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Great Ape Origins of Personality Maturation and Sex Differences

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Great Ape Origins of Personality Maturation and Sex Differences:

A Study of Orangutans and Chimpanzees

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Abstract

Human personality development evinces increased emotional stability, prosocial tendencies, and responsibility. One hypothesis offered to explain this pattern is Social-Investment Theory, which posits that culturally defined social roles, including marriage and employment, are responsible for the increased maturity. Alternatively, Five-Factor Theory emphasizes the role of biological factors, such as those governing physical development, which may predate the emergence of humans. Five-Factor Theory unlike Social-Investment Theory predicts that all or some of the human personality trends should be present in great apes, our closest evolutionary relatives. To test this prediction and to better understand the evolutionary origins of sex differences, we examined age and sex differences in the chimpanzee and orangutan personality dimensions Extraversion, Dominance, Neuroticism, and Agreeableness. We also examined the Activity and Gregariousness facets of Extraversion and the orangutan Intellect domain. In common with humans, Extraversion and Neuroticism declined across age groups in both species. Agreeableness declined in orangutans but increased in chimpanzees, as it does in humans, though this may reflect differences in how Agreeableness was defined in each species. Significant interactions indicated that male chimpanzees, unlike male orangutans, displayed higher Neuroticism scores than females, and maintained higher levels of Activity and Dominance into old age. Personality-age correlations were comparable across orangutans and chimpanzees, and similar to those reported in human studies. Sex differences were stronger in chimpanzees than in humans or orangutans. These findings support Five-Factor Theory, suggest the role of gene-culture coevolution in shaping personality development, and suggest that sex differences evolved independently in different species.

Keywords: personality, development, five-factor theory, Social-Investment Theory, primate

Introduction

Understanding how and why personality develops throughout life and why some personality traits differ between males and females is crucial to improving the lives of humans and animals and also to understanding personality evolution. To date, however, most research in personality development has focused on humans. Cross-sectional and longitudinal studies indicate that human aging brings with it a pattern of changes in personality reflecting greater maturity, self-control, and emotional stability (Roberts, Wood, & Caspi, 2008). In terms of the Five-Factor Model (Digman, 1990), the changes are declines in Neuroticism and Extraversion, increases in Agreeableness and Conscientiousness, and an increase and then decline in Openness to Experience (Bleidorn et al., 2013; Donnellan & Lucas, 2008; McCrae et al., 1999; McCrae et al., 2000; McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005; Roberts, Walton, & Viechtbauer, 2006; Soto, John, Gosling, & Potter, 2011; Srivastava, John, Gosling, & Potter, 2003; Terracciano, McCrae, Brant, & Costa, 2005).

One hypothesis offered to explain age-related changes in personality is Five-Factor Theory (McCrae & Costa, 2003). It posits that personality development, like personality itself, has biological and genetic origins, and is ultimately the product of evolution (McCrae & Costa, 2003). Five-Factor Theory thus predicts that developmental trends will differ only by small amounts across cultures. Studies highlighting the universality and genetic basis of human personality, such as those showing that age-related trends across cultures are similar (Bleidorn et al., 2013; McCrae et al., 1999; McCrae et al., 2000; McCrae et al., 2005), personality domains are heritable (Bouchard & Loehlin, 2001), the genetic structure of personality is similar across cultures (Yamagata et al., 2006), and genetic effects underlie the stabilities and trajectories of personality development (Bleidorn, Kandler, Riemann, Angleitner, & Spinath, 2009; McGue,

Bacon, & Lykken, 1993; Viken, Rose, Kaprio, & Koskenvuo, 1994), support Five-Factor

Theory.

Social-Investment Theory is another hypothesis offered to explain age-related changes in

personality (Roberts, Wood, & Smith, 2005). It posits that personality development arises from

individuals investing in age-related social roles, such as parenting and employment (Roberts et

al., 2005). Social-Investment Theory thus predicts that developmental trends will differ across

cultures in accordance with socially imposed constraints. Evidence supporting this hypothesis

includes data highlighting how social roles, such as those related to work and family, facilitate

increases in Agreeableness and Conscientiousness and decreases in Neuroticism and

Extraversion. A meta-analysis of cross-sectional studies found evidence for several such

associations and that, for some social roles, the associations were stronger where investment in

the role was greater (Lodi-Smith & Roberts, 2007). Moreover, a cross-sectional/cross-cultural

study found that cultures in which employment and family life started earlier showed stronger

age-related decreases in Neuroticism and Openness and stronger age-related increases in

Conscientiousness (Bleidorn et al., 2013). Social-investment theory also stresses environmental

contributions to personality, including non-shared environmental effects, identified in

longitudinal behavioral genetic studies (Bleidorn et al., 2009; McGue et al., 1993; Viken et al.,

1994).

These theories are not fundamentally incompatible. Instead the issue is whether

evolutionary processes that predated present day human social and cultural conditions selected

the pattern of human personality. Such processes would place strong constraints on

contemporary human populations, and are implied by Five-Factor Theory. Alternatively, is

human personality development based on social and cultural conditions, specific to humans, as

implied by the Social-Investment Theory? The controversy thus involves the question of whether these developmental changes are most accurately understood by an evolutionarily based explanation (an ultimate cause) or by a social-cultural explanation (a proximate cause) (Sherman, 1988; Tinbergen, 2005).

Unfortunately, there are no strong empirical tests in studies of humans that can clearly rule out either theory. However, Five-Factor Theory's assumption that personality development has an evolutionary basis leads to the prediction that developmental trends should be present in nonhuman primates, and especially our phylogenetically closest ancestors, the great apes.

Previous studies of nonhuman primates partially support Five-Factor Theory. For instance, species of monkeys, including captive rhesus macaques (Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Stevenson-Hinde & Zunz, 1978; Suomi, Novak, & Well, 1996), crab-eating macaques (Uher, Werner, & Gosselt, 2013), pigtailed macaques (Sussman, Mates, Ha, Bentson, & Crockett, 2014), and wild white-faced capuchin monkeys (Manson & Perry, 2013), display age-related personality changes similar to some of those in humans. These common changes extend to great apes. Kuhar, Stoinski, Lukas, and Maple (2006) found that the captive lowland gorilla factors "Dominant", "Understanding", and "Fearful" were not related to age, but the factor "Extroverted" was lower in older individuals. Also, echoing early descriptions (Yerkes, 1939), cross-sectional (Dutton, 2008; King, Weiss, & Farmer, 2005; King, Weiss, & Sisco, 2008; Massen, Antonides, Arnold, Bionda, & Koski, 2013; Weiss et al., 2009; Weiss, King, & Hopkins, 2007) studies suggest that personality development in chimpanzees and humans is similar.

Particularly noteworthy was a cross-sectional study of human and chimpanzee personality development (King et al., 2008). This study revealed broad similarities in the age-

related differences across these species. Also, after adjustment for the more rapid maturation of chimpanzees, the mean absolute change per year was similar in chimpanzees and humans. However, unlike humans (McCrae et al., 1999), male and female chimpanzees displayed different developmental trends. Male but not female chimpanzees maintained high levels of Activity, a facet of Extraversion, and Dominance, a domain combining elements of low fear, assertiveness, aggressiveness, and independence, into old age. Moreover, the age-related rise in Agreeableness was greater in females than in males.

The finding by King and his colleagues (2008) that chimpanzees, who are our closest living nonhuman relatives, exhibit a human like pattern of personality development is intriguing and seems to rule out Social-Investment Theory. However, as strong as these findings are, they are limited because, like humans, chimpanzees are an intensely social species (Goodall, 1986). Thus, these similarities may simply reflect the fact that personality development in chimpanzees (and presumably other highly social species) is a consequence of investing in social roles that are homologous or analogous to those of humans, such as attempts by males to increase their social status.

Thus, the main question addressed in the current study is whether the similarity between personality development in humans and chimpanzees is a consequence of the intense sociality of both species. If so, similarities between personality development in chimpanzees and humans may reflect social factors or life events, including cooperation and competition for status, that chimpanzees have in common with humans (de Waal, 2000; Goodall, 1986; Pusey & Schroepfer-Walker, 2013). Excluding this hypothesis requires examining personality development in species that share a recent common ancestor with humans and chimpanzees, but inhabit a different social environment. Orangutans (*Pongo pygmaeus* and *Pongo abelii*) are ideal

for this comparison. Orangutans share a common ancestor with humans and chimpanzees dating back 15 million years (Purvis, 1995). However, unlike humans and chimpanzees, orangutans are semi-solitary with an individual-based fission-fusion social structure, meaning that individual orangutans meet and maintain contact for short periods of time followed by separation (Galdikas, 1985a, 1985b, 1985c; van Schaik, 1999). Therefore, consistency between the age-related patterning of orangutan and chimpanzee personalities cannot be attributable to social factors or life events in common among highly social species.

Determining whether the comparability of chimpanzee and human personality is a consequence of the sociality of these species involves comparing age-related trends in the comparable chimpanzee and orangutan personality domains of Extraversion, Neuroticism, and Agreeableness. Five-Factor Theory would be supported to the extent that chimpanzee as well as orangutan development shows the human pattern of age-related changes, viz. decreases in Extraversion and Neuroticism as well as increases in Agreeableness. On the other hand, significant interactions between species (chimpanzees vs. orangutans) and age would diminish support for the Five-Factor Theory, especially if the direction of age effects differs between species. In addition, Five-Factor Theory would be supported if developmental rates as defined by the mean change per year are similar in orangutans, chimpanzees, and humans. This constancy would indicate an evolutionarily conserved rate of personality development and would be inconsistent with Social-Investment Theory to the extent that social-cultural influences constitute a key mechanism for personality development.

