

# Male coercion and the costs of promiscuous mating for female chimpanzees

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For reasons that are not yet clear, male aggression against females occurs frequently among primates with promiscuous mating systems. Here, we test the sexual coercion hypothesis that male aggression functions to constrain female mate choice. We use 10 years of behavioural and endocrine data from a community of wild chimpanzees (*Pan troglodytes schweinfurthii*) to show that sexual coercion is the probable primary function of male aggression against females. Specifically, we show that male aggression is targeted towards the most fecund females, is associated with high male mating success and is costly for the victims. Such aggression can be viewed as a counter-strategy to female attempts at paternity confusion, and a cost of multi-male mating.

**Keywords:** chimpanzee; sexual coercion; intersexual aggression; promiscuous mating; sexual selection; stress physiology

## 1. INTRODUCTION

Females in many mammalian species mate promiscuously, actively soliciting copulations from multiple partners (Dixson 1998; Wolff & Macdonald 2004). Primates represent a particularly interesting group in this regard because, in many Old World species, females display clear anatomical and physiological adaptations that promote multi-male mating (i.e. sexual swellings; Hrdy 1981; Nunn 1999; Zinner *et al.* 2004). In these species, male aggression against females is a common occurrence (van Schaik *et al.* 2004). However, this behaviour has not yet been fully explained. Hypotheses include male aggression towards females being an incidental outcome of male–male competition, or the result of intersexual dominance or feeding competition. The predominant hypothesis, however, is that male aggression towards females represents sexual coercion, making females more likely to mate with some males and less likely to mate with others (Smuts & Smuts 1993). Here, we test the sexual coercion hypothesis.

Clutton-Brock & Parker (1995) identified three types of sexual coercion: forced copulation, harassment and intimidation. These strategies are differentiated primarily by the temporal proximity of their effects. Forced copulation involves violent restraint, resulting in immediate mating. Harassment involves repeated attempts to copulate that impose costs on females, inducing eventual female submission. Intimidation involves physical punishment of female refusals to mate, increasing the likelihood of submission in the future. All of these strategies are expected to involve non-preferred males, as they presume female resistance.

Male mate guarding comprises a fourth form of coercion that involves directing aggression at females to prevent them from mating with other males (Smuts & Smuts 1993; van Schaik *et al.* 2004). Mate guarding may involve preferred males, as it functions to constrain female

promiscuity, rather than to overcome female reluctance. This form of coercion is expected to be prominent in species with high rates of multi-male mating, and can be viewed as a counter-strategy to female attempts at paternity confusion (van Schaik *et al.* 2004).

For male aggression to be interpreted as any form of sexual coercion, three specific conditions must be satisfied (Smuts & Smuts 1993). First, male aggression against females should intensify in reproductive contexts. Specifically, the most fecund females (i.e. those with the highest probability of conception) should receive the highest rates of male aggression. Second, male aggression against females should correlate with increased mating activity. Specifically, individual males should show higher copulation rates with the females that they are relatively more aggressive towards. Third, there must be a cost to male aggression, such that females would be better off not experiencing it. Although receiving aggression may appear inherently undesirable, it is possible that it might benefit females in some way, for example, by allowing them to test the quality of potential mates (Smuts & Smuts 1993; Szykman *et al.* 2003).

Individual predictions of the sexual coercion hypothesis find support in a range of mammals (Smuts & Smuts 1993; Clutton-Brock & Parker 1995). For example, male aggression against females frequently correlates with female fecundity, such that cycling females or females in oestrus receive more aggression than non-cycling or anoestrous females (ungulates: Clutton-Brock *et al.* 1992; primates: Smuts & Smuts 1993; Soltis *et al.* 1997; bottlenose dolphins (*Tursiops* sp.): Connor *et al.* 1996; Scott *et al.* 2005). Furthermore, in some species females that mate with multiple males experience lower reproductive rates and higher morbidity and/or mortality (sheep (*Ovis aries*): Reale *et al.* 1996; feral horses (*Equus caballus*): Linklater *et al.* 1999), costs probably associated with male mating aggression.

