

1 **Male chimpanzee aggression toward females: long-term intimidation increases likelihood**
2 **of paternity.**

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17 Running Title: **Male-female chimpanzee aggression and paternity**

18
19 SUMMARY

20
21 In sexually reproducing animals, male and female reproductive strategies often conflict [1]. In
22 some species, males use aggression to overcome female choice [2, 3], but debate persists over
23 the extent to which this strategy is successful. Previous studies of male aggression toward
24 females among wild chimpanzees have yielded contradictory results about the relationship
25 between aggression and mating behavior [4–11]. Critically, however, copulation frequency in
26 primates is not always predictive of reproductive success [12]. We analyzed a 17-year sample of
27 behavioral and genetic data from the Kasekela chimpanzee community in Gombe National Park,
28 Tanzania, to test the hypothesis that male aggression toward females increases male reproductive
29 success. We examined the effect of male aggression toward females during ovarian cycling,
30 including periods when the females were sexually receptive (swollen) and when they did not. We
31 found that, after controlling for confounding factors, male aggression during a female’s swollen
32 periods was positively correlated with copulation frequency. However, aggression toward
33 swollen females was *not* predictive of paternity. Instead, aggression by high-ranking males
34 toward females during their *non-swollen* periods was positively associated with likelihood of

35 paternity. This indicates that long-term patterns of intimidation allow high-ranking males to
36 increase their reproductive success, supporting the sexual coercion hypothesis. To our
37 knowledge, this is the first study to present genetic evidence of sexual coercion as an adaptive
38 strategy in a social mammal.

39

40 HIGHLIGHTS

- 41 • Aggression toward sexually receptive females correlated with male mating success
- 42 • Aggression toward non-sexually-receptive females was associated with paternity
- 43 • The effect of aggression on paternity was strongest for high-ranking males
- 44 • This represents the first genetic evidence of long-term sexual coercion in mammals

45

46 RESULTS

47 The sexual coercion hypothesis predicts that male aggression against females increases
48 male fitness [2, 10, 11]. We tested this prediction using behavioral and genetic data from wild
49 chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. Female
50 chimpanzees exhibit an anogenital swelling for about 10 days within a 36-day ovarian cycle [13].
51 During this time, a female mates with most males in the community, although high-ranking
52 males attempt to prevent this by directing aggression toward competitors and the female herself.
53 We consider male-female aggression during the period of maximal swelling (“swollen
54 aggression”) as potential short-term sexual coercion (but NOT forced copulation, as males rarely
55 attempt intromission during or immediately following aggression [11]). We view aggression
56 occurring outside this period (“non-swollen aggression”) as potential long-term coercion. Results

57 support the hypothesis that aggression toward a given female functions as an intimidation
58 strategy that increases a male's future chances of siring that female's offspring.

59

60 *Aggression and paternity*

61 We used generalized linear mixed models (GLMMs) to analyze the relationship between
62 aggression and likelihood of paternity within dyads. We included several additional potentially
63 influential factors (see Methods), and used Akaike's Information Criterion (ΔAICc , a measure of
64 the relative quality of a statistical model) [14] to identify the best predictors of paternity. Non-
65 swollen aggression rate, male dominance rank, the interaction between these two factors, and
66 dyadic relatedness were important predictors of paternity (Table 1; Figure 1a). Paternity
67 probability was greater for males of higher rank (Figure 1a, c), but lower if the male and female
68 were closely related (Figure 1a, d). Males that were more aggressive toward females during non-
69 swollen periods were more likely to conceive with those females. While this relationship was
70 positive for all males, it was very striking among high-ranking males – a high-ranking male with
71 the greatest rate of non-swollen aggression had a 47.9% chance of conceiving with that female
72 (Figure 1b). Among the subset of dyads in which the male's dominance rank score was one
73 standard deviation above the mean ($\text{MDS-Z} > 1$, $n = 47$), there was a strong positive association
74 between non-swollen aggression rate and paternity (Pearson correlation = 0.55, $p < 0.00001$,
75 Figure 2).