The second question emerges from the above-described finding that male chimpanzees show a different pattern of personality development than female chimpanzees or humans (King et al., 2008). These differences may reflect the fact that chimpanzee males, unlike human males,

do not invest in their offspring (Goodall, 1986). The fact that personality development in men resembles that in women could be a novel evolutionary adaptation in humans, viz. the ability of social roles including parenting to drive personality development, including a robust increase in Agreeableness. Alternatively, the pattern of personality development in male chimpanzees may be an evolutionarily recent adaptation specific to chimpanzees. The relative validities of these alternatives can be assessed by the significance of the sex by age by species interaction. Because male orangutans also do not care for their young (Galdikas & Wood, 1990), a significant three-way interaction would be consistent with a deviant developmental pattern for male chimpanzees, and thus would favor Five-Factor Theory.

In addition to studying age effects, we used this comparative approach to address questions about sex differences in personality, including which, if any, sex has higher scores, and the magnitude of the difference. On average, women score higher than men in traits related to Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness (Costa, Terracciano, & McCrae, 2001; Del Giudice, Booth, & Irwing, 2012; Feingold, 1994; McCrae et al., 2005; Schmitt, Realo, Voracek, & Allik, 2008). Although small, the magnitudes of these differences vary across cultures (Costa et al., 2001; McCrae et al., 2005; Schmitt et al., 2008). Considerable evidence suggests that these gender differences were affected by sexual selection, and reflect interactions between genetic and environmental effects (Schmitt et al., 2008).

Several studies of nonhuman primates confirm that the origins of sex differences in human personality are rooted in our primate ancestors. For example, sex differences in personality have been found in rhesus macaques (Stevenson-Hinde & Zunz, 1978; Suomi et al., 1996), crab-eating macaques (Uher et al., 2013), white-faced capuchins (Manson & Perry, 2013),

and chimpanzees (King et al., 2005; King et al., 2008; Koski, 2011; Weiss et al., 2009; Weiss et al., 2007). However, one study failed to find sex differences in problem solving, a skill that may reflect Openness (Hopper et al., 2013). Moreover, in studies where sex differences were found, the direction of differences varied even across closely related species. For example, Sussman, Ha, Bentson, and Crockett (2013) found that sex differences in Aggressiveness favored males in long-tailed macaques, females in pigtailed macaques, and neither sex in rhesus macaques. In addition, King and colleagues (2008) found that the tendency for women to be higher than men in Agreeableness and Conscientiousness is also seen in chimpanzees and is likely ancestral stemming from our common ancestor. However, they found that the tendency for men to be lower in Neuroticism and Extraversion than women was inconsistent with the chimpanzee data, suggesting that some human sex differences evolved after the human-chimpanzee split.

To further explore the evolutionary basis for human gender differences in personality, we compared sex differences in chimpanzees and orangutans. If the tendency for women to be higher in Neuroticism and Extraversion evolved recently, we would expect that, in orangutans and chimpanzees, males would have the highest scores on these two domains with the interaction of species and sex being non-significant. If this interaction is significant, it would suggest that sex differences in personality evolved independently many times throughout hominoid evolution. In addition, if, in common with chimpanzees and humans, female orangutans are higher in Agreeableness and the interaction of species and sex is non-significant, it would indicate that the origins of higher female Agreeableness can be traced back to the common ancestor of great apes, approximately 15 million years ago.

Our study brings a comparative, evolutionary perspective to the study of cross-sectional age differences and sex differences in personality. The interspecies comparisons are feasible

because five chimpanzee personality domains (Extraversion, Agreeableness, Conscientiousness, Neuroticism, and Openness) and three orangutan domains (Extraversion, Agreeableness, and Neuroticism) resemble human domains with the same names (King & Figueredo, 1997; King, Weiss, & Sisco, 2008). Therefore, the domains shared by chimpanzees and orangutans will be the focus of this study. However, we shall also examine age and sex differences in the Dominance domain shared between chimpanzees and orangutans, and the orangutan Intellect domain.

Methods

Subjects

Two samples described in previous studies (King et al., 2008; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012) were used. The orangutan sample included 70 males and 104 females living in 38 zoological parks located in the United States ($n = 34$), Canada ($n = 2$), Australia ($n = 1$), and Singapore ($n = 1$). Orangutan ages ranged from 1.8 to 51.2 years ($M = 21.6$; $SD = 12.0$). The chimpanzee sample included 77 males and 125 females living in 17 U.S. zoos and 1 Australian zoo. Chimpanzee ages ranged from .8 to 55.2 years ($M = 16.5$; $SD = 12.2$).

Raters

As detailed previously (King et al., 2008; Weiss et al., 2012), zoo personnel or volunteers who participated in an unrelated project involving chimpanzee behavioral observations rated the chimpanzees and zoo personnel rated the orangutans. Ninety raters assessed chimpanzee personality with a mean of 3.9 raters per chimpanzee and 8.7 chimpanzees per rater. One hundred and seven raters assessed orangutan personality with a mean of 2.6 raters per orangutan and 4.1 orangutans per rater.

Instruments

Each subject's personality was assessed by ratings questionnaires (King & Figueredo, 1997; Weiss et al., 2009; Weiss, King, & Perkins, 2006)[1]. Although ratings of primate personality arouses skepticism in some (e.g., Uher, 2008), there is ample evidence for the reliability and validity of observer ratings of primate personality (Freeman & Gosling, 2010).

Three questionnaires were used in the present study. Each questionnaire consisted of personality descriptive adjectives followed by one to three sentences that set the adjective in the context of primate behavior. One questionnaire comprised 41 adjectives derived from Goldberg's (1990) Big-Five taxonomy and 2 items, 'clumsy' and 'autistic' created for the original study (King & Figueredo, 1997). The second questionnaire comprised the 43 adjectives from the previously described questionnaire and five new items: 'anxious', 'vulnerable', 'cool', 'curious', and 'conventional' (Weiss et al., 2006). The third questionnaire comprised the 48 adjectives from the previously described questionnaire and six additional items: 'thoughtless', 'distractible', 'quitting', 'individualistic', 'innovative', and 'unperceptive' (Weiss et al., 2009).

Of the orangutans, 125 were assessed with the 48-item questionnaire, 12 were assessed with the 43-item questionnaire and a supplementary questionnaire that included the remaining 5 items, and 37 were assessed at a later time with the 54-item questionnaire. All of the chimpanzees were assessed with the 43-item questionnaire.

Domain and Facet *T*-Scores

Raw scores for the comparable chimpanzee and orangutan personality domains --- Extraversion, Dominance, Neuroticism, and Agreeableness --- and the orangutan Intellect domain were generated by unit-weighting and based on definitions of the domains for that species in previous studies (see Table 1). Chimpanzee domains were identified by principal axis factoring of 43 items on 100 of the subjects in our sample, as reported in King and Figueredo

(1997). Orangutan domains were identified by principal components analysis[2] of 48 items on 152

of the subjects in our sample, as reported in Weiss et al. (2006). Because correlations between

dimensions were modest and the varimax and promax rotations produced virtually identical

structures (King & Figueredo, 1997; Weiss et al., 2006), varimax solutions were interpreted.

Domain names were based, when applicable, on their similarity to human personality domains

(King & Weiss, 2011).

King et al. (2008) showed that, like humans (e.g., Terracciano et al., 2005), chimpanzee

personality facets do not necessarily have the same age-related trajectories as their parent

domain. We thus created unit-weighted scores for the chimpanzee and orangutan Extraversion

facets of Activity and Gregariousness (see Table 1). These facets were defined *a priori* based on

the distinction between items related to physical activity and social behavior (King & Weiss,

2011; King et al., 2008), and coincided with definitions of two human Extraversion facets with

the same names (see, e.g. Costa & McCrae, 1995). While King et al. (2008) also identified two

Conscientiousness facets, no Conscientiousness domain was found in orangutans (Weiss et al.,

2006). We therefore did not examine these facets in this study. No other domains contained

items that justified *a priori* separation into facets.

For ease of interpretability, we converted raw scores into T-scores ($M = 50$, $SD = 10$). To

make our results comparable with those from human studies (e.g., McCrae et al., 2000), T-scores

were based on the means and standard deviations of subjects who were the equivalent of

approximately 18 human years of age (aged 12 years or older).

When we compared orangutans and chimpanzees directly in a single model we used T-

scores based on the mean and standard deviation derived from a combined sample of 72 female

chimpanzees, 37 male chimpanzees, 84 female orangutans, and 47 male orangutans. For all other

analyses, we generated within-species *T*-scores. These were based on the mean and standard deviation derived from the individuals of a given species. For example, the within-species *T*-scores for orangutans was based on the 72 female and 37 male orangutans who were at least 12 years old.

