The Function of Male Agonistic Displays in Ursine Colobus Monkeys (*Colobus vellerosus*): Male Competition, Female Mate Choice or Sexual Coercion?

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Abstract

Male agonistic displays may allow males to assess competitors, females to assess mates, or could be directed at cycling females to sexually coerce them. We analysed the display output of 26 male ursine colobus monkeys (*Colobus vellerosus*) in four groups over 13-mo at the Boabeng-Fiema Monkey Sanctuary, Ghana. Display indices (including three behaviours, loud calls, stiff-legs, and jump-displays) were calculated for males in each group. Males vary in their expression of these behaviours suggesting they are sexually selected signals. We investigated the target of displays and whether display indices varied in relation to male dominance rank, eviction of other males, copulation rate, and proceptive behaviours received from females, to assess the primary function of these behaviours. Male displays decreased in vigour over time and were targeted to other groups and males. High-ranking males displayed more than low-ranking males. Alpha male display indices correlated with the number of other males evicted from the group. Display rates were generally higher when cycling females were present in the group. However, neither male display index nor rank correlated with copulation rates. Alpha and non-alpha males gave cycling females equal rates of sexual solicitations; likewise cycling females showed no difference in the rates of proceptive behaviours directed towards alpha and non-alpha males. Females mated promiscuously and did not seem to base mating decisions on male display output, although data on female hormones is needed to determine if they mate with strongly displaying males more in the periovulatory period. The male–male competition hypothesis received the greatest support, with some support for the female mate choice hypothesis. Although behaviours that appeared sexually coercive were observed, the function of male displays did not seem to be sexual coercion. Displays were rarely directed at females and males that displayed more did not have greater mating success.

Introduction

Male animals often invest substantial time and energy in behavioural displays, which involve quick movements, repeated vocalizations or both (Andersson 1994). These traits are sexually selected if they are sexually dimorphic, if males vary in their display output, and if conspecific discrimination of the signal leads to differential outcomes in mating and reproductive success for males (Snowdon 2004). When male displays are sexually selected, they may serve in intrasexual agonism (between males, to intimidate and assess opponents), in courtship (directed at females, for mate attraction) (Darwin 1871), or in sexual coercion (directed at females, to intimidate them and make them more likely to mate with that

male) (Smuts & Smuts 1993; Clutton-Brock & Parker 1995). However, some displays may serve multiple purposes (Berglund et al. 1996; Delaney et al. 2007; Morris et al. 2007).

When the energetic cost of male signals cannot be borne by lower-quality individuals, they may act as honest indicators of male viability and males may be able to display their superiority by withstanding the costs (Zahavi 1975, 1977; Grafen 1990). There is a large body of evidence showing that males that display at higher rates, for longer durations, at greater intensities, and with greater complexity than other males are most successful at mate attraction and in male–male competition (e.g. insects, Tachon et al. 1999; Berg & Greenfield 2005; Delaney et al. 2007; birds, Rintamaki et al. 1999; Gentner & Hulse 2000; frogs, Gerhardt et al. 2000; Schwartz et al. 2001; Pröhl 2003; mammals, Clutton-Brock & Albon 1979; Clutton-Brock et al. 1982; McElligott et al. 1999). Displays may indicate male condition (e.g. Møller 1991; Martin-Vivaldi et al. 2002; Morales et al. 2003) and call characteristics can indicate body size (birds, Ryan & Brenowitz 1985; Miyazaki & Waas 2003; toads, Davies & Halliday 1978; Arak 1988; frogs, Ryan 1985; mammals, Reby & McComb 2003; Harris et al. 2006; Rendall et al. 2005). If displays are costly, phenotypically variable, and indicative of the displaying individual's stamina (Kodric-Brown & Brown 1984), receivers could evaluate sender quality over time by using a cumulative receiver assessment rule (Sullivan 1990; Payne & Pagel 1996, 1997). According to this assessment rule, the quality of competitors or mates can be assessed by taking into account the sum of all display behaviours (Enquist & Leimar 1983).

Little is known about the function of male display behaviour in primates or even if these behaviours are sexually selected (Snowdon 2004). This is particularly true of behavioural displays, as some work has been done on vocalizations (reviewed in: Delgado 2006) and colour signalling (reviewed in: Bergman et al. 2009). Most primate studies are lacking some quantification of the variation in behavioural displays among males. This has only recently started to be documented in a few species (chacma baboons, Fischer et al. 2002, 2004; Kitchen et al. 2003; black howler monkeys, Kitchen 2004; guerezas, Harris 2006). Beyond male variation, work on the functional significance of behavioural signals is just beginning. One study by Utami & Mitra Setia (1995) on orangutans, showed that loud call rates were the best indicator of male attractiveness to females as measured by female approaches. Observa-

tions in mountain gorillas have shown that males direct displays at females, which do not seem to have a courtship function (Sicotte 2002) but rather appear sexually coercive (Robbins 2003). Preliminary work in lowland gorillas has shown that males perform more intense agonistic displays towards other males when greater numbers of females are present (Caillaud et al. 2008). For two other primate species (chacma baboons, Kitchen et al. 2009; chimpanzees, Muller et al. 2009), male behavioural displays (e.g. vocalizations, charging, branch-shaking) that are directed at females also appear to be sexually coercive and used to intimidate cycling females.

