscus	-1.32	NA	NA	NA	0	NA	NA	30	NA	9.11	-0.72	MMMF	MMMF	20
Avahi laniger	-0.49	NA	NA	NA	0	NA	NA	10	2.09	1.03	-1.94	NA	NA	2
Avahi occidentalis	-0.13	NA	NA	NA	0	NA	NA	6	NA	0.81	-0.57	NA	NA	3
Brachyteles arachnoides	-1.82	NA	NA	NA	0	NA	NA	57	NA	9.61	-0.27	MMMF	MMMF	19.6
Bunopithecus hoolock	-1.15	NA	NA	NA	0	NA	NA	24	NA	6.87	-1.04	MG	MG	3.2
Cacajao calvus	-0.56	NA	NA	NA	0	NA	NA	11	5.8	3.45	-0.12	MMMF	MMMF	23.7
Cacajao melanocephalus	-0.33	NA	NA	NA	0	NA	NA	8	NA	3.16	-0.24	NA	NA	30
Callicebus donacophilus	0.87	NA	NA	NA	0	NA	NA	1	NA	0.99	-0.41	NA	NA	1
Callicebus hoffmannsi	1.42	NA	NA	NA	0	NA	NA	0	NA	1.09	-0.55	NA	NA	1
Callicebus moloch	-0.93	NA	NA	NA	0	NA	NA	18	NA	1.02	-0.51	MG	MG	2.95
Callicebus personatus	-0.97	NA	NA	NA	0	NA	NA	19	NA	1.27	-1.21	MG	MMMF	2.35
Callicebus torquatus	0.14	NA	NA	NA	0	NA	NA	4	NA	1.28	-0.58	MG	MMMF	3.85
Callimico goeldii	-1.6	0	NA	NA	1	1	0	43	NA	NA	NA	MG	MG	6.85
Callithrix argentata	-0.84	0	NA	NA	0	NA	NA	16	1.83	0.33	-1.07	NA	NA	9.5
Callithrix aurita	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	6
Callithrix geoffroyi	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Callithrix humeralifera	0.14	NA	NA	NA	0	NA	NA	4	NA	0.36	-0.93	MG	PA	8.5
Callithrix jacchus	-0.92	0	NA	NA	1	0	1	161	1.3	0.36	-0.92	MG	PA	8.55
Callithrix mauesi	NA	NA	NA	NA	0	NA	NA	NA	NA	0.35	-1.33	NA	NA	NA
Callithrix penicillata	NA	NA	NA	NA	0	NA	NA	NA	NA	0.34	-0.16	NA	NA	5.9
Callithrix pygmaea	-0.84	NA	NA	NA	1	NA	NA	36	0.33	0.11	-1.01	MG	PA	6
Cebus albifrons	-0.17	NA	NA	NA	0	NA	NA	13	NA	3.18	0.56	MMMF	MMMF	25
Cebus apella	5.79	1	0	1	39	5	6	249	4.64	3.65	0.74	MMMF	MMMF	7.9
Cebus capucinus	2.66	0	NA	NA	4	1	0	60	NA	3.68	0.74	PG	PG	18.15
Cebus olivaceus	-0.31	NA	NA	NA	4	3	1	18	NA	3.29	0.27	PG	MMMF	11.45
Cercocebus agilis	NA	NA	NA	NA	NA	NA	NA	NA	NA	9.5	1.3	NA	NA	NA
Cercocebus galeritus	-0.07	NA	NA	NA	0	NA	NA	19	NA	NA	1.68	MMMF	MMMF	20.35
Cercocebus torquatus	-0.85	NA	NA	NA	0	NA	NA	32	25.1	9.47	1.41	MMMF	MMMF	26.85

Cercocebus torquatus atys	NA	NA	NA	NA	NA	NA	NA	NA	25.1	11	1.53	MMMF	MMMF	35
Cercopithecus ascanius	-0.03	0	NA	NA	1	1	0	26	3	3.7	0.12	PG	PG	26.3
Cercopithecus campbelli	-0.56	NA	NA	NA	0	NA	NA	11	NA	4.5	1.35	NA	NA	11
Cercopithecus cephus	-0.33	NA	NA	NA	0	NA	NA	8	NA	4.29	0.84	PG	PG	11
Cercopithecus diana	-0.08	1	1	0	0	NA	NA	28	NA	5.2	0.32	PG	PG	24.95
Cercopithecus erythrogaster	0.31	NA	NA	NA	0	NA	NA	3	NA	4.1	1.48	NA	NA	NA
Cercopithecus erythrotis	0.31	NA	NA	NA	0	NA	NA	3	NA	4.27	NA	NA	NA	NA
Cercopithecus hamlyni	0.14	NA	NA	NA	0	NA	NA	4	NA	5.49	1.24	PG	PG	NA
Cercopithecus lhoesti	-0.24	NA	NA	NA	0	NA	NA	7	NA	5.97	1.49	PG	PG	17.4
Cercopithecus mitis	-0.52	0	NA	NA	4	1	0	56	NA	7.93	1.8	PG	PG	16
Cercopithecus mona	0.99	3	2	0	0	NA	NA	8	NA	5.1	NA	PG	PG	NA
Cercopithecus neglectus	-0.89	NA	NA	NA	0	NA	NA	17	NA	7.35	1.59	PG	PG	4.5
Cercopithecus nictitans	-0.24	NA	NA	NA	0	NA	NA	7	NA	6.67	1.02	PG	PG	16
Cercopithecus petaurista	-0.01	NA	NA	NA	0	NA	NA	5	NA	4.4	0.93	NA	NA	14
Cercopithecus pogonias	-0.33	NA	NA	NA	0	NA	NA	8	NA	4.26	0.78	NA	NA	15
Cercopithecus preussi	0.54	NA	NA	NA	0	NA	NA	2	NA	NA	NA	NA	NA	3
Cercopithecus solatus	-0.13	NA	NA	NA	0	NA	NA	6	NA	6.89	1.54	PG	PG	10
Cercopithecus wolfi	-0.24	NA	NA	NA	0	NA	NA	7	NA	3.91	0.45	NA	NA	NA
Cheirogaleus major	0.31	NA	NA	NA	0	NA	NA	3	2.3	0.44	0.16	PG	PG	1
Cheirogaleus medius	-0.69	NA	NA	NA	0	NA	NA	13	1.12	0.19	-0.2	PG	MMMF	1
Chiropotes satanas	-1.05	NA	NA	NA	2	NA	NA	21	NA	2.9	-0.43	MMMF	MMMF	14.4
Chlorocebus aethiops	-0.19	1	1	0	4	1	1	91	13	4.26	0.66	MMMF	MMMF	NA
Chlorocebus sabaeus	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.3	1.16	NA	NA	NA
Colobus angolensis	-0.84	NA	NA	NA	0	NA	NA	16	NA	9.68	0.05	NA	NA	10.9
Colobus guereza	-1.58	0	NA	NA	1	1	0	42	2.98	13.5	0.64	PG	PG	7.6
Colobus polykomos	-0.89	0	NA	NA	0	NA	NA	17	10.7	9.9	-0.27	PG	MMMF	10.2
Colobus satanas	-0.49	0	NA	NA	0	NA	NA	10	NA	10.4	0.46	NA	NA	15.5
Colobus vellerosus	NA	NA	NA	NA	NA	NA	NA	NA	NA	8.5	-0.1	NA	NA	16
Daubentonia madagascariensis	-0.32	NA	NA	NA	4	NA	NA	52	NA	2.62	-0.68	PG	PG	1
Erythrocebus patas	1.61	1	1	0	1	1	0	33	7.2	12.4	1.85	PG	PG	28
Eulemur coronatus	-0.56	NA	NA	NA	0	NA	NA	11	NA	1.28	-0.06	MMMF	MMMF	6.95
Eulemur fulvus albocollaris	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.95	-1.33	NA	NA	NA
Eulemur fulvus fulvus	-1.58	NA	NA	NA	3	0	1	81	7.78	2.4	-0.91	MMMF	MMMF	9.15
Eulemur fulvus rufus	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.18	-1.04	NA	NA	9.5
Eulemur fulvus sanfordi	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.87	-0.78	NA	NA	7.7
Eulemur macaco flavifrons	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.88	-0.75	NA	NA	NA
Eulemur macaco macaco	0.06	NA	NA	NA	1	0	1	32	16.65	2.4	-1.07	MMMF	MMMF	9.2
Eulemur mongoz	-0.69	NA	NA	NA	1	NA	NA	13	NA	1.41	-1.3	MG	MG	2.7
Eulemur rubriventer	-0.69	NA	NA	NA	0	NA	NA	13	NA	1.98	-0.79	MG	MG	3.3
Euoticus elegantulus	0.87	NA	NA	NA	0	NA	NA	1	NA	0.29	-1.14	PG	PG	1
Galago alleni	0.54	NA	NA	NA	0	NA	NA	2	1.6	0.28	-0.52	PG	PG	6
Galago granti	1.42	NA	NA	NA	0	NA	NA	0	NA	NA	NA	NA	NA	NA
Galago matschiei	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.21	-0.73	NA	NA	1
Galago moholi	-0.74	NA	NA	NA	0	NA	NA	14	NA	0.19	-0.25	PG	MMMF	1
Galago senegalensis	-1.01	NA	NA	NA	0	NA	NA	20	1.66	0.23	-0.03	PG	MMMF	3.5
Galagoides demidoff	-0.01	NA	NA	NA	0	NA	NA	5	0.85	0.06	-0.25	PG	MMMF	5.5
Galagoides zanzibaricus	1.42	NA	NA	NA	0	NA	NA	0	NA	0.15	-0.19	MG	PG	1
Gorilla beringei	NA	NA	NA	NA	NA	NA	NA	NA	28.96	162.5	0.93	NA	NA	NA
Gorilla gorilla gorilla	4.68	13	8	8	25	3	6	517	15.01	170.4	2.55	PG	PG	6
Gorilla gorilla graueri	NA	NA	NA	NA	NA	NA	NA	NA	NA	175.2	2.71	NA	NA	NA

Hapalemur aureus	-0.01	NA	NA	NA	0	NA	NA	5	NA	1.52	-0.44	NA	NA	3
Hapalemur griseus	-1.54	NA	NA	NA	0	NA	NA	40	NA	0.75	-0.25	MG	MMMF	3.1
Hapalemur griseus griseus	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.75	-0.27	NA	NA	NA
Hapalemur simus	-0.33	NA	NA	NA	0	NA	NA	8	NA	2.15	1.4	NA	NA	NA
Hylobates agilis	-0.84	NA	NA	NA	0	NA	NA	16	6.32	5.88	-0.97	MG	MG	4.2
Hylobates klossii	0.14	NA	NA	NA	0	NA	NA	4	NA	5.67	-1.2	MG	MG	3
Hylobates lar	-2.14	NA	NA	NA	0	NA	NA	86	5.5	5.9	-0.56	MG	MG	3.2
Hylobates moloch	-0.84	NA	NA	NA	0	NA	NA	16	6.1	6.58	-0.79	MG	MG	2.15
Hylobates muelleri	-0.01	NA	NA	NA	0	NA	NA	5	NA	5.71	-0.71	MG	MG	3.2
Hylobates pileatus	0.44	1	0	1	1	1	0	16	NA	5.5	-0.95	MG	MG	3.25
Indri indri	-0.33	NA	NA	NA	0	NA	NA	8	NA	5.83	-1.74	MG	MG	3.1
Lagothrix lagotricha	-1.42	NA	NA	NA	0	NA	NA	34	11.2	7.28	-0.87	MMMF	MMMF	33
Lemur catta	-1.08	0	NA	NA	2	0	1	103	17.8	2.21	-0.9	MMMF	MMMF	16.45
Leontopithecus chrysomelas	-1.03	NA	NA	NA	1	NA	NA	46	NA	0.62	-0.07	NA	NA	6.7
Leontopithecus chrysopygus	-1.5	NA	NA	NA	0	NA	NA	38	NA	0.58	NA	NA	NA	3.6
Leontopithecus rosalia	-2.13	NA	NA	NA	0	NA	NA	85	1.48	0.62	-0.58	MG	MG	4.5
Lepilemur dorsalis	0.87	NA	NA	NA	0	NA	NA	1	NA	NA	NA	NA	NA	1
Lepilemur edwardsi	-0.01	NA	NA	NA	0	NA	NA	5	NA	0.91	-0.92	NA	NA	1
Lepilemur leucopus	0.54	NA	NA	NA	0	NA	NA	2	NA	0.62	-0.57	NA	NA	1
Lepilemur microdon	0.87	NA	NA	NA	0	NA	NA	1	NA	NA	NA	NA	NA	1
Lepilemur mustelinus	-0.01	NA	NA	NA	0	NA	NA	5	NA	0.62	-0.52	PG	MMMF	1
Lepilemur ruficaudatus	0.54	NA	NA	NA	0	NA	NA	2	NA	0.76	-0.99	PG	PG	1
Lepilemur septentrionalis	1.42	NA	NA	NA	0	NA	NA	0	NA	NA	NA	NA	NA	1
Lophocebus albigena	-0.75	1	0	1	0	NA	NA	34	NA	8.25	0.39	MMMF	MMMF	16
Lophocebus aterrimus	-0.13	NA	NA	NA	0	NA	NA	6	13.78	7.84	0.36	MMMF	MMMF	17.5
Loris lydekkerianus	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.26	-0.73	NA	NA	NA
Loris tardigradus	-0.12	NA	NA	NA	1	0	1	14	1.8	0.26	-0.82	PG	MMMF	1
Macaca arctoides	-0.12	2	1	1	1	NA	NA	48	48.2	12.2	0.61	MMMF	MMMF	NA
Macaca assamensis	-0.89	NA	NA	NA	0	NA	NA	17	NA	11.3	1.16	MMMF	MMMF	21
Macaca brunnescens	NA	NA	NA	NA	NA	NA	NA	NA	NA	16.6	NA	NA	NA	NA
Macaca cyclopis	-0.63	NA	NA	NA	0	NA	NA	12	NA	6	-0.13	PG	MMMF	20.2
Macaca fascicularis	2.48	3	0	3	7	1	1	174	35.2	5.36	0.83	MMMF	MMMF	27
Macaca fuscata	4.61	1	0	1	26	3	3	253	72.3	11	0.35	MMMF	MMMF	40.65
Macaca hecki	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Macaca maura	-1.08	NA	NA	NA	0	NA	NA	22	NA	9.72	1.09	MMMF	MMMF	NA
Macaca mulatta	1.75	1	0	1	5	1	2	296	46.2	7.7	0.6	MMMF	MMMF	38.5
Macaca nemestrina	0.82	NA	NA	NA	1	NA	NA	51	66.7	11.2	1.4	MMMF	MMMF	22.6
Macaca nemestrina leonina	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.02	NA	NA	NA
Macaca nigra	-1.24	NA	NA	NA	0	NA	NA	27	NA	9.89	1.63	MMMF	MMMF	35
Macaca ochreata	0.31	NA	NA	NA	0	NA	NA	3	NA	5.3	2.25	NA	NA	NA
Macaca radiata	0.1	NA	NA	NA	2	1	1	34	48.2	6.67	1.48	MMMF	MMMF	33.5
Macaca silenus	-1.17	NA	NA	NA	1	NA	NA	48	42	NA	NA	MMMF	MMMF	21
Macaca sinica	-0.63	NA	NA	NA	0	NA	NA	12	NA	5.68	1.61	MMMF	MMMF	20.1
Macaca sylvanus	0.01	2	NA	NA	0	NA	NA	67	NA	11.1	NA	MMMF	MMMF	18.3
Macaca thibetana	-1.06	NA	NA	NA	0	NA	NA	42	NA	15.2	1.02	MMMF	MMMF	21
Macaca tonkeana	-0.39	NA	NA	NA	1	1	0	26	NA	14.9	1.18	NA	NA	NA
Mandrillus leucophaeus	-0.93	0	NA	NA	0	NA	NA	18	41.05	17.5	0.39	PG	PG	17
Mandrillus sphinx	-0.28	NA	NA	NA	0	NA	NA	30	68	31.6	2.88	PG	PG	13.9
Microcebus murinus	-1.93	NA	NA	NA	0	NA	NA	66	2.49	0.06	-0.77	PG	MMMF	1
Microcebus myoxinus	NA	NA	NA	NA	0	NA	NA	NA	NA	0.03	-0.24	NA	NA	1

