



Sexual Coercion by Male Chimpanzees Shows That Female Choice May Be More Apparent than Real

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**Sexual coercion by male chimpanzees shows that female choice may be more
apparent than real**

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23 **Abstract**

24 The extent to which active female mating preferences influence male reproductive
25 success in mammals is unclear, particularly for promiscuously breeding species like
26 chimpanzees (*Pan troglodytes*). Previous studies from multiple long-term study sites have
27 shown that female chimpanzees mate more restrictively around ovulation, and this has
28 been taken as evidence for female choice. However, none of these studies rigorously
29 evaluated the alternative hypothesis, that restrictive mating results not from unconstrained
30 choice, but in response to coercive mate guarding, in which males use punishment and
31 intimidation to reduce female promiscuity and promote their own mating interests. Nor
32 did they consider evidence for the potential genetic or phenotypic benefits that females
33 might be choosing. Using 11 years of data from the Kanyawara community in Kibale
34 National Park, Uganda, we previously demonstrated that males achieve elevated mating
35 success with those females toward whom they direct high levels of aggression. Here we
36 extend those findings to show that even female copulatory approaches, which have
37 previously been attributed to female choice, may be influenced by male aggression.
38 Specifically, individual females at our site initiated periovulatory copulations most
39 frequently with the males who were most aggressive toward them throughout their cycles.
40 Those males showed high rates of aggression toward females throughout estrus, despite
41 achieving high copulation rates, demonstrating a continuing conflict of interest over the
42 exclusivity of mating access. Because sexual coercion is potentially widespread in
43 primates and other mammals, we conclude that male aggression must be taken into
44 account before mating preferences can be inferred from female behaviour.

45

46

47 **Key Words**

48 Female choice, sexual coercion, coercive mate guarding, mating preferences, mixed

49 mating strategy

50 **Introduction**

51 Females in a broad range of species, especially birds, are known to choose mates
52 that offer genetic or phenotypic benefits (Andersson 1994, Hill 2006, Mays et al. 2008).
53 Female choice is less well understood in mammals (Clutton-Brock & McAuliffe 2009).
54 Because most mammals are polygynous and rarely provide paternal care, male-male
55 competition for access to females is relatively intense. Consequently males that are
56 successful at mating tend to be high quality, which reduces the benefits of active female
57 choice (Clutton-Brock & McAuliffe 2009). Moreover, intense male mating competition
58 can select for both armaments and large body size, which males of some species employ
59 to constrain female mating behavior (Smuts & Smuts 1993, Clutton-Brock & Parker
60 1995, Muller & Wrangham 2009).

61 Primates present additional difficulties for the assessment of female choice.
62 Because female primates have slow life histories and produce relatively few offspring,
63 mate selectivity is expected to be particularly important in this order (Kappeler & van
64 Schaik 2004). Yet in many non-human primates, females mate promiscuously by actively
65 soliciting copulations from multiple partners (Dixson 1998, Hrdy 1981, Nunn 1999,
66 Zinner et al. 2004, Clarke et al. 2009). Multi-male mating appears to benefit females
67 primarily by confusing paternity, and thus reducing the risk of male infanticide (Hrdy
68 1979, van Noordwijk & van Schaik 2000, Paul 2002, van Schaik et al. 2004).

69 Given these problems, the extent and nature of female choice in promiscuously
70 mating primates is uncertain. However, there has been considerable interest in the idea
71 that a promiscuous strategy predominates only in the early follicular phase, when
72 conception is unlikely to occur, and that females exert a preference for particular males

73 around the time of ovulation, subtly attempting to concentrate paternity in those
74 individuals (Nunn 1999, van Schaik et al. 2004, Clarke et al. 2009). Female choice of
75 high-ranking males has been predicted in this context on the premise that those males
76 would provide the best defence against infanticide (Nunn 1999, van Schaik & Janson
77 2000, van Schaik et al. 2004, Clarke et al. 2009). Genetic benefits are also possible (Paul
78 2002, Byers & Waits 2006).

79 The prediction of biased mating during the periovulatory period (POP) has been
80 supported by the only empirical tests to date, from data on wild chimpanzees (*Pan*
81 *trogodytes*) (Matsumoto-Oda 1999; Stumpf & Boesch 2005, 2006; Pieta 2008).
82 Chimpanzees offer a relevant test because females copulate more than 500 times per
83 conception, normally mating with all of the adult males in their community (Wrangham
84 2002). Moreover, infanticide by adult males within the social group is an important risk
85 for females (Nishida & Kawanaka 1985, Arcadi & Wrangham 1999, Murray et al. 2007).

86 In the first study, at Mahale (Tanzania), Matsumoto-Oda (1999) found that the
87 proportion of a female's copulations with high-ranking males increased significantly
88 during the POP. She inferred from this result that females preferred to mate with high-
89 ranking males when they were likely to conceive. However her data cannot discriminate
90 between the hypothesis of female choice and the alternative hypothesis of female
91 constraint, i.e. that high-ranking males guard females more intensely during the POP and
92 thereby restrict female options. In support of the female-constraint hypothesis,
93 solicitations by adolescent males (who were low ranking) were more likely to succeed
94 when higher-ranking males were absent (34/48 attempts, i.e. 70.8% success) than when
95 they were present (6/23, i.e. 26.1%) (Table 5 in Matsumoto-Oda 1999).

