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Sexual coercion and courtship by male western gorillas

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Abstract Sexual coercion and courtship are possible explanations for why male primates may direct agonistic behavior towards females. If so, then in species where females exhibit mate choice by transferring between males: (a) females who are not lactating (potential migrants) should receive more agonistic behavior than other females, (b) males should exhibit more agonistic behavior towards females during intergroup encounters than when no rival males are nearby, and (c) males should show more herding behavior when their group contains potential migrant females. We tested those hypotheses in a population of approximately 150 western gorillas at Mbeli Bai, northern Congo. We also tested whether difference in male phenotypic traits influenced their rates of agonistic behavior towards females. Of the 332 observed cases of male agonistic behavior towards females, 29 % represented feeding competition, 7 % involved interventions in conflicts between females, and the remaining 64 % were considered potential evidence of sexual coercion and/or courtship. After excluding the cases of feeding competition and intervention, a multivariate analysis indicated that potential migrant females received agonistic behavior at a statistically significantly higher rate than other adult females.

Females also received agonistic behavior at a significantly higher rate during intergroup encounters than at other times. Herding occurred during 22 % of the 292 dyadic interunit encounters, and was significantly more likely to occur when the group contained a potential migrant female, but was not influenced by the number of adult females or the type of group encountered. Males with shorter body lengths had significantly higher rates of aggression, but phenotypic traits were not significantly correlated with herding. Collectively, our results are consistent with sexual coercion and/or courtship as an explanation for male-to-female agonistic behavior, but we are unable to distinguish between those two male mating strategies. Both types of behavior are likely due to a combination of perceived risks of female transfer and opportunity to advertise protector ability.

Keywords Agonistic behavior · Courtship · *Gorilla gorilla gorilla* · Herding · Intergroup encounter · Mate competition · Sexual coercion

Introduction

Males direct agonistic behavior towards females in many primate species including humans (Smuts and Smuts 1993; Clutton-Brock and Parker 1995; van Schaik et al. 2004; Muller et al. 2007, 2009). Such behavior can include displacements, aggressive vocalizations, displays, and physical aggression. In sexually dimorphic species, males are often larger than females and are dominant over them. Such dominance behavior can be seen in the feeding context, where males use agonistic acts such as displacements towards females to gain access to high-value food resources. Males also may use agonistic behavior as an

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intervention and policing strategy to curtail conflicts among females, which ultimately can contribute to mate retention (Watts 1997; Kahlenberg et al. 2008). Conflicts among females may increase as group size increases due to greater contest competition (e.g., Sterck et al. 1997), so agonistic behavior by males towards females as an intervention strategy may also increase accordingly.

In addition to feeding competition and policing, male agonistic behavior towards females can be seen as a mating strategy of courtship, sexual coercion, or a combination of both (Smuts and Smuts 1993; Clutton-Brock and Parker 1995; Robbins 2003, 2009; Muller et al. 2009). Courtship is defined as "a behavior that functions to advertise qualities of the courting individual and/or induce prospective partners to copulate" (Manson 1997). Hence, courtship allows males to demonstrate their qualities and facilitates female mate choice. Courtship is assumed to rarely cause physical injuries to the female (Knott 2009; Liu et al. 2013). Sexual coercion is defined as "the use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female" (Smuts and Smuts 1993). The costs of sexual coercion can include physiological and energetic costs, physical injuries, or in the extreme case infanticide (Alberts et al. 1996; Palombit 2000; Swedell et al. 2014; Polo et al. 2014; Archie et al. 2014; Emery Thompson et al. 2014). Coercion towards females can therefore be seen as a form of harassment and intimidation. If male agonistic behavior is used as either a mating strategy of courtship or coercion, then it may be directed towards sexually active females more often than towards lactating females (Muller et al. 2007; Kitchen et al. 2009; Swedell and Schreier 2009). Furthermore, assuming interunit encounters are a time to implement mate retention strategies, the rate of male agonistic behavior towards females may increase during encounters with another social unit.