Microcebus ravelobensis	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Microcebus rufus	-0.33	NA	NA	NA	0	NA	NA	8	2.9	0.04	-0.32	PG	MMMF	1
Miopithecus talapoin	0.14	NA	NA	NA	0	NA	NA	4	5.2	2.5	0.11	MMMF	MMMF	91.2
Mirza coquereli	0.31	NA	NA	NA	0	NA	NA	3	7.19	0.3	-0.98	PG	PG	1
Nasalis larvatus	-0.89	NA	NA	NA	0	NA	NA	17	13.8	20.4	2.18	PG	PG	11.25
Nomascus concolor	-0.38	1	1	0	0	NA	NA	21	NA	7.79	-0.94	MG	MG	4
Nomascus gabriellae	0.75	NA	NA	NA	1	NA	NA	4	NA	NA	NA	NA	NA	1
Nomascus leucogenys	-0.33	NA	NA	NA	0	NA	NA	8	NA	7.41	-0.98	NA	NA	1
Nycticebus bengalensis	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.1	-0.47	NA	NA	NA
Nycticebus coucang	-1.48	NA	NA	NA	0	NA	NA	37	2.17	0.68	-0.41	PG	MMMF	1
Nycticebus pygmaeus	-0.97	NA	NA	NA	0	NA	NA	19	4.25	NA	NA	PG	MMMF	1
Otolemur crassicaudatus	0.58	NA	NA	NA	2	0	1	36	13.32	1.19	-0.51	PG	MMMF	3.5
Otolemur garnettii	0.51	NA	NA	NA	1	NA	NA	12	NA	0.79	-0.42	PG	MMMF	1
Pan paniscus	6.45	12	11	1	10	4	0	225	135.2	45	0.14	MMMF	MMMF	85
Pan troglodytes schweinfurthii	NA	NA	NA	NA	NA	NA	NA	NA	NA	42.7	-0.17	NA	NA	NA
Pan troglodytes troglodytes	16.1	48	29	17	321	74	55	755	157.9	59.7	-0.08	MMMF	MMMF	50
Pan troglodytes verus	NA	NA	NA	NA	NA	NA	NA	NA	NA	46.3	-0.77	NA	NA	NA
Papio anubis	4.72	5	2	3	12	5	2	43	93.5	25.1	1.72	MMMF	MMMF	40
Papio cynocephalus	-0.49	2	2	1	0	NA	NA	114	52	21.8	1.45	MMMF	MMMF	48.2
Papio hamadryas	2.56	1	0	1	6	1	3	78	27.1	16.9	1.3	PG	PG	36.9
Papio papio	4.24	6	0	6	8	NA	NA	8	88.9	NA	NA	MMMF	MMMF	NA
Papio ursinus	4.73	6	6	0	4	2	0	22	72	29.8	1.99	MMMF	MMMF	47
Perodicticus potto	-0.49	NA	NA	NA	0	NA	NA	10	6.61	0.95	-0.98	PG	MMMF	1
Phaner furcifer	0.87	NA	NA	NA	0	NA	NA	1	NA	NA	NA	MG	MG	1
Piliocolobus badius	-1.08	1	NA	NA	1	NA	NA	52	NA	12.3	0.72	MMMF	MMMF	34
Piliocolobus kirkii	0.9	NA	NA	NA	NA	NA	NA	7	NA	5.8	-0.73	NA	NA	33.6
Piliocolobus pennantii	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Piliocolobus preussi	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	40
Piliocolobus rufomitratus	NA	NA	NA	NA	NA	NA	NA	NA	NA	9.67	0.27	NA	NA	24.5
Pithecia irrorata	-0.24	NA	NA	NA	0	NA	NA	7	NA	2.25	-0.52	MG	MG	4.4
Pithecia pithecia	-1.27	0	NA	NA	0	NA	NA	28	0.92	1.94	0.06	MG	MG	2.7
Pongo abelii	NA	NA	NA	NA	NA	NA	NA	NA	31.28	77.9	2.26	NA	NA	NA
Pongo pygmaeus	8.14	5	4	1	53	4	2	321	36.5	78.5	2.27	PG	PG	1
Presbytis comata	-0.56	NA	NA	NA	0	NA	NA	11	NA	6.68	-1.05	NA	NA	7.05
Presbytis melalophos	-0.13	NA	NA	NA	0	NA	NA	6	NA	6.59	-0.94	NA	NA	14
Procolobus verus	0.31	NA	NA	NA	0	NA	NA	3	NA	4.7	-0.47	NA	NA	6.3
Propithecus coquereli	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.7	-1.62	NA	NA	5.5
Propithecus diadema	-1.27	NA	NA	NA	0	NA	NA	28	NA	5.94	-1.25	MG	PG	4.95
Propithecus edwardsi	NA	NA	NA	NA	NA	NA	NA	NA	5.47	NA	NA	NA	NA	6
Propithecus tattersalli	-0.42	NA	NA	NA	0	NA	NA	9	NA	3.39	-1.21	PG	MMMF	4.1
Propithecus verreauxi	-1.04	0	NA	NA	0	NA	NA	41	5.78	3.25	-0.5	MMMF	MMMF	6.3
Pygathrix nemaeus	-1.18	NA	NA	NA	0	NA	NA	25	NA	11	0.12	NA	NA	9.3
Rhinopithecus avunculus	-0.56	NA	NA	NA	0	NA	NA	11	NA	NA	NA	NA	NA	30
Rhinopithecus bieti	NA	NA	NA	NA	0	NA	NA	NA	NA	15	0.75	NA	NA	50
Rhinopithecus brelichi	-0.84	NA	NA	NA	0	NA	NA	16	NA	15.8	NA	NA	NA	NA
Rhinopithecus roxellana	-1.46	NA	NA	NA	1	1	0	36	NA	17.9	0.84	MMMF	MMMF	65
Rungwecebus kipunji	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Saguinus bicolor	-0.42	NA	NA	NA	0	NA	NA	9	NA	0.43	-0.72	NA	NA	6.7
Saguinus fuscicollis	1.86	2	NA	NA	1	NA	NA	81	1.53	0.34	-0.87	MG	PA	6
Saguinus geoffroyi	NA	NA	NA	NA	0	NA	NA	NA	NA	0.48	-0.9	MMMF	MMMF	6.9

Saguinus imperator	-0.84	NA	NA	NA	0	NA	NA	16	NA	0.47	-0.72	MG	PA	5
Saguinus leucopus	0.31	NA	NA	NA	0	NA	NA	3	NA	0.49	-0.68	NA	NA	7.5
Saguinus midas	-0.89	NA	NA	NA	0	NA	NA	17	1.83	0.52	-1.23	MG	PA	5.55
Saguinus mystax	-0.22	NA	NA	NA	4	NA	NA	46	NA	0.51	-0.98	MG	PA	5.4
Saguinus oedipus	-2.6	0	NA	NA	0	NA	NA	153	3.4	0.42	-0.54	MG	PA	7.05
Saguinus tripartitus	-0.01	NA	NA	NA	0	NA	NA	5	NA	NA	NA	NA	NA	NA
Saimiri boliviensis	-1.46	NA	NA	NA	0	NA	NA	36	NA	0.91	0.34	MMMF	MMMF	60
Saimiri oerstedii	0.65	NA	NA	NA	0	NA	NA	4	NA	0.9	0.47	MMMF	MMMF	25.1
Saimiri sciureus	-1.03	NA	NA	NA	3	0	1	89	3.2	0.78	-0.03	MMMF	MMMF	34.85
Saimiri ustus	0.14	NA	NA	NA	0	NA	NA	4	NA	0.92	-0.03	NA	NA	NA
Semnopithecus entellus	1.06	2	0	2	7	0	1	98	11.1	13	0.14	PG	MMMF	19
Symphalangus syndactylus	-1.54	0	NA	NA	0	NA	NA	40	NA	11.9	-0.61	MG	MG	3.8
Tarsius bancanus	-0.33	NA	NA	NA	0	NA	NA	8	0.71	0.13	-0.15	MG	PG	1
Tarsius dentatus	NA	NA	NA	NA	0	NA	NA	2	NA	0.1	-0.66	NA	NA	1
Tarsius syrichta	-0.49	NA	NA	NA	0	NA	NA	10	0.72	NA	NA	PG	PG	1
Theropithecus gelada	-0.36	2	1	1	0	NA	NA	34	17.1	19	1.06	PG	PG	10
Trachypithecus auratus	0.54	NA	NA	NA	0	NA	NA	2	NA	NA	NA	NA	NA	11
Trachypithecus cristatus	-0.33	NA	NA	NA	0	NA	NA	8	6.2	6.61	-0.4	PG	PG	27.4
Trachypithecus delacouri	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Trachypithecus francoisi	-1.63	NA	NA	NA	0	NA	NA	45	NA	7.7	-0.83	NA	NA	NA
Trachypithecus geei	-0.24	NA	NA	NA	0	NA	NA	7	NA	10.8	-0.5	NA	NA	11
Trachypithecus johnii	0.1	NA	NA	NA	0	NA	NA	9	NA	12	-0.78	PG	PG	10
Trachypithecus obscurus	-0.13	NA	NA	NA	0	NA	NA	6	4.8	7.9	NA	PG	MMMF	10
Trachypithecus phayrei	-0.84	NA	NA	NA	0	NA	NA	16	NA	7.87	0.02	NA	NA	12.9
Trachypithecus pileatus	-0.01	NA	NA	NA	0	NA	NA	5	NA	12	-0.03	NA	NA	8.5
Trachypithecus poliocephalus	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.2	NA	NA	NA
Trachypithecus vetulus	0.54	NA	NA	NA	0	NA	NA	2	NA	5.67	0.43	NA	NA	8.35
Varecia rubra	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Varecia variegata variegata	-1.82	0	NA	NA	0	NA	NA	57	17.17	3.63	-0.81	NA	NA	2.8

Table C: *g_{s1} (composite measure of 'general intelligence', based on data from Reader et al. 2011, see Chapter 5 for details), deception count, deception count in males, deception count in females (all deception data from Byrne & Whiten 1990, see Chapter 5 for full details), innovation count, innovation count in males, innovation count in females (all innovation data from Reader et al. 2011, see Chapter 5 for full details), testes mas (g), male body mass (kg), size dimorphism (standardized residuals from regression of male on female body mass), mating system, social group size.*

