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**Supplementary Information for**  
**Facial Width-to-Height Ratio is Associated with Agonistic and Affiliative**  
**Dominance in Bonobos (*Pan paniscus*)**

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## 21 **Supplementary Methods and Results**

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### 22 *Subjects and measures*

23  
 24 A random sampling procedure was used to reduced researcher bias during facial measurement. NS  
 25 removed identifiable information from photographs and randomly selected a subset of subjects  
 26 from each zoo with available facial photographs, which were subsequently measured by JSM and  
 27 a research assistant, neither of whom took part in collection of the behavioral and psychometric  
 28 data. As described in the main text, appropriate photos with neutral expressions and forward-facing  
 29 orientation were subsequently selected and measured for these subjects. fWHRs were then paired  
 30 back with the remaining individual data after these measurements were completed.

31  
 32 Organizational effects of androgen exposure on behavior and facial morphology could plausibly  
 33 occur from the prenatal period until sexual maturity. We therefore sought to focus our analysis on  
 34 sexually mature bonobos. Previous research on captive bonobos suggests that the onset of puberty  
 35 is likely to occur from approximately 6-10 years of age, with the sharpest increase in urinary  
 36 testosterone around 8-9 years of age for males and an earlier but more gradual increase in females  
 37 [1]. We therefore excluded three 7 year old subjects from our final dataset who we could not  
 38 confidently classify as sexually mature. This resulted in a final sample of 38 individuals across  
 39 five social groups. Demographic data on the resultant sample is provided below (**Table S1**).

40  
 41 **Table S1.** Sample demographics.  
 42

Zoo	<i>n</i>	# Males	# Females	Average age (range)
Apenheul	5	2	3	19.6 (13-34)
Frankfurt	7	2	5	25.6 (11-62)
Planckendael	5	3	2	17.4 (10-27)
Twycross	8	3	5	22 (10-36)
Wilhelma	7	2	5	28.1 (11-48)
Wuppertal	6	3	3	28.3 (12-49)

43 *Footnote.* Age in listed in years.

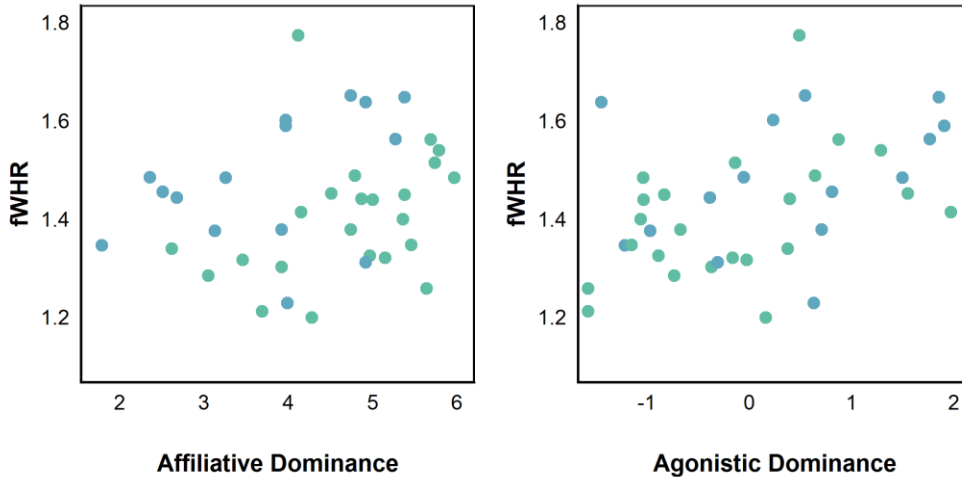
44  
 45 In the 22 subjects with available body weight measures, moderate to strong associations were also  
 46 observed between sex and weight ( $r_{\text{Biserial}} = 0.82$ ) and fWHR and weight ( $r = 0.36$ ). In our full  
 47 sample, fWHR and sex exhibit a similarly sized association ( $r_{\text{Biserial}} = 0.36$ ). While the relationship  
 48 between sex and fWHR may be mediated by body weight, as suggested by our primary regression  
 49 model (**M1**; see below), testosterone is also a known cause of individual differences in body size  
 50 [2]. It therefore remains unclear whether organizational androgen effects may be a latent common  
 51 cause of these associations. The statistically uncertain sex effect reported in the main text, after  
 52 conditioning on body weight, should therefore be cautiously interpreted.