76

77 *Aggression and copulation*

78 We used GLMMs to identify predictors of copulation rate. We again used ΔAICc as the
79 selection criterion, identifying several plausible models (Table 2). Therefore, we incorporated a

80 model averaging step, which identified both swollen and non-swollen aggression rates, female
81 age, male rank, alpha male despotism ratio (see Methods), relatedness, and two interaction terms
82 as the best predictors of copulation rate. Overall, males that showed higher levels of aggression
83 toward females tended to copulate with those females at higher rates. However, *swollen*
84 aggression had the strongest association with copulation rate. Copulation rates increased with
85 female age, but were lower in closely-related dyads and during periods when the alpha male was
86 particularly dominant (high despotism ratio).

87

88 *Timing of male-female aggression*

89 To determine if males directed more aggression at females when swollen than when non-
90 swollen, we pooled data across the entire study period. Among dyads that spent ≥ 25 hours
91 together during both swollen and non-swollen periods, swollen aggression rates were
92 significantly higher than non-swollen aggression rates ($n = 549$ dyads, 2.3 [range: 0 – 43.4] vs.
93 1.5 [0 – 25.2] events / 1000 hours together, Wilcoxon signed-rank test: $V = 32857$, $p < 0.001$).
94 This pattern was driven by parous females; there was no difference between swollen and non-
95 swollen aggression rates for nulliparous females ($n = 319$ dyads, 1.6 [range 0 – 22.2] vs. 1.2 [0 –
96 25.2] events/ 1000 hours, Wilcoxon signed-rank test: $V = 6904$, $p = 0.13$).

97

98 *Copulation and paternity*

99 Some primate studies have found little relationship between copulation rates and
100 paternity [12, 15]. However, a model including the terms from the best model for predicting
101 paternity (non-swollen aggression, relatedness, male rank, and male rank*non-swollen

102 aggression), demonstrated that copulation rate was significantly positively associated with
103 paternity (GLMM, $z = 2.157$, $p = 0.03$).

104

105 DISCUSSION

106 In this study of wild chimpanzees, aggression toward non-swollen females was positively
107 associated with paternity, particularly among high-ranking males. This indicates that at Gombe,
108 sexual coercion (as long-term intimidation) is a strategy that high-ranking males successfully
109 employ to increase fitness. Male rank was also positively associated with paternity,
110 independently of aggression. Although this could indicate female preference for dominant males,
111 the relationship between aggression and paternity in high-ranking males indicates that patterns of
112 paternity did not arise from unfettered female choice. Instead, the rank effect is most likely a
113 consequence of mate guarding by dominant males [11, 16].

114 Copulation data also support the sexual coercion hypothesis. Males that directed high
115 levels of aggression toward swollen, and to a lesser extent, non-swollen females, exhibited
116 higher copulation rates. However, although copulation rate predicted paternity, males who were
117 particularly aggressive toward swollen females were not more likely to sire those females'
118 offspring. This is probably because swollen females experience temporal variation in fertility,
119 with fertilization most likely during the peri-ovulatory period (POP) [17, 18]. Therefore,
120 aggression toward swollen females may allow some (e.g. low-ranking) males to increase their
121 mating success, but only during non-fertile portions of the females' swollen periods. This may
122 also explain the finding that while males directed more aggression toward swollen females, only
123 aggression toward non-swollen females increased paternity likelihood, especially for high-
124 ranking males. Also, as the dominance of the alpha increased relative to other males, overall

125 copulation rates decreased. This is intriguing evidence for effective mate guarding by strong
126 alpha males, and is consistent with previous work suggesting that alpha males sometimes trade
127 mating access to females for coalitionary support [19]. “Despotic” alphas may need less support
128 and thus may retain a greater share of copulations. As with paternity, male rank was positively
129 correlated with copulation rate, probably due to mate guarding by high-ranking males.

