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Citation for published version:

Wilson, V, Weiss, ALEXANDER, Lefevre, C, Ochiai, T, Matsuzawa, T, Inoue-murayama, M, Freeman, H, Herrelko, E & Altschul, D 2020, 'Facial width-to-height ratio in chimpanzees: Links to age, sex and personality', *Evolution and Human Behavior*. <https://doi.org/10.1016/j.evolhumbehav.2020.03.001>

Digital Object Identifier (DOI):

[10.1016/j.evolhumbehav.2020.03.001](https://doi.org/10.1016/j.evolhumbehav.2020.03.001)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Evolution and Human Behavior

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Facial width-to-height ratio in chimpanzees: links to age, sex and personality

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Acknowledgements

For providing images of the chimpanzees, the authors would like to thank Lisa Parr at the Yerkes National Primate Research Center, keepers and researchers at Edinburgh Zoo, particularly Roslin Talbot and Katie Slocombe, and the Great Ape Information Network Japan. We are also indebted to Steve Shapiro and Susan Lambeth at the National Center for Chimpanzee Care, funding source NIH U42-OD 011197, and the Great Ape Information Network, for providing demographic data. Thanks also to the Royal Zoological Society of Scotland, Edinburgh Zoo, for allowing research with their chimpanzees. TM acknowledges funding support from MEXT/JSPS KAKENHI Grant No.s 24000001 and 16H06283, and JSPS Core-to-Core Program A. CCSN. Funding bodies had no involvement in study design, analysis, write up or submission.

Declaration of interest

Declarations of interest: none

Word count

8142

Abstract

Links between the human facial width-to-height ratio (fWHR) and aggressive behaviours have been debated in recent years. The question of whether fWHR is a cue to dominance could benefit from the study of primate species that are closely-related to humans. We therefore built on the broad literature in humans, and recent research in capuchins, macaques and bonobos, and examined associations between fWHR in 131 captive chimpanzees from the United States, United Kingdom and Japan, and measures of age, sex, subspecies (*Pan troglodytes verus*, *P. t. schweinfurthii*, *P. t. troglodytes*), and six personality components (Dominance, Extraversion, Conscientiousness, Agreeableness, Neuroticism, and Openness). We found no evidence for sexual dimorphism in fWHR, as has been found in humans. We did find a positive relationship between fWHR and Dominance in *P. t. verus*, but only in adult females. This finding contrasts with that in humans, where dominant males have wider faces. We discuss these results in light of male-female differences in temporal rank stability, and in contrast to findings for bonobos, providing a useful perspective for fWHR research in humans.

Keywords: facial morphology, *Pan troglodytes verus*, dominance, sexual dimorphism, social cues

1. Introduction.

Interest in the measurement of facial metrics has grown in recent years (Haselhuhn, Ormiston, & Wong, 2015; Penton-Voak, Pound, Little, & Perrett, 2006). Starting with Weston et al.'s papers (2004; 2007) suggesting a link between bizygomatic width of skulls and traits pertinent to combat advantage (Haselhuhn et al., 2015), studies have found associations between male facial width-to-height ratio (fWHR) and aggressive and psychopathic traits in humans (Anderl et al., 2016; Goetz et al., 2013; Třebický et al., 2015; Zilioli et al., 2015), and how people rate individuals with different facial metrics on traits like aggression (Alrajih & Ward, 2014; Lefevre & Lewis, 2014; Mileva, Cowan, Cobey, Knowles, & Little, 2014; Stirrat & Perrett, 2010). Overall, these studies appear to indicate that men with higher fWHRs are more aggressive (Haselhuhn et al., 2015) and that fWHR is a cue for a propensity towards aggressive behaviour.

fWHR is not sexually dimorphic in humans (Kramer, 2012; Lefevre et al., 2012; Özener, 2012). The link between male aggressive tendencies and facial width may therefore be driven by male-male competition (Carré & McCormick, 2008). The evolutionary roots of this relationship, however, are still debated. A wider zygomatic arch could be linked to greater skull strength and thus a greater ability to withstand heavier blows, thereby providing an advantage in combat (Lefevre, Wilson, et al., 2014; Stirrat, Stulp, & Pollet, 2012). This possible function for a wider zygomatic arch could also explain its links to physical aggression in humans (Goetz et al., 2013; Třebický et al., 2015; Zilioli et al., 2015) and to traits related to high or low aggression, such as psychopathy (Noser, Schoch, & Ehlert, 2018) and cooperation (Haselhuhn, Wong, Ormiston, Inesi, & Galinsky, 2014), respectively.

The behavioural role of fWHR has however recently been questioned (Deaner, Goetz, Shattuck, & Schnotala, 2012; Goetz et al., 2013; Kosinski, 2017; Özener, 2012; Wang, Nair, Kouchaki, Zajac, & Zhao, 2019). One caveat in human studies is that they are often limited by their reliance on self-reported behavioural tendencies (Kosinski, 2017) or non-violent behaviours, such as a lack of cooperation (Haselhuhn et al., 2014), as well as samples from Western, wealthy populations (Hodges-Simeon, Hanson Sobraske, Samore, Gurven, & Gaulin, 2016). The latter limitation is particularly problematic, since for the biological role of a human trait to be established, it should be found across cultures.