We compared display output for 26 male ursine colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana, to determine whether these behaviours were sexually selected and analyse their function. Males in this species do not show courtship displays but they perform three ritualized agonistic displays, the loud call, jump-display and stiff-leg display. These behaviours are seen in females rarely (Sicotte et al. 2007). Male displays may be used between males to evaluate the strength of their competitors, which females could eavesdrop on and co-opt as indicators of mate quality (e.g. pre-existing trait hypothesis, Borgia 1979; Berglund et al. 1996; Morris et al. 2007). Alternatively, male displays may directly influence female mate choice, either because males are displaying their quality as a mate, or because displays intimidate the female and function as a form of sexual coercion.

Ursine colobus at BFMS are mainly folivorous (annual diet: 74% leaves, Saj et al. 2005) and group sizes vary (range: 9–38, x = 15.0, n = 15; Wong & Sicotte 2006) as does group composition, which can be multi-male/multi-female, uni-male/multi-female, or all-male bands (AMB's) (Teichroeb et al. 2003; Saj & Sicotte 2005). Males disperse from their natal group while female dispersal is facultative (Teichroeb et al. 2009). There is no mating or birth season (Teichroeb & Sicotte 2008b). Male-male competition is intense both for mating opportunities and for group membership (Sicotte et al. 2007; Teichroeb and Sicotte 2008a,b). Between-group encounters are usually aggressive, with adult males as the main participants. Group males, solitary males, and males in AMB's attack bisexual groups during male incursions (Sicotte & MacIntosh 2004). Male infanticide occurs after male takeovers and immigration and accounts for 38.5% of infant mortality (Teichroeb & Sicotte 2008a). If incoming males do not evict them, putative sires may aid females in infant defence

(Saj & Sicotte 2005; Teichroeb and Sicotte 2008a,b). The consequences of mate choice may be especially important for female *C. vellerosus* because male infanticide is common and putative sires act as infant protectors (Teichroeb & Sicotte 2008a).

We evaluate whether display behaviours are costly for male *C. vellerosus* and if the cumulative sum of male displays correlate best with indicators of male competitive ability, with measures of female mate choice, or with both. We also assess whether male displays occur primarily in situations where they could function in intimidating cycling females. If male agonistic displays in ursine colobus function as honest signals of competitive ability in male-male competition, we expected that: (1) male displays would be energetically costly; (2) male displays would be targeted towards other males; (3) males would vary in the frequency and intensity of their displays; (4) the cumulative sum of male displays would correlate with their rank, which is attained through contests with other males; (5) the display output of the alpha male in each group would correlate with the number of other males he evicts from the group (ability to exclude other males). If male displays function as honest signals for female mate choice, we predicted that: (1) male displays would be energetically costly; (2) male displays would occur in the presence of cycling females; (3) a males' display output would correlate with two indicators of female mate choice: (a) his copulation rate; and (b) female proceptive behaviour towards him. If male agonistic displays serve dual functions for *C. vellerosus*, we expected to find support for predictions under both the male-male competition and female mate choice hypotheses. Female freedom in mate choice may be influenced by male sexual and coercive behaviours (Smuts & Smuts 1993), so we also documented whether males varied in their mating solicitation attempts or their efforts to influence female choice using aggression. If male displays function to intimidate females, we predicted that:

(1) male displays would be targeted towards cycling females; (2) a males' display output would correlate with his copulation rate; (3) copulation or female proceptive behaviour would occur immediately after a display event.

Methods

Study Site and Data Collection

The Boabeng-Fiema Monkey Sanctuary (BFMS) is located in central Ghana ($7°43'N$ and $1°42'W$) and is a dry semi-deciduous forest, 191.6 ha in size. It is surrounded by farmland but connects to several smaller forest fragments in the area by a narrow, riparian forest. The vegetation is a mosaic of primary forest, regenerating farmland (secondary forest) and woodland (Fargey 1991; Saj et al. 2005).