130 This is the first genetic test of the sexual coercion hypothesis in any mammal. Importantly,
131 our molecular and behavioral data accord extremely well with extensive behavioral evidence of
132 long-term (indirect) sexual coercion in the Kanyawara chimpanzee (*P. t. schweinfurthii*)
133 community in Kibale National Park, Uganda, where dyadic copulation rate and male aggression
134 was also positively correlated [7]. As in our study, this relationship held for parous, but not
135 nulliparous females. Additionally, copulations during the POP were correlated with aggression
136 throughout the ovarian cycle, excluding POP [8], demonstrating the importance of long-term
137 coercion at Kanyawara [11]. Higher-ranking males were the most frequent aggressors toward
138 females [11] and when the alpha was present, there were fewer female solicitations (of other
139 males), [8], demonstrating the alpha’s effectiveness at mate-guarding. Our finding that older
140 females copulated more often than younger females is consistent with data from Kanyawara
141 showing that older females are more attractive to males [20] and that parous females are more
142 often the target of male aggression [21]. Such strong accordance between two research sites
143 provides confidence in the robustness of these findings, certainly among eastern chimpanzees.

144 By contrast, research on western chimpanzees (*P. t. verus*) in Tai National Park, Côte
145 D’Ivoire, found no evidence for sexual coercion, suggesting instead that females successfully
146 employ mate choice [4–6]. There are several possible explanations for these negative results. At
147 Tai, where females are more gregarious than at Gombe and Kanyawara [22], there may be fewer

148 opportunities to ‘sneak’ copulations in a more cohesive group, and thus less incentive for high-
149 ranking males to use aggression to attempt to constrain female choice. Further, our study
150 community had similar numbers of adult males to Kanyawara (11-14 and 10-11 adult males,
151 respectively) [7, 8], but more than double the number of adult males found in the two Tai
152 communities studied (3-4 adult males) [6]. In smaller groups, reproductive success tends to
153 correlate more closely with rank than in larger groups [12, 21, 23]. Thus a high-ranking male in a
154 small group may not need to resort to coercion to obtain a large share of paternities.

155 More comparative work is needed to disentangle the effects of biological and demographic
156 differences on the prevalence and efficacy of male sexual coercion. Although the results from
157 Gombe and Kanyawara clearly demonstrate that sexual coercion can be an effective component
158 of sexual selection in chimpanzees, it remains to be seen whether coercion is a ubiquitous
159 phenomenon, and whether alternative strategies exist. Further work is also needed to determine
160 the mechanism by which long-term patterns of aggression increase paternity probability.
161 Understanding the context in which non-swollen aggression by high-ranking males occurs and
162 how those males interact with female recipients of coercion during swollen periods may shed
163 light on why this strategy is effective for only some individuals.

164

165 METHODS

166 We used data from the long-term study of the Kasekela community at Gombe National
167 Park. We analyzed data from a 17-year period (1995-2011) for which relatedness and paternity
168 information was available from analysis of DNA obtained from fecal samples [24, 25]. During
169 daily, all-day focal follows of adult chimpanzees, researchers continuously recorded group
170 composition, reproductive state of all females, and all observed aggressive and copulation events

171 in the focal chimpanzee's party [13, 26]. We restricted analyses to 'reproductive windows', i.e.
172 when a given female was experiencing ovarian cycles. For nulliparous females this period started
173 at sexual maturity and ended with their first conception. For parous females this was the interval
174 between the first sexual swelling after post-partum amenorrhea and the next conception. We
175 estimated conception dates by backdating 226 days from the offspring's date of birth [27].

176 For analysis of copulation rates and paternity odds, we used data from reproductive
177 windows during which offspring of known paternity were conceived, and from those dyads
178 observed together during both swollen (mean \pm SD = 275 \pm 271 hours) and non-swollen periods
179 (312 \pm 283 hrs). The difference between these two means is not statistically significant ($t =$
180 1.7568, $p = 0.079$). Adult males were at least 12 years of age, the age of the youngest known sire
181 at Gombe [24, 25]. We classified females as adult after their first copulation with an adult male
182 (for natal females) or immigration date. The data set contained 31 reproductive windows (among
183 21 adult females) and 18 adult males, forming 250 unique dyads and 338 dyad-reproductive
184 windows.