Appendix D: dataset for analyses presented in chapter 6

Species	Whole brain volume	Neocortex volume	Cerebellum volume	Body mass Isler	Gs1	Social learning count	Innovation count	Tool use count	Extractive foraging count	Deception	Research effort	Group size	% fruit seeds	Diet breadth	Latitude range	Composite life history	Maximum longevity	Juvenile period
Allenopithecus nigroviridis	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	40	81	7	7.35	NA	276	NA
Allocebus trichotis	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	1	NA	3	5.19	NA	NA	NA
Alouatta belzebul	NA	NA	NA	NA	-0.73	0	0	0	0	0	15	7.4	NA	NA	13.77	NA	NA	NA
Alouatta caraya	NA	NA	NA	NA	-1.53	0	1	0	1	0	45	8.9	25	3	16.49	0.75	243.6	1276.72
Alouatta coibensis	NA	NA	NA	NA	NA	0	0	0	0	0	0	5.2	NA	2	0.63	NA	NA	NA
Alouatta guariba	NA	NA	NA	NA	NA	0	1	0	0	0	37	7.4	5	3	16.94	NA	NA	NA
Alouatta palliata	NA	NA	NA	NA	-0.26	3	0	0	0	1	79	13.1	42	3	23.51	1.48	300	1578.42
Alouatta pigra	NA	NA	NA	NA	-1.10	0	0	0	0	0	25	5.5	NA	3	5.6	NA	240	NA
Alouatta sara	NA	NA	NA	NA	0.14	0	0	0	0	0	4	NA	NA	NA	9.55	NA	NA	NA
Alouatta seniculus	NA	NA	NA	NA	0.03	0	4	1	0	0	82	7.9	42	3	23.04	1.24	300	1690.22
Aotus azarai	NA	NA	NA	NA	-1.00	0	0	0	0	0	22	4.1	NA	NA	14.28	NA	NA	NA
Aotus brumbacki	NA	NA	NA	NA	1.35	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA
Aotus hershkovitzi	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	1.06	NA	NA	NA
Aotus infulatus	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	NA	NA	NA	NA	NA	NA	NA
Aotus lemurinus	14646.57	7592.15	1701.99	752.8	-0.78	0	0	0	0	0	16	NA	NA	NA	9.79	NA	216	755.15
Aotus miconax	NA	NA	NA	NA	NA	0	0	0	0	0	2	NA	NA	NA	3.95	NA	NA	NA
Aotus nancymaae	NA	NA	NA	NA	0.01	0	0	0	0	0	5	4	NA	NA	3.75	NA	NA	NA
Aotus nigriceps	NA	NA	NA	NA	0.83	0	0	0	0	0	1	3.3	70	5	11.39	NA	NA	NA
Aotus trivirgatus	17005.23	9142.92	1623.46	1044	-1.71	0	0	0	0	0	58	3.15	45.5	4	9.82	-0.70	303.6	736.6
Aotus vociferans	NA	NA	NA	NA	0.05	0	1	0	0	0	12	3.3	NA	NA	12.04	NA	NA	NA
Arctocebus calabarensis	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	14	1	3.87	-1.47	156	298.91
Ateles belzebuth	NA	NA	NA	NA	-0.58	0	0	0	0	0	12	14.5	83	4	9.06	NA	336	NA
Ateles chamek	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	6	8.85	NA	NA	NA
Ateles fusciceps	104988.09	53189.05	12382.19	9160	0.14	0	0	0	0	0	4	NA	NA	2	9.34	1.71	288	1799.68
Ateles geoffroyi	101034	70856	12438	7535	-0.24	2	0	0	0	1	58	42	79.8	5	23.42	2.31	327.6	2104.57
Ateles paniscus	NA	NA	NA	NA	-1.23	0	0	0	0	0	30	20	82.9	5	10.42	2.33	453.6	2104.57
Avahi laniger	9798	4813	1489	1207	-0.45	0	0	0	0	0	10	2	0	4	11.09	NA	NA	NA
Avahi occidentalis	9124	4443	1383	801	-0.11	0	0	0	0	0	6	3	NA	4	3.54	NA	NA	NA
Brachyteles arachnoides	NA	NA	NA	NA	-1.70	0	0	0	0	0	57	19.6	32	4	0.9	NA	NA	2876.24
Bunopithecus hoolock	NA	NA	NA	NA	-1.07	0	0	0	0	0	24	3.2	67	5	8.72	NA	NA	2689.08
Cacajao calvus	NA	NA	NA	NA	-0.52	0	0	0	0	0	11	23.7	85	5	7.78	1.18	324	1262.74
Cacajao melanocephalus	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	30	NA	4	6.98	NA	216	NA
Cacajao rubicundus	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA
Callicebus brunneus	NA	NA	NA	NA	NA	0	0	0	0	0	3	2.5	NA	4	4.51	NA	NA	NA
Callicebus calligatus	NA	NA	NA	NA	NA	0	0	0	0	0	2	1	NA	NA	NA	NA	NA	NA
Callicebus cinerascens	NA	NA	NA	NA	NA	0	0	0	0	0	1	1	NA	NA	8.14	NA	NA	NA
Callicebus cupreus	NA	NA	NA	NA	NA	0	0	0	0	0	13	2.05	NA	NA	8.17	NA	NA	NA
Callicebus donacophilus	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	NA	NA	10.84	NA	NA	NA
Callicebus dubius	NA	NA	NA	NA	NA	0	0	0	0	0	0	1	NA	NA	NA	NA	NA	NA
Callicebus hoffmannsi	NA	NA	NA	NA	1.35	0	0	0	0	0	0	1	NA	NA	4.05	NA	NA	NA
Callicebus modestus	NA	NA	NA	NA	NA	0	0	0	0	0	0	1	NA	3	1.42	NA	NA	NA
Callicebus moloch	17944	11163	1622	875	-0.86	0	0	0	0	0	18	2.95	53.7	NA	12.8	-0.46	303.6	1262.74
Callicebus oenanthe	NA	NA	NA	NA	NA	0	0	0	0	0	0	1	NA	NA	0.82	NA	NA	NA
Callicebus olallae	NA	NA	NA	NA	NA	0	0	0	0	0	0	1	NA	NA	1.42	NA	NA	NA
Callicebus personatus	NA	NA	NA	NA	-0.90	0	0	0	0	0	19	2.35	NA	3	6.46	NA	NA	NA
Callicebus torquatus	NA	NA	NA	NA	0.14	0	0	0	0	0	4	3.85	70	4	NA	NA	NA	1683.65
Callimico goeldii	12112.34	6111.55	1270.39	499	-1.49	0	1	0	1	0	43	6.85	NA	3	12.61	-1.45	214.8	413.84
Callithrix argentata	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	9.5	NA	3	4	NA	201.6	701.52
Callithrix aurita	NA	NA	NA	NA	NA	0	0	0	0	0	NA	6	NA	3	2.99	NA	NA	NA

Callithrix flaviceps	NA	NA	NA	NA	NA	0	0	0	0	0	NA	9.8	NA	4	1.53	NA	NA	NA
Callithrix geoffroyi	7098.63	4040.03	713.35	534.4	NA	0	0	0	0	0	NA	NA	NA	3	4.17	NA	NA	NA
Callithrix humeralifera	NA	NA	NA	NA	0.14	0	0	0	0	0	4	8.5	NA	3	6.18	NA	180	NA
Callithrix jacchus	8124.76	4491.25	686.23	318	-0.75	2	1	0	2	0	161	8.55	22	3	7.6	-1.52	201.6	455.99
Callithrix kuhli	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	3	2.44	NA	NA	NA
Callithrix mauesi	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	NA	0.5	NA	NA	NA
Callithrix penicillata	6118.425	3232.995	727.005	328	NA	0	0	0	0	0	NA	5.9	NA	3	20.71	NA	NA	NA
Callithrix pygmaea	4301.02	2214	478.12	110	-0.74	0	1	0	0	0	36	6	0	4	13.11	-0.90	181.2	708.5
Cebus albifrons	NA	NA	NA	NA	-0.12	1	0	3	3	0	13	25	24.6	5	24.77	1.07	528	1501.69
Cebus apella	67156.14333	37699.39	5931.26	2787	5.95	17	39	64	56	1	249	7.9	52	6	35.78	1.31	541.2	1760.81
Cebus capucinus	NA	NA	NA	NA	2.77	5	4	7	3	0	60	18.15	67.5	8	14.56	1.86	657.6	2134.73
Cebus olivaceus	NA	NA	NA	NA	-0.24	0	4	3	2	0	18	11.45	46.7	3	13.17	NA	492	2525.48
Cercocebus galeritus	NA	NA	NA	NA	0.00	0	0	0	1	0	19	20.35	80.1	6	2.37	NA	252	2735.94
Cercocebus torquatus	NA	NA	NA	NA	-0.76	0	0	0	0	0	32	26.85	79	4	13.57	NA	360	1318.86
Cercopithecus ascanius	63505	45166	5828	3714	0.04	1	1	0	1	1	26	26.3	61.2	4	19	1.11	339.6	1718.73
Cercopithecus campbelli	NA	NA	NA	NA	-0.52	0	0	0	0	0	11	11	78	4	8.35	NA	396	NA
Cercopithecus cephus	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	11	79	5	11.25	NA	276	1521.9
Cercopithecus denti	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	7.21	NA	NA	NA
Cercopithecus diana	NA	NA	NA	NA	-0.01	1	0	0	0	1	28	24.95	52	6	4.6	NA	447.6	2279.95
Cercopithecus dryas	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	5.09	NA	NA	NA
Cercopithecus erythrogaster	NA	NA	NA	NA	0.31	0	0	0	0	0	3	NA	NA	3	3.21	NA	NA	NA
Cercopithecus erythrotis	NA	NA	NA	NA	0.31	0	0	0	0	0	3	NA	NA	3	3.54	NA	NA	NA
Cercopithecus hamlyni	70315.19	35627.18	6783.83	5490	0.14	0	0	0	0	0	4	NA	NA	3	8.52	NA	NA	NA
Cercopithecus lhoesti	NA	NA	NA	NA	-0.21	0	0	0	0	0	7	17.4	NA	3	9.76	NA	192	NA
Cercopithecus mitis	66443.85	34696.14	5433.24	7590.6	-0.41	0	4	0	3	1	56	16	54.5	5	27.82	1.85	325.2	2049.25
Cercopithecus mona	NA	NA	NA	NA	1.00	0	0	0	0	3	8	NA	NA	3	6.5	NA	360	NA
Cercopithecus neglectus	NA	NA	NA	NA	-0.82	0	0	0	0	0	17	4.5	77	6	19.19	1.47	315.6	2076.39
Cercopithecus nictitans	73183.47	37291.98	7283.92	6670	-0.21	0	0	0	0	0	7	16	67.1	3	15.49	NA	276	1684.59
Cercopithecus petaurista	NA	NA	NA	NA	0.01	0	0	0	0	0	5	14	NA	3	9.17	NA	228	NA
Cercopithecus pogonias	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	15	82.9	3	15.18	NA	289.2	1684.59
Cercopithecus preussi	NA	NA	NA	NA	0.53	0	0	0	0	0	2	3	NA	3	3.28	NA	NA	NA
Cercopithecus salongo	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA
Cercopithecus solatus	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	10	NA	NA	1.55	NA	NA	NA
Cercopithecus wolfi	NA	NA	NA	NA	-0.21	0	0	0	0	0	7	NA	NA	5	11.78	NA	NA	NA
Cheirogaleus major	6373	2938	947	400	0.31	0	0	0	0	0	3	1	NA	4	12.8	NA	180	420.91
Cheirogaleus medius	2961	1221	437	140	-0.63	0	0	0	0	0	13	1	NA	7	13.09	-1.33	231.6	413.84
Chiropotes albinasus	NA	NA	NA	NA	NA	0	0	0	0	0	3	22.5	NA	3	13.26	NA	204	NA
Chiropotes satanas	NA	NA	NA	NA	-0.97	0	2	0	2	0	21	14.4	91	4	NA	NA	216	NA
Chlorocebus aethiops	68955.92	NA	5988.25	3719.5	-0.06	5	4	2	3	1	91	NA	NA	5	13.79	NA	379.2	NA
Colobus angolensis	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	10.9	35	4	17.09	NA	NA	NA
Colobus guereza	77247.81	33411.22	7926.48	9673	-1.47	0	1	0	1	0	42	7.6	14	2	18.5	1.34	294	1929.19
Colobus polykomos	NA	NA	NA	NA	-0.82	0	0	0	0	0	17	10.2	36	2	9.43	1.04	366	1629.84
Colobus satanas	NA	NA	NA	NA	-0.45	0	0	0	0	0	10	15.5	57	3	6.35	NA	NA	NA
Daubentonia madagascariensis	42611	22127	6461	2555	-0.20	0	4	2	6	0	52	1	0	4	12.82	0.60	291.6	834.72
Erythrocebus patas	97005.79	48926.88	7298.02	12400	1.70	2	1	0	1	1	33	28	75	5	23.91	0.42	286.8	1246.07
Eulemur coronatus	NA	NA	NA	NA	-0.52	0	0	0	0	0	11	6.95	NA	5	1.51	NA	220.8	701.52
Eulemur fulvus fulvus	22106	12207	3328	2292	-1.44	1	3	0	3	0	81	9.15	46	6	6.7	0.12	444	791.75
Eulemur macaco macaco	NA	NA	NA	NA	0.15	0	1	1	2	0	32	9.2	NA	6	1.27	-0.15	360	660.75
Eulemur mongoz	NA	NA	NA	NA	-0.63	0	1	0	1	0	13	2.7	18	4	0.86	NA	360	1060.7
Eulemur rubriventer	NA	NA	NA	NA	-0.63	0	0	0	0	0	13	3.3	NA	4	9.31	NA	NA	566.36