Another reason why associations between fWHR and aggression may be fleeting in humans is that, for most of their history, humans lived in small-scale societies in which dominance hierarchies were not as steep and were centred on prestige (Boehm, 1999; Kaplan, Hooper, & Gurven, 2009). The tendency for humans to be egalitarian is evident in personality structure differences between humans and other primates. In humans, traits related to dominance are found across the Five-Factor Model's facets (Costa & McCrae, 1995). These traits include low anxiety, self-consciousness, and vulnerability, which are facets of Neuroticism, low straightforwardness, a facet of Agreeableness, high assertiveness and excitement-seeking, both facets of Extraversion, and high openness to actions, a facet of Openness (Ross, Benning, Patrick, Thompson, & Thurston, 2009). In contrast, chimpanzees (*Pan troglodytes*) have a sixth dimension, Dominance, which subsumes these traits related to competitive prowess (King & Figueredo, 1997). Not surprisingly, chimpanzees higher in Dominance display aggressive behaviours more frequently as do chimpanzees that are lower in Conscientiousness (low traits of

impulsive, defiant and aggressive) (Freeman et al., 2013; Pederson, King, & Landau, 2005).

These differences between human and chimpanzee personality might reflect the differences in how hierarchical their societies are and explain why, in humans, links between fWHR and behavioural traits associated with dominance and aggression are fleeting. One way to test this derives from the fact that, if fWHR is linked to combat advantage, one might expect to find an association between fWHR and the Dominance factor in chimpanzees, a species for which dominance and aggression play an important role in social interactions (Muller, 2002).

Studies of primates suggest that this is a promising avenue of research. At the species level, for example, there is an association between fWHR and despotism amongst macaque species: females in species with a more despotic matrilineal dominance style had higher fWHRs than species that were socially tolerant (Borgi & Majolo, 2016). These findings suggest that differences in sexual selection across different hierarchical systems play a role in the relationship between fWHR and despotic behaviours (Borgi & Majolo, 2016).

At the level of individuals, research on a distant relative of humans, the brown capuchin *Sapajus apella*, found a relationship between fWHR and Assertiveness, a personality dimension made up of traits such as *bullying, aggressive and dominant* (Lefevre, Wilson, et al., 2014; Morton et al., 2013; V. Wilson et al., 2014). This association was significant in males, as in humans, and in females. Unlike in humans, however, fWHR was sexually dimorphic in mature capuchins in that males had wider faces than females. Similar relationships were examined in rhesus macaques (*Macaca*

mulatta), a despotic macaque species (Thierry, 2000). Results revealed that the personality dimensions Dominance and Confidence were related to higher fWHR in young and adult samples, respectively (Altschul, Robinson, Coleman, Capitanio, & Wilson, 2019). Finally, in bonobos (*Pan paniscus*), which like chimpanzees are closely related to humans, fWHR has been linked to higher ratings of Assertiveness and to agonistic dominance in adult males and females (J. S. Martin, Staes, Weiss, Stevens, & Jaeggi, 2019). In bonobos, who are more socially tolerant than chimpanzees (Gruber & Clay, 2016), it is notable that Assertiveness reflects affiliative dominance such as high social status, rather than aggression.

These findings in Old- and New-World monkeys, and in bonobos, suggest that the relationship between fWHR and dominance-related traits may be ancestral to primate taxa. However, these data come from only three genera. Expanding this research to other species, and especially the other great apes, could provide a stronger ecological basis for understanding the relationship between dominance/aggression and fWHR in humans. Specifically, expanding the range of primate species studied to include those that differ from one another, and humans, with regards to their socioecology, would enable one to identify whether the association is ancestral, derived in each species, or whether the lack of an association is derived in humans. In addition, studies such as these allow one to test whether sex-specific selection pressures, such as differences in social tolerance or male-male competition, led to fWHR-dominance associations.

In the current study, we examined the relationship between fWHR and personality in chimpanzees, which are, for several reasons, an ideal species in which to study these associations. Chimpanzees are one of the closest extant relatives of humans, sharing a

common ancestor around 5 or more million years ago (Kuhlwilm et al., 2016). Expanding the study of fWHR and dominance to chimpanzees, therefore, helps to build a taxonomic tree of the similarities and differences in fWHR-dominance relationships amongst primates, including humans. The presence of a fWHR-dominance relationship in chimpanzees would suggest that this relationship did not evolve independently in different primate genera. More specifically, because chimpanzees, unlike humans and bonobos, live in male-dominated societies with high levels of aggression (Coe & Levin, 1980; Muller, 2002), if variance in fWHR is driven by low social tolerance, then chimpanzee fWHR should have a stronger relationship with agonistic behaviour than in humans or bonobos. Moreover, despite species differences in male dominance behaviour, like humans, sexual dimorphism in chimpanzees is moderate, with males being slightly larger than females (Leutenegger & Kelly, 1977). Thus, given the lack of sexual dimorphism in human fWHR (Kramer, 2012; Lefevre et al., 2012; Özener, 2012), we can examine the role of behavioural sex differences as a driver for sexual dimorphism in fWHR.