Age Groups

In the study comparing chimpanzee and human personality development (King et al., 2008), age groups for humans and chimpanzees were adjusted for the different development rates of the two species. However, defining comparable age groups for orangutans and chimpanzees is less clear. Developmental changes in physical traits are slower in orangutans than in chimpanzees, consistent with the slower life history of orangutans (Wich et al., 2004). However, the rates of chimpanzee and orangutan behavioral development overlap. For example, although weaning occurs later in orangutans than in chimpanzees, independence from maternal care occurs at similar ages (Pusey, 1983; van Adrichem, Utami, Wich, van Hooff, & Sterck, 2006). Likewise, the rate of sensorimotor development does not differ appreciably between the two species (Chevalier-Skolnikoff, 1983; Potì & Spinozzi, 1994). Therefore, we will use the same age-group categories for cross-species comparisons: late infancy to early adolescence (≤ 8 years), early to late adolescence (8.0 to 15.0 years), young adults (15.0 to 25.0 years), fully mature adults (25.0 to 35.0 years), and old adults (> 35.0 years) (see Table 2).

Analysis Strategy

Preliminary analyses. To be consistent with King et al. (2008), we computed inter-rater reliabilities and internal consistencies of raw scores for the orangutan domains for each age group. Inter-rater reliabilities consisted of two intraclass correlation coefficients or *ICC*s (Shrout & Fleiss, 1979). *ICC*(3,1) indicates the reliability of individual ratings; *ICC*(3,*k*) indicates the

reliability of mean scores based on k raters. *ICC*s were computed using mean squares from general linear models in which a domain score is predicted by rater effects, target effects, and the residual term representing the Rater $\times$ Target interaction (R Core Team, 2013). We used the alpha function in R (Revelle, 2013) to compute internal consistencies (Cronbach's alphas).

Although most subjects had lived in a zoo environment for their entire lives, 61 chimpanzees (mean age = 30.8; *SD* = 8.9) and 25 orangutans (mean age = 41.3; *SD* = 6.0) were wild born and transferred to zoos at an early age. Before ratings, wild-born animals had been in zoos for at least 20 years and most for more than 30 years. Therefore, if origin of birth was associated with personality, there would be confounding with age. All but one wild-born orangutan and none of the captive-born orangutans were older than 35 years when their personalities were rated. Thus, the lack of age overlap precluded testing for origin of birth effects independently of age in orangutans. On the other hand, both wild- and captive-born chimpanzees were represented with ages ranging from 15 to 35 years. Therefore, for chimpanzees, we tested whether origin of birth was a potential confound by conducting a general linear model with Type I sums of squares (R Core Team, 2013) where each domain score was predicted by origin of birth after controlling for age.

Age and sex effects. Six analyses, one for each of the four domains and two facets shared by chimpanzees and orangutans, were used to test for and to compare age and sex effects across species. A seventh analysis was conducted to determine whether there were age-related or sex differences in the orangutan Intellect domain.

Each of the first six analyses comparing orangutans and chimpanzees was a general linear model with Type III sums of squares (R Core Team, 2013). The domain or facet *T*-score served as the dependent variable. Predictors included species, sex, and age group, and all two-way

interactions, and the single three-way interaction. Because ratings were based on individual differences within species and not on differences between species, the species main effect was not meaningful and we did not interpret its effects. However, we included it in all models to allow testing for interactions.

In these models, species differences in age effects (significant Species ×Age Group interactions) would support the hypothesis that personality development in chimpanzees, a highly social species, differs from that of orangutans, a less considerably social species. Finding species differences in sex effects (significant Species × Sex interactions) would support the hypothesis that sex effects are relatively labile evolutionary characteristics that vary across species or group social structures. Finding that older male chimpanzees differ from orangutans and female chimpanzees (significant Species × Sex × Age interactions) in a direction suggesting that there was no later life Dominance and Activity decline and a slower rise in Agreeableness would support the hypothesis that there was selection for prolonged male aggression in chimpanzees.

The seventh analysis was also a general linear model with Type III sums of squares (R Core Team, 2013). The Intellect domain *T*-score served as the dependent variable in this model and predictors included the main effects of sex, age group, and their interaction.

We conducted two sets of follow-on analyses. First, if there were interactions, we conducted post-hoc general linear models to clarify the nature of the effects. These involved splitting the data by one of the interaction terms and examining the effect of the other term. For example, if there was a significant Species × Age Group interaction, we tested for age group effects in chimpanzees and orangutans separately. In the event of a significant three-way

interaction, we split the sample by species and tested for the sex, age group, and Sex × Age Group interaction.

Second, because of differences in how some domains and the Gregariousness facet were defined in orangutans and chimpanzees, any significant species differences might reflect the different composition of the domains or facets. Therefore, if we found species differences in age effects, sex effects, or their interaction, we determined whether these effects remained after scoring the domains or facets using only the items common to orangutans and chimpanzees. For example, if the Species × Age Group interaction for Neuroticism was significant, we re-ran the analyses substituting a domain T-score for Neuroticism that was computed when the raw score was defined as Excitable–Stable for chimpanzees and orangutans. We only reported the results of these analyses if they led to a change in results.

Rate of change. We tested whether the rate of change in orangutan personality was comparable to that of chimpanzees or humans. Similarity in rate of change across all three species would be inconsistent with developmental rates being strongly associated with life events common to highly social species. For these analyses, we made developmental years approximately comparable for humans and the apes. We assumed that maturation rate in chimpanzees and orangutans is about 50% higher than in humans (Napier & Napier, 1967; Riesen & Kinder, 1952). Therefore, the species-adjusted yearly change for the apes was defined as the change for 12-month year divided by 1.5. The proportion of total developmental change in one 12-month human year was then assumed to be approximately equal to the proportion of total developmental change in an 8-month ape year. In other words, 1 human year was assumed to be equivalent to .67 ape years.

Our first estimates described the absolute number of standard deviation units per species-adjusted year and was equal to slopes of regression lines relating the ungrouped age variable to within-species T-scores. We adjusted these slopes to account for the fact that 10 T-score units are equal to 1 standard deviation. In other words, the mean change in standard deviation units for each 8-month ape year was equal to: (change per human year in T-score units/10)/1.5. These analyses were conducted on the four domains and for the two Extraversion facets common to orangutans and chimpanzees and for the orangutan Intellect domain. To be consistent with the results of a human study that we include for comparison purposes (McCrae et al., 1999), we restricted these analyses to apes aged 12 years or older, which is the approximate equivalent of humans aged 18 or older. Our second measure of the relationship between age and personality scores was derived by obtaining the correlations between the ungrouped age variable and the within-species domain T-scores. These analyses were conducted on the four domains and for the two Extraversion facets common to orangutans and chimpanzees and for the orangutan Intellect domain. To be consistent with the comparable human study (McCrae et al., 2000), we excluded subjects in the first age group (age ≤ 8.0 years).

We computed the amount of change per year for Extraversion, Neuroticism, and Agreeableness in humans by taking the median of the absolute slopes presented in Figures 2, 1, and 4, respectively, from McCrae et al. (1999), and dividing these values by 100. We computed the amount of change per year for Activity and Gregariousness by taking the median of the absolute slopes of these facets presented in McCrae et al. (1999, Table 2), and dividing these values by 100. We obtained correlations between age and Extraversion, Neuroticism, and Agreeableness in humans from McCrae et al. (2000, p. 181). We could not find similar correlations for the Activity or Gregariousness facets.

Sex differences. To obtain mean z-score sex differences for the comparable chimpanzee and orangutan domains, the two facets, and the orangutan Intellect domain we used linear regressions. Data for apes less than 12 years old were excluded to be consistent with comparable human data, which is based on people over 18. In each regression, domain or facet z-scores that were standardized within species served as dependent variables. The ungrouped age variable and sex (0 = females, 1 = males) served as predictors. Thus, the regression coefficients for sex equaled the age-adjusted mean z-score sex differences.

Human personality gender differences were based on two large cross-cultural studies. The first (McCrae et al., 2005) assessed personality domains and facets with self- and rater-reports on the Revised NEO Personality Inventory (Costa & McCrae, 1992). The second (Schmitt et al., 2008) assessed personality domains with self-reports on the Big Five Inventory (BFI; Benet-Martínez & John, 1998). For Extraversion, Neuroticism, and Agreeableness, which are shared by all three species, we computed the average of the mean z-score differences reported on page 553 in McCrae et al. (2005) and in Table 1 of Schmitt et al. (2008). We also computed averages of the mean z-score differences between genders for rater-reports of the Activity and Gregariousness facets (Table 4, McCrae et al., 2005).

Results

Preliminary Analyses

Compared to chimpanzees (see Tables 2 and 5 in King et al., 2008), the mean inter-rater reliabilities for orangutans (see Table 3) tended to be higher and the internal consistency reliabilities (see Table 4) were similar. The only exceptions in both cases occurred in the oldest age group where, in the case of inter-rater reliabilities, the orangutans tended to be lower, and in the case of internal consistency reliabilities, the chimpanzees tended to be higher. For inter-rater

reliabilities (see Table 3)[3], mean reliabilities were lowest in the oldest age group. Agreeableness and Intellect inter-rater reliabilities decreased across age groups and Neuroticism inter-rater reliabilities increased. Dominance inter-rater reliabilities increased across the first two age groups and then declined. Extraversion inter-rater reliabilities declined across the first three age groups, increased, and then declined. Internal consistencies were fairly consistent across age groups, though they were lower for Intellect in the youngest and oldest age groups and for Neuroticism in the youngest age group (see Table 4).

Origin of birth was not associated with chimpanzee Extraversion, $F(1, 199) = 2.76$, $p = .098$; Dominance, $F(1, 199) = 1.42$, $p = .23$; Neuroticism, $F(1, 199) = 1.03$, $p = .31$; Agreeableness, $F(1, 199) = 1.94$, $p = .16$; Activity, $F(1, 199) = .70$, $p = .40$; or Gregariousness, $F(1, 199) = 3.21$, $p = .075$. We therefore did not include origin of birth in further analyses.