185 We defined aggressive events as directed displays, chases, or contact aggression by one
186 or more males toward a single female. We calculated rates of aggression for each dyad
187 (aggression events per 1000hr together), then standardized by Z-transformation within each
188 reproductive window. Thus dyadic aggression rates represented a male's aggression rate relative
189 to a female's average rate of received aggression from all males during a particular reproductive
190 window. We classified aggression according to whether it occurred during the swollen period of
191 a female's ovarian cycle (swollen aggression) or the non-swollen period (non-swollen
192 aggression). Male rank was calculated for each window using the Modified David's Score
193 (MDS) method [28], using submissive pant-grunt data from the year leading up to the end of the

194 window. Because the maximum possible MDS in any period is proportional to the square of the
195 number of individuals being ranked, we standardized the MDS scores (MDS-Z) by Z-
196 transformation within each reproductive window to facilitate comparison between periods. We
197 calculated a “despotism ratio” for each period to quantify the magnitude of rank difference
198 between the alpha and beta male by dividing the MDS of the highest-ranking male by that of the
199 second-highest. Finally, females were considered parous after having had one pregnancy carried
200 to term and nulliparous otherwise.

201 To determine whether male aggression toward females increased in reproductive
202 contexts, we pooled party association and aggression data for each dyad across the entire 17-year
203 study period. Subjects for this analysis were 38 cycling adult females and 20 adult males forming
204 549 dyads that spent at least 25 hours together during both swollen and non-swollen periods.

205 Of the 31 infants included in the study, paternities for 19 were previously reported by
206 Wroblewski et al. [24], and four by Gilby et al. [25]. Eight new paternities were identified for
207 this study using DNA extracted from fecal samples. Fecal samples were collected and preserved
208 in an equal volume of RNAlater (Ambion, Austin, Texas, USA), and DNA was extracted using
209 the QiaAmp DNA Stool Mini Kit (Qiagen) as described in Wroblewski et al. [24]. Individual
210 genotypes were determined for 8-11 microsatellite loci through PCR amplification and allele
211 sizing. Candidate males for paternity of each offspring were those that were ≥ 9 years of age at
212 the time of conception. The offspring, mother and candidate male genotypes were compared
213 across all loci, and in every case, only one male (the father) could have contributed the
214 complementary set of alleles to the offspring, given the maternal genotype. All other males had
215 mismatches with the offspring and maternal genotypes at ≥ 1 locus. Relatedness between males

216 and females was calculated using the Kinship v. 1.3.1 [29] and is the same as the frequency-
217 based calculations established by Queller & Goodnight [30].

218

219 **Analyses:**

220 For the GLMMs, we used swollen and non-swollen aggression rates to represent short-
221 and long-term coercion efforts by males, respectively. We included in our full models the
222 following factors, which, in addition to aggression, might influence paternity and copulation
223 rates. Female age is known to influence male chimpanzee mating interest [20]. Male rank could
224 increase dyadic paternity odds and copulation rates for dominant males via mate guarding [16,
225 31] or female preferences [32]. We included parity (nulliparous or parous) as a factor to
226 determine if it mediates the effect of male aggression on reproductive success as predicted by the
227 cost-of-sexual-attractiveness hypothesis [21]. As alpha males may trade mating for coalitionary
228 support [19], a more despotic alpha may receive a higher share of paternities because he needs
229 less support. Therefore, we calculated the despotism ratio (alpha MDS-Z / beta MDS-Z) for each
230 reproductive window. Finally, we included dyadic relatedness because evidence from birds and
231 mammals [32–35], suggests a cost to inbreeding, and Gombe chimpanzees are known to actively
232 avoid mating with close relatives [35, 36]. We included all first-order interactions between both
233 swollen and non-swollen aggression and these main effects, with the exception of despotism
234 ratio. This we only included in a first-order interaction with male rank, as despotism ratio would
235 seem unlikely to mediate the efficacy of male aggression.

236 All analyses were performed in R [37] using the lme4 package [38] for all GLMMs, and
237 the MuMIn package for model selection [39]. For all models, we determined the best set of
238 predictors using AIC as the model selection criterion [14, 40], and ranked the resulting models

239 by $\Delta AICc$, considering those with values ≤ 2 (with respect to the best model) to have substantial
240 support [41]. We then used model averaging [41] to generate final parameter estimates based on
241 this set of plausible models.