For our study, we first tested whether chimpanzee fWHR was related to sex or to age. We then examined the relationship of chimpanzee fWHR to a previously determined personality domain, Dominance (King & Figueredo, 1997; Weiss et al., 2009). We included the other five established domains - Openness, Conscientiousness, Extraversion, Agreeableness and Neuroticism - in our analyses, as they are relevant for social interactions (Pederson et al., 2005) and explain variance not accounted for by Dominance. As chimpanzees are highly agonistic (Muller, 2002) and exhibit sex differences in body size and aggressive behaviours (Leutenegger & Kelly, 1977; Muller,

2002; Riss & Goodall, 1973), we expected that (1) after reaching sexual maturity, males would have wider faces than females, consistent with earlier findings of adult sexual dimorphism (Weston et al., 2004); (2) similar to humans (Haselhuhn et al., 2015) and capuchins (Lefevre, Wilson, et al., 2014) we would find that, in males, higher Dominance, or lower Conscientiousness, which are associated with aggression in chimpanzees (Freeman et al., 2013; Pederson et al., 2005), would be related to greater fWHR. In addition to testing these hypotheses, because our data included several chimpanzee subspecies, we conducted exploratory analyses to determine whether there were differences in the strength of associations between subspecies.

2. Methods.

2.1 Subjects.

Images were collected from a total of 132 chimpanzees (61 male, 71 female). The sample was derived from three samples of chimpanzees whose personalities were assessed and for whom suitable images could be obtained: 58 chimpanzees came from 13 facilities in Japan, 21 chimpanzees came from Edinburgh Zoo in the United Kingdom, and 52 chimpanzees came from Bastrop, a research facility in the United States. Of the 114 chimpanzees for whom subspecies was known, 70 (35 male, 35 female) were *P. t. verus*, 42 (15 male, 27 female) were *P. t. troglodytes*, 1 female was *P. t. ellioti*, and 1 female was *P. t. schweinfurthii*. Subspecies classifications for 18 chimpanzees (11 male, 7 female) were not known either because the individuals were hybrids or because no data were available (see Table 1 for details). There was thus a good balance between males and females, and both *P. t. verus* and *P. t. troglodytes* chimpanzees were well-

represented, although we had only one each from the *P. t. ellioti* and *P. t. schweinfurthii* subspecies. The unknown category represents individuals whose background are truly unknown, as well as individuals who are known to be hybrids between subspecies. In these latter cases, the precise mixture of subspecies was not known.

----- Insert Table 1 here -----

2.2 Images.

For usable images, at the time the chimpanzees were photographed, their ages ranged from 4 to 49 years (mean = 22.1, SD = 11.2). Images were mostly provided by researchers or keepers at the facilities. Some images for the chimpanzees from Japan were obtained from the Great Ape Information Network website (<https://shigen.nig.ac.jp/gain/journal.jsp>). Additional images from Edinburgh Zoo were taken by VW. Images had to clearly depict a frontal view of the face with minimum angle or tilt (see Figure 1).

There were 259 images from Edinburgh and Japan. After excluding 20 images due to subject movement or poor quality/angle (for example, images where the chimpanzee was eating, the face was too small on the image, the image was taken from above, or the head was turned too far to the side), each chimpanzee had between 1 and 12 useable images (mean = 2.20, SD = 2.50; Edinburgh: mean = 7.42, SD = 2.99; Japan: mean = 1.72, SD = 1.15). For the Bastrop chimpanzees, we measured composite images created by morphing together original images, so each chimpanzee was represented by one composite image (see supplementary material).

2.3 Facial measurements.

Following Lefevre et al., (2014), fWHR was calculated as the bizygomatic width divided by the mid height of the face (see Figure 1). Measurements were taken by two individuals (researcher 1 = images for 76 chimpanzees; researcher 2 = images for 53 chimpanzees, all of which overlapped with the first 53) so that we could assess their reliability.

Researcher 1 calculated facial dimensions using Psychomorph (Lefevre, Wilson, et al., 2014), by placing delineation landmarks on images and calculating landmark distances.

Researcher 2 calculated facial dimensions by placing points manually and labelling pixel coordinates in image software GIMP, then calculating the distance between coordinates in R with the help of package “alphahull” (Altschul et al., 2019; Rodríguez Casal & Pateiro-López, 2010).