96 In more detailed studies, Stumpf and Boesch (2005, 2006) examined mating
97 patterns in two communities of wild chimpanzees living in Tai National Park (Ivory
98 Coast), quantifying female “preferences” by establishing rates of proceptivity (female-
99 initiated sexual behaviour) and resistance (avoidance of male solicitations) across male-
100 female dyads. They reported that males whose sexual advances were generally resisted by
101 a particular female were resisted by that female at higher rates, and solicited at lower
102 rates, during the POP. No such difference was evident for males who were generally
103 approached by a particular female for copulations.

104 A similar study by Pieta (2008) at our site in Kanyawara, Kibale National Park
105 (Uganda), showed a somewhat different pattern. As at Tai, males whose sexual advances
106 were generally resisted by a particular female were solicited by that female at lower rates
107 during the POP. However, no significant difference was found between rates of resistance
108 in the POP and non-POP. Additionally, and distinct from Tai, males at Kanyawara who
109 were generally approached by a particular female for copulations, were approached by
110 that female at higher rates, and resisted at lower rates, during the POP.

111 Both Stumpf and Boesch (2005, 2006) and Pieta (2008) construed their findings
112 as strong evidence for female choice in chimpanzees. However, neither study rigorously
113 tested the alternative hypothesis, that the distribution of female copulatory approaches
114 during the POP (when females were most attractive) was constrained by male aggression
115 (Muller et al. 2009a). For example, even if a female’s objective were to solicit all of the
116 males in a group equally, she might be thwarted by the efforts of a coercive male
117 interested in monopolizing her. Measures of female resistance were similarly difficult to
118 interpret. Although chimpanzee females might avoid a male’s advances owing to

119 negative preference, they might also do so because mating could invite punishment from
120 a higher-ranked suitor (Muller et al. 2009a). This is particularly problematic because both
121 studies defined resistance according to a female's initial response to the male solicitation
122 (including “ignoring the solicitation, avoiding the male, screaming, or leaving”, Stumpf
123 & Boesch, 2005). Thus, a female who waited for a high-ranking male to turn his
124 attention elsewhere before mating furtively with a soliciting male would have been
125 classified as “resistant”. Problems inherent in these assumptions of preference are
126 illustrated by the fact that in both Stumpf (2004: Appendix B) and Pieta’s (2008: Table 1)
127 studies, some females simultaneously “preferred” males based on measures of proceptive
128 behavior whom they “eschewed” based on measures of resistant behavior.

129 Controlling for the potential effects of male behavior on female mating decisions
130 is critical, because much evidence suggests that chimpanzee males use aggression as a
131 coercive mating tactic, making some females more likely to mate with them and less
132 likely to mate with rivals (Muller et al. 2007). For example, we have previously shown
133 that Kanyawara females experience increased rates of male aggression during periods of
134 maximal swelling (i.e. during estrus, Muller et al. 2007), when conception is most likely
135 to occur (Emery Thompson 2005). Parous females, who are more attractive to males
136 (Tutin 1979, Wrangham 2002, Muller et al. 2006), receive higher rates of male
137 aggression during maximal swelling than do less attractive nulliparous females (Muller et
138 al. 2007). Finally, individual males exhibit increased copulation rates with the parous
139 females toward whom they are most aggressive (Muller et al. 2007). This correlation may
140 partly result from females being compelled to copulate more frequently with their
141 aggressors (“direct coercion”), but it also seems likely to reflect a dynamic in which

142 aggressive males are able to prevent females from mating with other males (“indirect
143 coercion”) (Muller et al. 2009a).

144 We have also established that male aggression imposes significant costs on
145 Kanyawara females. Physical injury, including severe wounding, is a regular outcome of
146 the prolonged attacks that are sometimes directed at females (Muller et al. 2009a).
147 Furthermore, levels of stress hormones (cortisol) in females show dramatic increases
148 during periods of cycling and maximal swelling (Muller et al. 2007), a pattern that we
149 have recently shown is driven by an increase in male aggression during these periods
150 (Emery Thompson et al. 2010).

151 To date, attempts to control for the possible influence of male coercion on female
152 choice have mostly focused on the immediate context of mating. It is clear, however, that
153 chimpanzee males rarely use force directly in the act of copulation (Goodall 1986,
154 Stumpf & Boesch 2006). Stumpf and Boesch (2005), for example, reported no
155 significant correlation between rates of male aggression toward females and rates of
156 female proceptivity during the POP, and concluded that male coercion could therefore not
157 have been responsible for the more restrictive mating pattern at that time. This approach
158 assumes *a priori* that female behavior is not affected by previous social interactions with
159 males.