In primate species where females disperse, male agonism can include a behavior known as herding, in which a male prevents female(s) from joining other males during encounters with his competitors. Herding can include instances with agonistic behavior such as chasing female away from the extragroup males as well as behaviors without obvious agonism by positioning himself between the female(s) and the other social unit and hence blocking their movements (Cheney and Seyfarth 1977; Kummer 1995; Cooper et al. 2004; Kitchen et al. 2004; Robbins and Sawyer 2007). Additionally, herding is expected to be directed towards potential migrants more often than towards other females. We define potential migrants as females without a dependent offspring (Sicotte 1993), because females do not typically transfer while lactating

due to the threat of infanticide (Watts 1989; van Schaik and Kappeler 1997; Stokes et al. 2003).

The behavioral strategies of sexual coercion and courtship by primate males may vary according to their resource-holding potential, which would be similar to the plasticity that has been reported for strategies related to male–male mating competition (Jones 2006; Svensson et al. 2012). If so, then the amount of aggression that a male directs towards females may depend on the size of some physical traits; For example, males that have less fighting ability (smaller males) might compensate by showing higher rates of courtship and coercion towards the females in their harem. Therefore, investigating the rates of male aggression towards females in relation to measures of male phenotypic traits might help to elucidate the mechanism underlying the evolution of phenotypic correlates of reproductive success and hence sexual selection (Gross 1996).

Here, we investigate the patterns of agonistic behavior, including herding, by male western gorillas (*Gorilla gorilla gorilla*) towards the females in their group. Western gorilla groups typically consist of one adult male (silverback), several adult females and their offspring (Parnell 2002a; Stokes et al. 2003; Gatti et al. 2004). Male reproductive success is linked to harem size, tenure length, and offspring survival (Breuer et al. 2010), and extragroup paternity is likely to be absent or very low (Bradley et al. 2004). Silverbacks are about twice the size of adult females, which is considered evidence of strong sexual selection (Leigh and Shea 1995; Breuer et al. 2007). Silverbacks show variation in sexually dimorphic traits such as body length and the size of the sagittal crest, which have statistically significant correlations with fighting ability and reproductive success (Caillaud et al. 2008; Breuer et al. 2012). These physical traits are regularly displayed in all three contexts of sexual selection: male–male competition, female mate choice (e.g., courtship displays), and sexual coercion (e.g., intimidating females as mate guarding) (Schaller 1963; Parnell 2002b; Levréro 2005; Breuer 2008).

Agonistic behavior by male gorillas towards females can involve many different types of actions; it can occur in a variety of contexts; and it can reflect several different behavioral strategies and typically includes approach–retreat displacements, vocalizations, displays, and physical aggression (Robbins 2009). Displays can include chest beating, ground slapping, splash displaying, and head turning; contact aggression includes slapping, biting, and pinning down the female on the ground (Schaller 1963; Parnell and Buchanan-Smith 2001; Sicotte 2002; Parnell 2002b; Breuer 2008). Some agonistic acts represent feeding competition, as silverbacks may displace females from feeding spots (Watts 1992; Stokes 2004; Robbins 2008). Male agonism can also act as a policing behavior to reduce

conflicts among the females in his group, including harassment by long-term resident females towards recent immigrants (Watts 1991, 1992, 1997). However, the majority of agonistic behavior by males towards females appears to be linked to male mating strategies (Watts 1992; Sicotte 2002; Robbins 2003; Harcourt and Stewart 2007; Robbins 2008, 2009); For example, female mountain gorillas (*Gorilla beringei beringei*) receive higher rates of agonistic behavior from silverbacks on days when they mate compared with days without mating; and this is more frequently directed towards cycling (sexually active) females than towards lactating females (Robbins 2003, 2009). Infanticide, the most extreme case of sexual coercion, has been observed in mountain gorillas and has been suspected for western gorillas (Watts 1989; Stokes et al. 2003; Robbins et al. 2013). However, evidence of sexual coercion and courtship by male western gorillas is currently limited.