----- Insert Figure 1 here -----

2.4 Personality ratings.

Personality ratings were collected prior to the study for all 132 chimpanzees. Personality ratings for the 79 chimpanzees from the UK and Japan were collected using the 54 item Hominoid Personality Questionnaire (HPQ) (Weiss, 2017; Weiss et al., 2009). Each item from this questionnaire consists of an adjective followed by one to three sentences describing that trait. This questionnaire and an earlier 43-item version both revealed six components (King & Figueredo, 1997; King, Weiss, & Farmer, 2005; Weiss et al., 2009), labelled Dominance, Extraversion, Conscientiousness, Agreeableness, Neuroticism, and Openness. HPQ data from the Japanese sample were collected between 2006 and 2007

for a total of 146 chimpanzees (60 male, 86 female) from 10 facilities in Japan, ranging from just under 1 year to just under 52 years in age (mean = 22.0 years, SD = 10.5) (Weiss et al., 2009, p. 285). The personality of each chimpanzee was assessed by an average of 3.2 individuals who worked with and were familiar with that chimpanzee. HPQ data from the Edinburgh sample were collected for 22 chimpanzees (11 male, 11 female) in 2010. Ages ranged from 11 to 49 (mean = 25.7, SD = 11.0). All chimpanzees were assessed by between 3 and 4 raters who worked with and were familiar with the individuals. Chimpanzees from Bastrop (n = 99; 43 male, 56 female, aged 8 to 48 years old; mean age = 27 years, SD = 11.2) were previously rated between 2006 and 2008 by 17 raters on a 41-item questionnaire that was derived from other questionnaires, including the HPQ (Freeman et al., 2013).

Good convergent scoring properties exist between the Bastrop scale and the HPQ (Freeman et al., 2013). The personality components based on both instruments also have similar predictive validities: both Dominance dimensions were positively correlated with agonistic behaviours, both Extraversion dimensions were positively associated with play, both Agreeableness dimensions were positively associated with affiliation, and both the Reactivity/undependability dimension from the Bastrop questionnaire was associated with more agonistic behaviours, whilst its opposite, the Conscientiousness (Dependability) dimension of the HPQ, was associated with fewer agonistic behaviours (Freeman et al., 2013; Pederson et al., 2005).

For the personality analyses, we aggregated across raters so that, for each chimpanzee, we had a single mean score on each component, for each instrument. For the scoring of the HPQ, we followed the personality structure described in Weiss et al.

(2009) (Table 2). To ensure consistency in the scoring of items from both questionnaires, two authors (DMA and AW) examined the questionnaire used at Bastrop, and compared each item and its loading in both the six and five factor solutions (Freeman et al., 2013) to the descriptions of the HPQ items and those respective loadings (Weiss et al., 2009). The scoring system arrived at is described in Table S2. For the Bastrop chimpanzees, 8 items were included in Dominance, 6 items each were included in Extraversion and Conscientiousness, 3 items were included in Neuroticism, and 2 items each were included in Agreeableness and Openness. Further details on interrater reliability of the instruments are provided in the supplementary material.

----- Insert Table 2 here -----

2.5 Analyses.

2.5.1 Variables

Our outcome variable was fWHR. This and all six personality variables were treated as continuous variables, as were age, age² and age³. Age was calculated from the date each image was taken. The dates of some of the original Bastrop images were unknown, and so age for these images was unclear. In these instances, age was not included in the analyses. All continuous variables were scaled by centering and dividing by two standard deviations (Gelman, 2008). Subspecies was treated as a categorical variable with five levels, one for each of the four subspecies, and one for hybrids and other chimpanzees who did not have a distinct, known subspecies. Sex was a binary categorical variable, although when included as a predictor in mixed effects regression

models, sex was made numeric, scored as -0.4974 for females and 0.5009 for males, to be on approximately the same scale as the continuous variables. Location was treated as a single categorical variable, as was chimpanzee identity.

2.5.2 *Reliability*

To assess reliability between the two researchers who measured faces in different samples, one researcher reassessed 20 images that the first researcher had also rated. Reliability measures were calculated using Pearson's correlations and intraclass correlation coefficients (Shrout & Fleiss, 1979). We also examined the validity of the composite images from Bastrop (see the supplementary material for details).

2.5.3 *Statistical modelling*

To test for relationships between fWHR, age, sex, and the six personality dimensions, we conducted a series of linear mixed models and regression trees (R package 'REEMtree' (Sela & Simonoff, 2012); for a detailed description, see supplementary material). Facial measurements from one chimpanzee were excluded during analyses as these data represented an extreme outlier (> 3 SDs above the mean). For each chimpanzee, each measure from each photo represented one data point.

First, using mixed models, we examined the influence of subspecies, location, and identity, as random effects. Second, because of the possibility of interactions, as well as issues with false-positives in human-driven model building, we sought to identify variables and interactions of importance by examining the splitting variables and the branches of random effect expectation maximization decision trees. This allowed us to model our data as we might in a mixed effect model. Decision trees build what are essentially regression equations by identifying meaningful ways to split variables that are

given to the tree algorithm for investigation (Sela & Simonoff, 2012). A binary, categorical variable like sex is straightforward to split, whereas for a continuous variable, such as age, the algorithm can find cut-points that are best for model fit and so can create informed binary categories (branches) from continuous variables. On each side of a branch, a regression weight is determined for that category, and branching can occur recursively, creating multiple levels in the tree. Multiple branches are analogous to interactions. If a variable is given to the tree algorithm and does not have a relationship with the outcome variable, then it will simply not be used for branching. See the supplementary information for additional details on the decision trees. Third, we modelled the indicated branching variables in linear mixed-effect models, conducting additional post-hoc sensitivity analyses (see supplementary material).