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Despite such insights, no study has systematically tested all three predictions of the sexual coercion hypothesis. In this paper, we do so using long-term data from a study of wild chimpanzees (*Pan troglodytes schweinfurthii*). First, we evaluate the effects of female fecundity on rates of male–female aggression. Two independent measures of fecundity are employed, oestrous state and parity. Oestrous state is assessed by the presence of maximal sexual swellings, which in chimpanzees are oestrogen-dependent markers of the follicular phase (Graham 1981). We treat parity as a separate indicator of fecundity because, in our study population, parous females have higher probabilities of conception than nulliparous females (copulations per conception: parous females less than 500, nulliparous females more than 1000; Wrangham 2002).

Second, we assess whether male aggression correlates with increased mating activity. Using long-term data from 13 adult males and 15 parous females, we compare rates of copulation across dyads that exhibited varying amounts of male aggression. In these analyses, we test for the possible confounding effects of both male rank and male–female proximity.

Third, we examine the potential costs of male aggression to females in terms of increased physiological stress. To quantify such costs, we measured glucocorticoid excretion in urine samples collected opportunistically from individual females over more than 7 years. Although acute glucocorticoid secretion represents an adaptive response, it also constitutes a physiological cost, as energy must be redirected from processes, such as reproduction and growth, to meet the demands of the stressor (Sapolsky 2002). Chronic activation of the stress response incurs additional costs, as it is associated with a range of pathologies, including gastric ulcers and atherosclerosis (Sapolsky 2002). Further adverse effects of sustained glucocorticoid exposure include protein breakdown, muscle wasting and immunosuppression (Genuth 1993; Rabin 1999).

## 2. MATERIAL AND METHODS

### (a) Study population and long-term data

The subjects of the study were members of the Kanyawara chimpanzee community in Kibale National Park, Uganda, a population that has been studied continuously since 1987. Behaviour was recorded by a team of observers, which normally consisted of two to three long-term Ugandan field assistants, and one to two university-based researchers (graduate students, postdoctoral researchers or one of the authors). Whenever possible, observers followed the chimpanzees from the time that they woke in the morning until the time that they constructed their night nests.

Behavioural data came from two sources. For focal aggression rates, we used data collected by the first author between January and December 1998. To examine longer term patterns of aggression and mating behaviour, we used 10 years of all-occurrence sampling data collected between January 1994 and December 2003 by a team of field assistants. All-occurrence sampling of aggression is made possible by the boisterous nature of chimpanzee agonism, which renders it highly conspicuous to observers. Nevertheless, it is likely that the long-term data underestimate true rates of aggression, because some interactions are obscured by vegetation. In order to test whether

they do so in an unbiased manner, we compared focal data from 1998 with long-term data collected independently in the same year. A matrix correlation test (Hemelrijk 1990a) revealed a significant correlation between dyadic frequency of aggression in the long-term data and the focal data ( $K_r=460$ ,  $\tau_{rw}=0.53$ ,  $p=0.0005$ , 2000 permutations). Furthermore, mean rates of dyadic aggression calculated from the long-term data were significantly correlated with true rates from the focal data (Pearson correlation:  $r=0.93$ ,  $n=18$ ,  $p=0.000$ ). Each of these analyses included data from 7 adult females and 11 adult males. For rates, data were restricted to dyads with at least 25 observation hours in the focal data and 100 h in the long-term data. These results justify the use of long-term data for comparisons of relative aggression rates in different periods.

### (b) Behavioural data

Three categories of behaviour constituted male aggression: charging displays involved exaggerated locomotion, piloerection and branch shaking directed at specific females. Chases were recorded when a male pursued a fleeing female, who was generally screaming. All incidents of contact aggression were recorded as attacks. These included hits, kicks or slaps delivered in passing, as well as extended episodes of pounding, dragging and biting (Muller & Wrangham 2004a). Copulations, defined as mounting with intromission and pelvic thrusting, were recorded using all-occurrence sampling (Wrangham 2002). Male dominance ranks were assigned based on the direction of submissive vocalizations (pant-grunts) and decided agonistic encounters among male dyads (Muller & Wrangham 2004a).

### (c) Hormone assays

To quantify rates of glucocorticoid excretion by females, we assayed urine samples collected non-invasively between January 1998 and July 2005. When a chimpanzee urinated from a tree, M.N.M., M.E.T. or one of the long-term field assistants trapped urine in a disposable plastic bag attached to a 2 m pole. If a bag could not be placed in time, then urine was pipetted from leaves in the ground layer of vegetation. Immediately after collection, the identity of the chimpanzee, the date and the time of urination were recorded. To minimize the risk of sample cross-contamination, urine was collected from vegetation only when it was clear that multiple individuals had not urinated in the same area. Care was also taken to avoid collecting urine contaminated with faeces (see Muller & Wrangham (2004a) for additional details on the validation of sample collection procedures).