Ursine colobus monkeys (*Colobus vellerosus*) at BFMS have been studied under the supervision of PS since 2000. For this study, behavioural observations were performed on four groups (WW, DA, B2 and RT) during 13-mo (Jul. to Nov. 2004, Jan. to Aug. 2005). Group size and composition and the number of hours of data collection varied (Table 1). All males were individually recognized by features of the face and tail. All adult females in the small study groups (B2 and RT) and most in the larger study groups (DA, n = 5/10; WW, n = 8/11) were also recognized. We used observations from 26 males for this study, 22 adult males and four older subadult males that transitioned to adulthood. Only one of the 26 males for which data were used was presumed to be a natal male (adult male *Fi*), all others were immigrant males. Male *Fi* remained in his natal group (B2) for over a year as an adult and mated with all of the females except his suspected mother (female *G*). Proceptive behaviours and sexual solicitations were not observed between *Fi* and *G* either.

Groups were followed for two, 2-d periods per month from dawn to dusk (6:00 AM to 6:00 PM) by

Table 1: Study group composition and duration of observations

Name	Group size	Adults		Subadults		Juveniles/ infants	Contact hours[a]	Focal hours
		M	F	M	F			
RT	12–13	1–2	5	0–1	1	5	567.5	106.5
B2	13–17	1–3	4	2–4	0–1	4–5	574.5	102
DA	21–31	3–8	9–10	3–5	1–3	4–5	574	99.8
WW	28–33	6–10	10–11	2–6	2–3	2–5	690	125
Total							2406	433.3

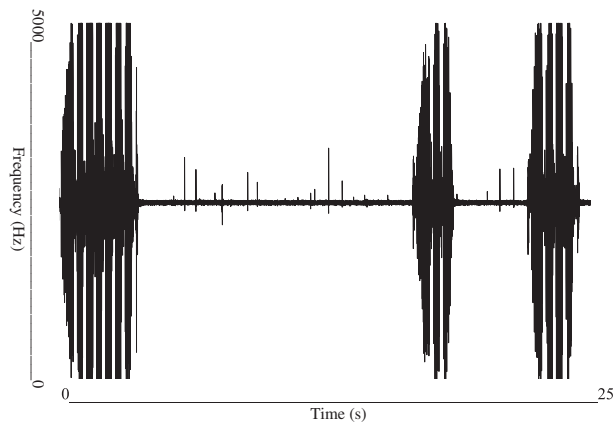[a]Including JAT and research assistants

Fig. 1: Three roaring bouts by a male *C. vellerosus*. The first bout is made up of seven roars, the second, three roars and the third, four roars. Bouts are distinct by the time lag between them (created using Praat software).

JAT with the help of a research assistant. In total, 202 full-day follows were conducted. Behavioural observations on adult and subadult individuals were recorded using 10-minute focal-animal samples that were alternated between the sexes (433.3 focal hours, 2406 contact hours; Table 1). *Ad libitum* data collection was employed to record agonistic events, copulations, and loud call displays that occurred outside of focal samples (Altmann 1974).

For *C. vellerosus*, loud call displays involve multiple roars ('rurr rurr rurr rurr') in several repeated bouts while leaping through the canopy (jump-display). Bouts of roaring within a loud call are usually separated by several seconds (Fig. 1). Roars can be counted during bouts and as with closely related *C. guereza*, each roar is made up by phrases of compound pulses, which can be plotted on a sonogram (Marler 1972; Harris 2006). For this study, we limit our analyses to roar number and duration and do not focus on the structure of the calls. Loud calls occur in the morning in contagious choruses with other groups and at other times of the day. Usually all the adult males in the group roar in relative synchrony, although some males produce more roars and/or tend to participate more often (58.6% of recorded calls were choruses, n = 75/128). Short bursts of roars are also released during contact aggression between individuals (males and females); however, these were not considered 'loud-calls' unless several repeated bouts of roaring were uttered.

When loud call bouts occurred, they were recorded on a hand held tape recorder (Sony TCM-400DV) and the observer (JAT) dictated during each

bout the identity of the calling male(s). When several males called together, observations focused on a single male (this was possible in 60% of choruses, n = 45/75), to determine his contribution to the chorus. In the cases where a male continued to call after the others had stopped, his identity was noted. Later, the numbers of roars per bout were extracted from the recording and the duration of roaring per call was timed.

The rates and durations of jump-displays and stiff-legs were recorded during focal samples. Jump-displays (leaping through the canopy with legs held stiffly) occur in the absence of loud-calls and are often associated with other display behaviours such as stiff-legs and aggressive open-mouths. Stiff-legs involves individuals holding their legs straight out from a branch, where they may be held for varying lengths of time (described for *C. guereza*, Oates 1977). During stiff-legs, males are sometimes seen with one leg held up by a branch as if they were 'cheating' (see below, J. A. Teichroeb, unpub. data).