To control for potential maturational changes, photos of 6 *P. t. verus*, 1 *P. t. troglodytes*, and 3 hybrids who were immature at the time of photograph were excluded from some analyses. Reports of chimpanzee age at maturation vary (Harcourt, Fossey, Stewart, & Watts, 1980; D. E. Martin, Swenson, & Collins, 1977; Pusey, Williams, & Goodall, 1997), but females are fully grown by age eight (Kraemer, Horvat, Doering, & McGinnis, 1982) and typically reach menarche between seven and eight years old (Atsalis & Videan, 2009). Males, on the other hand, may be fully grown by nine years (Kraemer et al., 1982) and have been known to father offspring at as young as ten years (Christophe Boesch, Kohou, Néné, & Vigilant, 2006). As such, we excluded photographs of females under eight years of age (four females with fourteen images taken across six different ages) and photographs of males under ten years of age (six males with eight images taken across six different ages).

3. Results.

For the facial measurements, interrater reliability using Pearson's correlation between the two raters' assessments was $r = 0.75$ ($P < 0.0001$), and the intraclass correlations were $ICC(3,1) = 0.69$ ($P = 0.0003$) and $ICC(3,k) = 0.81$ ($P = 0.0003$), indicating good agreement. We also found strong correlations between the Bastrop composite and original images (see supplementary information).

Proceeding with regression modelling, our first model included an intercept and random effects for location, subspecies, and identity nested within subspecies. Random effects of location and individual were associated with fWHR, but we found only very small differences between subspecies (Tables S4 and S5). All else being equal, different subspecies did not appear to have group-wide differences in fWHR. However, this finding does not indicate that there could not be meaningful differences in other variables within subspecies, that is, in a decision tree context, it may be that other variables, such as personality, could branch within certain subspecies but not others. Thus, in subsequent tree analyses, subspecies was included as a possible fixed effect (i.e., a variable that could be used for branching) rather than a random effect.

We next fitted mixed-effects regression trees to our data for 131 subjects (excluding the outlier). The first tree, a recursive partitioning and regression tree, branched on Agreeableness. On the lower Agreeableness branch, the tree then branched by subspecies, and on the *P. t. schweinfurthii-verus* branch, the tree branched by Neuroticism, and then Dominance (Table 3). The second, conditional inferential tree branched by subspecies again, though this time, the *P. t. schweinfurthii-verus* branch also included individuals who were hybrids or whose subspecies was not known (Figure S1).

Along this branch, the only other branch was by sex, which indicated that females had higher fWHR than males.

----- Insert Table 3 here -----

Informed by these results, we fitted mixed effect models in which Agreeableness predicted fWHR, excluding all 22 images of juveniles, which left 285 images from 124 individuals. In these models, Agreeableness was not associated with fWHR (Table S6), indicating that the dimension's primary contribution in the tree was as a branching criterion, rather than being meaningfully associated with fWHR. We next fitted mixed effects models with sex, Neuroticism, Dominance, and all two- and three-way interactions, in the *P. t. verus* subsample, again including only adults (Table 4). These results demonstrated a positive association between Dominance and fWHR, but only in females, such that females who had higher Dominance also had wider faces (Figure 2). Sensitivity analyses (Tables S7 and S8) supported this association; an identical model fitted to the data from all chimpanzees showed no significant associations (Table 4). Data divided by sex and major subspecies (*P. t. verus* and *P. t. troglodytes*) are presented in Figure 2.

----- Insert Table 4 here -----

----- Insert Figure 2 here -----

4. Discussion.

Contrary to our first prediction, we did not find any age or sex effects or age \times sex interactions. Regarding our second prediction, we did not find a main effect of Dominance, but in *P. t. verus* we did find a sex \times Dominance interaction: females, but not males, with higher Dominance had wider faces.

The null finding regarding age and sex differences runs counter to the findings of Weston et al., (2004) who found that facial width-to-height ratio was higher in male than in female chimpanzees. This difference may be attributable to the fact that their measurements were taken from skulls and not from photos. If one considers face width as a social signal or cue, measures that take not just bone but muscle and soft tissue into account are likely to be more informative than measures taken solely from bone. The difference between these two types of measures is illustrated by the fact that, in humans, sexual dimorphism in skulls was not replicated in measures taken from images (Kramer, 2017; Weston et al., 2007). The lack of age and sex differences also contrasts with findings in brown capuchin monkeys, in which mature males have wider faces than mature females (Lefevre, Wilson, et al., 2014). Our findings are, however, consistent with results in adult humans (Kramer, 2017; Lefevre et al., 2012) and in rhesus macaques (Altschul et al., 2019) and bonobos (J. S. Martin et al., 2019), which indicate that the fWHR at skin level is not sexually dimorphic. Given the small number of juveniles in our sample, it is possible that we were unable to detect differences between mature and immature individuals. Despite this, our relatively large adult sample revealed no sex difference in fWHR, which suggests that chimpanzees do not exhibit sexual dimorphism

in fWHR despite the fact that male chimpanzees exhibit more agonistic behaviour than females (Goodall, 1986; Muller, 2002).