Female gorillas do not travel alone, and they transfer between social units only during encounters with other silverbacks, so those encounters can be seen as a context where all three mechanisms of sexual selection occur (Sicotte 1993; Parnell 2002b; Levréro 2005; Harcourt and Stewart 2007; Robbins and Sawyer 2007). During those encounters, silverbacks frequently display and show herding behavior, especially when their group contains potential migrant females (ibid). It is also likely that herding might not only be a mate retention, but also a mate protection strategy, hence once would expect herding behavior to be more common in groups with more females. Furthermore, it has been suggested that herding is also more likely to occur when a group encounters solitary males (rather than another harem holder), as they may be more motivated to compete for access to females (Levréro 2005; Robbins and Sawyer 2007).

To better understand male agonistic behavior towards females in western gorillas, we tested several predictions. First, we predicted that feeding competition and policing will account for only a small proportion of the agonistic behavior from silverbacks towards females (as observed with mountain gorillas). After excluding those contexts, we predicted that the remaining agonistic behavior is primarily a mating strategy, so it should mainly be directed towards potential migrant females (instead of lactating females), and that the rate of agonism increases during encounters with another social unit (hence in the presence of rival males). Third, we predicted that herding is more common in groups that contain potential migrants and occurs more frequently as group size increases. Fourth, we predicted that herding is more likely during encounters with solitary males than during encounters with silverbacks holding a group. We also investigate the effect of female group size on agonistic behavior rates and herding. Lastly, we

predicted that rates of agonistic behavior towards females will be higher for males with smaller crests and shorter body lengths than for larger males. We use those results to discuss sexual coercion and courtship by male gorillas and other primates.

Methods

Study site and population

We studied western gorillas between November 2002 and December 2005 at Mbeli Bai, a 12.9-ha large swampy forest clearing in the southwest of Nouabalé-Ndoki National Park, Republic of Congo. Observations were made with 15–45 × 60 mm telescopes from a 9-m-high observation platform (mirador) overlooking the forest clearing with almost 100 % visibility. Gorillas have been habituated to the presence of observers on the mirador and were individually known since 1995 by features, such as the shape of their browridge, noseprint or coloration (Parnell 2002b; Stokes et al. 2003; Breuer et al. 2009, 2010). During the study period, the forest clearing was visited by approximately 150 gorillas from 17 different groups. Age–sex categories were based on Breuer et al. (2009), with offspring considered to be dependent (infants) until weaning at 4 years of age, and females considered as adults at 10 years of age. Potential migrants were defined as females without dependent offspring (Sicotte 1993; Robbins and Sawyer 2007). This definition included pregnant females and sexually active (cycling) females. Females were assumed to be pregnant during an estimated gestation period of 255 days prior to giving birth (Robbins 1999). Sexually active females were defined as either nulliparous or being without dependent offspring. Female group size was defined as number of adult females in the harem.

Data collection

We noted the time that each individual gorilla was visible in the clearing and all agonistic acts of silverbacks towards females in their group. Agonistic acts by the silverback included approach–retreat displacements, cough grunts (an aggressive vocalization), displays, contact aggression, and cases when a silverback slapped at a female without making physical contact. Based on Watts (1994), a displacement is defined as when the silverback made a nonaggressive approach towards a female, who watched the silverback and, when he was within two meters, moved more than two meters farther away. When ranked in order of increasing intensity, the types of male agonistic behavior towards females were: (a) displays: staring with a pursed-lipped facial expression, head turning, strutting, charging,

chest beating, ground slapping, and splash displaying; (b) slapping and lunging; (c) physical aggression (Schaller 1963; Parnell and Buchanan-Smith 2001; Parnell 2002b; Sicotte 2002; Levréro 2005). When a silverback showed multiple displays towards a female during a single display event (e.g., chest beating followed by a tight-lipped stiff-limbed body expression), we counted only one act with the highest intensity (see also Stokes 2004). We excluded 54 cases of agonistic behavior when it was not clear which female was the target of the display.