160 A growing body of evidence, however, suggests that sexual coercion in primates is
161 often a long-term strategy that achieves its goal by manipulating the future, rather than
162 simply the immediate behavior of the victim (Wrangham & Muller 2009). Male
163 punishment of both female mating resistance (Clutton-Brock & Parker 1995) and female
164 promiscuity (Clarke et al. 2009) can be effective strategies if females modify their

165 behavior in response to the actions of known males. The development of this response is
166 evident when female hamadryas baboons (*Papio hamadryas hamadryas*) are first
167 incorporated into a one-male unit (Swedell & Schreier 2009). Male hamadryas employ
168 aggression to enforce female proximity, promoting their long-term social bond. Once a
169 bond is established, and females learn to follow a male, and to avoid rival males, rates of
170 aggression drop (Swedell & Schreier 2009). Such a resolution may not occur, however, if
171 male and female mating interests are in conflict, or if threats to male mating exclusivity
172 emerge. For example, in mountain gorillas, encounters with strange males often provoke
173 aggression by resident silverbacks against their mates (Sicotte 1993).

174 Because chimpanzees, like hamadryas baboons, live in stable social networks and
175 exhibit cognitive abilities such as individual recognition, memory of specific events, and
176 sophisticated learning (Goodall 1986), male aggression might in theory affect female
177 behavior over the long term. We have previously shown that males in Kanyawara who
178 direct high levels of aggression toward individual females show increased rates of
179 copulation with those females compared to other males. We have also shown that the
180 majority of POP copulations are initiated by males rather than females (Emery Thompson
181 & Wrangham 2008). Nevertheless, it remains possible, as suggested by Stumpf and
182 Boesch (2005, 2006) that the copulations initiated by females represent a free expression
183 of preference. Here we employ 11 years of data from Kanyawara, to test whether patterns
184 of female-initiated copulation during the POP (when conception is most likely) reflect
185 primarily male coercion or female attempts to bias paternity toward specific males.
186 Because females might choose males based on a range of criteria, we consider predictions
187 for phenotypic and genetic benefits separately (See Table 1).

188 In theory females might practice unfettered promiscuity to gain protection from
189 infanticide, giving all males a more or less equal probability of conception. However,
190 previous work at Kanyawara suggests that this does not occur. For example, high-ranking
191 males at Kanyawara show higher rates of copulation with females during the POP, and
192 females show increased copulation rates with aggressors relative to non-aggressors
193 (Emery Thompson & Wrangham 2008; Muller et al. 2007). It is thus necessary to
194 consider alternative hypotheses to explain these biased mating patterns.

195 If females are actively concentrating paternity in particular males to gain
196 protection from infanticide (van Schaik et al. 2000), then all females are expected to
197 initiate periovulatory copulations most frequently with the alpha male (van Schaik et al.
198 2004). Consequently, the alpha is expected to show decreased rates of male-female
199 aggression during the POP, since his interest in sequestering females from competitors is
200 aligned with the female goal of concentrating paternity (Muller et al. 2009ab).

201 If female mate choice is directed toward maximizing genetic quality, then
202 predictions differ depending on whether females are choosing males with “good genes”
203 or males with “compatible genes” (Mays & Hill 2004, Neff & Pitcher 2005). In “good
204 genes” models, females choose mates based on a particular combination of alleles, and
205 females within a community are expected to bias paternity toward the same male or
206 males (as in pronghorn, *Antilocapra americana*: Byers & Waits 2006). In contrast to the
207 predictions of the infanticide-avoidance hypothesis, this male need not be the alpha (e.g.
208 female preference for brightly colored males in mandrills, *Mandrillus sphinx*: Setchell
209 2005). If females are choosing males based on genetic compatibility (i.e. dissimilarity),
210 then females are not expected to bias paternity toward the same males (e.g. potential

211 cryptic choice in the grey mouse lemur, *Microcebus murinus*: Schwensow et al. 2008). In
212 both models, males who are the targets of paternity concentration are expected to show
213 decreased rates of male-female aggression during the POP, since their interests are
214 aligned with those of the females.

215 If biases in female sexual initiations reflect constraints imposed by male
216 aggression, then females should solicit periovulatory copulations most frequently from
217 the males who are most aggressive toward them (Muller et al. 2007, 2009a). Such skew
218 could reflect direct coercion (a male increasing his absolute mating success with a
219 female), indirect coercion (a male restricting a female's ability to solicit other males), or
220 both. Furthermore, if biases in female copulatory initiations result from male constraints
221 on female promiscuity, and not female interest in paternity concentration, then conflict of
222 interest between males and females is expected to continue during the POP, as females
223 continue attempting to mate with males other than the aggressor. Consequently, rates of
224 male aggression against females are expected to remain steady or intensify around
225 ovulation. Finally, if biases in female copulatory initiations reflect primarily male mate
226 guarding (indirect coercion), then females are expected to show increased solicitation
227 rates toward males in the absence of the males who are most aggressive toward them.

228

229 **Methods**

230 Study population and long-term data

231 The subjects of the study were members of the Kanyawara community in Kibale
232 National Park, Uganda, a chimpanzee population that has been studied continuously since
233 1987. This study incorporates data from 29,488 observation hours from January 1996 to

234 December 2006. The community consisted of 47 chimpanzees at the beginning of the
235 study (including 11 adult males and 17 adult females) and 52 individuals at the end of the
236 study (including 10 adult males and 16 adult females).