Urine samples were stored in a propane-powered freezer (below  $-18^\circ\text{C}$ ) prior to transport to Boston University's Reproductive Ecology Laboratory (Muller & Wrangham 2004a). Enzyme immunoassay for urinary cortisol was performed with reagents provided by C. J. Munro in the Clinical Endocrinology Laboratory at University of California, Davis. Samples, urine controls and standards (50  $\mu\text{l}$  diluted 1 : 100 in 0.1 M phosphate buffer) were assayed in duplicate with horseradish-peroxidase-labelled cortisol competitor in pre-coated Nunc Maxisorp Immunoplates. After 2 h incubation at room temperature, plates were washed, developed with 40 mM ABTS substrate solution and incubated for an additional 30–60 min before optical scanning with 405 and 620 nm filters. To correct for variation in urine concentration, cortisol measures were indexed to creatinine (Lasley *et al.* 1994).

Interassay coefficients of variation for 94 assays were 11.5 and 14.4% for high and low pools, respectively. Coefficients of variation for 12 replicates were 5.4 and 9.5% for high and low pools, respectively. Parallelism was examined by comparing the regression curves of per cent binding on log-transformed cortisol dose for the standard curve ( $y = -0.34x + 1.06$ ) versus serial dilution of a urine sample ( $y = -0.38x + 1.23$ ); the slopes of these curves did not differ significantly ( $t = -0.688$ ,  $d = 12$ ,  $p = 0.50$ ).

### 3. RESULTS

#### (a) Male aggression and female fecundity

Focal data indicate that intersexual aggression occurs regularly among Kanyawara chimpanzees, with individual females suffering charges, chases or physical attacks from individual males at a mean rate of  $0.017 \pm 0.004$  (all are  $\pm$ s.e.) times per hour. A female travelling in a party with five adult males could thus be expected to receive aggression, on average, once per day (i.e. 12 h of observation), a rate indistinguishable from that of male aggression received by males ( $0.015 \pm 0.003$  times  $h^{-1}$ ; Mann-Whitney  $U$ -test:  $Z = -0.165$ ,  $N_1 = 8$  adult females,  $N_2 = 11$  adult males,  $p = 0.869$ , all are two-tailed).

As predicted by the sexual coercion hypothesis, parous females were subject to significantly higher rates of male aggression when cycling and maximally swollen than during periods of lactational amenorrhea (figure 1). Furthermore, a cross-sectional comparison showed that median rates of received male aggression for maximally swollen parous females ( $0.049 \pm 0.010$  times  $h^{-1}$ ) were significantly higher than those for maximally swollen nulliparous females ( $0.015 \pm 0.008$  times  $h^{-1}$ ; Mann-Whitney  $U$ -test:  $Z = -2.7$ ,  $N_1 = 13$  parous females,  $N_2 = 9$  nulliparous females,  $p = 0.006$ ). This comparison is based on absolute rates of received aggression. Dyadic rates of male-female aggression showed the same pattern (parous median:  $0.006 \pm 0.002$  times  $h^{-1}$ ; nulliparous median:  $0.000 \pm 0.001$  times  $h^{-1}$ ; Mann-Whitney  $U$ -test:  $Z = -3.0$ ,  $N_1 = 11$  parous females,  $N_2 = 9$  nulliparous females,  $p = 0.003$ ; includes data from dyads observed together for at least 50 h, 7-11 males (median = 10) per parous female, 8-11 males (median = 10) per nulliparous female). Finally, four females who began the study as nulliparous, all experienced increased levels of male aggression when they mated as parous females (nulliparous median:  $0.016 \pm 0.010$  times  $h^{-1}$ ; parous median:  $0.055 \pm 0.025$  times  $h^{-1}$ ). This comparison is based on absolute rates of received aggression. Dyadic rates of male-female aggression showed the same pattern (nulliparous median:  $0.000 \pm 0.001$  times  $h^{-1}$ , 10-11 males (median = 11) per female; parous median:  $0.008 \pm 0.003$  times  $h^{-1}$ , 7-11 males (median = 9.5) per female).