Our second finding was that *P. t. verus* females who are higher in Dominance have wider faces. This finding is not consistent with findings from studies of humans, which find that males with wider faces have more dominant or aggressive tendencies (Haselhuhn et al., 2015). One explanation for why we did not find any relationship between fWHR and Dominance in males in this subspecies and, indeed, in the other subspecies, is that we assessed Dominance ratings rather than social rank. However, in the wild, higher rank is correlated with aggressive and dominant behaviour (Muller, 2002) and ratings-based measures of dominance correlate with rank (Buirski, Plutchik, & Kellerman, 1978). Thus, it is unlikely that we would obtain different results if we used chimpanzee rank as opposed to Dominance.

Our findings for males are surprising. Testosterone has been proposed as the mechanism linking aggressive behaviour and fWHR in humans (Eisenbruch, Lukaszewski, Simmons, Arai, & Roney, 2017; Lefevre, Lewis, Perrett, & Penke, 2013; Welker, Goetz, & Carré, 2015; Whitehouse et al., 2015) and male chimpanzees, starting at approximately six years of age, experience an increase in testosterone, which is linked to social rank (Muehlenbein, Watts, & Whitten, 2004) and coincides with an increase in aggressive behaviour (Kraemer et al., 1982). However, several recent studies have not found an association between fWHR and testosterone in humans (Bird et al., 2016; Eisenbruch et al., 2017; Hodges-Simeon et al., 2016; Kordsmeyer, Freund, Pita, Jünger, & Penke, 2018). As such, the earlier findings may be false positives. Our findings for a

lack of relationship between fWHR and Dominance in male chimpanzees are consistent with this possibility.

An alternative explanation for the lack of a Dominance-fWHR association within males pertains to chimpanzee group dynamics. Wild chimpanzees live in fission-fusion societies, meaning that the social make-up of their group changes frequently (Aureli et al., 2008; Lehmann & Boesch, 2004). Male chimpanzees compete for social status, with dynamic changes in rank across their lifespan (Foerster et al., 2016). They are thus prone to frequent displays of aggression (Coe & Levin, 1980), which may be a way for them to maintain their social status in their constantly changing group environments (Muller, 2002). It is possible that these displays of dominance reduce the need for morphological cues of dominance. This possible explanation for our null results suggests that associations between fWHR and traits like Dominance would be stronger in species for which rank is not strongly determined by aggressive displays.

In contrast to males, morphological cues of dominance could be important in females, who are less prone to aggressive displays than males (Goodall, 1986; Muller, 2002). Females exhibit relatively stable ranks across their lifespan, that is, they do not compete for dominance (C. Boesch & Boesch-Achermann, 2000; Foerster et al., 2016; Pusey et al., 1997). It is thus possible that sex differences in how rank is obtained and how stable rank is, may explain the sex-specific relationships between facial morphology and dominance in chimpanzees, something that warrants further investigation.

Placing our findings into a broader context, it is important to consider how these results aid in our understanding of fWHR links to aggression and dominance in humans. Firstly, this paper contributes to the growing body of data indicating that fWHR is related

to dominance and aggression in nonhuman primates (Altschul et al., 2019; Borgi & Majolo, 2016; Lefevre, Wilson, et al., 2014; J. S. Martin et al., 2019; V. Wilson et al., 2014). Given that this relationship has now been found not only in humans but also in *Pan* (chimpanzees and bonobos), the Old World *Macaca* genus and New World *Sapajus apella*, these findings point to the fWHR as an evolutionary ancient cue to behaviour that predates the divergence of the Catarrhini and Platyrrhini. This encourages further comparative assessments of fWHR and its association with behaviour. Secondly, as with humans (Lefevre et al., 2012; Özener, 2012) we found no evidence for sexual dimorphism in chimpanzee fWHR. This suggests that, as in humans (Carré & McCormick, 2008), the fWHR-dominance association may be driven by intrasexual competition, except this occurs in females rather than males.

Finally, given the differences in social style between humans, bonobos and chimpanzees (with humans and chimpanzees being the most and least tolerant, respectively), it is worth considering whether there are species differences in the strength of relationship between fWHR and dominant traits. We translated the f^2 reported by Martin et al., (2019) for bonobos and the sample-size weighted average correlation between fWHR and aggression in Haselhuhn's meta-analysis (2015) to correlation coefficients, and compared them with the correlation coefficients derived in our study. The estimated correlation coefficients for human males, $r = 0.11$, and for chimpanzee males, $r = 0.03$, indicated that the effect size was negligible in comparison to the small effect size for chimpanzee females, $r = 0.24$, bonobo Agonistic Dominance, $r = 0.38$, and bonobo Affiliative Dominance, $r = 0.21$ (Sullivan & Feinn, 2012). Although these results suggest that the relationship between fWHR and dominance does not vary in a linear

fashion with social style, it is apparent that in humans, the strength of this relationship is weaker than that for chimpanzee females or bonobos. This could be a result of higher social tolerance amongst humans; however, given that bonobos are generally less aggressive than chimpanzees (M. Wilson et al., 2014), differences in other factors, such as group dynamics and rank stability, probably also play a role. For humans, this low effect size could also result from the development of human language and culture (Whiten & Erdal, 2012) which, by providing alternative avenues to communicate dominance, could obviate the need for morphological cues. However, such a hypothesis would require further investigation, especially in non-Western cultures.