237 Behavior was recorded by a team of observers, which normally consisted of 2-3
238 long-term Ugandan field assistants and 1-2 university-based researchers (graduate
239 students, postdoctoral researchers, or one of the authors). Confidence in the accuracy of
240 long-term behavioral data comes from tests documenting close agreement between focal
241 data collected by researchers and all-occurrence sampling data collected independently
242 by field assistants (Muller et al. 2007), together with routine measures of inter-observer
243 reliability (Kibale Chimpanzee Project, unpublished data).

244 Chimpanzees were located by following their tracks, listening for calls or waiting
245 near fruiting trees. Whenever possible, observers followed chimpanzees from the time
246 that they woke in the morning until they constructed their night nests. Observers
247 identified all individuals present in a focal party at 15 min intervals throughout the day. A
248 party was defined as all chimpanzees within 50 continuous meters of each other.
249 Observers also detailed the behavior of individual party members during 10 min focal
250 sessions. Focal targets consisted of all age-sex classes, and were randomly selected
251 throughout the day from observable party members. Observers attempted to record all
252 overt submissive vocalizations (pant-grunts) and behaviors, and any aggression that
253 occurred within the party, including the identities of the actors.

254 Aggression was defined as any directed charge, chase or attack (see Muller 2002
255 for definitions). These types of aggression are accompanied by exaggerated movements
256 and vocalizations (e.g. screams) from victims, rendering them highly conspicuous to

257 observers. Thus, our sampling of aggression is equivalent to all-occurrence sampling
258 (Altmann 1974). Nevertheless, the long-term data underestimate true rates of aggression,
259 because some interactions are obscured by vegetation. Muller et al. (2007) compared
260 focal data on intersexual aggression collected by a single observer with long-term data
261 and showed that these underestimates represent an unbiased sample of the behavior.

262 Dyadic rates of male-female aggression are reported from three different time
263 periods. “POP aggression” was calculated by summing the number of charges, chases and
264 attacks a male directed at a female across all POP days (see definition below), and
265 dividing by the number of hours the pair were observed together on those days. “Pre-POP
266 aggression” was calculated in the same manner, but for days of maximal swelling prior to
267 the POP. “Cycling aggression” was the same measure again, but calculated over all days
268 in which the female was actively cycling (i.e. not pregnant or experiencing lactational
269 amenorrhea), regardless of whether she was maximally swollen on that day. Thus, all
270 aggression rates controlled for dyadic association times, which are reported in Tables 2
271 and 3.

272 Male dominance ranks were assigned based on the direction of submissive
273 vocalizations (pant-grunts) and decided agonistic encounters among male dyads (Muller
274 & Wrangham 2004). Ordinal ranks (r) were assigned to each male on a yearly basis, and
275 these were standardized by the number of adult males in the hierarchy (n_M) using the
276 formula: $(n_M - r) / (n_M - 1)$. Each male was assigned a mean rank over the period of female
277 sexual cycling sampled, based on these standardized yearly ranks.

278

279 Ovarian cycle data

280 Observers used a simple scale to record the degree of tumescence of the sexual
281 swelling for each female in a party. Females with sexual skins that were completely flat
282 received scores of 1. Females with sexual skins that were partially inflated (i.e. soft
283 and/or wrinkled rather than tense and shiny) received scores of 2. Females with sexual
284 skins that were maximally tumescent (i.e. tense and shiny with no drooping) received
285 scores of 3. Estrous females were defined as having maximally tumescent swellings.
286 Nonestrous females were those with partial or flat swellings.

287 In wild chimpanzees, ovulation occurs within the period of maximal swelling
288 tumescence and, according to independent examinations of ovarian cycle profiles, is most
289 probable (>75%) between 2 and 5 days before the end of swelling, designated D-2 to D-5
290 if D0 is the first day of detumescence (Deschner et al. 2003; Emery Thompson 2005;
291 Emery Thompson & Wrangham 2008). Because mammalian sperm are predicted to
292 survive in the female reproductive tract for approximately 48-72 hours (Johnson and
293 Everitt, 1988; Royston, 1982; Wilcox et al. 1995), these models also assign a high
294 probability of fertile mating to cycle days D-6 and D-7. Thus, we define the probable
295 periovulatory period (POP) as days D-2 to D-7. Days of low fertilization potential (non-
296 POP) included the last day of sexual swelling when ovulation probability is low and
297 female attractiveness drops substantially (Emery Thompson & Wrangham 2008) and up
298 to 10 pre-POP days with maximal swelling tumescence. We excluded both cycles from
299 females known to be pregnant (from hCG testing or other hormonal data), and cycles for
300 which the first day of maximal swelling or the day of detumescence were not observed
301 (Emery Thompson 2005).

302 We limited our analyses to interactions between adult males (aged 15 years and

303 over) and parous females. Nulliparous female chimpanzees experience both a prolonged
304 period of subfecund cycling following menarche, and relatively high rates of neonatal
305 mortality (Roof et al. 2005, Brewer-Marsden et al. 2006). Consequently, males prefer
306 parous females as mates, and compete more intensely for access to them (Muller et al.
307 2006). Table 4 shows, for each female, the number of cycles sampled in both POP and
308 non-POP periods.