Age and Sex Effects

Results for the general linear models for the four domains and two facets are presented in Table 5. Results of the general linear model for the Intellect domain are presented in Table 6.

Extraversion significantly declined across age groups and was more pronounced in the orangutans than in the chimpanzees, resulting in a Species × Age Group interaction (see Figure 1). Post-hoc analyses revealed declines over age groups for chimpanzees, $\eta_p^2 = .52$, $F(4,192) = 52.23$, $p < .001$ as well as orangutans, $\eta_p^2 = .46$, $F(4,164) = 35.11$, $p < .001$.

Activity displayed a developmental pattern different from Extraversion (see left panel of Figure 2). It strongly and significantly declined across age groups and was significantly higher in males than females. All interaction effects were significant. Post-hoc analyses indicated that the male advantage over females in Activity was a characteristic of chimpanzees, $\eta_p^2 = .09$, $F(1,192) = 18.09$, $p < .001$, but not orangutans, $\eta_p^2 < .01$, $F(1,164) = .15$, $p = .69$. Post-hoc analyses also

revealed that Activity declined in chimpanzees, $\eta_p^2 = .64$, $F(4,192) = 86.37$, $p < .001$ and

orangutans, $\eta_p^2 = .45$, $F(1,164) = 34.03$, $p < .001$. Finally, post-hoc analyses indicated that

declines in Activity across age groups were greater in female than in male chimpanzees, $\eta_p^2 =$

$.08$, $F(4,192) = 4.00$, $p = .004$, but the comparable difference was not significant in orangutans,

$\eta_p^2 = .05$, $F(4,164) = .15$, $p = .078$. Age differences in the Gregariousness facet paralleled those

for Extraversion (see right panel of Figure 2). Gregariousness declined across age groups, but the

decline did not extend to the oldest chimpanzee age group, leading to a significant Species $\times$ Age

Group interaction. Post-hoc analyses revealed that Gregariousness declined across age groups in

chimpanzees, $\eta_p^2 = .43$, $F(4,192) = 35.82$, $p < .001$, and orangutans, $\eta_p^2 = .51$, $F(4,164) = 42.68$,

$p < .001$.

Dominance was significantly higher in males than in females. The age group effect was

also significant: Dominance increased and then decreased over age groups (see Figure 3). The

Species $\times$ Sex $\times$ Age Group effect was significant as older male chimpanzees consistently

surpassed females whereas male and female orangutans were mostly similar in each age group.

Post-hoc analyses confirmed this: the Sex $\times$ Age Group effect was significant in chimpanzees,

$\eta_p^2 = .07$, $F(4, 192) = 3.47$, $p = .009$, but not orangutans, $\eta_p^2 = .03$, $F(4,164) = 1.07$, $p = .37$.

Neuroticism declined significantly across age groups (see Figure 4). The non-significant

Species $\times$ Age interaction indicated that the declines in both species were similar. In addition,

there was a significant Species $\times$ Sex interaction. Post-hoc analyses revealed that male

chimpanzees had higher Neuroticism scores than females, $\eta_p^2 = .04$, $F(1,192) = 8.62$, $p = .004$

whereas male orangutans had lower scores than females, $\eta_p^2 = .03$, $F(1,164) = 4.64$, $p = .036$.

Analysis of the Agreeableness domain showed a significant effect of age group and a

significant Species $\times$ Age Group interaction. Post-hoc analyses revealed that the direction was

significantly positive in chimpanzees, $\eta_p^2 = .06$, $F(4,192) = 3.04$, $p = .019$, and negative in orangutans, $\eta_p^2 = .10$, $F(4,164) = 4.34$, $p = .002$ (see left panel of Figure 5). There was also a significant Species $\times$ Sex interaction. Post-hoc analyses revealed that this came about because female chimpanzees were significantly higher in Agreeableness than their male counterparts, $\eta_p^2 = .04$, $F(1,192) = 8.48$, $p = .004$, while there were no significant sex differences in Agreeableness between male and female orangutans, $\eta_p^2 < .01$, $F(1,164) = .19$, $p = .66$. However, when Agreeableness was defined using just the defining items common to both species, the Species $\times$ Sex ($p = .065$) and Species $\times$ Age Group ($p = .073$) interactions were not significant (see right panel of Figure 5).

The orangutan Intellect domain was significantly higher in males than in females (see Figure 6). Intellect increased from the first to the second age group followed by more modest increases.

Rate of Change

The rates of change for each 8-month ape year in orangutans were similar to those of chimpanzees and the rate of change per year in humans (see Table 7). With the exception of Dominance and Gregariousness, the correlations between age and personality scores in orangutans were strikingly similar to those of chimpanzees (see Table 7).

Sex Differences

Sex differences in absolute standard deviation units for orangutans, chimpanzees, and humans are presented in Table 8. Across all species, sex differences were largest for Neuroticism and smallest for Gregariousness. For the Extraversion facets and Dominance, Neuroticism, and Agreeableness, orangutans showed the greatest sex differences in Neuroticism (higher in females) and Activity (higher in females); chimpanzees showed the greatest sex differences in

Dominance (higher in males) and Agreeableness (higher in females). Across these domains and facets, absolute sex differences were larger in chimpanzees (median $|\Delta z| = .48$) than orangutans (median $|\Delta z| = .17$). For the Extraversion facets, Neuroticism, and Agreeableness, sex differences were comparable for orangutans (median $|\Delta z| = .26$) and humans (median $|\Delta z| = .22$), both of which were less than those of chimpanzees (median $|\Delta z| = .44$). These results did not differ appreciably when we analyzed the entire Extraversion domain instead of its two component facets.

Discussion

In terms of age-related personality differences, we found that Extraversion and its Gregariousness facet decreased in both species, though the correlation with age was greater in orangutans. The pattern for the Activity facet of Extraversion was similar, though the decreases leveled off in male chimpanzees. We also found evidence for a rise and decline in Dominance in later life, though this decline was not present in male chimpanzees. Our study also revealed evidence for Neuroticism declines in both species. A pattern of age differences suggested that Agreeableness declines in orangutans but increases in chimpanzees. Finally, for the orangutan Intellect domain, we found evidence for increases in early life and then a leveling off in adulthood. The magnitudes of age based personality differences were similar in chimpanzees, orangutans, and in two studies of human personality (McCrae et al., 1999; McCrae et al., 2000).

Human personality development is characterized by individuals becoming more introverted, less competitive, less emotional, and having greater behavioral controls (Roberts et al., 2008). This pattern is largely preserved in chimpanzees (King et al., 2008). However, with the exception of large cross-sectional studies (e.g., Soto et al., 2011; Srivastava et al., 2003), there has been little evidence for more than very modest gender differences in human personality

development (McCrae & Costa, 2003; Roberts et al., 2006; Terracciano et al., 2005; Terracciano, McCrae, & Costa, 2006). Therefore, finding sex differences in the magnitude or in the direction of age related differences in Activity and Dominance was unexpected.

The finding that Extraversion and its facets as well as Neuroticism decline in a semi-solitary species (orangutans) as well as in a highly social species (chimpanzees) suggests phylogenetic universality in these developmental trajectories. These parallels, and the fact that declines in Extraversion were stronger in orangutans than in chimpanzees, rule out explanations for Extraversion and Neuroticism declines that rest on investment in social roles common in highly social species, such as humans (Roberts et al., 2005). Moreover, given that, unlike humans, male chimpanzees and male orangutans do not care for their young (Galdikas, 1985a; Goodall, 1986), it is unlikely that social roles related to establishing a family are responsible for these declines.

On the other hand, the species differences in Agreeableness trajectories show that age-related personality changes in humans may not generalize to all great apes. This finding suggests that developmental increases in Agreeableness may have evolved in response to an increased need in adulthood to maintain social cohesion. In contrast, among orangutans, a semi-solitary species (Galdikas, 1985a, 1985b, 1985c; van Schaik, 1999), there would be less selection for such increased Agreeableness during development. However, this interpretation is not supported by findings in white-faced capuchins, a species with a social structure similar to that of chimpanzees (Aureli et al., 2008), in which a factor similar to Agreeableness is inversely associated with age (Manson & Perry, 2013). One possible explanation for this discrepancy is that, as is the case with brown capuchin monkeys, *Sapajus apella* (Morton et al., 2013), white-faced capuchin Agreeableness is a blend of Extraversion and Agreeableness. Another possibility

is that this difference in age effects may have arisen from the different item content in the

chimpanzee and orangutan Agreeableness scales. Further studies should thus examine whether

there are species-level associations between the intensity of social interactions and age-related

trends in Agreeableness.

That species-adjusted change per year was similar in orangutans, chimpanzees, and

humans (Donnellan & Lucas, 2008; McCrae et al., 1999; McCrae et al., 2000; Roberts et al.,

2006; Soto et al., 2011; Srivastava et al., 2003; Terracciano et al., 2005) is striking. This suggests

that rate of change is governed by processes related to species lifespan and that the influence of

modern human cultures or specific human social environments is, at best, modest.