Our findings raise several important questions. First, why is Dominance related to greater fWHR in female chimpanzees, which are less aggressive than their male conspecifics (Muller, 2002; M. Wilson et al., 2014)? It is unlikely that the mechanisms proposed earlier, such as these associations being rooted in testosterone or combat advantage, provide an answer. Future research could benefit from exploring the role of rank stability. Second, why was an association between dominance and fWHR found in *P. t. verus* females, but not in the other subspecies and sexes? One possibility arises from the observation that western chimpanzees are more bonobo-like in that they exhibit lower levels of lethal aggression (M. Wilson et al., 2014) and more gregarious behaviour (Gruber & Clay, 2016), and females of this species exert more influence within groups (Gruber & Clay, 2016). This fits with recent findings linking fWHR to Dominance in bonobos (J. S. Martin et al., 2019). Ultimately, studies comparing *P. t. verus* and central (*P. t. troglodytes*) and eastern (*P. t. schweinfurthii*) chimpanzees, both of which display

more typical male-dominated social dynamics (Gruber & Clay, 2016), will be needed to test this hypothesis.

These findings offer interesting insights into the relationship between personality and fWHR in chimpanzees. The link between fWHR and Dominance in females is unusual, especially in contrast to findings in human females (Haselhuhn et al., 2015; Lefevre, Eтчells, Howell, Clark, & Penton-Voak, 2014; Stirrat & Perrett, 2010). These findings encourage further research on whether fWHR is a social cue in primates other than humans (Alrajih & Ward, 2014; Lefevre & Lewis, 2014; Mileva et al., 2014; Stirrat & Perrett, 2010; V. Wilson et al., 2018), and what role such a cue might play in social interactions. Most importantly, further studies on relationships between facial morphology and social behaviour from a comparative perspective may help elucidate similar relationships in humans.

Data availability

The data associated with this research are available at [link].

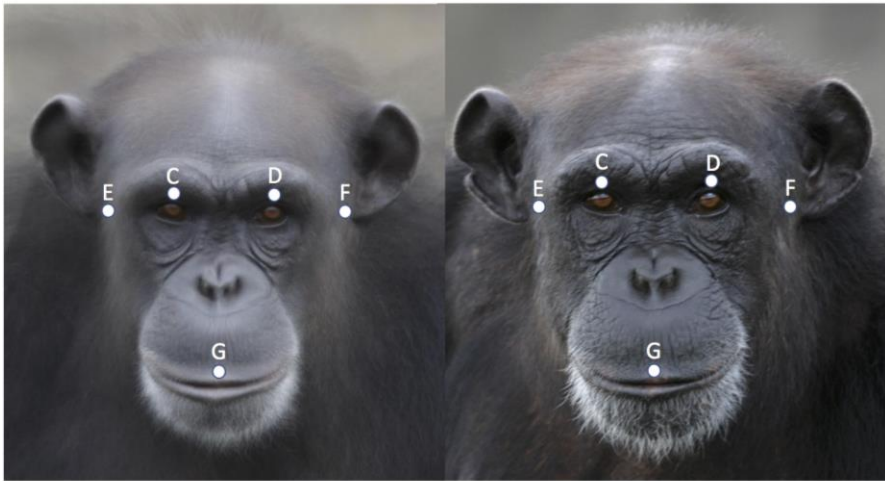


Figure 1. Facial points used for morphometric calculations. Left: morphed image; Right: original image. Measure for Facial width-to-height ratio: $e-f/cd-g$.