309

310 Female proceptivity

311 Chimpanzee copulations are normally initiated by a clear solicitation from either
312 the male or the female (Goodall 1986). Male courtship behaviour includes direct gaze,
313 branch shaking, bipedal swagger, knuckle-rapping, or outstretched arms, all accompanied
314 by penile erection. Female solicitations normally consist of a female approaching a male
315 and crouching with her sexual swelling toward him. Copulation was defined as mounting
316 with intromission and pelvic thrusting (Wrangham 2002). We have omitted cases where
317 observers could not determine who initiated the copulation. This produced a total of 996
318 copulations in non-pregnant cycles with known POP dates.

319 Following Stumpf and Boesch (2005) and Pieta (2008), we assigned each male to
320 one of three categories for each female, depending on whether he was generally solicited
321 by that female for copulation. “Approached” males were those whose average solicitation
322 rate by a female, during periods of maximal swelling, exceeded that female’s mean rate
323 of male solicitation by at least 25%. “Non-approached” males were those who fell below
324 a female’s mean solicitation rate by at least 25%. All other males were designated
325 “Neutral.” We favour these terms over Stumpf and Boesch’s “Preferred” and “Non-

326 preferred” males, because they describe behaviour without attributing motivation.
327 Proceptivity rates were calculated for each male-female dyad by dividing the number of
328 female-initiated POP copulations by the number of hours the pair were observed together
329 during the POP.

330 Previous chimpanzee studies have employed rates of “resistance” (defined as
331 ignoring a male solicitation or actively avoiding a copulation attempt) as an additional
332 measure of female choice (Stumpf & Boesch 2005, Pieta 2008). For three reasons we did
333 not incorporate resistance in the present study. First, Pieta’s (2008) data show that, at
334 Kanyawara, female proceptivity rates showed larger and more reliable changes during the
335 POP than did rates of resistance. Second, *active* female resistance of male copulatory
336 attempts (i.e. screaming at and fleeing from, struggling with, or striking a male) is rare
337 enough to be of questionable significance as an effective mode of female choice (4% at
338 Gombe: Goodall 1986; ~3% overall rate at Kanyawara: Kibale Chimpanzee Project,
339 unpublished data). In the current dataset (which is limited to fully adult males and non-
340 pregnant cycles) fewer than 1.2% of POP copulations were actively resisted by females
341 (n=5), making it impossible to establish meaningful patterns. Third, the operational
342 definition of resistance is problematic, with rates recorded by different observers varying
343 markedly within sites. At Tai, for example, Boesch & Boesch-Achermann (2000)
344 reported a rate of 8%, whereas Stumpf & Boesch (2005) reported 28%. Similar
345 differences are seen between resistance rates in the long-term data at Kanyawara, and
346 those reported by Pieta (2008). At Kanyawara, the lower rates reflect active resistance by
347 females. The higher rates reported by Pieta can only be generated by classifying females
348 who initially ignore a male’s solicitation as resistant, whether or not they later copulate

349 with him. As discussed previously, this assumption results in behaviors that may have
350 nothing to do with negative preference being classified as resistant (e.g. if a female delays
351 her positive response to a male's solicitation until the attention of a high-ranking male is
352 directed elsewhere).

353 Interpreting female resistance is further complicated by the fact that a female may
354 ignore or even flee from a male because she does not want to mate with him, but also out
355 of anxiety -- male solicitations frequently include moderately aggressive behaviours such
356 as branch shaking, foot stomping, and piloerection -- or from fear of another male nearby.
357 At Kanyawara we sometimes see females fleeing male copulatory approaches following
358 threats from nearby males. These observations are consistent with the hypothesis that
359 male coercion in this species functions to constrain female mating behavior (Muller et al.
360 2006). In practice, a female's motivation can be impossible to determine. This difficulty
361 may explain inconsistencies in prior choice studies, which reported some females having
362 both high proceptivity and high resistance rates to the same male (Stumpf & Boesch
363 2005, Pieta 2008).

364

365 Analyses

366 Dyadic rates of male-female aggression during cycling and rates of copulation
367 (both overall and female-initiated) during the periovulatory period (POP), were compared
368 for 8 females and 12 males using the Kr row-wise matrix partial correlation test
369 (Hemelrijk 1990). Because our data span multiple years, it was impossible for some
370 individuals in the dataset to interact (e.g., if a female had died before a male entered
371 adulthood). Consequently, there were missing values in our matrices (25% of 96 cells).

372 To deal with such values, we created a third matrix containing dummy variables -- zero
373 for non-missing values, and a constant for missing values (Hemelrijk 1990). The constant
374 was also added to missing values within the aggression and copulation matrices, and the
375 dummy matrix was then partialled out. Statistics were calculated using Matman 1.1
376 software (Noldus Information Technology, Wageningen, The Netherlands). Significance
377 of the correlation coefficient was estimated with 2,000 permutations.

378 All other statistical analyses were conducted using SPSS 16.0 (SPSS Inc., Chicago,
379 IL, U.S.A.) Comparisons between dependent groups employed the Wilcoxon signed-rank
380 test. All correlations report Kendall's rank correlation coefficient (τ). All statistical tests
381 are two tailed, and means are reported \pm s.e.