There were also substantial sex differences in both ape species. Male orangutans and

male chimpanzees were higher in Dominance but lower in Gregariousness than their female

counterparts. Moreover, while orangutan males in common with humans (McCrae et al., 2005)

had lower Neuroticism scores than females, the opposite was true for chimpanzees. The

magnitude of sex differences was highest in chimpanzees and of a similar, lower magnitude in

orangutans and humans. These findings suggest that sex differences, and particularly those in

Neuroticism, were evolutionarily labile and varied substantially among ape species throughout

the evolution of great apes and humans.

Sex differences in personality can be viewed as a type of sexual dimorphism. In

nonhuman primates, sexual dimorphism is usually defined as physical or behavioral differences

between sexes, although body size and secondary sexual characteristics are the most commonly

used indicators (Dixson, 2009; Plavcan, 2011). High levels of sexual dimorphism in nonhuman

primates are often associated with increased agonistic male competition (Plavcan, 2012).

Sexual dimorphism defined by size and weight is greater in orangutans than in chimpanzees (Smith & Jungers, 1997). However, the size-based sexual dimorphism of orangutans is probably not based entirely on male-male competition (Plavcam, 2004; Plavcan, 2012). The orangutan dimorphism may instead be a consequence of Rensch's rule stating that size dimorphism of a species increases with the mean species body size (Gordon, 2006; Plavcam, 2001; Rensch, 1959).

Perhaps the most interesting findings are those showing that male rather than female chimpanzees are higher in Neuroticism and that, among male chimpanzees, Dominance and Activity remain high into older age. These findings are consistent with the well-documented agonistic temperament of wild chimpanzee males (Goodall, 1986). Nonlethal intragroup aggression attributable to wild male chimpanzees was found to be 384 times greater than estimates for human hunter-gatherer groups while the comparable figure for female chimpanzees was 182 (Wrangham, Wilson, & Muller, 2006).

However, aggressiveness can take more nuanced forms than simple competition between individual males. For example, male chimpanzees who form coalitions of at least two members to direct aggression towards an outsider have increased reproductive success (Gilby et al., 2013), a result consistent with the heighted Dominance scores of male chimpanzees as well as the stable Activity scores in chimpanzees older than 15 years. Among wild chimpanzees, male attacks on promiscuous female chimpanzees occur mainly when the females are multiparous and in estrus and are likely to result in copulation. This suggests that the attacks are not simply an expression of overall aggressiveness but are focused on females most likely to conceive and are therefore a component of a mating strategy (Muller, Thompson, Kahlenberg, & Wrangham, 2011).

The combined findings of this study go some way to resolving the controversy about whether human personality development is based mainly on biological foundations, as predicted by Five-Factor Theory, or on social/cultural foundations, as predicted by Social-Investment Theory. With the possible exception of Agreeableness, the congruence between age-related changes in chimpanzee and human personality domains, and the fact that similar trends are also found in orangutans, is more consistent with Five-Factor Theory. In other words, the human pattern of personality change is based on an evolutionary continuity, is homologous with the pattern in chimpanzees, and is not attributable to shared characteristics of highly social species. However, this phylogenetic continuity is not wholly at odds with Social-Investment Theory since species-level modification of these developmental rates within the basic pattern may be a consequence of environmental effects.

This study indicates that the biological constraints on personality development based on human evolutionary history are consistent with human cultural constraints favoring increased emotional stability, responsibility, and agreeableness with increased age. One explanation for these findings, the unique developmental pattern of male chimpanzees (King et al., 2008), and findings in support of the Social Investment Hypothesis (Roberts et al., 2005) and Five-Factor Theory (McCrae & Costa, 2003) is that the patterns of personality change reflect gene-culture co-evolution (Laland, Odling-Smee, & Myles, 2010; Lumsden & Wilson, 1981; Richerson & Boyd, 2005). This explanation would posit that the species level of normative change is a product of trends that humans, chimpanzees, and orangutans inherited from a common ancestor species. As developmental trajectories vary across individuals and are heritable (Bleidorn et al., 2009; Terracciano et al., 2005; Terracciano et al., 2006), human cultures would thus vary in the frequencies of genes associated with slower or faster change for one or more traits.

These gene-influenced cultural differences in trajectories would be reflected in the cultures (cf. McCrae et al., 1999, p. 475), and would lead to different fitness outcomes for individuals who possessed genes related to faster or slower change in personality traits. For example, in cultures in which the frequency of genes related to faster maturation is high, individuals that possess genotypes that lead them to mature slowly would be disadvantaged; they would enter the workforce later, marry later than their peers, and would produce fewer offspring. Thus, mismatched individuals would have lower fitness, leave fewer descendants in later generations, or be driven to emigrate to cultures more consistent with their rate of maturation, perhaps as a result of active gene by environment correlations (Scarr & McCartney, 1983).

The assumption that personality development is a consequence of gene-culture co-evolution is consistent with associations between cultural dimensions and personality mean levels (Hofstede & McCrae, 2004) and findings showing that humans and animals seek out physical and social environments consistent with their personalities (Jaffee & Price, 2007; Massen & Koski, 2014; Stamps & Groothuis, 2010). The gene-culture co-evolution hypothesis leads to novel predictions. For example, individuals whose rate and direction of personality maturation deviates from that favored by their current cultural environment would be expected to be poorer at acquiring resources, perhaps represented by having a lower socioeconomic status, and would reproduce later and less often. In addition, the developmental trajectories of immigrants and their children should differ from those found in their country of origin. Furthermore, differences in developmental trajectories across cultures (see, e.g. Bleidorn et al., 2013) should be a function of the genetic distance between the peoples of those cultures. Finally, the gene-culture hypothesis predicts genetic correlations between personality trajectories and their purported environmental triggers, such as time of marriage.

There were some limitations to this study. First, raters knew the sex and approximate age of subjects. This was unavoidable, as it is in human studies. However, the emergence of substantive differences between chimpanzees and orangutans makes it unlikely that age-related differences in personality reflected projections of human age differences onto the subjects. Second, the present study was cross-sectional and not longitudinal, so it is possible that the present findings could contain cohort effects (Costa & McCrae, 1982). However, it is difficult to imagine what cohort effects would lead to the present pattern of similarities and differences across orangutans, chimpanzees, and humans. They also would not explain why, after adjusting for rate of development, the magnitudes of age differences in these great apes is comparable to those in humans. Nonetheless, future longitudinal studies of great apes that use ratings and behavioral measures would be invaluable.

This study demonstrates the promise of using a comparative approach to study personality development and sex differences. While it reveals further questions, it highlights life courses that we, and our great ape contemporaries, inherited from a common ancestor species, but also one which which evolved later.

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Footnotes

[1] The Hominoid Personality Questionnaire is freely available at

http://extras.springer.com/2011/978-1-4614-0175-9/weiss_chimpanzee_personality.pdf

[2] Principal axis factoring yielded nearly identical results (see footnote 4 in Weiss et al.,

2006, p. 505).

[3] Inter-rater reliabilities for the total orangutan sample are higher than in the original

paper (Weiss et al., 2006). This likely reflects the additional subjects and the fact that the mean

squares used to estimate inter-rater reliabilities in Weiss et al. were derived without a term for

rater effects.

Table 1

Orangutan and Chimpanzee Domain Definitions Used to Create Unit-Weighting Scores

Domain	Species	
	Orangutan[a]	Chimpanzee[b]
Extraversion	Active – Conventional + Curious – Depressed + Imitative + Inquisitive + Inventive – Lazy + Playful – Solitary– Unemotional	Active + Affectionate – Depressed + Friendly + Imitative – Lazy + Playful + Sociable – Solitary
Dominance	Aggressive + Bullying + Defiant + Dominant – Gentle + Irritable + Jealous + Manipulative + Persistent + Reckless + Stingy – Submissive	Bullying – Cautious + Decisive – Dependent + Dominant – Fearful + Independent + Intelligent + Persistent + Stingy – Submissive – Timid
Neuroticism	Anxious + Cautious – Cool + Erratic + Excitable + Fearful + Impulsive – Predictable – Stable +Timid + Vulnerable	Excitable – Stable – Unemotional
Agreeableness	Affectionate + Friendly + Helpful + Protective + Sensitive + Sociable + Sympathetic	Helpful + Gentle + Protective + Sensitive + Sympathetic
Intellect	– Clumsy + Decisive – Dependent – Disorganized + Independent + Intelligent	
Facets		
Activity	Active – Lazy	Active – Lazy
Gregariousness	Playful + Imitative – Solitary – Depressed	Playful + Sociable + Affectionate + Imitative + Friendly – Solitary – Depressed

Note. [a]Domain definitions based on Table 1 in King and Figueredo (1997). [b]Domain definitions based on Table 3 in Weiss et al. (2006).

Table 2

Sample Composition by Sex and Age Group

	Age Group				
	≤ 8	8-15	15-25	25-35	> 35
Orangutan					
Male	14	15	20	13	8
Female	8	20	36	23	17
Total	22	35	56	36	25
Chimpanzee					
Male	25	23	15	7	7
Female	39	25	27	22	12
Total	64	48	42	29	19

Table 3

Inter-rater reliabilities for Orangutan Domains by Age Group and in the Total Sample

Domain	$\leq 8^a$		8-15[a]		15-25[b]		25-35[c]		> 35[c,d]		Total	
					Age Group							
Extraversion	.89	(.95)	.68	(.85)	.55	(.76)	.83	(.92)	.13	(.27)	.76	(.89)
Dominance	.74	(.88)	.83	(.93)	.71	(.87)	.66	(.82)	.62	(.80)	.74	(.88)
Neuroticism	.40	(.63)	.37	(.60)	.65	(.83)	.64	(.81)	.67	(.83)	.55	(.76)
Agreeableness	.67	(.84)	.59	(.79)	.51	(.74)	.37	(.58)	.32	(.54)	.59	(.78)
Intellect	.78	(.90)	.68	(.85)	.51	(.74)	.53	(.73)	.15	(.30)	.66	(.83)
M	.70	(.84)	.63	(.80)	.59	(.79)	.61	(.77)	.38	(.55)	.66	(.83)

Note. Values outside parentheses are *ICC*(3,1) estimates. Values insider parentheses are *ICC*(3,k) estimates. [a]mean number of raters per subject = 2.6; [b]mean number of raters per subject = 2.7; [c]mean number of raters per subject = 2.4; [d]One subject omitted because they were rated by only one rater.