Male Display Index

We combined display behaviours and constructed a 'display index' for each male (Table 2). We used a male's performance over the entire study period because the sexes reside together in *C. vellerosus,* so individuals have long sampling periods in which to assess males (Sullivan 1990). A male's index was determined by ranking him relative to all other males in his group for each display behaviour and then taking a mean for all his available rankings (Table 2). Thus, a mean rank was assigned for each male, which indicated his total display output relative to other males in his group, such that a lower number indicates a high level of display (Table 2). For males that changed dominance rank, we constructed three indices: (1) one index, as described above, which ranked the male over the entire study period relative to the other males in his group; and (2) two separate indices that compared the male relative with himself when he occupied a higher vs. a lower rank. Two indices were also constructed for alpha males, one ranking their display output compared to males within their own group and one relative to the alpha males in other groups. The data used to construct display indices comes only from focal-animal samples (n = 1074, 178.46 h), except for roaring, for which *ad libitum* observations were used because of its rarity (n = 98 calls where a single male's contribution was known). Stiff-legs and jump

Table 2: Calculation of male display index in each group showing rankings for each behaviour

Group	Male	Age[a]	Loud call displays Mean no. roars per bout	Loud call displays Mean duration roaring per call (s)	Stiff leg displays No encounters Mean duration (s)	Stiff leg displays No encounters Rate (no./min.)	Stiff leg displays During encounters Mean duration (s)	Stiff leg displays During encounters Rate (no./min.)	Jump displays No encounters Mean duration (s)	Jump displays No encounters Rate (no./min.)	Jump displays During encounters Mean duration (s)	Jump displays During encounters Rate (no./min.)	Overall w/i Group Display Index	Mean dominance rank[b]
RT	St	A	1	1	1	1	1	1		1	2	1	1.11	1
B2	Hu	SA/A	2	2	2	2	2	2		2	1	2	1.89	2
	Lx	A	1	1	3.5	1		1.5	2	2	3	1.5	1.83	1
	Lo	A	3		3.5	3	1	4	1	1	4	4	2.76	2.5
	Wo	A	2	2	2	4	3	3		4.5	2	3	2.83	1.5
	Le	A				5.5				4.5			5	3
	T	A	4	3		5.5	2	1.5		4.5		5	3.7	2
	Fi	A	1	3	1	2	4	5		4.5	1	1.5	2.89	3.3
DA	Cy	A	1	3	2	1	1	1	3	1	1	3.5	1.75	1
	Do	A	4		5	2	2	4	2	2	3	1	2.67	1.5
	Ry	A	2	1	4	3	4	2.5		6	4	3.5	3.33	1
	Td	A			1	5				6			4	2
	Mc	A	6	2	6	4	5	5	1	3	2	5	3.8	2.5
	Ma	SA/A	3		3	6		6		6		6	4.92	4.3
	Sh	SA/A				7	3	2.5		6		2	4.1	5.3
	Mo	SA/A	5			8				6			6.33	6.5
WW	Pe	A			4	1			1.5	7.5			4.17	1
	Ha	A			1	8	3	4		3	1	3	2.81	1
	Q	A	1		2	5	1	6	3	1	3	2	2.67	2.5
	Cl	A			7.5	9			1.5	2		5.5	5.08	4
	Jr	A	2	1	3	4	4	2	4	4	2	1	2.7	3.5
	Be	A	3		5.5	3	5	5		7.5		5.5	4.36	4
	Er	A				7	6	7		7.5		5.5	6.6	5
	Ac	A			5.5	2		1		7.5			5	6
	Ru	A			7.5	6	2	3		7.5		5.5	5.17	6
	No	A				10				7.5			8.75	7