382

383 **Results**

384 Proceptivity rates varied across females. Average rates of female proceptivity
385 across the adult males ranged from 0.005 to 0.014 times per hour for all periods of
386 maximal swelling (mean: 0.01 ± 0.002). These figures are comparable to those reported
387 by Stumpf and Boesch (2005). On average, females initiated 28.4% of their copulations
388 with males (female range: 19.6 - 47.4%; $n=8$ parous females; $stdev=8.91$) whereas male
389 initiation accounted for, on average, 71.6% of copulations.

390 Patterns of female proceptivity during estrus are summarized in Table 5, which
391 shows *approached*, *non-approached* and *neutral* males for each female. The alpha male
392 (MS) is a conspicuous outlier in these data, as he was classified as *approached* for all of
393 the parous females in our sample. For ranks below alpha, there was no consistency
394 among females as to which males received high rates of proceptivity, and which went

395 unsolicited. Every male except the alpha was categorized as *non-approached* by at least
396 one female, and every male except the lowest-ranking individual was classified as
397 *approached* by at least one female. Figure 1 shows, for each male, the absolute number of
398 females for whom he was an *approached* or *non-approached* male. Neither of these
399 measures correlated with average male rank across the study period (Kendall correlation;
400 *approached*: $\tau=0.287$, $p=0.220$, $n=12$; *non-approached*: $\tau=-0.097$, $p=0.674$, $n=12$).

401 It was necessary to use mean male rank for statistical purposes, but it should be
402 noted that the lack of an association between male rank and approach preference cannot
403 be explained by male ranks changing over the study period (e.g. if a male interacted with
404 one estrous female while low-ranking and another while high-ranking). Our results were
405 similar for the subset of males ($n=6$) who remained high- (MS, BB), medium- (BF), or
406 low-ranking (YB, PG, SY) throughout the study period.

407 Counter to the predictions of hypotheses based on active female paternity
408 concentration, the alpha male (MS) showed no decrease in aggression toward estrous
409 females during the POP compared to pre-POP days of maximal swelling (Figure 2). On
410 average, parous females received aggression from the alpha male 0.0183 ± 0.009 times
411 per hour during the POP. This rate was marginally higher than that on non-POP days of
412 maximal swelling (0.0166 ± 0.004 times per hour), but the difference was not statistically
413 significant (Wilcoxon signed ranks test: $Z=-0.105$, $p=0.917$, $n=8$ parous females).

414 Similarly, individual *approached* males showed no difference in rates of
415 aggression, between POP and pre-POP days of maximal swelling, directed toward the
416 females who solicited copulations from them at high rates (Figure 2). On average, parous
417 females received aggression from their *approached* males 0.0102 ± 0.003 times per hour

418 during the POP. This was identical to the rate on non-POP days of maximal swelling
419 (0.0102 ± 0.003 times per hour; Wilcoxon signed ranks test: $Z=-0.14$, $p=0.889$, $n=8$
420 parous females).

421 Consistent with the coercion hypothesis, when females were most likely to
422 conceive (i.e. during the POP), they initiated copulations most frequently with the males
423 who were most aggressive toward them throughout periods of ovarian cycling. A matrix
424 partial correlation procedure (Hemelrijk 1990) revealed a significant positive association
425 between the amount of aggression directed by males at individual parous females during
426 all periods when they were cycling, and the number of times females approached those
427 males for copulation during the POP ($\tau_{rw; xy.z} = 0.37$, $p<0.001$, $n=8$ females, 12 males).
428 There was also a significant positive association between the amount of aggression
429 directed by males at individual cycling females and the number of times females
430 copulated with those males during the POP, regardless of who initiated the copulation
431 ($\tau_{rw; xy.z} = 0.32$, $p=0.001$, $n=8$ females, 12 males). There was no significant correlation
432 between the amount of aggression directed by males at individual cycling females during
433 the POP and the number of times females copulated with those males during the POP
434 ($\tau_{rw; xy.z} = 0.106$, $p=0.12$, $n=8$ females, 12 males).

435 As an additional test of the relationship between male aggression and female
436 proceptivity, we compared, for each of 8 parous females, periovulatory proceptivity rates
437 toward males who were aggressive toward the female at rates above and below the
438 median amount of male aggression received by her (Figure 3). As expected, individual
439 females solicited periovulatory copulations at significantly higher rates from the males
440 that were more aggressive toward them (0.013 ± 0.002 solicitations per hour), than those

441 who were less aggressive toward them (0.002 ± 0.001 solicitations per hour; Wilcoxon
442 signed rank test: $Z=-2.52$, $p=0.012$, $n=8$ females). Strikingly, half of the females in our
443 sample never solicited a periovulatory copulation from any of the males who directed less
444 than the median amount of aggression toward them.