Euoticus elegantulus	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	5	4	11.56	NA	180	NA
Euoticus inustus	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA
Galago alleni	NA	NA	NA	NA	0.53	0	0	0	0	0	2	6	73	3	0.58	NA	144	283.18
Galago granti	NA	NA	NA	NA	1.35	0	0	0	0	0	0	NA	NA	NA	11.24	NA	NA	NA
Galago moholi	NA	NA	NA	NA	-0.68	0	0	0	0	0	14	1	NA	2	27.4	-1.50	198	420.91
Galago senegalensis	3408.35	1649.89	578.05	200.3	-0.94	0	0	0	0	0	20	3.5	0	2	31.78	-1.24	204	330.37
Galagoides demidoff	3203	1568	413	75	0.01	0	0	0	0	0	5	5.5	19	4	20.16	-1.73	168	345.24
Galagoides thomasi	NA	NA	NA	NA	NA	0	0	0	0	0	NA	1	NA	NA	21.65	NA	NA	NA
Galagoides zanzibaricus	NA	NA	NA	NA	1.35	0	0	0	0	0	0	1	NA	3	27.83	NA	NA	322.75
Gorilla gorilla gorilla	410960.86	202127.6	54971.24	104467	4.86	13	25	21	12	7	517	6	67	6	13.87	3.06	648	3353.12
Hapalemur aureus	NA	NA	NA	NA	0.01	0	0	0	0	0	5	3	NA	2	1.87	NA	NA	NA
Hapalemur griseus	NA	NA	NA	NA	-1.44	0	0	0	0	0	40	3.1	NA	1	11.41	-0.13	205.2	1003.17
Hapalemur simus	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	7.5	NA	4	2.22	NA	144	NA
Hylobates agilis	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	4.2	61	4	12.21	NA	528	NA
Hylobates klossii	NA	NA	NA	NA	0.14	0	0	0	0	0	4	3	72	3	2.43	NA	NA	NA
Hylobates lar	97505	65800	12078	5595	-2.00	0	0	0	0	0	86	3.2	60	4	23.63	2.67	480	3852.57
Hylobates moloch	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	2.15	61	4	1.03	NA	NA	NA
Hylobates muelleri	NA	NA	NA	NA	0.01	0	0	0	0	0	5	3.2	NA	4	10.63	NA	NA	NA
Hylobates pileatus	NA	NA	NA	NA	0.50	0	1	0	0	1	16	3.25	79.4	4	4.87	NA	432	2454.24
Indri indri	36285	20114	5504	6335	-0.30	0	0	0	0	0	8	3.1	43	3	5.16	NA	NA	1605.69
Lagothrix flavicauda	NA	NA	NA	NA	NA	0	0	0	0	0	2	9.1	NA	4	3.25	NA	NA	1683.65
Lagothrix lagotricha	91676.7	46788.56	9707.56	7160	-1.32	0	0	0	0	0	34	33	79	6	8.45	1.47	360	1729.33
Lemur catta	NA	NA	NA	NA	-0.94	4	2	0	2	0	103	16.45	54	5	5.11	-0.04	360	831.62
Leontopithecus chrysomelas	NA	NA	NA	NA	-0.92	0	1	0	0	0	46	6.7	NA	4	2.04	NA	NA	NA
Leontopithecus chrysopygus	NA	NA	NA	NA	-1.40	0	0	0	0	0	38	3.6	NA	3	3.19	NA	NA	NA
Leontopithecus rosalia	11355.29	6405.48	1089.9	609	-2.00	0	0	0	0	0	85	4.5	84	6	1.79	-0.82	297.6	890.34
Lepilemur dorsalis	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	NA	3	1.19	NA	NA	NA
Lepilemur edwardsi	NA	NA	NA	NA	0.01	0	0	0	0	0	5	1	NA	4	3.72	NA	NA	NA
Lepilemur leucopus	NA	NA	NA	NA	0.53	0	0	0	0	0	2	1	NA	2	1.97	NA	103	620.76
Lepilemur microdon	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	NA	NA	7.4	NA	NA	NA
Lepilemur mustelinus	NA	NA	NA	NA	0.01	0	0	0	0	0	5	1	6	3	3.97	NA	144	663.81
Lepilemur ruficaudatus	7175	3282	1165	805	0.53	0	0	0	0	0	2	1	NA	2	3.96	NA	NA	NA
Lepilemur septentrionalis	NA	NA	NA	NA	1.35	0	0	0	0	0	0	1	NA	1	NA	NA	NA	377.57
Lophocebus albigena	89810.41	44831.96	8125.75	6010	-0.67	0	0	0	0	1	34	16	64	4	12.48	1.19	392.4	2525.48
Lophocebus aterrimus	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	17.5	NA	6	7.29	NA	321.6	NA
Loris tardigradus	6269	3524	728	193	-0.06	0	1	0	0	0	14	1	15	5	1.68	-0.83	196.8	350.76
Macaca arctoides	90976.42	47067.49	7583.76	9666.6667	-0.02	1	1	1	1	2	48	NA	NA	6	22.58	1.27	360	1570.01
Macaca assamensis	NA	NA	NA	NA	-0.82	0	0	0	0	0	17	21	NA	4	16.15	NA	NA	NA
Macaca cyclopis	NA	NA	NA	NA	-0.58	0	0	0	0	0	12	20.2	NA	3	1.9	NA	NA	1650.01
Macaca fascicularis	53845.39	26653.01	5145.91	4251	2.63	7	7	3	2	3	174	27	66.9	5	29.02	0.88	456	1319.5
Macaca fuscata	88479.69	51584.87	6413.89	8030	4.80	45	26	5	16	1	253	40.65	44	6	11.32	1.03	396	1460.77
Macaca maura	NA	NA	NA	NA	-1.00	0	0	0	0	0	22	NA	NA	1	1.45	NA	NA	NA
Macaca mulatta	87449.97	44453.46	7677.54	5670.5	1.93	15	5	2	4	1	296	38.5	63	7	22.76	0.85	432	1101.07
Macaca nemestrina	95411.15	42583.16	7126.3	11102.7	0.94	3	1	1	2	0	51	22.6	75	6	15.87	0.92	411.6	1427.17
Macaca nigra	76340.29	34146.24	6995.1	9890	-1.15	0	0	1	1	0	27	35	NA	3	1.48	1.30	216	1984.51
Macaca ochreata	NA	NA	NA	NA	0.31	0	0	0	0	0	3	NA	NA	1	2	NA	NA	NA
Macaca radiata	NA	NA	NA	NA	0.20	0	2	1	1	0	34	33.5	53	6	13.06	1.02	360	1785.78
Macaca silenus	95121.19	50982.8	8282.98	8900	-1.06	1	1	1	1	0	48	21	NA	6	5.96	1.40	480	1912.19
Macaca sinica	NA	NA	NA	NA	-0.58	0	0	0	0	0	12	20.1	75	4	3.92	NA	420	1894.11
Macaca sylvanus	83284.63	45170.79	7259.82	9625	0.12	0	0	0	1	2	67	18.3	33	8	5.42	0.71	264	1542.25

Macaca thibetana	NA	NA	NA	NA	-0.96	1	0	0	0	0	42	21	NA	5	9.32	NA	NA	NA
Macaca tonkeana	NA	NA	NA	NA	-0.31	2	1	2	2	0	26	NA	NA	NA	4.92	NA	NA	NA
Mandrillus leucophaeus	NA	NA	NA	NA	-0.86	0	0	0	0	0	18	17	NA	5	4.02	1.54	400.8	1745.96
Mandrillus sphinx	126188.36	66537.98	13347.95	12800	-0.20	3	0	0	0	0	30	13.9	92	7	10.5	1.38	555.96	2122.11
Microcebus murinus	1696.29	749.38	257.44	63	-1.81	0	0	0	0	0	66	1	51	6	13.25	-1.80	186	355.53
Microcebus myoxinus	NA	NA	NA	NA	NA	0	0	0	0	0	NA	1	NA	NA	0.55	NA	NA	NA
Microcebus ravelobensis	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	NA	0.4	NA	NA	NA
Microcebus rufus	NA	NA	NA	NA	NA	0	0	0	0	0	8	1	NA	4	11.73	NA	144	NA
Miopithecus talapoin	37776	26427	3374	1350	0.14	0	0	0	0	0	4	91.2	54	5	9.37	0.62	370.8	1733.36
Mirza coquereli	NA	NA	NA	NA	0.31	0	0	0	0	0	3	1	NA	7	10.18	-0.80	183.6	343.74
Nasalis concolor	NA	NA	NA	NA	NA	0	0	0	0	0	4	2.75	NA	NA	2.43	NA	NA	NA
Nasalis larvatus	92797	62685	12113	14561	-0.82	0	0	0	0	0	17	11.25	43	5	11.21	0.86	252	1894.11
Nomascus concolor	NA	NA	NA	NA	-0.32	0	0	0	0	1	21	4	NA	3	5.23	2.34	529.2	2454.24
Nomascus gabriellae	NA	NA	NA	NA	0.77	0	1	0	0	0	4	1	NA	NA	4.28	NA	NA	NA
Nomascus leucogenys	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	1	NA	NA	5.68	NA	NA	NA
Nycticebus coucang	11755	6192	1310	653	-1.38	0	0	0	0	0	37	1	60	5	18.11	0.06	318	660.82
Nycticebus pygmaeus	NA	NA	NA	NA	-0.90	0	0	0	0	0	19	1	NA	NA	13.01	NA	NA	NA
Otolemur crassicaudatus	9668	4723	1414	1150	0.68	1	2	0	2	0	36	3.5	27	4	31.53	-0.41	225.6	609.86
Otolemur garnettii	NA	NA	NA	NA	0.56	1	1	0	0	0	12	1	NA	3	14.25	-0.70	204	592.15
Pan paniscus	306268.18	143189.6	42118.37	39100	6.58	5	10	27	15	6	225	85	NA	5	6.67	NA	576	5465.72
Pan troglodytes troglodytes	344981.5	166441.4	47789.24	44047	16.26	214	321	371	217	31	755	50	66	6	21.85	3.57	720	3897.96
Papio anubis	190957	140142	18683	18150	4.80	4	12	2	8	5	43	40	31.4	7	27.69	NA	302.4	NA
Papio cynocephalus	NA	NA	NA	NA	-0.36	2	0	0	0	2	114	48.2	62	7	25.91	1.84	540	2560.56
Papio hamadryas	168266.3	85245.15	14639.32	18000	2.67	1	6	12	10	1	78	36.9	88	5	9.39	1.43	450	1652.37
Papio papio	NA	NA	NA	NA	4.25	3	8	4	5	4	8	NA	NA	4	4.65	NA	480	NA
Papio ursinus	NA	NA	NA	NA	4.77	5	4	4	7	4	22	47	87	6	20.82	2.10	540	1543.35
Perodicticus potto	13212	6683	1699	835	-0.45	0	0	0	0	0	10	1	65	3	25.94	-0.23	312	561.58
Phaner furcifer	NA	NA	NA	NA	0.83	0	0	0	0	0	1	1	85	5	1.15	NA	144	NA
Piliocolobus badius	73818	50906	8648	8285	-0.98	0	0	0	0	1	52	34	26	3	10.69	NA	NA	1473.2
Piliocolobus kirkii	NA	NA	NA	NA	0.93	1	1	0	0	0	7	33.6	NA	NA	0.76	NA	NA	NA
Piliocolobus pennantii	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	3	9.52	NA	NA	NA
Piliocolobus preussi	NA	NA	NA	NA	NA	0	0	0	0	0	NA	40	NA	2	3.25	NA	NA	NA
Pithecia aequatorialis	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	3	3.96	NA	178.8	NA
Pithecia albicans	NA	NA	NA	NA	NA	0	0	0	0	0	1	4.6	NA	8	2.9	NA	NA	NA
Pithecia irrorata	NA	NA	NA	NA	-0.21	0	0	0	0	0	7	4.4	NA	NA	11.8	NA	NA	NA
Pithecia monachus	32867	NA	NA	2360	NA	0	0	0	0	0	1	2.5	55	5	15.52	NA	295.2	NA
Pithecia pithecia	NA	21028	3908	NA	-1.18	0	0	0	0	0	28	2.7	92	5	11.88	-0.14	248.4	1089.37
Pongo pygmaeus	323450.54	164030.4	37797.51	58542.5	8.27	86	53	114	22	5	321	1	64	5	8.01	3.34	720	3318.62
Presbytis comata	NA	NA	NA	NA	NA	0	0	0	0	0	11	7.05	14	5	1.79	NA	NA	NA
Presbytis frontata	NA	NA	NA	NA	NA	0	0	0	0	0	1	NA	NA	NA	7.89	NA	NA	NA
Presbytis melalophos	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	14	49	4	5.21	NA	192	NA
Presbytis potenziani	NA	NA	NA	NA	NA	0	0	0	0	0	3	3.7	NA	3	2.43	NA	NA	NA
Presbytis rubicunda	NA	NA	NA	NA	NA	0	0	0	0	0	3	6.5	49	5	11.21	NA	NA	NA
Presbytis thomasi	NA	NA	NA	NA	NA	0	0	0	0	0	NA	8	NA	4	2.39	NA	NA	NA
Procolobus verus	NA	NA	NA	NA	0.31	0	0	0	0	0	3	6.3	24	4	5.06	NA	NA	NA
Propithecus diadema	NA	NA	NA	NA	-1.18	0	0	0	0	0	28	4.95	55	4	5.48	NA	NA	1683.65
Propithecus tattersalli	NA	NA	NA	NA	-0.38	0	0	0	0	0	9	4.1	NA	2	0.31	NA	NA	NA
Propithecus verreauxi	25194	13170	3957	2955	-0.94	1	0	0	0	0	41	6.3	41	4	5.9	0.30	247.2	943.94
Pygathrix nemaeus	72530	48763	8063	9720	-1.10	0	0	0	0	0	25	9.3	NA	4	5.84	NA	300	NA
Rhinopithecus avunculus	NA	NA	NA	NA	-0.52	0	0	0	0	0	11	30	NA	3	1.57	NA	NA	NA

Rhinopithecus bieti	NA	NA	NA	NA	NA	0	0	0	0	0	NA	50	NA	3	2.82	NA	NA	755.15
Rhinopithecus brelichi	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	NA	NA	3	2.29	NA	NA	NA
Rhinopithecus roxellana	NA	NA	NA	NA	-1.36	0	1	0	1	0	36	65	NA	3	5.97	NA	NA	NA
Saguinus bicolor	NA	NA	NA	NA	-0.38	0	0	0	0	0	9	6.7	NA	4	2.89	NA	NA	NA
Saguinus fuscicollis	8200.26	4195.73	827.38	396.6	1.97	2	1	1	1	2	81	6	60.4	6	16.93	-0.78	294	406.61
Saguinus geoffroyi	NA	NA	NA	NA	NA	0	0	0	0	0	NA	6.9	NA	5	5.51	NA	NA	NA
Saguinus imperator	9370.88	4988.26	824.25	518.5	-0.78	0	0	0	0	0	16	5	NA	6	4.8	NA	242.4	NA
Saguinus inustus	NA	NA	NA	NA	NA	0	0	0	0	0	0	NA	NA	NA	6.42	NA	NA	NA
Saguinus labiatus	NA	NA	NA	NA	NA	2	0	0	0	0	27	5.25	NA	4	9.33	NA	NA	NA
Saguinus leucopus	NA	NA	NA	NA	0.31	0	0	0	0	0	3	7.5	NA	1	4.96	NA	NA	NA
Saguinus midas	10782.87	5775.38	1045.43	591	-0.82	0	0	0	0	0	17	5.55	69	4	16.39	-1.01	184.8	841.82
Saguinus mystax	NA	NA	NA	NA	-0.10	0	4	0	0	0	46	5.4	NA	3	7.17	NA	NA	556.85
Saguinus nigricollis	NA	NA	NA	NA	NA	0	0	0	0	0	3	6.3	NA	5	2.42	NA	182.4	NA
Saguinus oedipus	10673.28	5910.78	874.42	445.1	-2.43	0	0	0	0	0	153	7.05	NA	5	3.6	-1.07	277.2	680.38
Saguinus tripartitus	NA	NA	NA	NA	0.01	0	0	0	0	0	5	NA	NA	2	0.99	NA	NA	NA
Saimiri boliviensis	NA	NA	NA	NA	-1.36	0	0	0	0	0	36	60	NA	3	16.7	NA	NA	NA
Saimiri oerstedii	NA	NA	NA	NA	0.66	1	0	0	0	0	4	25.1	NA	4	1.5	NA	NA	NA
Saimiri sciureus	21642.56	12147.92	1671.98	742.5	-0.89	1	3	0	2	0	89	34.85	28	2	16.52	0.38	324	1399.88
Saimiri ustus	NA	NA	NA	NA	0.14	0	0	0	0	0	4	NA	NA	NA	14.32	NA	NA	NA
Saimiri vanzolinii	NA	NA	NA	NA	NA	0	0	0	0	0	0	40	NA	2	0.76	NA	NA	NA
Semnopithecus entellus	NA	NA	NA	NA	1.20	2	7	0	3	2	98	19	24.4	6	12.92	1.18	300	1497.64
Symphalangus syndactylus	NA	NA	NA	NA	-1.44	0	0	0	0	0	40	3.8	47	4	11.01	2.57	456	3788.23
Tarsius bancanus	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	1	NA	2	12.93	-0.94	144	658.68
Tarsius dianae	NA	NA	NA	NA	NA	0	0	0	0	0	2	1	NA	2	0.98	NA	NA	NA
Tarsius pumilis	NA	NA	NA	NA	NA	0	0	0	0	0	0	1	NA	1	2.08	NA	NA	NA
Tarsius spectrum	NA	NA	NA	NA	NA	0	0	0	0	0	9	3.25	0	1	7.45	NA	144	596.29
Tarsius syrichta	3393	1768	428	126	-0.45	0	0	0	0	0	10	1	0	2	7.03	NA	180	NA
Theropithecus gelada	NA	NA	NA	NA	-0.29	0	0	0	0	2	34	10	26	5	6.49	1.65	336	1894.11
Trachypithecus auratus	NA	NA	NA	NA	0.53	0	0	0	0	0	2	11	NA	4	3.09	NA	NA	NA
Trachypithecus cristatus	NA	NA	NA	NA	-0.30	0	0	0	0	0	8	27.4	32	2	12.97	NA	373.2	NA
Trachypithecus delacouri	NA	NA	NA	NA	NA	0	0	0	0	0	NA	NA	NA	1	3.29	NA	NA	NA
Trachypithecus francoisi	NA	NA	NA	NA	-1.53	0	0	0	0	0	45	NA	NA	NA	11.38	NA	NA	NA
Trachypithecus geei	NA	NA	NA	NA	-0.21	0	0	0	0	0	7	11	NA	3	0.98	NA	NA	NA
Trachypithecus johnii	NA	NA	NA	NA	0.14	1	0	0	0	0	9	10	21	3	2.82	NA	NA	NA
Trachypithecus obscurus	NA	NA	NA	NA	-0.11	0	0	0	0	0	6	10	35	4	11.12	NA	300	NA
Trachypithecus phayrei	NA	NA	NA	NA	-0.78	0	0	0	0	0	16	12.9	NA	2	12.27	NA	NA	NA
Trachypithecus pileatus	NA	NA	NA	NA	0.01	0	0	0	0	0	5	8.5	NA	6	7.23	NA	NA	NA
Trachypithecus vetulus	NA	NA	NA	NA	0.53	0	0	0	0	0	2	8.35	NA	3	3.59	0.93	276	1113.7
Varecia variegata variegata	29713	15293	4286	3575	-1.70	0	0	0	0	0	57	2.8	NA	4	8.15	-0.54	384	701.52