53  
 54 Scatterplots of our raw data provide initial support for the association between fWHR and both  
 55 affiliative and agonistic dominance (**Fig S1**), but also suggest that the strength of affiliative  
 56 dominance in particular is enhanced by controlling for sex, age and body weight. Consistent with

57 this interpretation, a clearer affiliative dominance association is observed with fWHR residuals  
 58 after controlling for these factors (**Fig S2**).

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 61

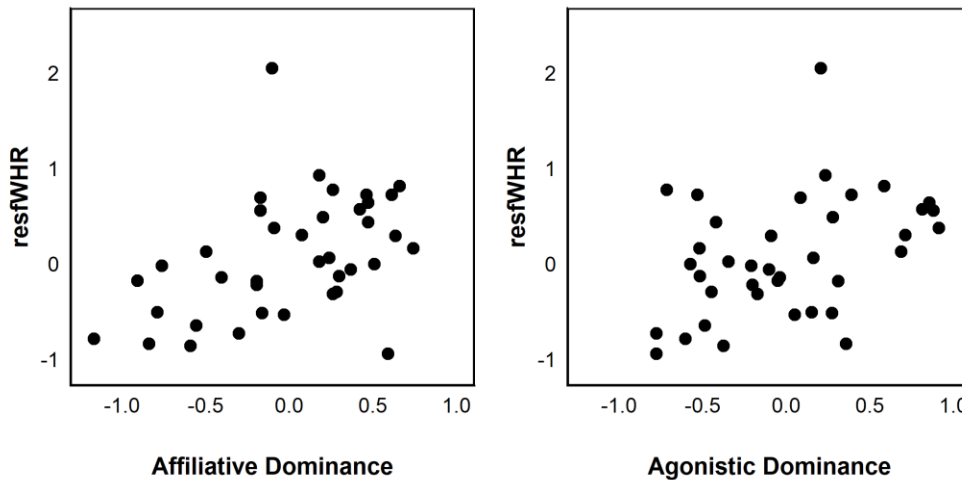
**Fig S1.** Scatterplots of fWHR and the social dominance measures.



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*Footnote.* Datapoints are colored separately for females (green) and males (blue). Social dominance measures are shown on the original data scale.

**Fig S2.** Scatterplots of fWHR residuals and the social dominance measures.



69  
 70  
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 72  
 73

*Footnote.* Social dominance measures are standardized to 2 SD. resfWHR = residual fWHR controlling for age, sex, and body weight.

74 It is important to emphasize that our agonistic dominance measure was analyzed using within-  
 75 group deviations rather than absolute scores. By centering individual scores within zoos, we  
 76 effectively accounted for differential opportunities for agonistic encounters across zoos. This is  
 77 necessary because the raw David's scores used as a measure of agonistic dominance are contingent

78 upon the sample size within each zoo. As further described below, we did not find support for  
 79 further zoo-specific effects in a random slopes model (**M11** below).  
 80

---

81 *Statistical Analysis*

82  
 83 We estimated Bayesian linear measurement error models for all analyses using the R package  
 84 ‘brms’ [3], which interfaces with the Stan statistical programming language [4]. As noted in the  
 85 main text, we employed a fully Bayesian approach to statistical estimation and inference.  
 86 Therefore, rather than relying upon null hypothesis tests and arbitrary designations of statistical  
 87 significance, we used multiple sources of information to summarize and draw inferences from our  
 88 posterior model estimates [5]. The R Code and dataset for this manuscript have been provided as  
 89 additional supplementary material and can be used to replicate all analyses described below.  
 90