Table 4

Internal Consistency Reliabilities for Orangutan Domains by Age Group and in the Total Sample

Domain	Age group (years)					Total
	≤ 8	8-15	15-25	25-35	> 35	
Extraversion	.87	.86	.85	.87	.81	.91
Dominance	.91	.93	.92	.87	.88	.91
Neuroticism	.69	.87	.86	.89	.74	.86
Agreeableness	.77	.88	.92	.89	.86	.88
Intellect	.68	.74	.81	.78	.61	.80
M	.78	.86	.87	.86	.78	.87

Table 5

General Linear Model Results for Comparing Orangutans and Chimpanzees

Predictor	df	SS	MS	F	p	η_p^2
		Extraversion				
Species	1	8.21	8.21	.11	.74	< .01
Sex	1	7.03	7.03	.09	.76	< .01
Age Group	4	20834.48	5208.62	70.31	< .001	.44
Species × Sex	1	96.18	96.18	1.30	.26	< .01
Species × Age Group	4	1365.60	341.40	4.61	.001	.05
Sex × Age Group	4	557.23	139.31	1.88	.11	.02
Species × Sex × Age Group	4	416.03	104.01	1.40	.23	.02
Residual	356	26371.28	74.08			
		Activity				
Species	1	56.86	56.86	.90	.34	< .01
Sex	1	244.69	244.69	3.89	.049	.01
Age Group	4	22680.41	5670.10	90.12	< .001	.50
Species × Sex	1	442.28	442.28	7.03	.008	.02
Species × Age Group	4	665.37	166.34	2.64	.033	.03
Sex × Age Group	4	781.04	195.26	3.10	.016	.03
Species × Sex × Age Group	4	687.51	171.88	2.73	.029	.03
Residual	356	22398.04	62.92			
		Gregariousness				
Species	1	18.80	18.80	.25	.62	< .01
Sex	1	4.41	4.41	.06	.81	< .01
Age Group	4	21265.27	5316.32	69.46	< .001	.44
Species × Sex	1	4.95	4.95	.06	.80	< .01
Species × Age Group	4	2151.20	537.80	7.03	< .001	.07
Sex × Age Group	4	296.13	74.03	.97	.43	.01
Species × Sex × Age Group	4	214.54	53.63	.70	.59	.01
Residual	356	27247.73	76.54			
		Dominance				
Species	1	5375.99	5375.99	68.10	< .001	.16
Sex	1	829.10	829.10	10.50	.001	.03
Age Group	4	3612.66	903.17	11.44	< .001	.11
Species × Sex	1	105.92	105.92	1.34	.25	< .01
Species × Age Group	4	660.10	165.03	2.09	.082	.02
Sex × Age Group	4	263.63	65.91	.83	.50	.01
Species × Sex × Age Group	4	1058.53	264.63	3.35	.010	.04
Residual	356	28104.73	78.95			

Predictor	df	SS	MS	F	p	η_p^2
Neuroticism						
Species	1	9606.68	9606.68	172.03	< .001	.33
Sex	1	13.97	13.97	.25	.62	< .01
Age Group	4	1274.54	318.63	5.71	< .001	.06
Species × Sex	1	708.04	708.04	12.68	< .001	.03
Species × Age Group	4	386.41	96.60	1.73	.14	.02
Sex × Age Group	4	194.20	48.55	.87	.48	.01
Species × Sex × Age Group	4	459.21	114.80	2.06	.086	.02
Residual	356	19880.60	55.84			
Agreeableness						
Species	1	12.39	12.39	.15	.70	< .01
Sex	1	170.24	170.24	2.05	.15	.01
Age Group	4	896.54	224.14	2.70	.031	.03
Species × Sex	1	380.57	380.57	4.58	.033	.01
Species × Age Group	4	1858.94	464.74	5.59	< .001	.06
Sex × Age Group	4	31.80	7.95	.10	.98	< .01
Species × Sex × Age Group	4	51.47	12.87	.15	.96	< .01
Residual	356	29580.50	83.09			

Note. η_p^2 = partial eta-squared

Table 6

General Linear Model Results for the Orangutan Intellect Domain

Predictor	df	SS	MS	F	p	η_p^2
Sex	1	651.66	651.66	6.60	.011	.04
Age Group	4	8081.07	2020.27	20.47	$< .001$	.33
Sex × Age Group	4	182.72	45.68	.46	.76	.01
Residual	164	16186.60	98.70			

Note. η_p^2 = partial eta-squared

Table 7

Absolute Rate of Change per Species Adjusted Year and Correlations with Age

Variable	Orangutans		Chimpanzees		Humans	
	$|\Delta z|$	r	$|\Delta z|$	r	$|\Delta z|$	r
Domain						
Extraversion	.033	-.60	.020	-.38	.014[a]	-.21[b]
Dominance	.013	-.06	.012	.21	---	---
Neuroticism	.018	-.27	.012	-.25	.002[c]	-.17[b]
Agreeableness	.006	-.21	.013	.28	.017[d]	.09[b]
Intellect	.008	.19	---	---	---	---
Facet						
Activity	.028	-.56	.033	-.58	.003[e]	---
Gregariousness	.031	-.59	.013	-.26	.015[e]	---

Note. The general linear model revealed that the main effect of age group was significant for all domains and facets. Absolute rate of change estimates ($|\Delta z|$) for orangutans and chimpanzees were based on 131 and 109 subjective, respectively. Correlations (*r*) for orangutans and chimpanzees were based on 152 and 138 subjects, respectively. [a]Estimate computed using published regression coefficients (McCrae et al., 1999, Figure 2). [b]Estimate from McCrae et al. (2000, p. 181). [c]Estimate computed using published regression coefficients (McCrae et al., 1999, Figure 1). [d]Estimate computed using published regression coefficients (McCrae et al., 1999, Figure 4). [e]Estimate computed using published regression coefficients (McCrae et al., 1999, Table 2)

Table 8

Absolute Standardized Sex Differences

Variable	Orangutans		Chimpanzees		Humans	
	$|\Delta z|$	Direction	$|\Delta z|$	Direction	$|\Delta z|$	Direction
Domain						
Extraversion	.29	F	.05	M	.12[a]	F
Dominance	.04	F	.70[***]	M	---	---
Neuroticism	.48[**]	F	.48[*]	M	.44[a]	F
Agreeableness	.13	M	.54[**]	F	.24[a]	F
Intellect	.36[*]	M	---	---	---	---
Facet						
Activity	.34[*]	F	.39[*]	M	.12	F
Gregariousness	.17	F	.08	F	.20	F

Note. Orangutan and chimpanzee estimates were based on 131 and 109 subjects, respectively. F = females higher, M = males higher. [a]Estimated using values from page 553 of McCrae et al. (2005) and Table 1 of Schmitt et al. (2008). [b]Estimated using values from page 553 of McCrae et al. (2005).

[*]$p < .05$, two-tailed. [**]$p < .01$, two-tailed. [***]$p < .001$, two-tailed.