445 Because the alpha male, MS, was both solicited by, and highly aggressive toward,
446 every female in our sample, we wanted to test whether female proceptive behavior
447 changed in his absence. If female promiscuity is constrained by male aggression, in the
448 form of coercive mate guarding, then females are expected to show higher rates of
449 proceptivity when MS is not in a party. Unfortunately, MS was rarely absent when parous
450 females were observed with full swellings. For the eight females in our sample, the mean
451 of mean dyadic association times with males in parties containing MS was 243 hours for
452 periods of maximal swelling. For parties without MS, this figure was only 12 hours. Out
453 of 88 potential adult male/estrous female dyads, 45 were *never* observed in the absence of
454 MS, and 31 were seen together for less than 8 hours. The remaining 13 dyads all included
455 either AL or NL (the two females with the largest sample of cycles), who were observed
456 with other males in MS's absence for an average of 70 hours per dyad. Looking at the
457 data from these females, a strong effect of the alpha's presence on mating behavior is
458 evident, for both male-initiated and female-initiated copulations. Consistent with the male
459 coercion hypothesis, individual males were solicited by AL and NL at significantly
460 higher rates in parties where MS was absent (0.039 ± 0.016 times per hour) than in
461 parties where he was present (0.007 ± 0.002 times per hour; Wilcoxon signed ranks test:
462 $Z=-2.366$, $p=0.018$, $n=8$ males; Figure 4). In turn, males solicited AL and NL at
463 significantly higher rates in parties without MS (0.317 ± 0.126 times per hour) than in

464 parties with him (0.006 ± 0.002 times per hour; Wilcoxon signed ranks test: $Z=-2.366$,
465 $p=0.018$; $n=8$ males).

466

467 **Discussion**

468 Our study is the first research on female choice in wild primates to rigorously test
469 for the confounding effects of male aggression on female behavior. Using a larger pool of
470 male mating partners than previous studies, and incorporating more female cycles, we
471 found that female copulatory approaches in chimpanzees are not consistent with
472 unfettered female choice, but instead appear constrained by persistent coercive aggression
473 from males. All the females in our sample showed elevated rates of periovulatory
474 proceptivity toward the alpha male (MS), who became dominant in 1997 and maintained
475 his position through the end of this study in 2006. Each female solicited between one and
476 five additional males at high rates during the POP. The identity of solicited males differed
477 by female, and male rank did not appear to be an important criterion for selection.

478 Although universal proceptivity toward the alpha male might ostensibly support a model
479 of female choice for good genes, and the idiosyncratic distribution of proceptivity toward
480 other males could fit with a model of choice for genetic compatibility, additional
481 observations favor the alternative hypothesis that patterns of female proceptivity
482 primarily reflect male sexual coercion (Wrangham & Muller 2009).

483 First, the males who were most aggressive toward individual females, not only
484 during periods of maximal swelling, but also in contexts not directly related to mating,
485 were the ones most frequently solicited by those females during the POP. This result
486 explains the systematic bias toward the alpha male since, compared to other males, he

487 showed high levels of aggression to all of the females in our sample (Muller et al. 2009a).
488 The present data cannot distinguish whether this bias occurs (1) because aggressive males
489 compel females to solicit them more than they would have otherwise, (2) because
490 aggressive males receive a higher relative share of solicitations by reducing the
491 probability that a female will solicit other males, or (3) both. However, the fact that
492 females increased their solicitation rates of all males in the absence of the most
493 aggressive male supports the occurrence of indirect coercion (i.e. coercive mate
494 guarding).

495 Second, patterns of female-directed aggression by the alpha male and other
496 *approached* males, during periods of maximal swelling, challenge the notion that females
497 are actively concentrating paternity. If, for example, females are eager to bias conceptions
498 toward the alpha male, and the alpha male is concerned with paternity certainty, then the
499 interests of the pair should be aligned during the POP. Consequently, the alpha male
500 should be less aggressive toward females as ovulation approaches, and the females
501 become more compliant, mating primarily with him. The fact that the alpha male at
502 Kanyawara continued to show high rates of female-directed aggression in periods
503 immediately preceding ovulation indicates a conflict of interest. The existence of such
504 conflict suggests that females were resistant to the alpha's mate-guarding efforts, and that
505 they were interested in mating with additional males. This interpretation is further
506 supported by the fact that females showed increased rates of male solicitation when the
507 alpha male was absent. A similar argument applies generally to *approached* males, who
508 also showed a steady rate of aggression throughout the period of maximal swelling
509 toward the females who solicited them most frequently.

510 Although it is possible that males may simply differ in their overall propensity for
511 aggression, and be incapable of modulating their behavior in response to female
512 compliance or resistance, this seems unlikely for two reasons. First, previous studies from
513 Kanyawara have shown that male aggression is elegantly tailored to context. Males are
514 more aggressive toward attractive, parous females than they are toward subfecund,
515 nulliparous females (Muller et al. 2007). Males aggressively interfere in copulations at
516 higher rates in the POP than the non-POP, and exhibit elevated rates of male-male
517 aggression in conceptive vs. nonconceptive cycles (Emery Thompson & Wrangham
518 2008). Finally, the alpha male, MS, is less likely to aggressively interfere in copulations
519 involving his male allies, than in those involving non-allies (Duffy et al. 2007). Thus, if
520 females are amenable to being mate-guarded by males, there is no reason to suppose that
521 males should not be capable of tempering their aggression in reply.