242

243 *Paternity*

244 To test whether aggression was correlated with likelihood of paternity, we ran a series of
245 GLMM regressions, with paternity (Yes/No) as the dependent variable, our candidate predictors
246 of paternity and first-order interactions as factors and female ID as a random effect. By
247 standardizing aggression rates, we accounted for most of the variability that could be attributed
248 to individual males. Therefore did not include Male ID as a random effect in our final models,
249 although inclusion resulted in minimal or no change in our parameter estimates.

250

251 *Copulation rate*

252 To test whether aggression was correlated with copulation rates, we ran negative
253 binomial GLMM regressions for count data (data over-dispersion prevented the use of Poisson
254 regression), with copulation counts as the outcome variable, time spent together as an offset,
255 female ID as a random effect, and our candidate predictors of copulation rate (and first-order
256 interaction terms) as factors. We did not account for zero inflation because the zero-inflated
257 model produced no increase of fit over the standard model.

258

259 *Copulation rate vs. likelihood of paternity*

260 To test whether copulation rates were positively correlated with likelihood of paternity,
261 we ran a logistic GLMM regression, with paternity (Yes/No) as the outcome variable, female ID

262 as a random effect, and the four terms from the best model for predicting paternity, plus
263 copulation rate as factors.

264

265 **Author contributions:**

266 J.T.F., A.E.P., and I.C.G. designed the project, E.E.W., R.S.R., and B.H.H. assigned paternities
267 and calculated relatedness values, and M.C.-R. and T.P. designed and implemented the
268 regression analyses. All authors analyzed data. J.T.F., A.E.P., and I.C.G. wrote the manuscript,
269 with input from E.E.W. All authors read and commented on the manuscript.

270

271 **Data curation:**

272 Dryad repository: “Data from: Male chimpanzee aggression toward females: long-term
273 intimidation increases likelihood of paternity”. Accession: doi:10.5061/dryad.v4h76, data files:
274 1) Aggression rate by swollen state data set; 2) Regression analysis data set.

275

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290 **References**

- 291 1. Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and*
292 *the Descent of Man*, B. Campbell, ed. (Chicago: Aldine), pp. 136–179.
- 293 2. Smuts, B. B., and Smuts, R. W. (1993). Male aggression and sexual coercion of females in
294 nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Stud.*
295 *Behav.* 22, 1–63.
- 296 3. Clutton-Brock, T. H., and Parker, G. A. (1995). Sexual coercion in animal societies.
297 *Anim. Behav.* 49, 1345–1365.
- 298 4. Stumpf, R. M., and Boesch, C. (2006). The efficacy of female choice in chimpanzees of
299 the Taï Forest, Côte d'Ivoire. *Behav. Ecol. Sociobiol.* 60, 749–765.
- 300 5. Stumpf, R. M., and Boesch, C. (2005). Does promiscuous mating preclude female choice?
301 Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park,
302 Côte d'Ivoire. *Behav. Ecol. Sociobiol.* 57, 511–524.
- 303 6. Stumpf, R. M., and Boesch, C. (2010). Male aggression and sexual coercion in wild West
304 African chimpanzees, *Pan troglodytes verus*. *Anim. Behav.* 79, 333–342.
- 305 7. Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., and Wrangham, R. W. (2007).
306 Male coercion and the costs of promiscuous mating for female chimpanzees. *Proc. R. Soc.*
307 *B-Biological Sci.* 274, 1009–1014.
- 308 8. Muller, M. N., Thompson, M. E., Kahlenberg, S. M., and Wrangham, R. W. (2011).
309 Sexual coercion by male chimpanzees shows that female choice may be more apparent
310 than real. *Behav. Ecol. Sociobiol.* 65, 921–933.
- 311 9. Pieta, K. (2008). Female mate preferences among *Pan troglodytes schweinfurthii* of
312 Kanyawara, Kibale National Park, Uganda. *Int. J. Primatol.* 29, 845–864.
- 313 10. Muller, M. N., Kahlenberg, S. M., and Wrangham, R. W. (2009). Male aggression and
314 sexual coercion of females in primates. In *Sexual coercion in primates and humans: An*
315 *evolutionary perspective on male aggression against females*, M. N. Muller and R. W.
316 Wrangham, eds. (Cambridge, MA: Harvard University Press), pp. 3–22.
- 317 11. Muller, M. N., Kahlenberg, S. M., and Wrangham, R. W. (2009). Male aggression against
318 females and sexual coercion in chimpanzees. In *Sexual coercion in primates: An*
319 *evolutionary perspective on male aggression against females*, M. N. Muller and R. W.
320 Wrangham, eds. (Cambridge, MA: Belknap Press of Harvard University Press), pp. 184–
321 217.
- 322 12. Alberts, S. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew
323 in male savannah baboons, *Papio cynocephalus*. *Anim. Behav.* 65, 821–840.