Table D: *whole brain volume (cubic cm), neocortex volume (cubic cm), cerebellum volume (cubic cm), body mass (kg, from Isler et al. 2008, see Chapter 6 for full citation), gs1 (composite measure of 'general intelligence' based on data from Reader et al. 2011, see Chapter 6 for full details), counts of social learning, innovation, tool use, extractive foraging and deception, research effort (from Reader et al. 2011, see Chapter 6 for full details), social group size, % fruit & seeds in diet, diet breadth, latitude range, composite measure of life history speed (see Chapter 6 for full details), maximum longevity (days), juvenile period length (days)*

Appendix E: full results for multi-variate PGLS analyses presented in Chapters 3-4

E.i) Chapter 3: 3.2.5 (Methods), 3.3.3 (Results)

Duration of peak swelling, predicted by cycle length and swelling type

	Predictor variables with effect sizes & p-values				
Outcome variables	Cycle length (days)	Swelling size (categorical)	N	R^2	λ
Duration of peak swelling (days, weighted mean from per-article dataset)	β=0.10, p=0.87	Small vs. medium: β=0.52, p=0.92 Small vs. large: β=2.78, p=0.70 Large vs. medium: β=2.25, p=0.57	12	0.11	0.00

E.ii) Chapter 4: 4.2.2 (Methods), 4.3.1 (Results)

*Testes mass, predicted by male body mass*swellings (all species)*

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln male body mass (Non-swelling species)	Ln male body mass (Swelling species)	N	R^2	λ
Ln-testes mass	β=0.29, p=0.13 (swellings 'up-coded')	β=1.11, p<0.001 (swellings 'up-coded')	32	0.47	0.84
Ln-testes mass	β=0.28, p=0.13 (swellings 'down-coded')	β=1.13, p<0.001 (swellings 'down-coded')	32	0.47	0.87

*Testes mass, predicted by male body mass*swellings (multi-male, multi-female only 'up-coded')*

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln male body mass (Non-swelling species)	Ln male body mass (Swelling species)	N	R^2	λ
Ln-testes mass	β=0.13, p=0.80 (swellings 'up-coded')	β=1.11, p<0.001 (swellings 'up-coded')	20	0.44	0.83
Ln-testes mass	β=0.16, p=0.73 (swellings 'down-coded')	β=1.17, p<0.001 (swellings 'down-coded')	20	0.45	0.84

*Testes mass, predicted by male body mass*swellings (multi-male, multi-female only 'down-coded')*

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln male body mass (Non-swelling species)	Ln male body mass (Swelling species)	N	R^2	λ
Ln-testes mass	β=-0.22, p=0.73 (swellings 'up-coded')	β=1.09, p<0.001 (swellings 'up-coded')	18	0.44	0.87
Ln-testes mass	β=-0.06, p=0.91 (swellings 'down-coded')	β=1.15, p=0.001 (swellings 'down-coded')	18	0.46	0.84

E. iii) Chapter 4: 4.2.2 (Methods), 4.3.2 (Results)

Male body mass, predicted by female body mass & swellings (all species)

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-male body mass	$\beta=1.04$, $p<0.001$ (swellings 'up-coded')	$\beta=0.05$, $p=0.42$ (swellings 'up-coded')	68	0.86	1
Ln-male body mass	$\beta=1.04$, $p<0.001$ (swellings 'down-coded')	$\beta=0.05$, $p=0.43$ (swellings 'down-coded')	68	0.86	1

Male body mass, predicted by female body mass & swellings (multi-male, multi-female only 'up-coded')

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-male body mass	$\beta=1.05$, $p<0.001$ (swellings 'up-coded')	$\beta=0.01$, $p=0.85$ (swellings 'up-coded')	32	0.88	1
Ln-male body mass	$\beta=1.05$, $p<0.001$ (swellings 'down-coded')	$\beta=0.006$, $p=0.92$ (swellings 'down-coded')	32	0.88	1

Male body mass, predicted by female body mass & swellings (multi-male, multi-female only 'down-coded')

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-male body mass	$\beta=1.00$, $p<0.001$ (swellings 'up-coded')	$\beta=-0.06$, $p=0.40$ (swellings 'up-coded')	27	0.89	0.99
Ln-male body mass	$\beta=1.00$, $p<0.001$ (swellings 'down-coded')	$\beta=-0.11$, $p=0.20$ (swellings 'down-coded')	27	0.90	0.99

E. iv) Chapter 4: 4.2.2 (Methods), 4.3.4 (Results)

*Male group size, predicted by female group size*swellings (all species)*

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female group size (Non-swelling species)	Ln female group size (Swelling species)	N	R^2	λ
Ln-male group size	$\beta=0.30$, $p=0.13$ (swellings 'up-coded')	$\beta=0.99$, $p<0.001$ (swellings 'up-coded')	45	0.54	0.77
Ln-male group size	$\beta=0.26$, $p=0.18$ (swellings 'down-coded')	$\beta=0.99$, $p<0.001$ (swellings 'down-coded')	45	0.56	0.78

Male group size, predicted by female group size & swellings (multi-male, multi-female only 'up-coded')

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female group size	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-male group size	$\beta=0.42$, $p=0.02$ (swellings 'up-coded')	$\beta=0.38$, $p=0.17$ (swellings 'up-coded')	23	0.38	0
Ln-male group	$\beta=0.40$, $p=0.02$ (swellings	$\beta=0.45$, $p=0.09$ (swellings	23	0.42	0

size	‘down-coded’)	‘down-coded’)			

Male group size, predicted by female group size & swellings (multi-male, multi-female only ‘down-coded’)

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female group size	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-male group size	β=0.58, p=0.01 (swellings ‘up-coded’)	β=0.46, p=0.13 (swellings ‘up-coded’)	19	0.49	0
Ln-male group size	β=0.54, p=0.02 (swellings ‘down-coded’)	β=0.53, p=0.07 (swellings ‘down-coded’)	19	0.52	0

E.v) Chapter 4: 4.2.2 (Methods), 4.3.7 (Results)

Female canine length, predicted by female body mass & swellings (all species)

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-female canine length	β=0.15, p=0.004 (swellings ‘up-coded’)	β=-0.14, p=0.02 (swellings ‘up-coded’)	47	0.22	0.51
Ln-female canine length	β=0.16, p=0.002 (swellings ‘down-coded’)	B=, p= (swellings ‘down-coded’)	47	0.25	0.53

Female canine length, predicted by female body mass & swellings (multi-male, multi-female only ‘up-coded’)

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-female canine length	β=0.16, p=0.01 (swellings ‘up-coded’)	β=0.00, p=0.99 (swellings ‘up-coded’)	24	0.20	0
Ln-female canine length	β=0.17, p=0.01 (swellings ‘down-coded’)	β=-0.03, p=73 (swellings ‘down-coded’)	24	0.21	0

Female canine length, predicted by female body mass & swellings (multi-male, multi-female only ‘down-coded’)

	Predictor variables with effect sizes & p-values				
Outcome variables	Ln female body mass	Swellings (none vs. exaggerated)	N	R^2	λ
Ln-female canine length	β=0.16, p=0.02 (swellings ‘up-coded’)	β=-0.01, p=0.91 (swellings ‘up-coded’)	20	0.20	0
Ln-female canine length	β=0.17, p=0.02 (swellings ‘down-coded’)	β=-0.04, p=0.66 (swellings ‘down-coded’)	20	0.21	0

Appendix F: full results for PGLS analyses presented in Chapter 5

F.i) Chapter 5: 5.2.3 (Methods) 5.3.1 (Results)

Tactical deception rate, predicted by testes mass, body mass and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1	β=-0.24, p=0.09 β=0.02, p<0.001 β=0.29, p=0.002 β=0.28, p=0.006	31	0.73	0.00

Tactical deception rate in males, predicted by testes mass, body mass and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception males+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1	β=-0.54, p=0.09 β=0.02, p=0.009 β=0.61, p<0.001 β=-0.05, p=0.70	19	0.73	0.00

Tactical deception rate in females, predicted by testes mass, body mass and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception females+1	Ln-testes mass Ln-male body mass Ln-research effort+1	β=0.06, p=0.70 β=0.23, p=0.14 β=0.38, p=0.02	19	0.42	0.00

Tactical deception rate, predicted by testes mass, body mass, research effort and social group size

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1 Ln-social group size	β=-0.26, p=0.10 β=0.02, p=0.001 β=0.30, p=0.004 β=0.29, p=0.01 β=0.0002, p=1	29	0.72	0.00

F.ii) Chapter 5: 5.2.3 (Methods) 5.3.2 (Results)

Innovation rate, predicted by testes mass, body mass and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-innovation+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1	β=-0.19, p=0.19 β=0.02, p<0.001 β=0.10, p=0.27 β=0.50, p<0.001	68	0.60	0.00

Innovation rate in males, predicted by testes mass, body mass and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-innovation males+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1	β=-0.38, p=0.03 β=0.02, p<0.001 β=0.25, p=0.01 β=0.20, p=0.09	24	0.75	0.00

Innovation rate in females, predicted by testes mass, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation females+1	Ln-testes mass Ln-male body mass Ln-research effort+1	β=0.11, p=0.45 β=-0.06, p=0.65 β=0.54, p=0.002	24	0.39	0.00

Innovation rate, predicted by testes mass, body mass, research effort and social group size

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1 Ln-social group size	β=-0.18, p=0.24 β=0.02, p<0.001 β=0.12, p=0.20 β=0.49, p<0.001 β=-0.08, p=0.37	66	0.60	0.00

Innovation rate, predicted by testes mass, body mass, research effort and social group size (removing an outlier, Cebus apella)

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation+1	Ln-testes mass Testes mass Ln-male body mass Ln-research effort+1 Ln-social group size	β=-0.17, p=0.25 β=0.02, p<0.001 β=0.11, p=0.19 β=0.43, p<0.001 β=-0.08, p=0.32	65	0.62	0.00

F.iii) Chapter 5: 5.2.3 (Methods) 5.3.2 (Results)

g_{s1}, predicted by testes mass, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-testes mass Testes mass Ln-male body mass	β=-0.99, p=0.01 β=0.09, p<0.001 β=0.46, p=0.03	68	0.57	0.00

g_{s1}, predicted by testes mass, body mass and research effort (removing outliers, Pongo pygmaeus and Cebus apella)

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-testes mass Testes mass Ln-male body mass	β=-0.88, p=0.005 β=0.09, p<0.001 β=0.27, p=0.13	66	0.67	0.00

g_{s1}, predicted by testes mass, body mass, research effort and social group size

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-testes mass Testes mass Ln-male body mass Ln-social group size	β=-0.89, p=0.02 β=0.09, p<0.001 β=0.53, p=0.02 β=-0.35, p=0.14	66	0.58	0.00

g_{s1}, predicted by testes mass, body mass, research effort and social group size (removing an outlier, Pan troglodytes)

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
g_{s1}	Ln-testes mass	β=-0.46, p=0.22	65	0.37	0.00
	Testes mass	β=0.06, p<0.001			
	Ln-male body mass	β=0.45, p=0.03			
	Ln-social group size	β=-0.29, p=0.19			

F.iv) Chapter 5: 5.2.3 (Methods) 5.3.3 (Results)

Tactical deception rate, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception+1	Body mass dimorphism	β=0.15, p=0.26	40	0.21	0.68
	Ln-research effort+1	β=0.32, p=0.008			

Tactical deception rate in males, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception males+1	Body mass dimorphism	β=0.27, p=0.18	23	0.03	0.80
	Ln-research effort+1	β=0.07, p=0.70			

Tactical deception rate in females, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-deception females+1	Body mass dimorphism	β=-0.03, p=0.82	23	0.35	0.00
	Ln-research effort+1	β=0.42, p=0.002			

Innovation rate, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-innovation+1	Body mass dimorphism	β=0.10, p=0.17	165	0.37	0.52
	Ln-research effort+1	β=0.42, p<0.001			

Innovation rate in males, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-innovation males+1	Body mass dimorphism	β=0.22, p=0.12	30	0.26	0.00
	Ln-research effort+1	β=0.37, p=0.009			

Innovation rate in females, predicted by body mass dimorphism and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-innovation females+1	Body mass dimorphism	β=-0.08, p=0.50	30	0.44	0.00
	Ln-research effort+1	β=0.55, p<0.001			

g_{s1}, predicted by body mass dimorphism

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
g_{s1}	Body mass dimorphism	β=0.12, p=0.53	165	0.0	0.85

F.v) Chapter 5: 5.2.3 (Methods) 5.3.5 (Results)