We categorized the agonistic acts into three contexts (see also Watts 1992; Stokes 2004). The feeding context includes displacements in which the silverback typically started feeding where the female had been located. The intervention context includes all agonistic behavior by the silverback as a reaction to a conflict between females. Cough grunting vocalizations were included as agonism in both feeding competition and interventions (they were never observed to occur in another context). The remaining aggressive acts were hypothesized to be a male mating strategy in a reproductive context.

We defined interunit interactions as any event when two social units (groups or solitary males) were in the clearing at the same time. During interunit encounters we noted all events of herding, the identities of involved individuals, the type of group encountered (solitary male, harem holder, or nonbreeding group without fertile females), and the behaviors exhibited. We defined herding as any agonistic behavior by a silverback towards at least one of his females during an encounter with another social unit. This included instances in which the silverback positioned himself between the female(s) and the other social unit which clearly forced his female(s) away from the other social unit.

Measures of body length and crest size

We used photogrammetric measurements of body length and crest size as reported in Breuer et al. (2007). The digital photos were taken of the side profile of the silverbacks, and the distance to the gorillas was measured with a laser range finder. We used rump length as a measure of body length. Crest size was calculated as the first component of a principal component analysis based on six linear measures of the head.

Rates of aggression received by females

After excluding cases of feeding competition and intervention strategy, we tested whether the remaining aggressive acts were consistent with our classification as a male mating strategy. We calculated the rate of aggression of each silverback–female dyad as the number of aggressive acts divided by the length of observation time that the

silverback and the female were in the *bai* simultaneously. To avoid excessive influence from dyads with infrequent observations, the mean and standard deviation were weighted according to the amount of time that each female was observed with the silverback.

We performed a multivariate analysis to test the predictions that potential migrant females receive higher rates of aggression than lactating females, and that rates were higher when encountering another unit compared with visits without the presence of another unit. We ran a generalized linear mixed model (GLMM) which included the following predictor variables: whether the female was a potential migrant (no = 0, yes = 1), whether the group was encountering another silverback (yes or no), and the number of adult females in the group. The model also included random effects variables for the identity of each female and the silverback in her group. The model used one data point for each observed combination of those predictor and random effect variables. The response variable was the number of aggressive acts received by the female. The model also included a control variable for the (log-transformed) number of minutes that the dyad was observed (essentially an offset term). Rather than using the aggression rate directly as the response variable, our offset approach was intended to avoid excessive influence from data points with few observation hours.

Rates of aggression performed by silverbacks

The rate of aggression performed by each silverback was calculated as the number of aggressive events divided by the length of observation time that the silverback was seen in the clearing. To avoid excessive influence from males with infrequent observations, the mean and standard deviation were weighted according to the amount of time that each silverback was observed.

We ran a GLMM to test whether the rates of aggression performed by silverbacks were higher when potential migrant females were present and whether other rival males were present (during interunit encounters). The model included the following predictor variables: the proportion of adult females who were potential migrants, whether the group was encountering another silverback (yes or no), and the number of adult females in the group. The identity of each silverback was a random factor. The response variable was the number of aggressive acts performed by the silverback, and we followed a similar transformation as in the first model. The model also included a control variable for the (log-transformed) number of minutes that the silverback was observed (essentially an offset term).

We ran two additional GLMM to test the prediction that smaller males show higher rates of aggression towards

females in their group. As we did not have measurements of phenotypic traits for all silverbacks, we used subsets of data in which body length ($n = 10$ harem holders; $n = 17$ opponent silverbacks) or crest size ($n = 9$ harem holders; $n = 17$ opponent silverbacks) was available. We ran two separate models (rather than incorporating both variables into a single model) because both measurements were not available for each silverback. Each model was similar to the previous model of aggression rates per silverback, except that we added a predictor variable for one of the body size measurements.