- 324 13. Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior* (Cambridge:
325 Harvard University Press).
- 326 14. Burnham, K. P., Anderson, D. R., and Huyvaert, K. P. (2010). AIC model selection and
327 multimodel inference in behavioral ecology: some background, observations, and
328 comparisons. *Behav. Ecol. Sociobiol.* *65*, 23–35.
- 329 15. Stern, B. R., and Smith, D. G. (1984). Sexual behavior and paternity in three captive
330 groups of rhesus monkeys (*Macaca mulatta*). *Anim. Behav.* *32*, 23–32.
- 331 16. Muller, M. N., and Wrangham, R. W. (2004). Dominance, aggression and testosterone in
332 wild chimpanzees: a test of the “challenge hypothesis.” *Anim. Behav.* *67*, 113–123.
- 333 17. Emery Thompson, M. (2005). Reproductive endocrinology of wild female chimpanzees
334 (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones
335 in sex and conception. *Am. J. Primatol.* *67*, 137–58.
- 336 18. Deschner, T., Heistermann, M., Hodges, K., and Boesch, C. (2003). Timing and
337 probability of ovulation in relation to sex skin swelling in wild West African chimpanzees,
338 *Pan troglodytes verus*. *Anim. Behav.* *66*, 551–560.
- 339 19. Duffy, K. G., Wrangham, R. W., and Silk, J. B. (2007). Male chimpanzees exchange
340 political support for mating opportunities. *Curr. Biol.* *17*, R586–7.
- 341 20. Muller, M. N., Thompson, M. E., and Wrangham, R. W. (2006). Male chimpanzees prefer
342 mating with old females. *Curr. Biol.* *16*, 2234–2238.
- 343 21. Wrangham, R. W. (2002). The cost of sexual attraction: is there a trade-off in female Pan
344 between sex appeal and received coercion? In *Behavioural diversity in chimpanzees and*
345 *bonobos*, C. Boesch, G. Hohmann, and L. Marchant, eds. (Cambridge: Cambridge
346 University Press), pp. 204–215.
- 347 22. Wittiger, L., and Boesch, C. (2013). Female gregariousness in Western chimpanzees (*Pan*
348 *troglodytes verus*) is influenced by resource aggregation and the number of females in
349 estrus. *Behav. Ecol. Sociobiol.* *67*, 1097–1111.
- 350 23. Cowlshaw, G., and Dunbar, R. I. M. (1991). Dominance rank and mating success in male
351 primates. *Anim. Behav.* *41*, 1045–1056.
- 352 24. Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H.,
353 and Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees,
354 *Pan troglodytes schweinfurthii*. *Anim. Behav.* *77*, 873–885
- 355 25. Gilby, I. C., Brent, L. J. N., Wroblewski, E., Rudicell, R. S., Hahn, B. H., Goodall, J., and
356 Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees.
357 *Behav. Ecol. Sociobiol.* *67*, 373–381.