Main effect of mating system on tactical deception rate

Model	**AIC**
Deception predicted by mating system (‘down-coded’) & research effort	87.26*
Deception predicted by mating system (‘up-coded’) & research effort	89.07*
Deception predicted by research effort only	92.90

* = more complex model favoured by >2 AIC units

Main effect of mating system on tactical deception rate in males

Model	**AIC**
Deception in males predicted by mating system (‘down-coded’) & research effort	65.13
Deception in males predicted by mating system (‘up-coded’) & research effort	65.64
Deception in males predicted by research effort only	62.70

* = more complex model favoured by >2 AIC units

Main effect of mating system on tactical deception rate in females

Model	**AIC**
Deception in females predicted by mating system (‘down-coded’) & research effort	56.58
Deception in females predicted by mating system (‘up-coded’) & research effort	56.39
Deception in females predicted by research effort only	52.76

* = more complex model favoured by >2 AIC units

Main effect of mating system on innovation rate

Model	**AIC**
Innovation predicted by mating system (‘down-coded’) & research effort	297.76
Innovation predicted by mating system (‘up-coded’) & research effort	298.34
Innovation predicted by research effort only	299.50

* = more complex model favoured by >2 AIC units

Main effect of mating system on innovation rate in males

Model	**AIC**
Innovation in males predicted by mating system (‘down-coded’) & research effort	74.67
Innovation in males predicted by mating system (‘up-coded’) & research effort	75.00
Innovation in males predicted by research effort only	72/14

* = more complex model favoured by >2 AIC units

Main effect of mating system on innovation rate in females

Model	**AIC**
Innovation in females predicted by mating system (‘down-coded’) & research effort	63.52
Innovation in females predicted by mating system (‘up-coded’) & research effort	63.62
Innovation in females predicted by research effort only	60.17

* = more complex model favoured by >2 AIC units

Main effect of mating system on g_{s1}

Model	**AIC**
$g_{s1,}$ predicted by mating system (‘down-coded’) & research effort	553.47
$g_{s1,}$ predicted by mating system (‘up-coded’) & research effort	555.09
$g_{s1,}$ predicted by research effort only	552.66

* = more complex model favoured by >2 AIC units

Tactical deception rate, predicted by mating system ('downcoded') and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.49, p=0.26	41	0.17	0.87
	Monogamous vs. multi-male, multi-female	β=1.05, p=0.02			
	Multi-male, multi-female vs. polygynous	β=0.55, p=0.02			
	Ln-research effort+1	β=0.008, p=0.94			

Tactical deception rate, predicted by mating system ('upcoded') and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.70, p=0.16	41	0.15	0.87
	Monogamous vs. multi-male, multi-female	β=1.22, p=0.02			
	Multi-male, multi-female vs. polygynous	β=0.52, p=0.02			
	Ln-research effort+1	β=-0.009, p=0.94			

Tactical deception rate, predicted by mating system ('downcoded') and research effort (removing an outlier, Pan troglodytes)

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.59, p=0.18	40	0.24	0.97
	Monogamous vs. multi-male, multi-female	β=1.14, p=0.01			
	Multi-male, multi-female vs. polygynous	β=0.54, p=0.005			
	Ln-research effort+1	β=-0.16, p=0.09			

Tactical deception rate, predicted by mating system ('upcoded') and research effort (removing an outlier, Pan troglodytes)

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.82, p=0.08	40	0.17	0.93
	Monogamous vs. multi-male, multi-female	β=1.28, p=0.008			
	Multi-male, multi-female vs. polygynous	β=0.45, p=0.02			
	Ln-research effort+1	β=-0.13, p=0.21			

Tactical deception rate, predicted by mating system ('downcoded'), research effort and social group size

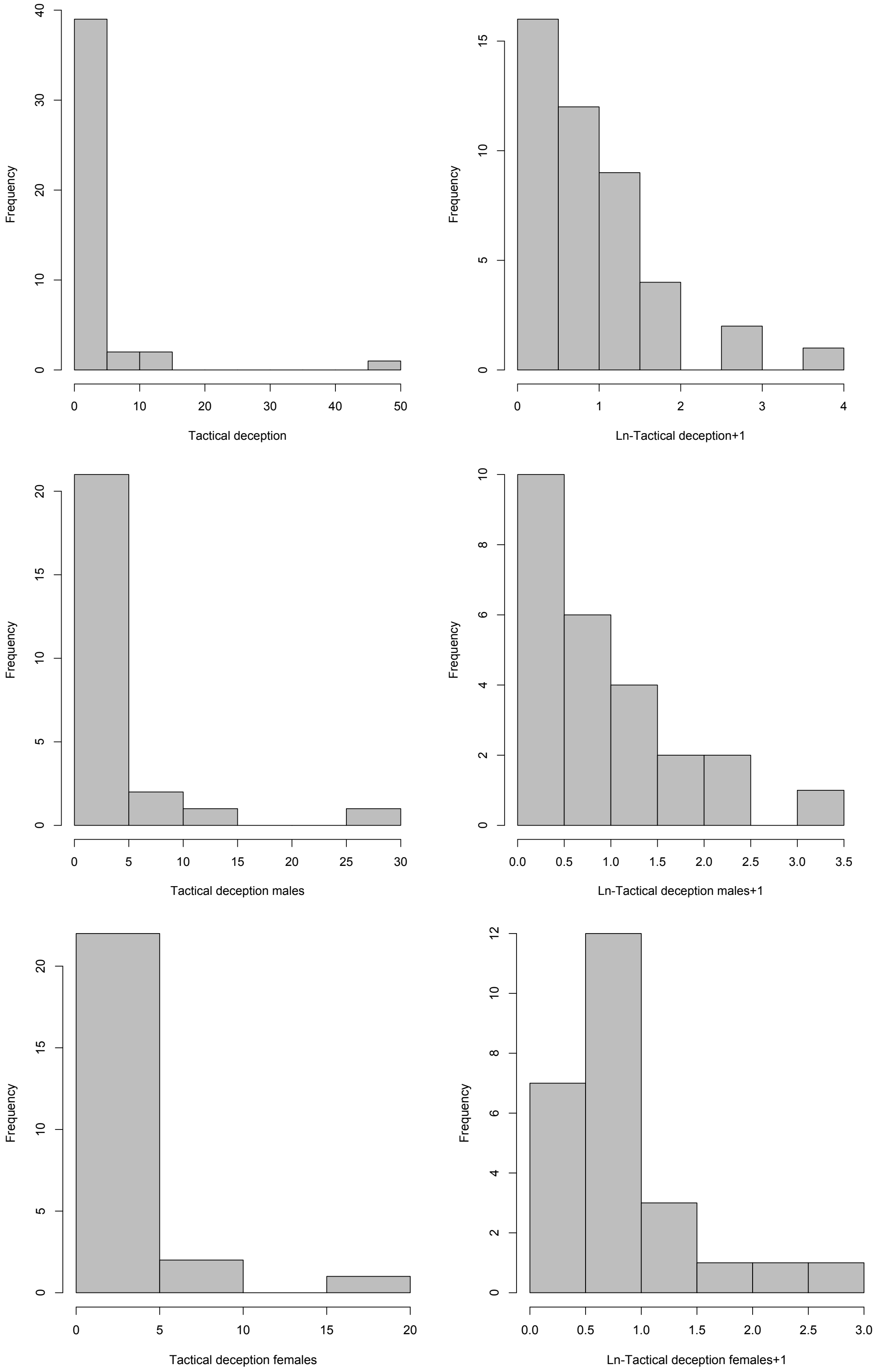
Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.27, p=0.51	37	0.24	0.78
	Monogamous vs. multi-male, multi-female	β=0.73, p=0.11			
	Multi-male, multi-female vs. polygynous	β=0.46, p=0.09			
	Ln-research effort+1	β=0.23, p=0.08			
	Ln-social group size	β=0.05, p=0.74			

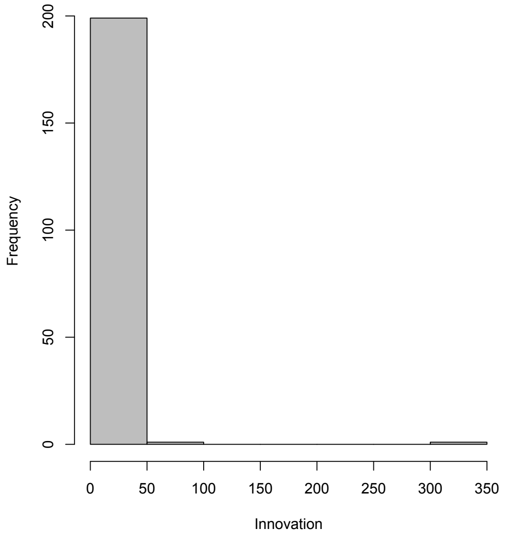
Tactical deception rate, predicted by mating system ('upcoded') research effort and social group size

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-deception+1	Monogamous vs. polygynous	β=0.32, p=0.51	37	0.21	0.79
	Monogamous vs. multi-male, multi-female	β=0.76, p=0.16			
	Multi-male, multi-female vs. polygynous	β=0.44, p=0.1			
	Ln-research effort+1	β=0.23, p=0.11			
	Ln-social group size	β=0.05, p=0.72			

F.vii) Chapter 5: 5.2.2 (Methods)

Comparison of distributions for log transformed and untransformed continuous variables

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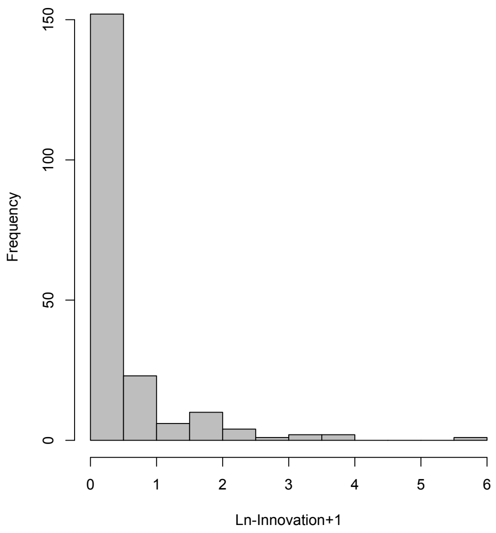
Innovation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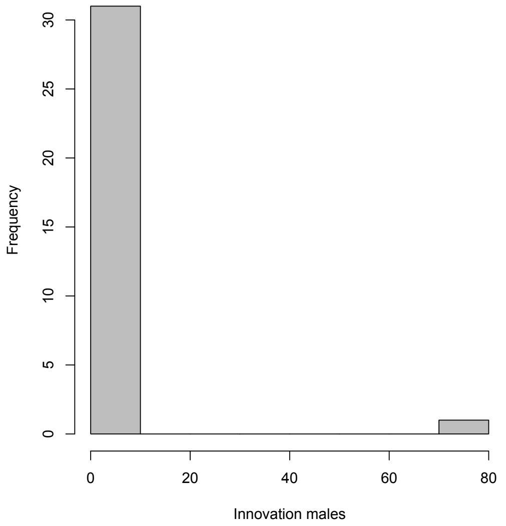
Ln-Innovation+1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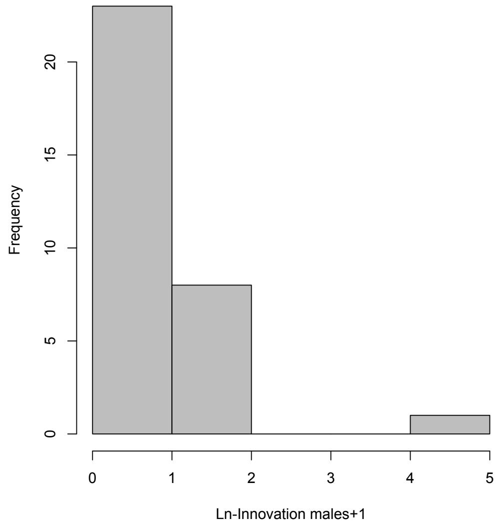
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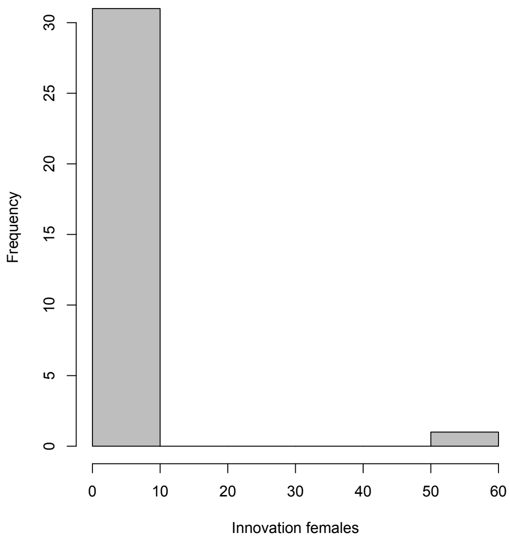
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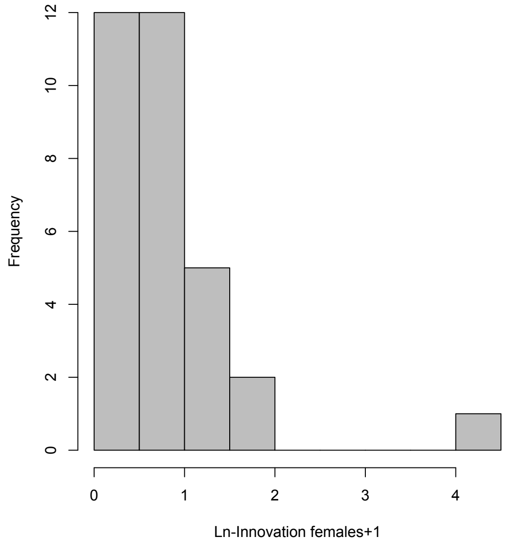
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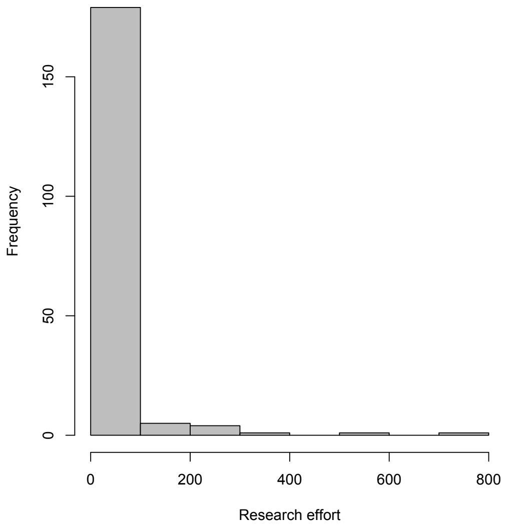
Ln-Innovation females+1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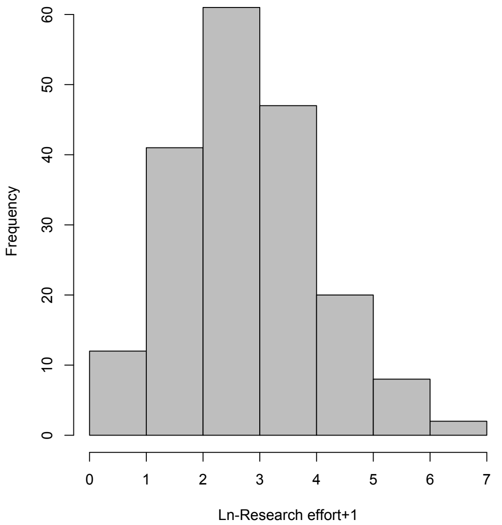
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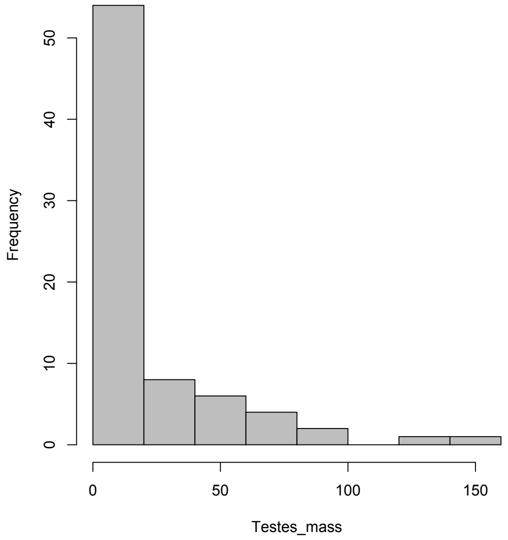
Ln-Research effort+1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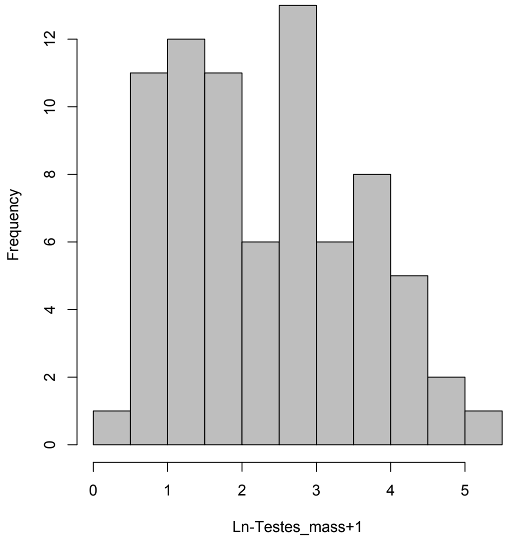
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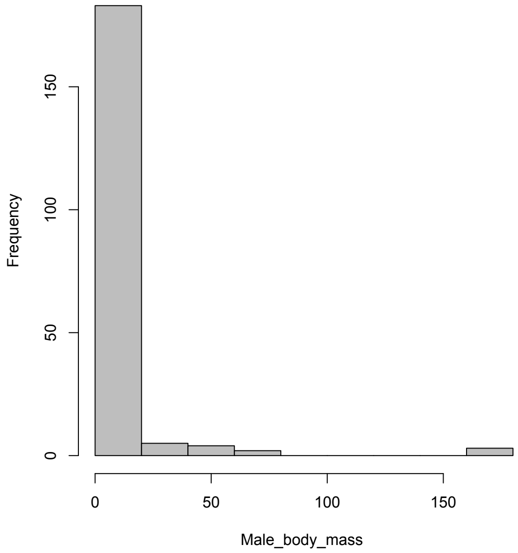
Ln-Testes_mass+1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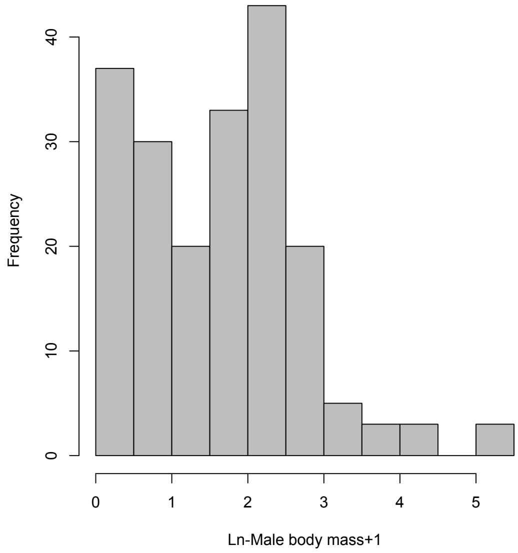
Frequency
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30
40
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2
3
4
5
Ln-Male body mass+1