Figure 1. Mean levels ± 1 standard error for Extraversion expressed as within-species *T*-scores across the five age groups for male and female orangutans and chimpanzees. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.
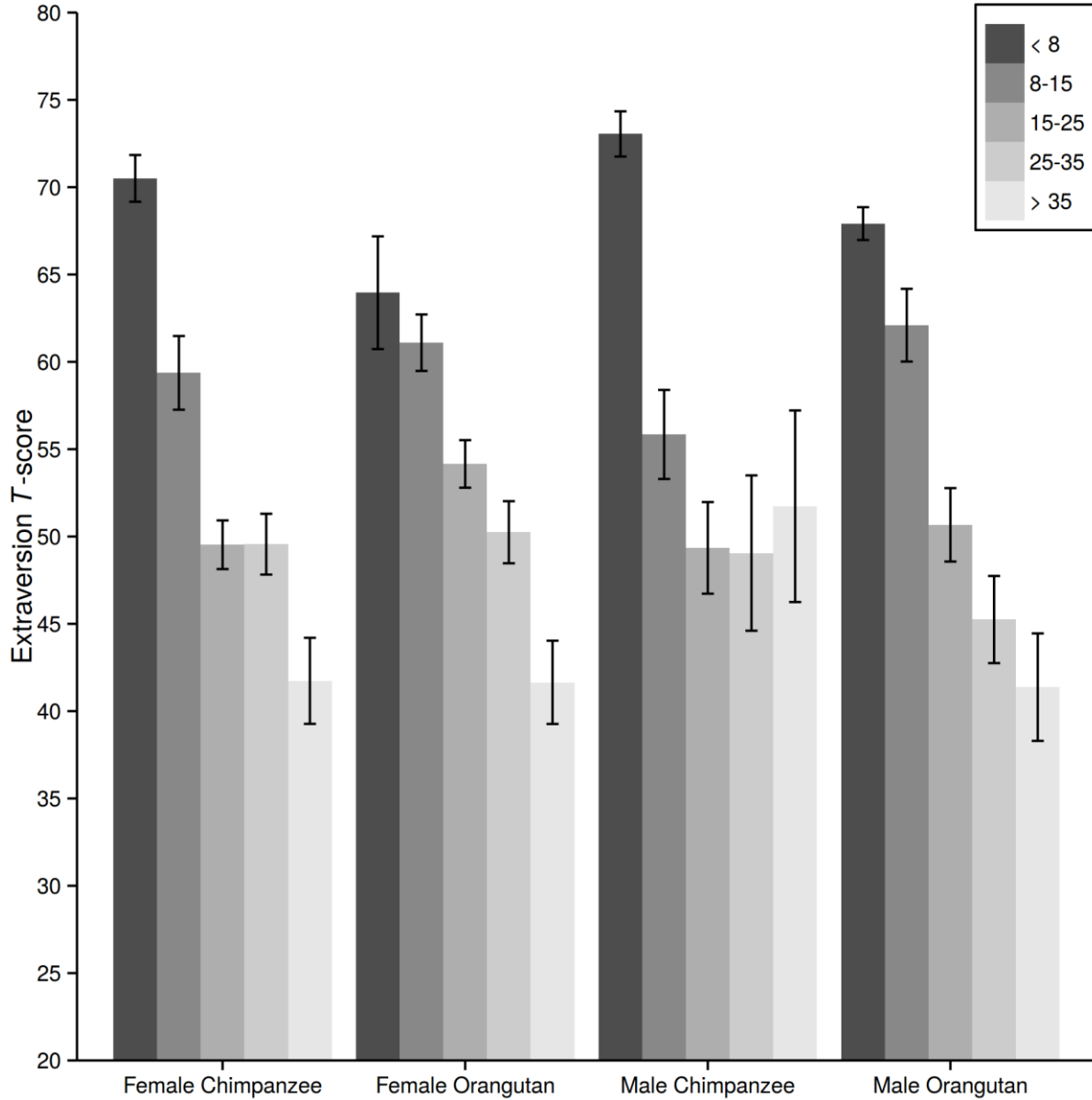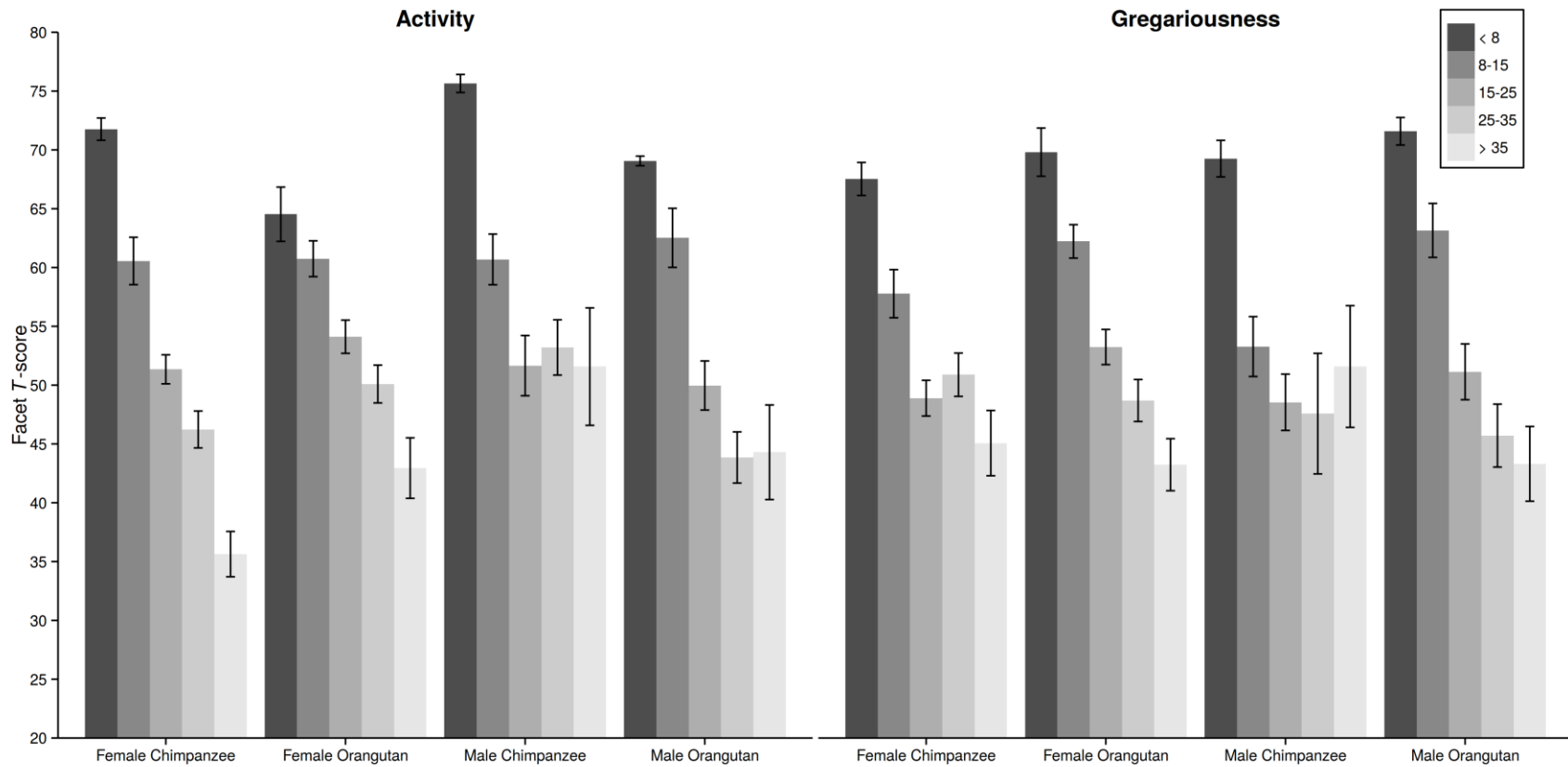
Figure 2. Mean levels ± 1 standard error for Activity and Gregariousness expressed as within-species *T*-scores across the five age groups for male and female orangutans and chimpanzees. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.
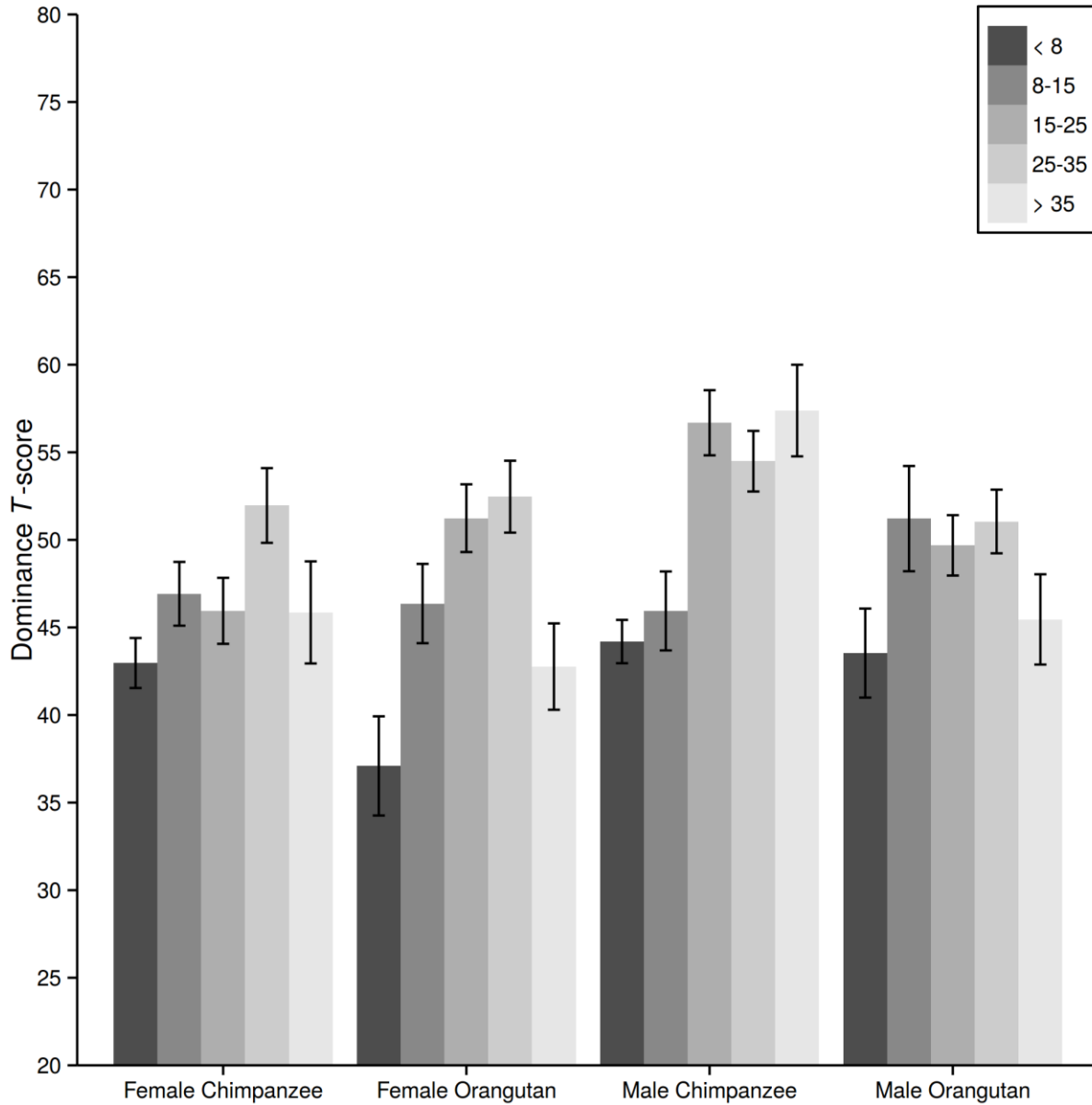
Figure 3. Mean levels ± 1 standard error for Dominance expressed as within-species *T*-scores across the five age groups for male and female orangutans and chimpanzees. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.