High rankings (low numbers) indicate a high display output; Missing values indicate that no data were available.
[a]A, adult; SA/A, subadult maturing to adult.
[b]Mean dominance rank in the male's own group, if males changed rank, their mean rank is presented.
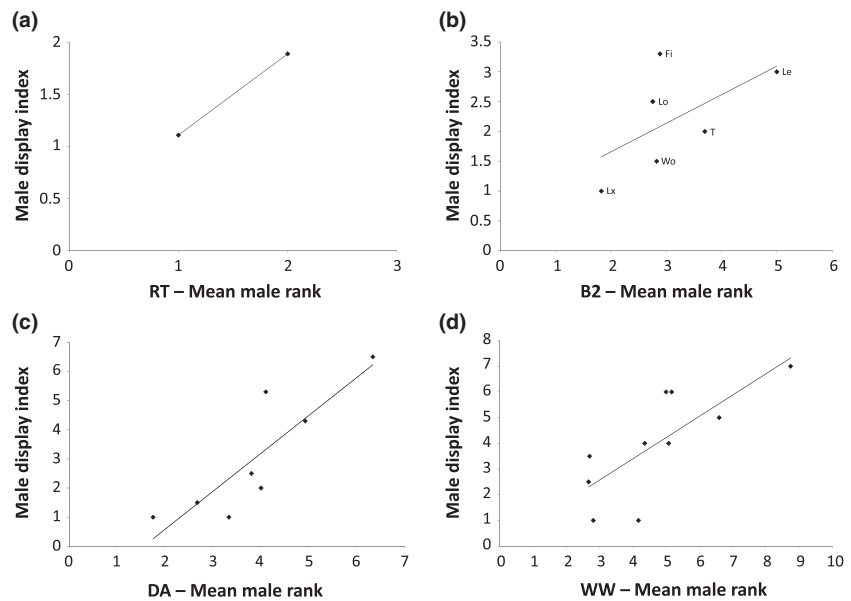
Fig. 2: Scatterplots for male display index and mean dominance rank in each group showing trend lines (a. RT; b. B2; c. DA; d. WW). For (b), note that males *Lx, T* and *Le* were present in group B2 at a different time period than *Lo, Wo* and *Fi*, while the females remained the same.

displays were ranked separately in two contexts: when encounters were occurring (between-group encounters and male incursions, see below) and when they were not (Table 2).

The measures of display behaviours used in the indices are as follows: (1) the mean number of roars per loud call bout; (2) the mean duration of roaring per call (s); (3) the rate of stiff-leg displays (no./min.); (4) the mean duration of stiff-leg displays (s); (5) the rate of jump-displays (no./min.); and (6) the mean duration of jump-displays (s) (Table 2). Stiff-legs and jump-displays often occurred in sequence, so that males effectively increased the vigour of that display. We thus decided to count these two behaviours separately for calculation of the display indices.

Male dominance relationships were determined from the direction of aggressive and submissive behaviours during focal samples and *ad libitum* observations. Subordinate males usually make a grimace and a pant-grunt (a characteristic snuffling vocalization, described for *C. guereza*, Oates 1977) when they are approached by a dominant male. Male dominance relationships within each group were linear and males could be assigned a numerical rank. Changes in male dominance relationships were detectable immediately as interactions between males usually included the subordinate individual producing submissive pant-grunts. Bidirectionality in aggression within these relationships rarely occurred, and was only observed in WW group, where we have a few cases of subordinate individuals directing

displacements, agonism, or threats towards dominants (RT, 2 males, 31 unidirectional interactions; B2, 6 males, 33 unidirectional interactions; DA, 8 males, 37 unidirectional interactions; WW, 10 males, 62 interactions, 4 showing bidirectional aggression, 3 of these 4 cases were the same long-tenured male (*Jr*) directing aggression towards new dominant males). Male evictions were defined as increased aggression (e.g. threats, chasing, contact aggression) between two males within a group in the days preceding one of them emigrating from the group.

Between-group encounters (BGE's) and male incursions occurred when individuals from two groups came within 50 m of one another (Oates 1977). They differed in that BGE's (n = 163) involved whole groups and both sexes coming into proximity whereas male incursions (n = 85) involved only male(s) from one group approaching individuals from another group (Sicotte & MacIntosh 2004). Encounters separated by at least 1 h were considered distinct.

Measures of Female Mate Choice

Female *C. vellerosus* lack external signals of ovulation, so we were unable to determine a probable fertile period as can sometimes be done for species with sexual swellings. Females were presumably cycling in months where they were seen mating or showing sexual behaviour. These months were defined as the female's 'cycling period' for calculation of solicitations, proceptivity, and aggressive behaviours

received in relation to the males. For females that gave birth and those whose observations of the cycling period were truncated, we back-dated an approximate gestation time of 6-mo (Harris & Monfort 2006) from the end of the study so that none of the calculations were based on months where females were pregnant and may have been mating non-conceptively. Females were often still in the process of weaning an older infant (>1 yr old) when they began to show sexual behaviour.

Copulation rates for males were calculated as the number of copulations observed per cycling female per month in the group (using both focal-animal and *ad libitum* data). Mating in ursine colobus is characterized by multiple intromissions (Campbell 2007), so copulations have relatively long durations and include several mounts and dismounts. Copulations were considered complete when mounts with intromission ceased and distinct when mounting bouts were separated by at least 1 h.