#### (b) Male aggression and mating activity

Males in the study were aggressive towards different females at markedly different rates. A matrix partial correlation procedure (Hemelrijk 1990b) revealed a significant association between the amount of aggression directed by males at individual oestrous females and the number of times males copulated with those females, controlling for the amount of time spent together ( $rK_r = 0.36$ ,  $p = 0.000$ , 2000 permutations). As an additional test of the relationship between male aggression

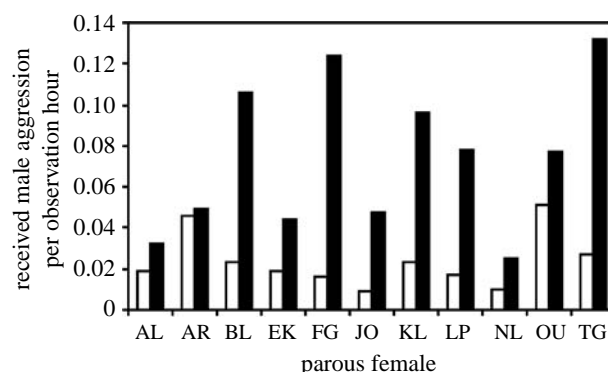


Figure 1. Male aggression against females intensifies in reproductive contexts. Parous females received significantly higher median rates of male aggression when they were in oestrus (black bars:  $0.074 \pm 0.011$  times  $h^{-1}$ ) than during periods of lactational amenorrhea (white bars:  $0.019 \pm 0.004$  times  $h^{-1}$ ; Wilcoxon signed-rank test:  $Z = -2.9$ ,  $N = 11$ ,  $p = 0.003$ ). Oestrous periods included observations when females maintained maximally tumescent sexual swellings, but were not pregnant. Periods of lactational amenorrhea included observations from the birth of an infant until the female resumed full sexual swellings. Females were observed for at least 100 h in each reproductive state. The figure shows absolute rates of received aggression. Rates of received aggression per male/female dyad showed the same pattern (oestrus median:  $0.008 \pm 0.002$  times  $h^{-1}$ ; lactational amenorrhea:  $0.003 \pm 0.001$  times  $h^{-1}$ ; Wilcoxon signed-rank test:  $Z = -2.7$ ,  $N = 9$  females,  $p = 0.008$ ; includes data from dyads observed for at least 50 h in each reproductive state, 8-13 males (median = 11) per lactating female, 7-11 males (median = 10) per oestrous female).

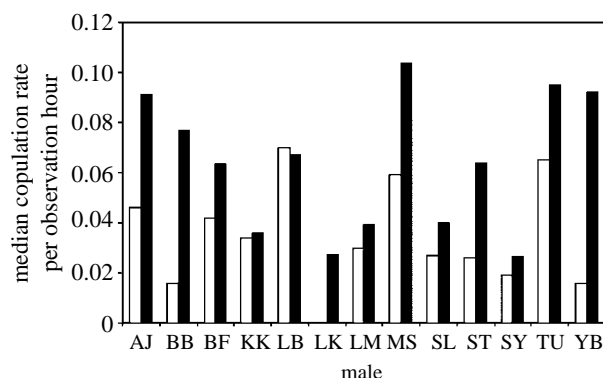


Figure 2. We examined median dyadic rates of aggression for each of 13 males with 15 parous females. For each male, we calculated median copulation rates with females who received (a) more or (b) less than or equal to the median amount of aggression for that male. All dyads were observed together for at least 25 h when the female was in oestrus (2-14 females per male, median = 11). Males copulated at significantly higher rates with the parous females that they were more aggressive towards (black bars: median =  $0.064 \pm 0.008$  cops  $h^{-1}$ ) than those they were less aggressive towards (white bars: median =  $0.03 \pm 0.006$  cops  $h^{-1}$ ; Wilcoxon signed-rank test:  $Z = -3.04$ ,  $n = 13$  males,  $p = 0.002$ ).

and mating, we compared, for each of 13 adult males, copulation rates with females who received more or less than the median amount of aggression from that male. As predicted, individual males copulated at significantly higher rates with females that they were more aggressive towards, than those they were less aggressive towards (figure 2).