Frequency of herding performed by silverbacks

We performed a multivariate analysis to examine the probability that the silverback herded a female during an encounter with another male. The GLMM included three predictor variables: whether the group contained a potential migrant female (yes or no), the number of adult females in the group, and the type of group encountered (solitary male, harem, or nonbreeding group). The model also included one random effect variable for the identity of the silverback in the focal group, and another random effect variable for the identity of the silverback that was encountered. The model used one data point for each observed encounter, with a control variable for the number of minutes observed. The response variable indicated whether herding occurred (no = 0, yes = 1), so the model was fit with a binomial error structure and logit link.

In the subset of data in which body size measurements were available, we ran two additional models to examine whether the probability of herding by each silverback was correlated with: (1) the difference between his body length versus the male he encountered, and (2) the difference between his crest size versus the male he encountered. Each model was similar to the previous model of herding frequencies, except that we added a predictor variable for one of the body size measurements. Again, we ran two separate models (rather than incorporating both variables into a single model) because both measurements were not available for each silverback.

Statistical analyses

Unless otherwise stated, we ran the GLMM with a Poisson error structure and a log link function. To assess the statistical significance of each predictor variable, we conducted likelihood ratio tests by comparing the full model with a reduced model in which the predictor was excluded. We also compared each full model with a corresponding null model that contained none of the predictor variables. Throughout the text, the term "significant" refers to statistical significance ($p < 0.05$). All models were run in R

(R Development Core Team 2011) using the glmer functions of the R-package lme4 (Bates et al. 2014).

Results

We recorded 332 cases of agonistic behavior by silverbacks towards females, including 96 cases in a feeding context (29 %), 22 cases of intervening in female conflicts (7 %), and 214 cases that were hypothesized to be a male mating strategy in a reproductive context (64 %). The feeding context included 84 approach–retreat displacements (25 % of all agonistic acts) and 12 cases of cough grunting (4 %). Interventions included four cases of cough grunting (1 %) and 18 cases in which the silverback ran towards the fighting females, sometimes slapping at female(s) or using physical aggression to separate them. Potential migrant females were the target in 176 of the 214 cases within a reproductive context (82 %), which is significantly higher than the 33 of 118 (28 %) cases in other contexts (Fisher exact test, $p < 0.001$).

Of the 214 cases that were hypothesized to be in a reproductive context, 197 cases were displays (92 %), ten cases involved contact aggression (5 %), and in seven cases (3 %) the silverback slapped at a female without physical contact. Seven of those ten cases of contact aggression occurred during interunit interactions. In two cases we noticed wounds after a silverback jumped on a female, pinned her to the ground, and bit her on the neck. We noted 63 cases of herding during 292 dyadic interunit encounters. We next investigate the factors influencing rates of aggression in the reproductive context only.

Rates of aggression received by females in reproductive context

Among the 40 females observed in this study, the average rate of aggression received was 0.07 ± 0.10 acts per hour. A multivariate analysis indicated that potential migrants received aggression at a significantly higher rate than other adult females (Table 1; Fig. 1). Females received aggression at a significantly higher rate when the group encountered another silverback (versus when no other silverback was present). The rate of aggression received by females also had a significant negative correlation with group size, which suggests that females in larger groups receive less aggression (Table 1).

Rates of aggression performed by silverbacks in reproductive context

The average rate of aggression performed by the 12 silverbacks was 0.24 ± 0.30 acts per hour. The rate of

Table 1 Results of a multivariate generalized linear mixed model for the rate of male aggression received by each female versus the number of minutes she was observed (log transformed), her reproductive status (potential migrant versus other), whether her group encountered another silverback, and the number of females in her group

	Estimate	Standard error	z-Value	p-Value
Intercept	−4.45	0.87	−5.1	
Minutes observed	0.51	0.10	5.1	
Potential migrant	1.91	0.22	8.9	<0.001
Encounter	0.84	0.15	5.5	<0.001
Group size	−0.36	0.10	−3.5	<0.001

Table 2 Results of a multivariate generalized linear mixed model for the rate of male aggression performed by each silverback versus the number of minutes he was observed (log transformed), the proportion of his females who were potential migrants, whether his group encountered another silverback, and the number of adult females in his group