Rates of solicitations, proceptive behaviours, and aggressive behaviours between males and cycling females were calculated per dyad as number of events per focal minute. Male sexual solicitations towards females included: follows; touches (to hips, face or back); sniffs and licks to the anal-genital region; hip grabs; pushes to the back to induce a sexual presentation; mounts before copulating; and licks to the face. Female proceptive behaviours to males included: sexual presentations; touches (to face, back or penis); hip grabs; licks (to face or penis); and back mounts. Male aggressive behaviours towards cycling females and male aggressive behaviours that influenced female mate choice were: (1) mate-guarding: males sitting near cycling females, aggressively keeping other males from making contact with them; (2) mate-herding: males

approaching cycling females and forcing them to shift direction, usually away from another group or male; (3) harassment: males using a combination of sexual solicitations and aggressive behaviours (e.g. chases, hits, slaps, etc.) to attempt to mate with apparently reluctant cycling females or when already mating with females. Reluctance to mate for females occurred when they stayed sitting and refused to present to the male, moved away from the male, or directed aggression to the male; (4) aggressive behaviours directed to cycling females without an obvious, direct attempt to mate by the male.

Data Analyses

To determine if male displays were energetically costly, we used Pearson and Spearman correlations to see if display behaviours performed in several repeated bouts decreased in duration or in the number of display elements with an increasing number of bouts performed. A Wilcoxon signed-rank test was also used to see whether 'cheating' and 'non-cheating' stiff-leg durations varied for the same males.

When we examined the target or the stimulus of displays, for two groups (B2 and RT), there were months where there were no cycling females present in the group (B2, n = 2 mo; RT, n = 5 mo). Thus, for three males, it was possible to calculate the rates of male displays during these months compared with when cycling females were present in the group. We were only able to compare rates for stiff-legs and jump-displays (Table 3). During loud calls, males often roared in synchrony, and although a single male could sometimes be followed, an accurate rate of calling per minute of study for each male could not be calculated.

Table 3: Comparison of the stiff-leg and jump-display rates for three males when there were cycling females in the group compared with when there were not. Separate rates are shown for when extra-group males were within 50 m of the groups (i.e. a between-group encounter or male incursion was occurring)

| | | Situation and rate of display behaviour (no./min.) | | | |
| | | Regular observation hours | | Extra-group males present | |
Male	Behaviour	No cycling females present	Cycling females present	No cycling females present	Cycling females present
St	Stiff-leg	0.022	0.028	0.191	0.229
	Jump-display	0.003	0.008	0.046	0.077
Hu	Stiff-leg	0.009	0.011	0	0.200
	Jump-display	0	0	0	0.033
Wo	Stiff-leg	0.007	0.011	0	0.050
	Jump-display	0	0	0.100	0.033

Mann–Whitney U-tests were used to compare alpha and non-alpha males in their number of roars per loud call bout, rates of sexual solicitations given to cycling females and rates of proceptive behaviours received from cycling females. We also used Mann–Whitney U-tests to compare alpha and non-alpha males in their: (1) mean stiff-leg rates; (2) mean stiff-leg durations; (3) mean jump-display rates; and (4) mean jump-display durations. As these are multiple tests on the same behaviours a Bonferroni correction was applied for these tests, lowering the alpha level to 0.025. When males changed rank, Wilcoxon signed-rank tests were used to compare their copulation rates and display indices when they were higher to when they were lower-ranked.

We compared the mean dominance rank of males who did not participate in loud call bouts to that of males that tended to call longer or more often. In this analysis, RT group was excluded because the subordinate male (*Hu*) was just reaching adulthood and his participation in loud calls was only intermittent. A Pearson correlation was used to see whether display index and proceptive behaviour received from females were related. We also used a Pearson correlation to see whether copulation rate and dominance rank were correlated for males that did not change rank during the study. Spearman correlations were used to determine if dominance rank and male display index or copulation rates and display index were related for males in each group. Spearman correlations were also used to see whether the number of other males evicted by alpha males divided by the number of males available for eviction correlated with their display index or if it correlated with the time they had been alpha. A Bonferroni correction was applied for these two tests, lowering the alpha level to 0.025. Statistics were two-tailed and were performed using SPSS 16.0. Except where a Bonferroni correction was applied, the alpha level was set at $p \leq 0.05$.

Results

Are Male Displays Energetically Costly?

During loud-call displays, males roared with a mean of 16.0 roars per bout (n = 16 males, range: 1–56). The mean number of roars per bout decreased with an increasing number of bouts performed (n = 29, r = −0.65, p = 0.0001). Mean stiff-leg duration was 12.8 s (n = 337, range: 2–262 s). When several stiff-leg displays were performed by a male in a single focal sample, the mean duration of stiff-legs

decreased with an increasing number of bouts (n = 9, r_s = −0.83, p = 0.005). 'Cheating' stiff-legs (holding at least one leg up on a branch) were longer than non-cheating stiff-legs when the same males were compared (n = 13 males, cheating x = 19.08 s, non-cheating x = 7.05 s, W = 85, p = 0.003). Mean jump-display duration was 3.8 s (n = 119, range: 1–32 s). The duration of jump-displays did not decrease with an increasing number of bouts within the same focal sample (n = 7, r_s = −0.39, p = 0.38).