Appendix G: full results for PGLS analyses presented in Chapter 6 (6.3.1-6.3.2)

G.i) Chapter 6: 6.3.1 (Results)

$g_{s1,}$ predicted by whole brain volume

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-brain volume	$\beta=-0.61$, $p=0.05$	62	0.58	0.00
	Brain volume	$\beta<0.01$, $p<0.001$			

$g_{s1,}$ predicted by whole brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-brain volume	$\beta=0.33$, $p=0.69$	62	0.59	0.00
	Brain volume	$\beta<0.01$, $p<0.001$			
	Ln-body mass	$\beta=-0.78$, $p=0.23$			

$g_{s1,}$ predicted by neocortex volume, remaining (whole – neocortex) brain volume, and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-neocortex volume	$\beta=-1.68$, $p=0.05$	62	0.58	0.00
	Neocortex volume	$\beta<0.01$, $p<0.001$			
	Ln-remaining brain volume	$\beta=2.60$, $p=0.02$			
	Ln-body mass	$\beta=-1.12$, $p=0.11$			

$g_{s1,}$ predicted by cerebellum volume, remaining (whole – cerebellum) brain volume, and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-cerebellum volume	$\beta=-1.24$, $p=0.41$	62	0.56	0.00
	Cerebellum volume	$\beta<0.01$, $p<0.001$			
	Ln-remaining brain volume	$\beta=1.48$, $p=0.17$			
	Ln-body mass	$\beta=-0.05$, $p=0.49$			

Social learning, predicted by whole brain volume and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Social learning+1	Ln-brain volume	$\beta=-0.07$, $p=0.57$	62	0.62	0.00
	Brain volume	$\beta<0.01$, $p<0.001$			
	Ln-research effort+1	$\beta=0.05$, $p<0.001$			

Social learning, predicted by whole brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Social learning+1	Ln-brain volume	$\beta=0.01$, $p=0.73$	62	0.62	0.00
	Brain volume	$\beta<0.01$, $p<0.001$			
	Ln-body mass	$\beta=-0.15$, $p=0.56$			
	Ln-research effort+1	$\beta=0.05$, $p<0.001$			

Social learning, predicted by neocortex volume, remaining (whole – neocortex) brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ

Ln-Social learning+1	Ln-neocortex volume	β=-0.38, p=0.24	61	0.62	0.00
	Neocortex volume	β<0.01, p=0.001			
	Ln-remaining brain volume	β=0.55, p=0.20			
	Ln-body mass	β=-0.18, p=0.49			
	Ln-research effort+1	β=0.44, p<0.001			

Social learning, predicted by cerebellum volume, remaining (whole – cerebellum) brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Social learning+1	Ln-cerebellum volume	β=-0.29, p=0.62	62	0.59	0.00
	Cerebellum volume	β<0.01, p=0.008			
	Ln-remaining brain volume	β=0.36, p=0.41			
	Ln-body mass	β=-0.07, p=0.81			
	Ln-research effort+1	β=0.45, p<0.001			

Innovation, predicted by whole brain volume and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Innovation+1	Ln-brain volume	β=-0.01, p=0.26	62	0.64	0.00
	Brain volume	β<0.01, p<0.001			
	Ln-research effort+1	β=0.05, p<0.001			

Innovation, predicted by whole brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Innovation+1	Ln-brain volume	β=0.02, p=0.54	62	0.64	0.00
	Brain volume	β<0.01, p<0.001			
	Ln-body mass	β=-0.03, p=0.28			
	Ln-research effort+1	β=0.04, p<0.001			

Innovation, predicted by neocortex volume, remaining (whole – neocortex) brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Innovation+1	Ln-neocortex volume	β=-0.43, p=0.18	61	0.65	0.00
	Neocortex volume	β<0.01, p<0.001			
	Ln-remaining brain volume	β=0.76, p=0.08			
	Ln-body mass	β=-0.35, p=0.19			
	Ln-research effort+1	β=0.44, p<0.001			

Innovation, predicted by cerebellum volume, remaining (whole – cerebellum) brain volume, body mass and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Innovation+1	Ln-cerebellum volume	β=-0.02, p=0.97	62	0.62	0.00
	Cerebellum volume	β<0.01, p=0.003			
	Ln-remaining brain volume	β=0.31, p=0.48			
	Ln-body mass	β=-0.27, p=0.36			
	Ln-research effort+1	β=0.46, p<0.001			

G.ii) Chapter 6: 6.3.2.1 (Results)

Whole brain volume, predicted by social group size

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Ln-group size	$\beta=0.15, p=0.13$	58	0.02	1.00

Whole brain volume, predicted by social group size and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Ln-group size	$\beta=0.11, p=0.002$	58	0.89	0.93
	Ln-body mass	$\beta=0.64, p<0.001$			

Neocortex volume, predicted by social group size, remaining (whole – neocortex) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-neocortex volume	Ln-group size	$\beta=0.09, p=0.02$	58	0.93	0.20
	Ln-remaining brain volume	$\beta=0.53, p<0.001$			
	Ln-body mass	$\beta=0.33, p=0.002$			

Cerebellum volume, predicted by social group size, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-cerebellum volume	Ln-group size	$\beta=0.006\ p=0.80$	58	0.96	0.80
	Ln-remaining brain volume	$\beta=0.83, p<0.001$			
	Ln-body mass	$\beta=0.12, p=0.05$			

$g_{s1,}$, predicted by social group size

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-group size	$\beta=0.23, p=0.21$	166	0.003	0.83

Social learning, predicted by social group size and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-social learning+1	Ln-group size	$\beta=-0.17, p=0.02$	169	0.40	0.00
	Group size	$\beta=0.02, p<0.001$			
	Ln-research effort+1	$\beta=0.38, p<0.001$			

Innovation, predicted by social group size and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation+1	Ln-group size	$\beta=-0.22, p=0.004$	169	0.42	0.00
	Group size	$\beta=0.02, p=0.001$			
	Ln-research effort+1	$\beta=0.44, p<0.001$			

G.iii) Chapter 6: 6.3.2.2 (Results)

Whole brain volume, predicted by percentage fruit & seeds in diet

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	% fruit & seeds	$\beta=0.004$, $p=0.23$	45	0.01	1.00

Whole brain volume, predicted by percentage fruit & seeds in diet and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	% fruit & seeds	$\beta<0.01$, $p=0.93$	45	0.88	0.95
	Ln-body mass	$\beta=0.64$, $p<0.001$			

Neocortex volume, predicted by percentage fruit & seeds in diet, remaining (whole – neocortex) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-neocortex volume	% fruit & seeds	$\beta<0.01$, $p=0.98$	45	0.93	0.11
	Ln-remaining brain volume	$\beta=0.66$, $p<0.001$			
	Ln-body mass	$\beta=0.26$, $p=0.04$			

Cerebellum volume, predicted by percentage fruit & seeds in diet, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-cerebellum volume	% fruit & seeds	$\beta<0.01$, $p=0.54$	45	0.96	0.82
	Ln-remaining brain volume	$\beta=0.89$, $p<0.001$			
	Ln-body mass	$\beta=0.09$, $p=0.19$			

$g_{s1,}$, predicted by percentage fruit & seeds in diet

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	% fruit & seeds	$\beta<0.01$, $p=0.48$	94	0.00	0.91

Social learning, predicted by percentage fruit & seeds in diet and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-social learning+1	% fruit & seeds	$\beta<0.01$, $p=0.21$	97	0.45	0.00
	Ln-research effort+1	$\beta=0.55$, $p<0.001$			

Innovation, predicted by percentage fruit & seeds in diet and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation+1	% fruit & seeds	$\beta<0.01$, $p=0.78$	97	0.44	0.00
	Ln-research effort+1	$\beta=0.57$, $p<0.001$			

Whole brain volume, predicted by diet breadth

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Diet breadth	β=0.04, p=0.34	62	0.00	1.00

Whole brain volume, predicted by diet breadth and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Diet breadth	β=0.03, p=0.21	62	0.86	0.92
	Ln-body mass	β=0.63, p<0.001			

Neocortex volume, predicted by diet breadth, remaining (whole – neocortex) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-neocortex volume	Diet breadth	β=0.02, p=0.33	61	0.92	0.32
	Ln-remaining brain volume	β=0.56, p<0.001			
	Ln-body mass	β=0.32, p=0.002			

Cerebellum volume, predicted by diet breadth, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-cerebellum volume	Diet breadth	β=-0.01, p=0.40	62	0.96	0.82
	Ln-remaining brain volume	β=0.87, p<0.001			
	Ln-body mass	β=0.10 p=0.07			

$g_{s1,}$, predicted by diet breadth

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Diet breadth	β=0.20, p=0.03	165	0.02	0.85

Social learning, predicted by diet breadth and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-social learning+1	Diet breadth	β=0.09, p=0.02	168	0.33	0.63
	Ln-research effort+1	β=0.33, p<0.001			

Innovation, predicted by diet breadth and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-innovation+1	Diet breadth	β=0.02, p=0.57	168	0.32	0.62
	Ln-research effort+1	β=0.40, p<0.001			

G.iv) Chapter 6: 6.3.2.3 (Results)

Whole brain volume, predicted by latitude range

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Latitude range	β<0.01, p=0.89	64	0.00	1.00

Whole brain volume, predicted by latitude range and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Latitude range	β=0.05, p=0.17	64	0.86	0.92
	Ln-body mass	β=0.63, p<0.001			

Neocortex volume, predicted by latitude range, remaining (whole – neocortex) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Neocortex volume	Ln-Latitude range	β=0.04, p=0.40	63	0.92	0.30
	Ln-remaining brain volume	β=0.55, p<0.001			
	Ln-body mass	β=0.33, p=0.002			