	Estimate	Standard error	z-Value	p-Value
Intercept	−4.48	1.11	−4.0	
Minutes observed	0.33	0.12	2.7	
Potential migrants	3.23	0.62	5.2	<0.001
Encounter	0.85	0.16	5.5	<0.001
Group size	0.36	0.22	1.6	0.10

Fig. 1 Rate of male aggression received per female versus their reproductive status (non-PMF = lactating female; PMF = potential migrant female), depending on whether their group was encountering another silverback (*grey bars*) or not (*white bars*)
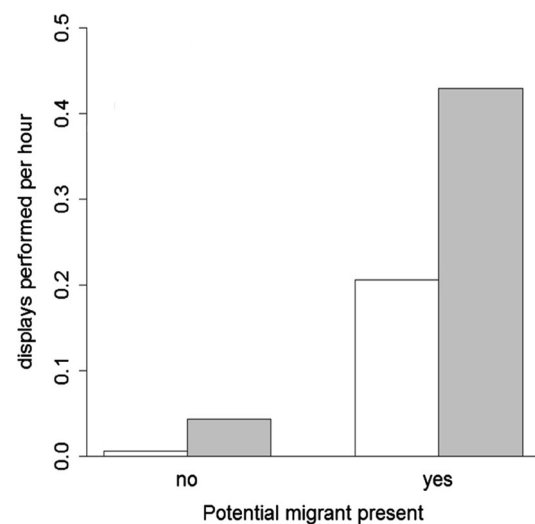

Fig. 2 Rate of male aggression performed by each silverback, depending on whether his group contained at least one potential migrant female present or not, and whether his group was encountering another silverback (*grey bars*) or not (*white bars*)

aggression performed per silverback had a significant positive correlation with the proportion of his adult females who were potential migrants, and the aggression occurred at a significantly higher rate during interunit encounters than other contexts (Table 2; Fig. 2). The rate of aggression was not significantly correlated with the number of adult females in the group (Table 2).

To further examine if the significantly higher rate of aggression during interunit encounters was influenced by whether the other silverback had a breeding group or was solitary, we ran a post hoc test that controlled for group size and the proportion of adult females who were potential migrants, with random effect variables for the identity of each silverback involved. Silverbacks performed 0.35 aggressive acts per hour towards their females during encounters with another harem holder group, which is not significantly different than 0.20 during encounters with a solitary male or a nonbreeding group (coefficient = 0.17,

$\chi^2 = 0.6$, $df = 1$, $p = 0.43$). Thus, we found no significant evidence that aggression rates depend on the type of social unit encountered.

In the subset of data in which body size measurements were available, the rate of aggression performed by silverbacks had a significant negative correlation with their body length, which suggests that smaller males were more aggressive (coefficient = −0.24, $\chi^2 = 5.8$, $df = 1$, $p = 0.016$). The rate of aggression performed by silverbacks was not significantly correlated with their crest size (coefficient = 0.79, $\chi^2 = 1.8$, $df = 1$, $p = 0.185$). Thus, we found mixed results regarding whether aggression rates are correlated with body size measurements.

Frequency of herding performed by silverbacks

The full multivariate model for herding frequency was significantly better than the null model with all three

predictors removed (presence of potential migrants, the number of females in the group, and the type of unit encountered), but only one of these predictors was significant when evaluated separately (the presence of potential migrants; Table 3). Herding occurred during 56 of the 177 encounters when the group contained a potential migrant (32 %), which was significantly higher than the 7 of 115 encounters (6.1 %) when the group did not contain a potential migrant ($\chi^2 = 7.2$; $df = 1$; $p = 0.007$). The probability of herding was not significantly related to the total number of adult females in the group nor to the type of unit encountered (Table 3).

In the subset of data in which body size measurements were available, the frequency of herding performed by each silverback was not significantly correlated with the difference between his body length versus the male he encountered ($\chi^2 = 0.88$; $df = 1$; $p = 0.35$), nor the difference in crest size ($\chi^2 < 0.21$; $df = 1$; $p = 0.65$). Thus, we found no significant evidence that the frequency of herding is correlated with body size measurements.