Target or Stimulus for Male Displays

It was typically not clear whether there were specific targets for loud calls; however, the stimulus for calling by males in the focal group was usually other groups and/or single males in other groups calling (77.1%, n = 54/70). When males in the focal group initiated loud-calling (n = 16), 62.5% of calls occurred while the group was undergoing an incursion by extra-group males. The remainder seemed caused by within-group individuals issuing 'che' vocalizations (18.8%) (a sound that sometimes precedes loud calls, see Sicotte et al. 2007 for a description), mona monkey calling (12.5%), and unknown factors (6.3%). A target could be determined in 67.1% (n = 284/423) of stiff-legs. Of these 284 stiff-legs, 47.2% were directed at other groups (134/284), 48.9% at individual males (139/284) and 3.9%, at females (11/284). Eight of the 11 (72.7%) stiff-legs directed at females occurred during or immediately after mating. A target could be determined in 72.2% (n = 92/126) of jump-displays, of these 45.7% (42/92) were directed towards other groups and 54.3% (50/92) were targeted at individual males. Jump-displays were never directed at individual females.

For the three males that could be tested, the rates of stiff-legs increased when cycling females were in the group compared with when no cycling females were present, both during regular observation hours and during BGE's or male incursions (Table 3). The rate of jump-displays also increased in two of the three males. The highest rates of both display behaviours tended to occur when both cycling females and extra-group males were present (Table 3).

Male Display and Dominance Rank

Males varied in their display outputs (Table 2). During loud calls, alpha males produced more roars per bout than non-alpha males (n_{Alpha} = 8, x = 20.6,

$n_{Non-alpha}$ = 8, x = 11.5, U = 12.5, p = 0.05). The mean dominance rank of males that were observed not participating in loud call bouts was 4.17 (n = 12 bouts), while the mean rank of males that tended to call alone was 2.59 (n = 49 bouts) and the mean rank of males that continued calling longer than other males was 1.3 (n = 10 bouts). For stiff-legs, alpha males showed a trend towards greater rates than non-alpha males (n_{Alpha} = 7, x = 0.08/min., $n_{Non-alpha}$ = 15, x = 0.03/min., U = 24, p = 0.05) and for jump-displays, alpha male rates were significantly higher than those for non-alpha males (n_{Alpha} = 7, x = 0.09/min., $n_{Non-alpha}$ = 14, x = 0.005/min., U = 17, p = 0.02). The mean duration of jump-displays and stiff-legs did not differ for alpha and non-alpha males (jump-displays: n_{Alpha} = 5, x = 3.58 s, $n_{Non-alpha}$ = 5, x = 3.2 s, U = 15, p = 0.67; stiff-legs: n_{Alpha} = 7, x = 13.22 s, $n_{Non-alpha}$ = 14, x = 11.7 s, U = 36, p = 0.35). Alpha males were found to 'cheat' during 8.7% of their stiff-legs (17/195), while non-alpha males 'cheated' on 14% of their stiff-legs (21/150).

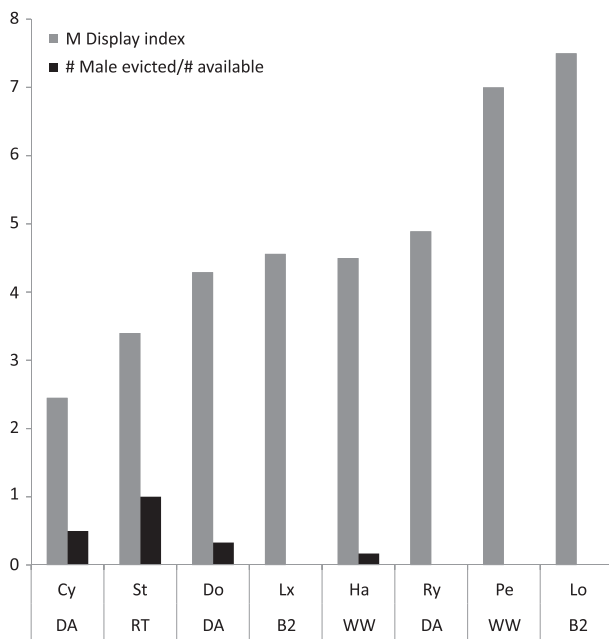In each group, higher ranked males had a propensity to display more often and/or for longer durations (Fig. 2). For groups where a test could be done, mean male rank correlated significantly with their display index (DA: n = 8, r_s = 0.91, p = 0.002; WW: n = 10, r_s = 0.82, p = 0.004). A similar pattern was seen in groups where tests could not be performed (RT and B2, see Table 2 and Fig. 2). However, when males changed rank, there was no difference in their display index at higher and lower ranks (n = 9, W = −18, p = 0.28).