Cerebellum volume, predicted by latitude range, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Cerebellum volume	Ln-Latitude range	β=0.02, p=0.36	64	0.96	0.80
	Ln-remaining brain volume	β=0.84, p<0.001			
	Ln-body mass	β=0.12, p=0.04			

$g_{s1,}$, predicted by latitude range

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
g_{s1}	Ln-Latitude range	β=-0.42, p=0.10	182	0.03	0.85
	Latitude range	β=0.08, p=0.02			

Social learning, predicted by latitude range and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Social learning+1	Ln-Latitude range	β=-0.12, p=0.24	185	0.29	0.65
	Latitude range	β=0.03, p=0.05			
	Ln-research effort+1	β=0.29, p<0.001			

Innovation, predicted by latitude range and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Innovation+1	Ln-Latitude range	β=-0.13, p=0.23	185	0.30	0.65
	Latitude range	β=0.03, p=0.06			
	Ln-research effort+1	β=0.32, p<0.001			

G.v) Chapter 6: 6.3.2.4 (Results)

Whole brain volume, predicted by composite life history length

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Composite life history length	β=0.79, p<0.001	47	0.73	0.58

Whole brain volume, predicted by composite life history length and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Composite life history length	β=0.23, p<0.001	47	0.94	0.67
	Ln-body mass	β=0.54, p<0.001			

Neocortex volume, predicted by composite life history length, remaining (whole – neocortex) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Neocortex volume	Composite life history length	β=0.21, p=0.006	47	0.93	0.32
	Ln-remaining brain volume	β=0.47, p=0.01			
	Ln-body mass	β=0.23, p=0.05			

Cerebellum volume, predicted by composite life history length, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Cerebellum volume	Composite life history length	β=0.12, p=0.007	47	0.96	0.93
	Ln-remaining brain volume	β=0.76, p<0.001			
	Ln-body mass	β=0.10, p=0.10			

$g_{s1,}$, predicted by composite life history length

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
g_{s1}	Composite life history length	β=-0.45, p=0.09	74	0.51	0.00
	Exp-Composite life history length	β=0.39, p<0.001			

Social learning, predicted by composite life history length and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Social learning+1	Composite life history length	β=-0.08, p=0.43	74	0.57	0.00
	Exp-Composite life history length	β=0.09, p<0.001			
	Ln-research effort+1	β=0.47, p<0.001			

Innovation, predicted by composite life history length and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Innovation+1	Composite life history length	β=-0.10, p=0.33	74	0.56	0.00
	Exp-Composite life history length	β=0.09, p<0.001			
	Ln-research effort+1	β=0.50, p<0.001			

Whole brain volume, predicted by juvenile period length

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-juvenile period	β=1.75, p<0.001	53	0.84	0.00

Whole brain volume, predicted by juvenile period length and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-juvenile period	β=0.28, p=0.003	53	0.91	0.87
	Ln-body mass	β=0.58, p<0.001			

Neocortex volume, predicted by juvenile period length, remaining (whole – neocortex) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Neocortex volume	Ln-juvenile period	β=0.41, p<0.001	53	0.95	0.16
	Ln-remaining brain volume	β=0.47, p=0.002			
	Ln-body mass	β=0.25, p=0.02			

Cerebellum volume, predicted by juvenile period length, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Cerebellum volume	Ln-juvenile period	β=0.29, p=0.002	53	0.95	0.57
	Ln-remaining brain volume	β=0.49, p<0.001			
	Ln-body mass	β=0.29, p<0.001			

$g_{s1,}$*, predicted by juvenile period length*

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
g_{s1}	Ln-juvenile period	β=-0.23, p=0.70	103	0.00	0.80

Social learning, predicted by juvenile period length and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Social learning+1	Ln-juvenile period	β=-0.46, p=0.11	103	0.42	0.00
	Juvenile period	β<0.01, p=0.04			
	Ln-research effort+1	β=0.47, p<0.001			

Innovation, predicted by juvenile period length and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Innovation+1	Ln-juvenile period	β=-0.60, p=0.04	103	0.43	0.00
	Juvenile period	β<0.01, p=0.02			
	Ln-research effort+1	β=0.50, p<0.001			

Whole brain volume, predicted by maximum longevity

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Ln-max longevity	β=0.54, p=0.005	56	0.12	1.00

Whole brain volume, predicted by maximum longevity and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Brain volume	Ln-max longevity	β=0.33, p=0.002	56	0.90	0.93
	Ln-body mass	β=0.61, p<0.001			

Neocortex volume, predicted by maximum longevity, remaining (whole – neocortex) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Neocortex volume	Ln-max longevity	β=0.25, p=0.15	55	0.92	0.34
	Ln-remaining brain volume	β=0.41, p=0.02			
	Ln-body mass	β=0.39, p=0.002			

Cerebellum volume, predicted by maximum longevity, remaining (whole – cerebellum) brain volume and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Cerebellum volume	Ln-max longevity	β=-0.08, p=0.37	55	0.96	0.87
	Ln-remaining brain volume	β=0.94, p<0.001			
	Ln-body mass	β=0.06, p=0.35			

g_{s1}*,, predicted by maximum longevity*

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
g_{s1}	Ln-max longevity	β=-11.13, p<0.001	116	0.44	0.04
	Max longevity	β=0.04, p<0.001			

Social learning, predicted by maximum longevity and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Social learning+1	Ln-max longevity	β=-3.67, p<0.001	117	0.63	0.08
	Max longevity	β=0.01, p<0.001			
	Ln-research effort+1	β=0.42, p<0.001			

Innovation, predicted by maximum longevity and research effort

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Innovation+1	Ln-max longevity	β=-3.09, p<0.001	117	0.56	0.00
	Max longevity	β=0.01, p<0.001			
	Ln-research effort+1	β=0.44, p<0.001			

G.vi) Chapter 6: 6.3.2.5 (Results)

Whole brain volume, predicted by g_{s1}

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	g_{s1}	β=0.04, p=0.08	62	0.04	1.00

Whole brain volume, predicted by social learning and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Social learning+1	β=0.08, p=0.18	62	0.05	1.00
	Ln-research effort+1	β=0.05, p=0.35			

Whole brain volume, predicted by innovation and research effort

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Innovation+1	β=0.09, p=0.13	62	0.06	1.00
	Ln-research effort+1	β=0.05, p=0.32			

Whole brain volume, predicted by g_{s1} and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	g_{s1}	β=0.02, p=0.04	62	0.87	1.00
	Ln-body mass	β=0.60, p<0.001			

Whole brain volume, predicted by social learning, research effort and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Social learning+1	β=0.06, p=0.006	62	0.87	1.00
	Ln-research effort+1	β=-0.02, p=0.33			
	Ln-body mass	β=0.60, p<0.001			

Whole brain volume, predicted by innovation, research effort and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Brain volume	Ln-Innovation+1	β=0.04, p=0.08	62	0.87	0.99
	Ln-research effort+1	β=-0.002, p=0.93			
	Ln-body mass	β=0.60, p<0.001			

Neocortex volume, predicted by $g_{s1,}$ remaining brain volume (whole brain – neocortex) and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Neocortex volume	g_{s1}	β=-0.004, p=0.80	62	0.92	0.29
	Ln-remaining brain volume	β=0.55, p<0.001			
	Ln-body mass	β=0.33, p=0.003			

Neocortex volume, predicted by social learning, remaining brain volume (whole brain – neocortex), research effort and body mass

Outcome variables	Predictor variables with effect sizes & p-values		N	R^2	λ
Ln-Neocortex volume	Ln-Social learning+1	β=0.005, p=0.91	61	0.91	0.33
	Ln-remaining brain volume	β=0.52, p=0.001			
	Ln-research effort+1	β=0.001, p=0.98			

	Ln-body mass	β=0.35, p=0.002			

Neocortex volume, predicted by innovation, remaining brain volume (whole brain – neocortex), research effort and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Neocortex volume	Ln-Innovation+1	β=0.005, p=0.91	61	0.91	0.33
	Ln-remaining brain volume	β=0.52, p=0.001			
	Ln-research effort+1	β=0.001, p=0.98			
	Ln-body mass	β=0.35, p=0.002			

Cerebellum volume, predicted by g_{s1}, remaining brain volume (whole brain – cerebellum) and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Cerebellum volume	g_{s1}	β=0.003, p=0.72	62	0.96	0.84
	Ln-remaining brain volume	β=0.88, p<0.001			
	Ln-body mass	β=0.09, p=0.12			

Cerebellum volume, predicted by social learning, remaining brain volume (whole brain – cerebellum), research effort and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln-Cerebellum volume	Ln-Social learning+1	β=0.009, p=0.65	62	0.96	0.88
	Ln-remaining brain volume	β=0.92, p<0.001			
	Ln-research effort+1	β=-0.04, p=0.07			
	Ln-body mass	β=0.07, p=0.22			

Cerebellum volume, predicted by innovation, remaining brain volume (whole brain – cerebellum), research effort and body mass

Outcome variables	**Predictor variables with effect sizes & p-values**		N	R^2	λ
Ln- Cerebellum volume	Ln-Innovation+1	β=0.003, p=0.87	62	0.96	0.88
	Ln-remaining brain volume	β=0.92, p<0.001			
	Ln-research effort+1	β=-0.03, p=0.09			
	Ln-body mass	β=0.07, p=0.24			

Appendix H: full results for PGLS analyses presented in Chapter 6 (6.3.3)

H.i) Chapter 6: 6.3.3.1 (Results)

Outcome variables	Predictor variables with effect sizes & p-values		AIC	N	R^2	λ
Ln-whole brain volume	Ln-Juvenile period Ln-Maximum longevity gs_1	β=1.17, p<0.001 β=0.68, p=0.03 β=0.04, p=0.13	76.60	51	0.67	0.58
Ln-whole brain volume	Ln-Juvenile period Ln-Maximum longevity	β=1.42, p<0.001 β=0.85, p=0.005	76.55	51	0.87	0.00
Ln-whole brain volume	Ln-Juvenile period	β=1.76, p<0.001	83.16	51	0.85	0.00
Ln-whole brain volume	Ln-Maximum longevity	β=0.67, p=0.001	87.96	51	0.18	1.00

H.ii) Chapter 6: 6.3.3.2 (Results)

Outcome variables	Predictor variables with effect sizes & p-values		AIC	N	R^2	λ
Ln-whole brain volume	Ln-Group size Ln-Juvenile period Ln-Maximum longevity Ln-Social learning+1 Ln-Innovation+1 Ln-Research effort+1 Ln-Body mass	β=0.09, p=0.0009 β=0.17, p=0.05 β=0.36, p=0.002 β=0.07, p=0.09 β=-0.03, p=0.50 β=-0.05, p=0.16 β=0.56, p<0.001	-16.78	48	0.92	1.00
Ln-whole brain volume	Ln-Group size Ln-Maximum longevity Ln-Body mass	β=0.10, p=0.003 β=0.39, p<0.001 β=0.58, p<0.001	-15.59	48	0.92	0.97
Ln-whole brain volume	Ln-Group size Ln-Body mass	β=0.10, p=0.01 β=0.63, p<0.001	-2.35	48	0.89	0.95
Ln-whole brain volume	Ln-Maximum longevity Ln-Body mass	β=0.39, p<0.001 β=0.59, p<0.001	-8.60	48	0.90	0.96

H.iii) Chapter 6: 6.3.3.3 (Results)

Outcome variables	Predictor variables with effect sizes & p-values		AIC	N	R^2	λ
Ln-neocortex volume	Ln-Group size Ln-Juvenile period Ln-Remaining brain volume Ln-Body mass	β=0.07, p=0.05 β=0.39, p=0.002 β=0.48, p=0.002 β=0.23, p=0.03	8.72	50	0.97	0.00
Ln-neocortex volume	Ln-Group size Ln-Remaining brain volume Ln-Body mass	β=0.09, p=0.02 β=0.64, p<0.001 β=0.24, p=0.03	17.81	50	0.96	0.00
Ln-neocortex volume	Ln-Juvenile period Ln-Remaining brain volume Ln-Body mass	β=0.40, p=0.001 β=0.48, p=0.002 β=0.25, p=0.02	10.57	50	0.95	0.16

H.iv) Chapter 6: 6.3.3.4 (Results)

Outcome variables	Predictor variables with effect sizes & p-values		AIC	N	R^2	λ
gs_1	Diet breadth Ln-Latitude range Latitude range Ln-Maximum longevity Maximum longevity	β=0.19, p=0.10 β=-0.31, p=0.49 β=0.08, p=0.09 β=-11.74, p<0.001 β=0.04, p<0.001	445.96	113	0.46	0.05

gs_1	Ln-Maximum longevity	β=-11.12, p<0.001	449.12	113	0.44	0.04
	Maximum longevity	β=0.04, p<0.001				

H.v) Chapter 6: 6.3.3.5 (Results)

Outcome variables	**Predictor variables with effect sizes & p-values**		AIC	N	R^2	λ
Ln-social learning+1	Ln-group size	β=0.007, p=0.95	158.22	88	0.71	0.00
	Group size	β=0.01, p=0.08				
	Diet breadth	β=0.02, p=0.63				
	Ln-Latitude range	β=-0.05, p=0.75				
	Latitude range	β=0.02, p=0.29				
	Ln-Juvenile period	β=0.18, p=0.56				
	Juvenile period	β<0.01, p=0.07				
	Ln-Maximum longevity	β=-4.52, p<0.001				
	Maximum longevity	β=0.02, p<0.001				
	Ln-Research effort+1	β=0.43, p<0.001				
Ln-social learning+1	Ln-Maximum longevity	β=-3.83, p<0.001	164.20	88	0.66	0.00
	Maximum longevity	β=0.01, p<0.001				
	Ln-Research effort+1	β=0.46, p<0.001				

H.vi) Chapter 6: 6.3.3.6 (Results)

Outcome variables	**Predictor variables with effect sizes & p-values**		AIC	N	R^2	λ
Ln-innovation+1	Ln-group size	β=-0.11, p=0.43	191.93	89	0.60	0.00
	Group size	β=0.01, p=0.14				
	Ln-Latitude range	β=-0.19, p=0.34				
	Latitude range	β=0.03, p=0.16				
	Ln-Juvenile period	β=0.20, p=0.59				
	Juvenile period	β<0.01, p=0.34				
	Ln-Maximum longevity	β=-3.59, p<0.001				
	Maximum longevity	β=0.01, p<0.001				
	Ln-Research effort+1	β=0.49, p<0.001				
Ln-innovation+1	Ln-Maximum longevity	β=-3.50, p<0.001	186.48	89	0.60	0.00
	Maximum longevity	β=0.01, p<0.001				
	Ln-Research effort+1	β=0.50, p<0.001				