The association between mating and aggression could theoretically have resulted from processes other than

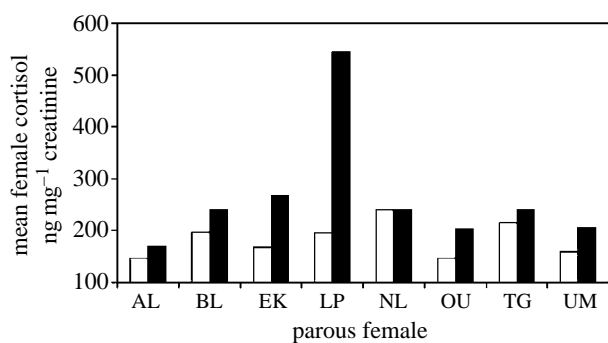


Figure 3. We calculated mean monthly cortisol levels for the eight parous females observed in cycling and non-cycling conditions between 1998 and 2005. Parous females showed elevated levels of mean glucocorticoid excretion on oestrous days (black bars:  $265 \pm 41$  ng mg<sup>-1</sup> creatinine) compared with periods of lactational amenorrhoea (white bars:  $184 \pm 12$  ng mg<sup>-1</sup>; Wilcoxon signed-rank test:  $N=8$ ,  $p=0.01$ ).

sexual coercion. We therefore conducted additional analyses to test two alternative hypotheses. First, it is possible that females were not actually coerced, but preferred to mate with high-ranking males, who happened to be more aggressive. This logic is supported by the observation that high-ranking males at Kanyawara exhibit higher overall rates of aggression than low-ranking males (Muller & Wrangham 2004a). However, two observations contradict this interpretation. First, as clear in figure 2, the relationship between aggression and copulation rates was not limited to high-ranking males. Out of 13 males, 12 showed elevated copulation rates with the females they were most aggressive towards. Second, although focal data indicate that high-ranking males are more aggressive overall, this is driven by a correlation between rank and male aggression against males (Kendall correlation:  $\tau = -0.62$ ,  $n=11$ ,  $p=0.008$ ). There was correlation neither between male rank and aggression directed at females ( $\tau = -0.37$ ,  $n=11$ ,  $p=0.12$ ), nor between rates of male aggression against males and male aggression against females ( $\tau = 0.24$ ,  $n=11$ ,  $p=0.31$ ). These patterns also challenge the alternative hypothesis that male aggression against females represents an incidental outcome of male-male competition.

A second potential alternative explanation for the association between mating and aggression is that males were generally aggressive towards any female in direct proximity with them, and that females necessarily approached males in order to copulate (Soltis *et al.* 1997). We tested this hypothesis by analysing long-term aggression and mating data from nine nulliparous females. If aggression is the inevitable result of close male proximity, then nulliparous females should exhibit the same correlation between mating and aggression found in parous females. If, however, the relationship results from sexual coercion, then no correlation between aggression and mating should exist for nulliparous females because they are less attractive to males, and males show little interest in monopolizing them (Wrangham 2002; Muller & Wrangham 2004a; Muller *et al.* 2006). A matrix partial correlation test (Hemelryk 1990b) revealed no association between the amount of aggression directed by males at oestrous nulliparous females and the number of times males copulated with those females, controlling for the amount of time spent together ( $\tau K_r = 0.08$ ,  $p=0.31$ , 2000

permutations). Furthermore, individual males did not copulate at significantly higher rates with the nulliparous females that they were more aggressive towards, than those they were less aggressive towards (Wilcoxon signed-rank test:  $Z = -1.4$ ,  $n=12$  males,  $p=0.16$ , includes dyads observed together for at least 25 h when the female was in oestrus; two to nine females per male, median = 8.5). Thus, these alternatives to the sexual coercion hypothesis do not account for our findings.

### (c) Male aggression and female stress

In accordance with the idea that male aggression imposes physiological costs on females, female cortisol excretion was elevated in reproductive contexts; these increases were correlated with fecundity in a similar manner as rates of aggression. Accordingly, cycling parous females exhibited significantly higher levels of urinary cortisol ( $214 \pm 25$  ng mg<sup>-1</sup> creatinine) than cycling nulliparous females ( $120 \pm 14.6$  ng mg<sup>-1</sup> creatinine; Mann-Whitney  $U$ -test:  $Z = -2.7$ ,  $N_1=6$  nulliparous females,  $N_2=11$  parous females,  $p=0.007$ ), and parous females showed elevated levels of cortisol excretion during oestrous periods compared with periods of lactational amenorrhoea (figure 3). Nulliparous females, in contrast, showed no difference between average levels of glucocorticoid excretion on oestrous ( $120.4 \pm 30.1$  ng mg<sup>-1</sup> creatinine) versus non-oestrous days ( $113.8 \pm 13.6$  ng mg<sup>-1</sup> creatinine; Wilcoxon signed-rank test:  $N=5$ ,  $p=0.89$ ).