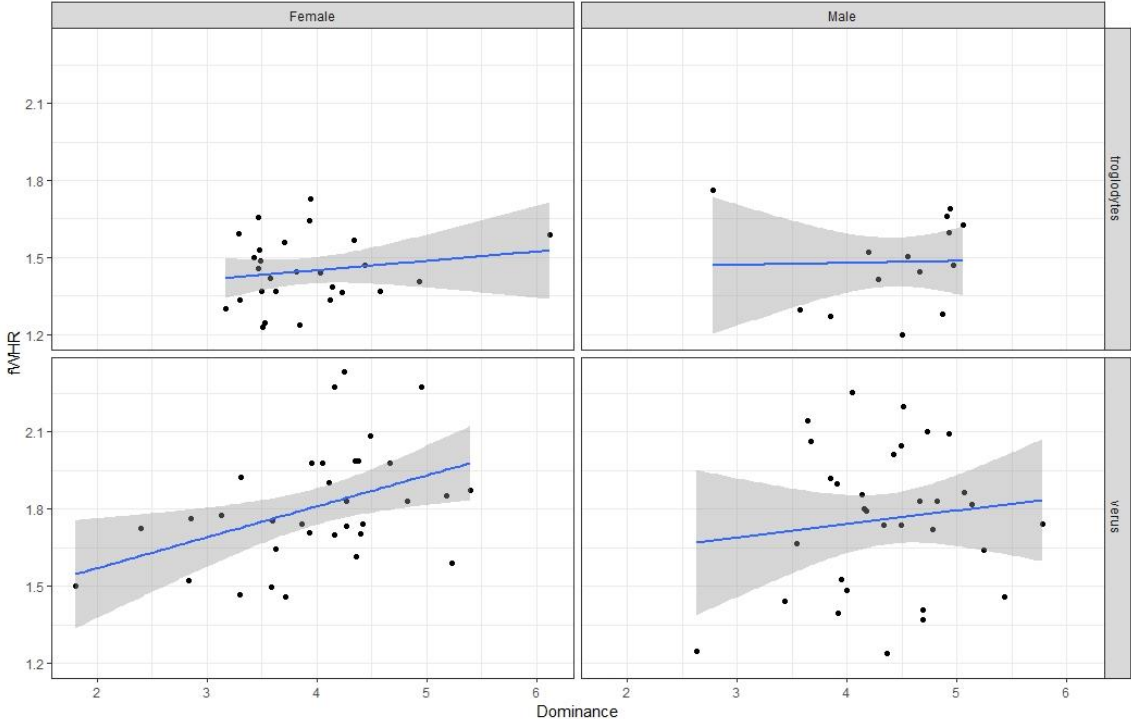


Figure 2. fWHR and Dominance personality dimensions, divided by sex and major subspecies. The line is the best fit linear regression line for each subset of data.

Table 1. Summary table of all chimpanzees, divided by location, sex and subspecies

	Edinburgh	Japan	Bastrop	Total
Total	21	53	58	132
Sex				
Male	10	24	27	61
Female	11	29	31	71
Subspecies				
<i>P. t. verus</i>	9	52	9	70
<i>P. t. troglodytes</i>	1	1	40	42
<i>P. t. schweinfurthii</i>	0	1	0	1
<i>P. t. ellioti</i>	1	0	0	1
Unknown or hybrid	10	4	4	18

Table 2. Item scoring for six personality components derived from the Hominoid Personality Questionnaire.

<i>Personality components</i>						
Positive loading items	Dominance	Extraversion	Conscientiousness	Agreeableness	Neuroticism	Openness
	Dominant	Active	Predictable	Sympathetic	Excitable	Inquisitive
	Independent	Playful		Helpful	Autistic	Inventive
	Decisive	Social		Sensitive		Curious
	Intelligent	Friendly		Protective		Innovative
	Persistent	Affectionate		Gentle		
	Bullying	Imitative		Conventional		
	Stingy					
	Manipulative					
Negative loading items	Submissive	Solitary	Impulsive		Stable	
	Dependent	Lazy	Defiant		Cool	
	Fearful	Individualistic	Reckless			
	Timid	Depressed	Erratic			
	Cautious		Irritable			
	Vulnerable		Aggressive			
	Anxious		Jealous			
			Disorganised			
			Thoughtless			
			Distractible			
		Unperceptive				
		Quitting				
		Clumsy				

Table 3. Recursive partitioning regression tree of fWHR predicted by age, sex, subspecies, and personality.

Branch	n	Deviance	Outcome value
Root	285	7.036	1.574
Agreeableness ≥ 1.052	56	0.657	1.504
Agreeableness < 1.052	229	6.081	1.590
<i>P. t. troglodytes</i> , unknown	138	2.185	1.604
<i>P. t. schweinfurthii</i> , <i>verus</i>	125	4.211	1.681
Neuroticism ≥ 0.7	24	0.916	1.579
Neuroticism < 0.7	91	2.901	1.715
Dominance ≥ 1.498	10	0.073	1.508
Dominance < 1.498	81	2.340	1.738
Variance of errors	0.023		
Log-likelihood	81.514		

Agreeableness, Neuroticism, and Dominance are scaled and centred. Unknown subspecies includes hybrid chimpanzees.

Table 4. Mixed models of fWHR predicted by personality in the *verus* subspecies and full sample

Effect	<i>P. t. verus</i>		All	
	Estimate	95% CI	Estimate	95% CI
Sex	-0.011	[-0.177, 0.203]	0.008	[-0.110, 0.140]
Dominance	0.042	[-0.254, 0.338]	-0.044	[-0.189, 0.109]
Neuroticism	-0.207	[-0.422, 0.044]	-0.029	[-0.178, 0.120]
Sex × Dominance	-0.708	[-1.254, -0.119]	-0.294	[-0.612, 0.003]
Sex × Neuroticism	-0.338	[-0.812, 0.099]	-0.234	[-0.489, 0.084]
Dominance × Neuroticism	0.197	[-0.325, 0.739]	0.136	[-0.185, 0.507]
Sex × Dominance × Neuroticism	0.765	[-0.160, 1.712]	0.115	[-0.451, 0.718]

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