91  
 92 We examined the association between fWHR and measures of affiliative and agonistic dominance,  
 93 while accounting for error in the measurement of fWHR across photos. In addition to these  
 94 covariates, we also included fixed effects for years of age and sex in all models. We found that  
 95 inclusion of random zoo-specific intercepts did not account for a meaningful degree of variance in  
 96 fWHR ( $\tilde{\sigma}^2 = 0.03$  [MAD = 0.04]) and reduced the efficiency of MCMC model convergence. We  
 97 therefore excluded this term from our statistical models.  
 98

99 Our first model (**M0**) excluded information on body weight to assess potential sexual dimorphism  
 100 in fWHR irrespective of body size. We therefore estimated the following formal model structure  
 101 conditional on the average fWHR measurement for subject  $i$  using Hamiltonian Markov Chain  
 102 Monte Carlo.  
 103

104 **Model 0 (M0).** Main effects without body weight covariate.

$$105 \text{fWHR}_{\text{EST},i} \sim \text{Normal}(\mu_i, \sigma)$$

$$106 \mu_i = \alpha + \beta_{\text{AssR}} + \beta_{\text{wgDS}} + \beta_{\text{Age}} + \beta_{\text{Sex}}$$

$$107 \text{fWHR}_{\text{OBS},i} \sim \text{Normal}(\text{fWHR}_{\text{EST},i}, \text{fWHR}_{\text{SD},i})$$

$$108 \alpha, \beta \sim \text{Normal}(0, 2)$$

$$109 \sigma \sim \text{Half - Cauchy}(0, 2)$$

110  
 111 Here, the expected subject-specific fWHR  $\mu_i$  is represented as a function of the population-level  
 112 intercept  $\alpha$  and population-level/fixed effects  $\beta$  for Assertiveness scores of affiliative dominance  
 113 (AssR), within-group David’s scores of agonistic dominance (wgDS), age, and sex. We account  
 114 for measurement error in fWHR measurements by parameterizing observed fWHR measurements  
 115  $\text{fWHR}_{\text{OBS},i}$  as arising from a normal distribution characterized by unknown mean parameter  
 116  $\text{fWHR}_{\text{EST},i}$  and the standard deviation  $\text{fWHR}_{\text{SD},i}$  of fWHR measurements for each subject. This  
 117 structure effectively accounts for uncertainty in our response variable while estimating the  
 118

119 regression parameters, and vice versa [5]. The expected measurement error for subjects with  
 120 multiple photographs was assigned to 3 subjects with single photographs. Please note that we  
 121 simplify specification of model priors to represent shared priors over fixed effects ( $\alpha, \beta$ ) and  
 122 residual and effects ( $\sigma$ ). We also suppress observed covariate values to ease interpretation, so that  
 123 terms such as  $\beta_{\text{AssR}}$  implicitly denote  $\beta_{\text{AssR} \text{AssR}_i}$ .

124

125 For our primary analysis (**M1**), we then included body weight as an additional covariate to assess  
 126 whether links between fWHR, sex, and social dominance were independent of body size. Recent  
 127 body weight measures were only available for a subset of our sample, and we therefore used a  
 128 Bayesian imputation procedure to avoid an appreciable loss of information and statistical power.  
 129 We used an inclusive predictive model for estimating unmeasured body weights, incorporating all  
 130 main effect terms in the primary regression model, so as to reduce systematic error and better  
 131 approximate data missing completely at random (MCAR) [6]. We therefore estimated the  
 132 following model conditional on our dataset

133

134

135 **Model 1 (M1)**. Main effects with body weight covariate.