Discussion

Although agonistic behavior by males towards females can serve several functions, our results agree with previous studies on gorillas which suggest that the majority of such behavior occurs as a mating strategy (Watts 1992; Stokes 2004; Robbins 2008). After excluding the cases of feeding competition and intervening or policing of female conflicts, we found significantly higher rates of agonistic behavior towards potential migrants than other females, significantly higher rates of agonistic behavior during interunit encounters than other contexts, and significantly greater occurrence of herding when the group contained a potential migrant. Thus, our study suggests that, in the one-male

Table 3 Results of a multivariate generalized linear mixed model of the probability that a silverback performed herding during an encounter with another male

	Estimate	Standard error	z-Value	p-Value
Intercept	−3.354	0.74	−4.37	
Minutes observed	0.295	0.16	1.86	
Potential migrant	1.378	0.53	2.61	0.007
Number of females	0.089	0.15	0.67	0.547
Nonbreeding group	−0.256	0.79	−0.36	0.373
Solitary silverback	−0.544	0.42	−1.30	0.373

Predictor variables indicated whether the group contains a potential migrant, the number of females in the group, and the type of unit encountered (breeding group versus nonbreeding group or solitary male). The length of the observations was a control variable

harem system in western gorillas, male agonistic behavior towards females serves as a reproductive strategy in both the presence and absence of rival (extragroup) males. As discussed below, male agonistic behavior (including herding) is seen as both a short-term and long-term strategy to enhance male reproductive success in a variety of ways.

Male-to-female feeding competition and male interventions in female conflicts

Approximately one-third of agonistic behavior by males towards females was related to feeding competition (displacements and cough grunts). A previous study at Mbeli Bai concluded that around 50 % of male agonistic acts towards females were approach–retreat interactions in the feeding context (Stokes 2004), but the author excluded observations when more than one group was present in the clearing, so the study may have underestimated the contribution of male displays towards females as a mating strategy (Watts 1992; Robbins 2008). Additionally both Stokes (2004) and the current study focused on behavior in a *bai* where the vegetation is abundant and evenly distributed, so contest competition may be higher when gorillas feed at high-quality monopolizable fruiting trees in the surrounding forest (Doran and McNeilage 2001).

Less that 10 % of the agonistic behavior by males towards females was related to interventions in conflicts among the females. Such interventions were also rare in previous studies of western and mountain gorillas (Watts 1992; Stokes 2004). Conflicts among female gorillas can include competition for both food and proximity to the dominant male (Watts 1994). As both western and mountain gorillas indeed show higher contest competition over fruit (Robbins 2008; Lodwick 2014), it is likely that male intervention rates are also higher in the surrounding forest. To compare levels of male agonistic behavior towards females in different contexts and environments, we suggest initiating studies with habituated groups to provide a complete picture of male-to-female agonistic behavior in western gorillas.

Herding and male-to-female agonistic behavior in reproductive context

After excluding the cases that were due to feeding competition or intervention in female conflicts, we found that rates of male agonistic behavior towards females were significantly higher during interunit encounters than other times in the *bai*. Female gorillas transfer only during interunit encounters, so males may show heightened agonistic behavior towards potential migrant females of their own group as a mate guarding strategy.

Potential migrant females received significantly higher rates of agonistic behavior than females with dependent offspring, providing support for the coercion/courtship hypothesis. In mountain gorillas, cycling and pregnant females also receive significantly higher amounts of male agonistic behavior than lactating females (Robbins 2009). The results are consistent with findings from other primates that showed heightened rates of agonistic behavior during periods of increased mating activity (Kitchen et al. 2009; Swedell and Schreier 2009). We also found evidence of increased herding behavior within groups that contain potential migrant females, supporting the mate retention hypothesis.