## 4. DISCUSSION AND CONCLUSIONS

Our data show that male chimpanzees directed more aggression towards more fecund females, and achieved more matings with females towards whom they were more aggressive. They also suggest that male aggression imposed physiological costs on females, in terms of increased glucocorticoid secretion. It is difficult to demonstrate conclusively that male aggression caused elevations in female cortisol, because energetic stress resulting from increased travel or feeding competition can also affect cortisol excretion (e.g. Muller & Wrangham 2004b). However, the contrast between parous and nulliparous females suggests that aggression was likely the relevant stressor. Even when they are not in oestrus, nulliparous females spend more time than parous females in parties with males, incurring associated travel and feeding costs (Wrangham 2000). Yet nulliparous females maintained significantly lower cortisol levels than parous females. Furthermore, oestrous nulliparous females at Kanyawara mate with males at rates equivalent to those of oestrous parous females (Wrangham 2002; Emery Thompson 2005), yet they did not show the marked increase in cortisol excretion during periods of maximal swelling that parous females did. The salient difference between nulliparous and parous females appears to be their attractiveness to males (Muller *et al.* 2006), which results in heightened male coercion.

Since male aggression against females both constrained female mate choice and imposed costs on females, we conclude that such aggression functioned as sexual coercion. Coercive aggression could increase male copulation rates through at least two mechanisms: by overcoming female resistance (direct coercion), and/or by limiting female promiscuity (mate guarding). We expect

the choice of such strategies to vary with female reproductive state and with male rank. Specifically, low-ranking or non-preferred males might employ aggression to overcome female resistance, which appears to increase during the periovulatory period, whereas high-ranking or preferred males might do so to constrain female promiscuity, which appears to decrease during the periovulatory period (Stumpf & Boesch 2005). Detailed data on the timing of mating and aggression by males of different ranks in relation to ovulation are necessary to fully address this issue.

Whether the benefits lie primarily in overcoming female resistance or in constraining female promiscuity, these data represent the strongest evidence found that in a wild primate, male aggression against females functions as part of a mating strategy. As such, they represent the best demonstration of male coercion as a mechanism of sexual selection distinct from male–male competition and female choice in primates (Smuts & Smuts 1993; Clutton-Brock & Parker 1995).

A cycling female chimpanzee can escape the costs of male coercion by accompanying an individual male to a peripheral part of the community range in an exclusive 'consortship' (Goodall 1986). Females do not regularly form consortships, however, and when they do, initial coercion by the consorting male can play a role (Goodall 1986; Smuts & Smuts 1993; Muller & Wrangham 2001). This implies that mating promiscuously in multi-male settings is beneficial for females. In primates generally, much evidence suggests that multi-male mating functions to confuse paternity, and thereby decrease the risk of infanticide by males (Hrdy 1979; van Schaik & Janson 2000; Wolff & Macdonald 2004). This is plausible for chimpanzees, for whom infanticide by adult males within the social group is an important risk (Nishida & Kawanaka 1985; Clark Arcadi & Wrangham 1999). An additional possibility is that paternity confusion induces males to invest in infants indirectly, through cooperative defence of a community feeding range (Wrangham 1979). Such functional reasons for female promiscuity can be expected to vary among primates. Wherever female promiscuity is favoured, however, there is a potential for conflict between male and female mating strategies. We therefore expect similar evidence of an evolved function for sexual coercion to be widespread in other primate species.

For sponsoring long-term research in Kibale National Park, we thank the Uganda Wildlife Authority and Makerere University Biological Field Station. For assistance in the field, we thank J. Barwoeza, the late J. Basagara, D. Kateeba, C. Katongole, F. Mugurusi, the late D. Muhangyi, C. Muruuli, D. Sebugwawo and P. Tuhairwe. Research at Kibale was supported by grants from the U.S. National Science Foundation (awards 9807448 and 0416125), NIH, the L.S.B. Leakey Foundation, the National Geographic Society and the Wenner-Gren Foundation.

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