136

137

138

$$\text{fWHR}_{\text{EST},i} \sim \text{Normal}(\mu_i, \sigma)$$

139

$$\mu_i = \alpha + \beta_{\text{AssR}} + \beta_{\text{wgDS}} + \beta_{\text{Age}} + \beta_{\text{Sex}} + \beta_{\text{Weight}}$$

140

$$\text{fWHR}_{\text{OBS},i} \sim \text{Normal}(\text{fWHR}_{\text{EST},i}, \text{fWHR}_{\text{SD},i})$$

141

$$\text{Weight}_i \sim \text{Normal}(v_i, \sigma_{\text{Weight}})$$

142

$$v_i = \alpha_{\text{Weight}} + \gamma_{\text{AssR}_v} + \gamma_{\text{wgDS}_v} + \gamma_{\text{Age}_v} + \gamma_{\text{Sex}_v} + \gamma_{\text{fWHR}_v}$$

143

$$\alpha, \beta, \gamma \sim \text{Normal}(0, 2)$$

144

$$\sigma \sim \text{Half - Cauchy}(0, 2)$$

145 Here, missing values for body weight are imputed using the regression function defined for the  
 146 subject-specific expectation  $v_i$ , with random predictive uncertainty  $\sigma_{\text{Weight}}$ . Fixed effect terms in  
 147 this predictive imputation model are noted by  $\gamma$ , rather than the  $\beta$  notation for fixed effects in the  
 148 main fWHR model, to aid interpretation.

149

150 Cohen's  $f^2$  [7] were calculated as suggested by Selya and colleagues [8] to provide a standardized  
 151 metric of local effect size

152

$$f^2 = \frac{R_{AB}^2 - R_A^2}{1 - R_{AB}^2}$$

153 Here  $R_{AB}^2$  is the variance explained by a model containing the parameter of interest B, and  $R_A^2$  is  
 154 the variance explained by a model of all other parameters A excluding B. An estimated  $f^2$  can be  
 155 negative as the sampled posterior of  $R_{AB}^2$  may be smaller than  $R_A^2$ . For ease of interpretation, we

156 report negative values as 0 to denote that no support was found for a relative increase in the  
157 explanatory power of the model.

158

159 *Additional interaction effect models.*

160

161 For comparison with previous research on capuchins, we also estimated additional interaction  
162 models with sex-specific effects for affiliative (**M2**; see R Code for further details) and agonistic  
163 dominance (**M3**), as well as an interaction between these dominance measures (**M4**). Given that  
164 associations between personality and dominance rank have been found to vary across the lifespan  
165 [e.g., 9], we also fit supplementary exploratory models estimating interactions between age and  
166 affiliative (**M5**) and agonistic dominance (**M6**), as well as age by sex interactions with affiliative  
167 (**M7**) and agonistic dominance (**M8**). No clear interaction effects were observed across models. In  
168 addition to the absence of sex-specific interactions reported in the main text, we also did not find  
169 support for age interaction effects with affiliative ( $\tilde{\beta} = 0.03$  [0.37], 90% CI [-0.57, 0.66],  $p_{>0} =$   
170  $0.54$ ,  $\tilde{f}^2 = 0$ ) or agonistic dominance ( $\tilde{\beta} = 0.01$  [0.35], 90% CI [-0.57, 0.58],  $p_{<0} = 0.51$ ,  $\tilde{f}^2 = 0$ ).  
171 Sex-specific age interactions were also not present for affiliative ( $\tilde{\beta} = 0.14$  [0.88], 90% CI [-1.28,  
172  $1.60$ ],  $p_{>0} = 0.56$ ,  $\tilde{f}^2 = 0$ ) or agonistic dominance ( $\tilde{\beta} = -0.20$  [0.94], 90% CI [-1.75, 1.20],  $p_{>0} =$   
173  $0.59$ ,  $\tilde{f}^2 = 0$ ).

174

175 It is possible that such age by sex interactions for social dominance are non-linear across the  
176 lifespan, particularly for male bonobos. We therefore further explored non-linear sex by age  
177 interactions for affiliative (**M9**) and agonistic dominance (**M10**) using tensor product smoothing  
178 [10]. Given the difficulty of directly interpreting non-linear regression coefficients, we used the  
179 Watanabe-Akaike information criterion (WAIC) to conduct a fully Bayesian model comparison  
180 [11] between the main effects model (**M1**) and these more complex non-linear interaction models.  
181 As with other information criteria such as AIC or BIC, smaller values indicate greater relative  
182 model quality and expected predictive validity, such that  $WAIC_{\text{Model A}} - WAIC_{\text{Model B}} \leq -2$   
183 provides minimal support for selection of the more complex Model A. Consistent with the  
184 aforementioned results, we found that allowing for non-linear interaction effects did not  
185 meaningfully enhance the quality of our models and their expected predictive validity ( $WAIC_{\text{M9}} -$   
186  $WAIC_{\text{M1}} = 4.87$  [SE = 9.33];  $WAIC_{\text{M10}} - WAIC_{\text{M1}} = 5.85$  [SE = 6.47]).