We did not find a significant effect of the group type encountered on the rates of male-to-female agonistic behavior or the occurrence of herding. In contrast, a previous *bai* study showed significantly more herding during encounters with another breeding group than with a solitary male (Levréro 2005). Conversely, studies of mountain gorillas have shown increased agonistic and herding behavior when encountering a solitary male compared with breeding groups (Sicotte 1993; Robbins and Sawyer 2007). Comparisons among studies should be considered tentative, not only due to differences in the definition of herding, but also because the observations of encounters differ between *bai* studies versus habituated groups. Analyses that control for the age of the silverback would be useful because the competitiveness of solitary males may vary depending on whether they are young males who have not yet acquired a group or if they have lost all females in their harem and are at the end of their reproductive tenure (Breuer unpublished results). Such a life history approach towards investigating male–male competition might confirm findings from other studies that have shown that younger males often exhibit more agonistic behavior than older ones (Swedell and Schreier 2009). Finally, we could not find an effect of the number of adult females (both potential migrants and lactating females) in a group on the occurrence of herding behavior. Thus, as herding is mainly directed towards potential migrant females, it appears to act as a mate retention strategy rather than a protective strategy against infanticide as it does not seem to be targeted towards females with dependent infants.

Mechanisms of sexual selection in gorillas

Male agonistic behavior is often used in a variety of different contexts (Berglund et al. 1996). It may be used in male–male combat to intimidate and assess rivals, in courtship (to attract mates), or as sexual coercive strategies (Snowdon 2004; Teichroeb and Sicotte 2010). Similar to other sexually dimorphic primates (Kitchen et al. 2009), it appears that in gorillas many behaviors directed to mates

are also used towards rivals, suggesting that several mechanisms of sexual selection work in concert. In gorillas, threat displays that indicate fighting ability, health, and vigor to rivals can simultaneously be assessed by group females and extragroup females during intergroup encounters, particularly if they are related to protective ability (Breuer et al. 2012). Similarly, such behavior serves dual interests of the males: attract females, while at the same time protect mates and dissuade them from seeking another male. The relative role of each of those mechanisms remains difficult to assess as they often work in concert and their effects are diluted by different counterstrategies.

The rate of aggression performed by silverbacks had a significant negative correlation with their body length, which suggests that smaller males were more aggressive. Previous studies have indicated that smaller males have poorer fighting ability and lower reproductive success (Caillaud et al. 2008; Breuer et al. 2012), so they may try to compensate through greater courtship and/or coercion of their females. Such a conclusion should be considered tentative, however, because results for body size measurements were not significant in our other three analyses of aggression and herding. Thus, we found mixed results regarding whether courtship behavior or sexual coercion are influenced by the size of sexually dimorphic traits, even though such traits are believed to arise from sexual selection (Plavcan 2001; Lindenfors et al. 2007). Taken at face value, the nonsignificant results might suggest that sexual selection for such traits is more strongly influenced by male mating competition, rather than by female mate choice or sexual coercion. Such a conclusion could be complicated because female mate choice likely depends on the performance of males during intrasexual competition, such as their defense of offspring (Sicotte 2001; Harcourt and Stewart 2007).

In sum, our results indicate that male western gorillas use agonistic behavior as a strategy primarily targeting potential migrant females, particularly during periods of increased transfer risk. As with many studies, however, we could not measure any fitness costs to the female, so it was not possible to investigate whether the agonistic behavior occurs as a courtship behavior, or as a sexually coercive strategy, or both (Robbins 2009). As seen in previous studies of gorillas, agonistic behavior most often takes the form of displays, and physical aggression resulting in wounds is rare (Watts 1992; Stokes 2004; Levréro 2005; Harcourt and Stewart 2007; Robbins 2009). Although some physical aggression by males resulted in females being wounded, it was impossible to measure the exact impact of these wounds or to assess stress levels of females (MacCormick et al. 2012), as collecting fecal samples in the swampy environment of Mbeli Bai is extremely challenging. Regardless, sexual coercion

and courtship are both likely due to a combination of perceived risks of female transfer and opportunity to advertise protector ability.

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