- 358 26. Wilson, M. L. (2012). Long-term studies of the chimpanzees of Gombe National Park,
359 Tanzania. In Long-term field studies of primates, P. M. Kappeler and D. P. Watts, eds.
360 (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 357–384.
- 361 27. Boehm, E. E., and Pusey, A. E. (2013). Measuring gestation length in the chimpanzees of
362 Gombe National Park. *Am. J. Phys. Anthropol.* *150* (S56), 84.
- 363 28. De Vries, H., Stevens, J. M. G., and Vervaecke, H. (2006). Measuring and testing the
364 steepness of dominance hierarchies. *Anim. Behav.* *71*, 585–592.
- 365 29. Goodnight, K. F., and Queller, D. C. (1999). Computer software for performing likelihood
366 tests of pedigree relationship using genetic markers. *Mol. Ecol.* *8*, 1231–1234.
- 367 30. Queller, D. C., and Goodnight, K. F. (1989). Estimating Relatedness Using Genetic
368 Markers. *Evolution* (N. Y.) *43*, 258–275.
- 369 31. Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale
370 National Park, Uganda. *Behav. Ecol. Sociobiol.* *44*, 43–55.
- 371 32. Matsumoto-Oda, A. (1999). Female choice in the opportunistic mating of wild
372 chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behav. Ecol. Sociobiol.* *46*,
373 258–266.
- 374 33. Crnokrak, P., and Roff, D. a (1999). Inbreeding depression in the wild. *Heredity.* *83*, 260–
375 70.
- 376 34. Ralls, K., Ballou, J. D., and Templeton, A. (1988). Estimates of lethal equivalents and the
377 cost of inbreeding in mammals. *Conserv. Biol.* *2*, 185–193.
- 378 35. Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Anim. Behav.* *28*, 543–552.
- 379 36. Pusey, A. (2005). Inbreeding avoidance in primates. In *Inbreeding, incest, and the incest*
380 *taboo*, A. P. Wolf and W. H. Durham, eds. (Stanford: Stanford University Press), pp. 61–
381 75.
- 382 37. R Core Team. (2014). *R: A Language and Environment for Statistical Computing.*
- 383 38. Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., and
384 Dai, B. (2014). *lme4* package.
- 385 39. Bartoń, K. (2014). *MuMIn: Multi-model inference.*
- 386 40. Anderson, D. R., Burnham, K. P., and Thompson, W. L. (2000). Null hypothesis testing:
387 problems, prevalence, and an alternative. *J. Wildl. Manage.* *64*, 912–923.

388 41. Burnham, K. P., and Anderson, D. R. (1998). Model selection and inference: a practical
389 information-theoretic approach (New York: Springer Verlag New York).

390

391 **Figure and Table Legends**

392 **Figure 1:** Predicted likelihood of paternity based on covariates from the best model.

393

394 a) Effect sizes and 95% confidence intervals of variables from the best model (Model 1 in Table
395 1) on probability of paternity. MRank = Male dominance rank (MDS-Z), NSagg = standardized
396 non-swollen aggression rate, and Relatedness = Queller and Goodnight's R (see Methods).

397 b) Lines indicate effect of aggression rates toward non-swollen females when all other covariates
398 are at their average values. Solid line = middle-ranking males; dotted line = high-ranking males;
399 dashed line = low-ranking males.

400 c) Lines represent the effect of male rank (MDS-Z) on likelihood of paternity when other
401 covariates are at their average values; Solid line = average levels of non-swollen aggression;
402 dotted line = high levels of non-swollen aggression toward the female; dashed line= low non-
403 swollen aggression.

404 d) Solid line represents the effect of relatedness on likelihood of paternity among all dyads.

405

406 **Figure 2:** Paternity among highly-ranked males by non-swollen aggression rate

407

408 Observed frequency of paternities among dyads with high-ranking males (MDS-Z > 1) vs. non-
409 swollen aggression rate. **Low** represents standardized aggression rates toward non-swollen
410 females < -1, **Med-Low:** [-1, 0), **Med-High:** [0, 1), and **High:** ≥ 1 .

411

412 **Table 1:** Factors influencing likelihood of paternity
413 Models and effect sizes for averaged model and all models with $\Delta AICc \leq 2$. See Methods for
414 description of full model. **Fem Age:** centered female age (years) **Rank:** male standardized
415 Modified David's Score (MDS-Z); **NS Agg:** standardized dyadic aggression rates toward
416 females during their non-swollen periods; **Parity:** binary (1 = parous, 0 = nulliparous); **Despot**
417 **ratio:** despotism ratio, the ratio of α -male MDS-Z to β -male MDS-Z; **Relatedness:** Queller and
418 Goodnight's R; **S Agg:** standardized dyadic aggression rates toward females during their swollen
419 periods. Columns with a * represent first-order interaction terms.