187

188 Finally, although we used within-zoo centering on David's scores, thus controlling for differential  
189 opportunities for agonistic encounters among zoos, it is possible that other unmeasured zoo-  
190 specific effects could still confound our main results. We therefore also estimated a supplementary  
191 model (**M11**) examining whether random zoo-specific slopes between social dominance and  
192 fWHR enhanced model quality. In support of our main effects model (**M1**), we found that adding  
193 parameters for zoo-specific slopes reduced the expected predictive validity of our model  
194 ( $WAIC_{\text{M11}} - WAIC_{\text{M1}} = 4.89$  [SE = 2.26]).

195

196 Our data therefore do not provide support for more complex relationships between social  
197 dominance and fWHR than are described in our main effects model. For these reasons, we relied  
198 on **M1** for drawing statistical inferences. Nonetheless, it is important to emphasize that our data  
199 provide only modest statistical power for detecting interaction and random slope effects, which  
200 would be more effectively examined in larger samples.

201

202 **Supplementary References**

203

- 204 1. Behringer, V., Deschner, T., Deimel, C., Stevens, J. M., & Hohmann, G. (2014). Age-  
205 related changes in urinary testosterone levels suggest differences in puberty onset and  
206 divergent life history strategies in bonobos and chimpanzees. *Hormones and*  
207 *Behavior, 66*, 525-533.
- 208 2. Veldhuis, J. D., Roemmich, J. N., Richmond, E. J., Rogol, A. D., Lovejoy, J. C.,  
209 Sheffield-Moore, M., ... & Bowers, C. Y. (2004). Endocrine control of body composition  
210 in infancy, childhood, and puberty. *Endocrine Reviews, 26*, 114-146.
- 211 3. Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using  
212 Stan. *Journal of Statistical Software, 80*, 1-28.
- 213 4. Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., ... &  
214 Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical*  
215 *Software, 76*. DOI: 10.18637/jss.v076.i01
- 216 5. McElreath, R. (2016) *Statistical Rethinking: A Bayesian course with examples in R and*  
217 *Stan*. Boca Raton: CRC Press.
- 218 6. Collins, L. M., Schafer, J. L., & Kam, C. M. (2001). A comparison of inclusive and  
219 restrictive strategies in modern missing data procedures. *Psychological Methods, 6*, 330–  
220 351.
- 221 7. Cohen, J. E. (1988). *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ:  
222 Lawrence Erlbaum Associates.
- 223 8. Selya, A. S., Rose, J. S., Dierker, L. C., Hedeker, D., & Mermelstein, R. J. (2012). A  
224 practical guide to calculating Cohen's  $f^2$ , a measure of local effect size, from PROC  
225 MIXED. *Frontiers in Psychology, 3*, 111.
- 226 9. Altschul, D. M., Hopkins, W. D., Herrelko, E. S., Inoue-Murayama, M., Matsuzawa, T.,  
227 King, J. E., ... & Weiss, A. (2018). Personality links with lifespan in chimpanzees. *eLife*,  
228 7, e33781.
- 229 10. Wood, S. N., Scheipl, F., & Faraway, J. J. (2012). Straightforward intermediate rank  
230 tensor product smoothing in mixed models. *Statistics and Computing, 23*, 341–360.
- 231 11. Gelman, A., Hwang, J., & Vehtari, A. (2014). Understanding predictive information  
232 criteria for Bayesian models. *Statistics and Computing, 24*, 997-1016.