



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

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2 **Sexual coercion by male chimpanzees shows that female choice may be more**
3 **apparent than real**
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9 Martin N. Muller^{1,*}, Melissa Emery Thompson¹, Sonya M. Kahlenberg²
10 & Richard W. Wrangham³
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16 ¹Department of Anthropology, University of New Mexico, MSC 1040-01, Albuquerque,
17 New Mexico 87131, USA

18 ²Department of Biology, Bates College, Lewiston, Maine 04240, USA

19 ³Department of Human Evolutionary Biology, Harvard University, Cambridge,
20 Massachusetts 02138, USA
21

22 **To whom correspondence should be addressed. E-mail: muller@unm.edu*

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.

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47 **Key Words**

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

49 mating strategy

Introduction

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

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

Given these problems, the extent and nature of female choice in promiscuously mating primates is uncertain. However, there has been considerable interest in the idea that a promiscuous strategy predominates only in the early follicular phase, when 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 *troglydites*) (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 Taï 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 Taï, 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 Taï, 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

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

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

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

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

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

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

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

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

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

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

Methods

Study population and long-term data

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

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

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

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

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

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

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

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

Ovarian cycle data

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

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

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

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

Female proceptivity

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

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

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

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

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

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

Analyses

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

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

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

Results

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

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

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

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

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

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

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

Consistent with the coercion hypothesis, when females were most likely to conceive (i.e. during the POP), they initiated copulations most frequently with the males who were most aggressive toward them throughout periods of ovarian cycling. A matrix partial correlation procedure (Hemelrijk 1990) revealed a significant positive association between the amount of aggression directed by males at individual parous females during all periods when they were cycling, and the number of times females approached those males for copulation during the POP ($\tau_{rw; xy.z} = 0.37$, $p<0.001$, $n=8$ females, 12 males).

There was also a significant positive association between the amount of aggression directed by males at individual cycling females and the number of times females copulated with those males during the POP, regardless of who initiated the copulation ($\tau_{rw; xy.z} = 0.32$, $p=0.001$, $n=8$ females, 12 males). There was no significant correlation between the amount of aggression directed by males at individual cycling females during the POP and the number of times females copulated with those males during the POP ($\tau_{rw; xy.z} = 0.106$, $p=0.12$, $n=8$ females, 12 males).

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

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

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

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

Discussion

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

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

First, the males who were most aggressive toward individual females, not only during periods of maximal swelling, but also in contexts not directly related to mating, were the ones most frequently solicited by those females during the POP. This result 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.

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

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

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

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

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

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

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

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

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

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

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