522 Second, with the exception of the alpha, no individual male in the study was
523 generally aggressive toward all parous females. Males showed variable rates of
524 aggression across potential mating partners, clearly singling out individual females for
525 special consideration. Why a male should focus his coercive efforts on a particular female
526 or females is not clear, but the fact that across male-female dyads, total copulation rates
527 during the POP and rates of male aggression during cycling were correlated, suggests that
528 the strategy is a successful one.

529 Although our data are consistent with the idea that male aggression limits female
530 promiscuity over the long-term, this idea is difficult to test directly. Evidence for such a
531 dynamic in hamadryas baboons is more straightforward, because male-female
532 relationships can be tracked from their inception, and it is clear that male aggression

533 decreases once females reliably maintain proximity and avoid other males (Swedell &
534 Schreier 2009). The current chimpanzee study followed ongoing, long-term relationships,
535 so there was no way to show a direct decrease of female promiscuity in response to male
536 aggression. However, the fact that females showed increased proceptivity in the absence
537 of the most aggressive male suggests a distinct dynamic from that of hamadryas, in which
538 females are resistant to male mate guarding. Future studies will examine the evidence for
539 coercive mate guarding more directly by tracking the development of specific male-
540 female relationships from adolescence.

541 Why should a female be resistant toward the mate-guarding efforts of a high-
542 ranking male like the alpha? One possibility is that the cost of acquiescence is high, if it
543 invites intense efforts from other males at direct sexual coercion in the form of
544 intimidation and harassment. Another is that the benefits provided by high-ranking males
545 are few. Male chimpanzees provide little or no direct paternal care. And because female
546 chimpanzees frequently travel alone or in small groups, they regularly encounter
547 potentially infanticidal males in the absence of the alpha (Clarke et al. 2009).
548 Consequently, even high-ranking males may not be able to offer reliable protection from
549 infanticide. The most likely potential benefit to females of biasing paternity toward high-
550 ranking males in fission-fusion species is therefore “good genes.” Whether such benefits
551 ever outweigh the risk of infanticide inherent in any attempt to actively concentrate
552 paternity in a single male is an open question.

553 Furthermore, females could conceivably gain the same genetic benefits under a
554 scenario of passive choice, whereby the “best-male” (Clutton-Brock & Harvey 1976)
555 emerges from the conclusion of male-male competition, mate guarding, and sperm-

556 competition. Evidence from our site supports the hypothesis that male chimpanzees both
557 detect and respond to changes in female conception risk without behavioral cues (for Tai
558 see Deschner et al. 2004), and that shifting mating dynamics over the cycle can be
559 accounted for primarily by shifts in the competitive investment and solicitation behavior
560 of high-ranking males (Emery Thompson 2005, Emery Thompson & Wrangham 2008).
561 Even at Tai, where female choice has been argued to be particularly important (Stumpf &
562 Boesch 2005, 2006), long-term paternity data show a precise fit with the predictions of
563 the priority-of-access model, which posits male dominance status as the primary
564 determinant of mating access (Boesch et al. 2006).

565 The assumption that female chimpanzees should subtly try to realize secret
566 preferences for chosen males makes sense from an anthropocentric perspective, given
567 that women express obvious preferences for certain men over others. However, there is
568 little evidence that chimpanzee females evince this type of mating psychology, or that it
569 would provide a clear evolutionary benefit if they did. If the result of male-male
570 competition for mates, sperm competition, and effective mate guarding were a reliable
571 indicator of male quality in chimpanzees, then attempts by females to thwart these
572 mechanisms via active mate choice would make little sense. And although females might
573 reinforce these mechanisms through active choice, such a strategy would appear not only
574 superfluous, but, in the face of persistent infanticide risk, dangerous. We do not suggest
575 that females are passive players in the chimpanzee mating game. Rather, we acknowledge
576 the possibility that female agency is directed primarily at maximizing offspring survival
577 through a strategy of paternity confusion, and that the evolved mating psychology of
578 female chimpanzees is profoundly different from that of human females.

579 The Kanyawara data are thus consistent with either of two conclusions: (1) active
580 female choice is absent, and females instead pursue a strategy of unbiased promiscuity to
581 confuse paternity; (2) female mate preferences exist but are constrained by male-male
582 competition and sexual coercion in this male-dominant species. The data do not support a
583 “mixed” strategy in which females attempt to concentrate paternity in preferred males.

584 Although our study was entirely observational, our results are consistent with the
585 one experimental study conducted on a promiscuous primate (*Macaca fascicularis*) that
586 gave females complete control over access to males, thus reducing the potential for male
587 coercion (Nikitopolous et al. 2005). In that study, no effect of cycle phase on female
588 preferences was evident, as females apportioned their mating choices to spread
589 copulations evenly across all the males in their social group. In wild studies female
590 preferences are not so easily isolated from the effects of male aggression. Because such
591 aggression is widespread in primates (Muller & Wrangham 2009) and other mammals
592 (Clutton-Brock & Parker 1995), the potential for male coercion must be taken into
593 account before mating preferences can be inferred from female behavior.

594

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