420
421 Effect sizes are multiplicative effects on paternity odds ratio of a one-unit change in the variable.
422 Values above 1 will increase likelihood of paternity, while values below 1 will decrease
423 likelihood of paternity. In Model 1, the only variable of the four significantly associated with
424 likelihood of paternity was the interaction between male rank and non-swollen aggression ($p =$
425 0.04). In the averaged model, important predictors of paternity are highlighted in bold.

426
427 **Table 2:** Factors influencing copulation rates
428 Models and effect sizes for the average model and the best 10 models. See Methods for
429 description of original full model. **Fem Age:** centered female age (years) **Rank:** male
430 standardized Modified David's Score (MDS-Z); **NS Agg:** standardized dyadic aggression rates
431 toward females during their non-swollen periods; **Despot ratio:** despotism ratio, the ratio of α Z-
432 MDS to β Z-MDS; **Relatedness:** Queller and Goodnight's R; **S Agg:** standardized dyadic
433 aggression rates toward females during their swollen periods. Columns with a * represent first-
434 order interaction terms.

435

436 Effect sizes are multiplicative effects of a one-unit change in the variable on predicted copulation
437 rates. Values above 1 will increase predicted dyadic copulation rates, while values below 1 will
438 decrease predicted dyadic copulation rates. In Model 1, swollen aggression rate is significantly
439 positively correlated with copulation rate ($p < 0.000001$). Other factors significant in predicting
440 copulation rate were female age ($p < 0.001$), despotism ratio ($p = 0.04$), and the interaction
441 between swollen aggression rate and relatedness ($p = 0.03$). There was a trend toward
442 significance for dyadic relatedness ($p = 0.07$). In the averaged model, important predictors of
443 paternity are highlighted in bold.

444

445 Table 1:
446

Model	Fem Age	Rank	NS Agg	Parity	Despot ratio	Related-ness	S Agg	NS Agg* Rank	NS Agg* Related	AICc	Δ	Weight
1		1.26	1.06			0.17		1.48		204.83	0.00	0.287
2		1.19	1.05					1.55		205.81	0.98	0.176
3		1.26	1.06	0.88		0.17		1.49		206.76	1.93	0.109
4		1.25	1.05			0.16	1.05	1.48		206.77	1.94	0.109
5	1.00	1.26	1.06			0.17		1.48		206.79	1.96	0.108
6		1.26	1.06		0.99	0.17		1.48		206.82	1.99	0.106
7		1.26	1.05			0.17		1.48	0.90	206.82	1.99	0.106
Average	1.00	1.24	1.06	0.99	1.00	0.23	1.01	1.49	0.99	-	-	-

447
448 Table 2:
449

Model	Fem Age	Rank	NS Agg	Despot ratio	Related-ness	S Agg	NS Agg* FemAge	NS Agg* Rank	Rank* Despot Ratio	S Agg* Related-ness	AICc	Δ	Weight
1	1.05			0.90	0.58	1.28				0.55	1610.53	0.00	0.15
2	1.05	1.23		0.90	0.55	1.28			0.95	0.54	1610.83	0.30	0.13
3	1.05	1.07		0.90	0.56	1.27				0.54	1610.85	0.32	0.13
4	1.05		1.06	0.90	0.59	1.27				0.56	1611.44	0.91	0.10
5	1.05		1.05	0.90	0.62	1.28	1.01			0.57	1611.56	1.03	0.09
6	1.05	1.07	1.06	0.90	0.57	1.26				0.55	1611.70	1.17	0.09
7	1.05	1.23	1.06	0.90	0.56	1.26			0.95	0.54	1611.71	1.18	0.08
8	1.05	1.23	1.05	0.90	0.58	1.27	1.01		0.95	0.55	1611.78	1.25	0.08
9	1.05	1.07	1.05	0.90	0.59	1.26	1.01			0.56	1611.92	1.39	0.08
10	1.05	1.22	1.06	0.90	0.59	1.26		1.06	0.95	0.51	1612.11	1.58	0.07
Average	1.05	1.10	1.03	0.90	0.58	1.27	1.00	1.00	0.98	0.55	-	-	-

450