Figure 4. Mean levels ± 1 standard error for Neuroticism expressed as within-species *T*-scores across the five age groups for male and female orangutans and chimpanzees. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.
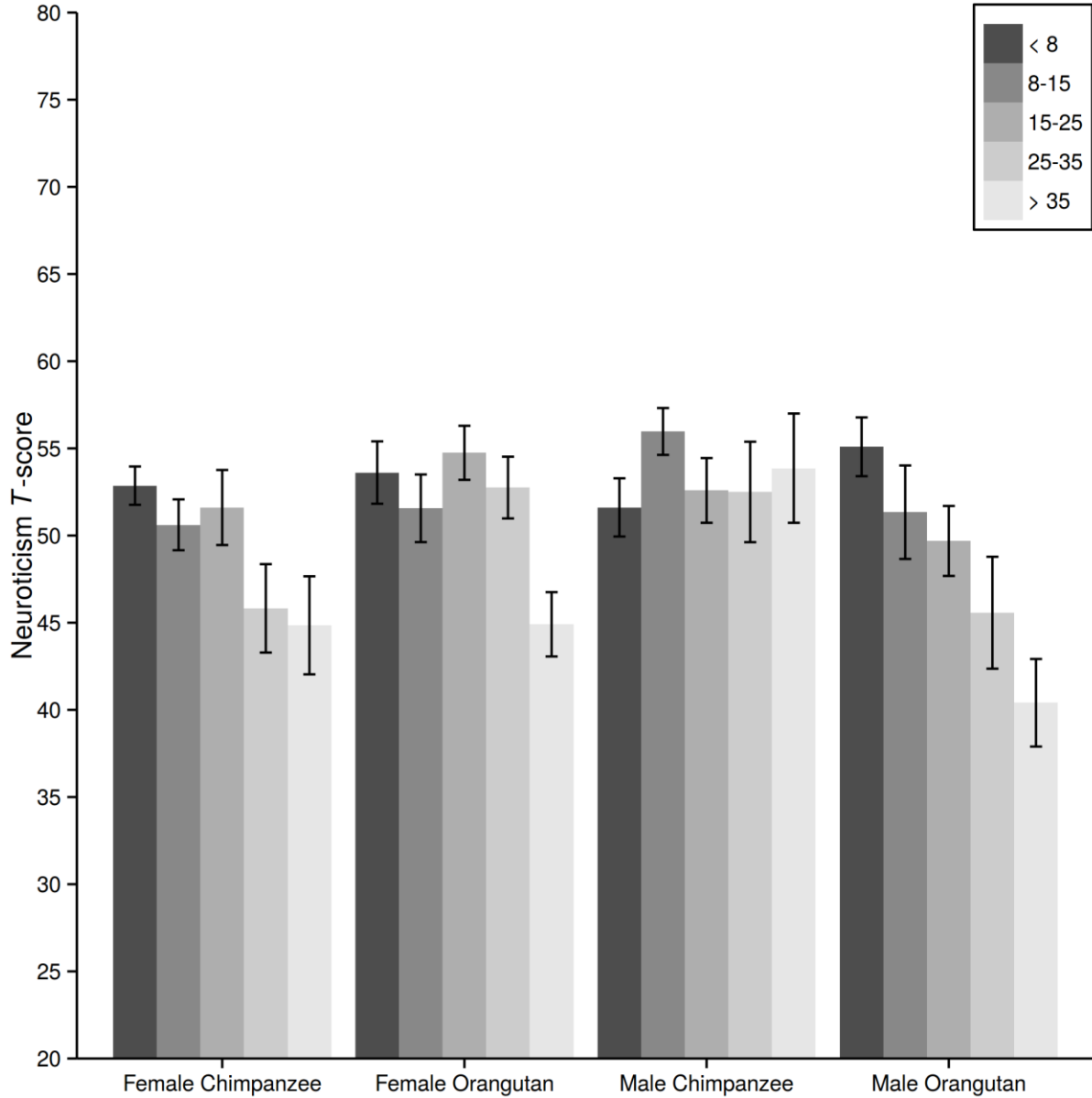
Figure 5. Mean levels ± 1 standard error for Agreeableness expressed as within-species *T*-scores across the five age groups for male and female orangutans and chimpanzees. The left panel depicts these values for the original definitions of Agreeableness for both species. The right panel depicts these values for the definition of Agreeableness common to both species. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.
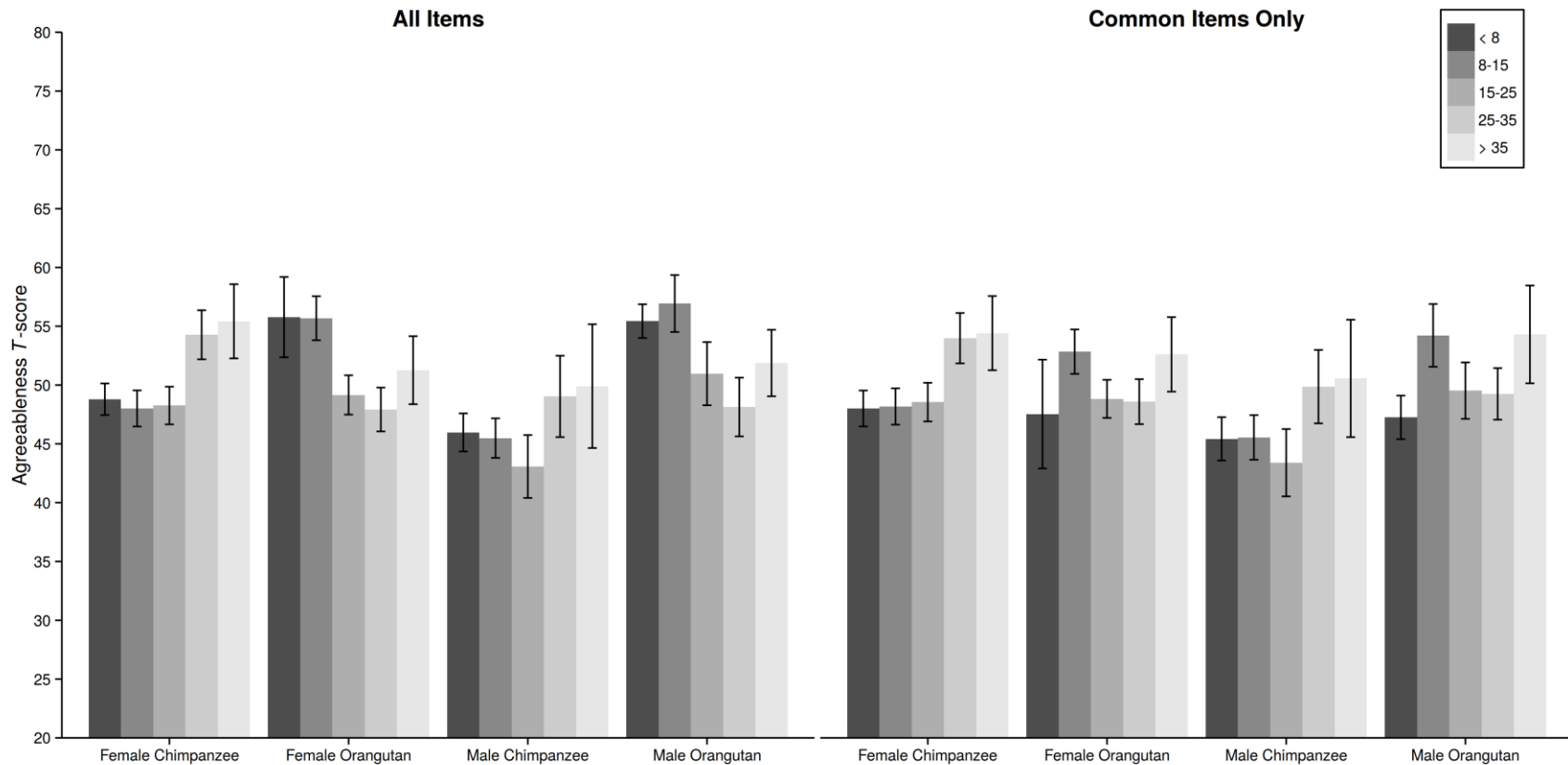
Figure 6. Mean levels ± 1 standard error for Intellect expressed as within-species *T*-scores across the five age groups for male and female orangutans. Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported License and published under the terms of this license. For more details see http://creativecommons.org/licenses/by/3.0/.