Male Display and Male Eviction

Display indices comparing alpha males in each group were found to correlate with the number of other males that they successfully evicted from their group/the number of males available for eviction (n = 8, r_s = −0.91, p = 0.002) (Fig. 3). The time that a male had been alpha did not correlate with the number of other males he evicted (n = 8, r_s = 0.58, p = 0.13).

Copulation Rates and Female Proceptive Behaviour

We observed 81 copulations during the study, although after backdating to ensure females were cycling, 32 were used in calculating copulation rates. For males that did not change rank, copulation rates (no. cop./no. cycling females/mo) were not correlated with their dominance rank (n = 17, r = −0.07, p = 0.78). Copulation rates also did not correlate with male display index in any of the three groups for which a comparison could be made (B2: n = 6, r_s = 0.06, p = 0.91; DA: n = 8, r_s = 0.32, p = 0.44; WW: n = 9, r_s = −0.59, p = 0.10; Fig. 4). Among males that changed rank, copulation rates did not differ between higher vs. lower ranking conditions (n = 11, W = 21, p = 0.30).

The mean rate of female proceptive behaviour towards males did not correlate with male display index (n = 16, r = −0.09, p = 0.72). The rates of proceptive behaviours given to alpha and non-alpha males by cycling females also showed no difference (n_{Alpha} = 6, x = 0.002/min., $n_{Non-alpha}$ = 10, x = 0.002/min., U = 24, p = 0.55).

Male Sexual Solicitation and Behaviours to Influence Female Choice

Alpha and non-alpha males gave sexual solicitations to cycling females at similar rates (n_{Alpha} = 7, x = 0.003/min., $n_{Non-alpha}$ = 9, x = 0.002/min., U = 25, p = 0.52). However, during focal-samples, cycling females were only followed by alpha males (n = 3) and only alpha males used aggression to

Fig. 3: Alpha males in each group arranged in order of decreasing display output with the number of other males he evicted divided by the number available for eviction. Sampling time for each male while he was at alpha male status varied (*Cy* – 4 mo; *St* – 13 mo; *Do* – 6 mo; *Lx* – 3.5 mo; *Ha* – 10.5 mo; *Ry* – 4 mo; *Lo* – 8 mo; *Pe* – 3.5 mo).
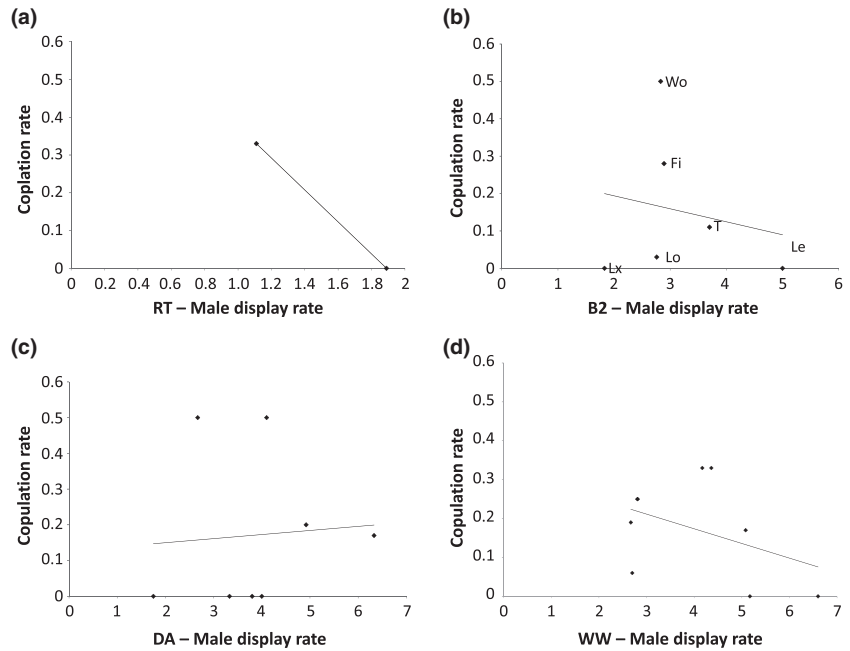
Fig. 4: Scatterplot and trend line for copulation rate (no. copulations/no. cycling females/mo) and display rate for males in each group (a. RT; b. B2; c. DA; d. WW). For (b), note that males *Lx*, *T* and *Le* were present in group B2 at a different time period than *Lo*, *Wo* and *Fi*, while the females remained the same.
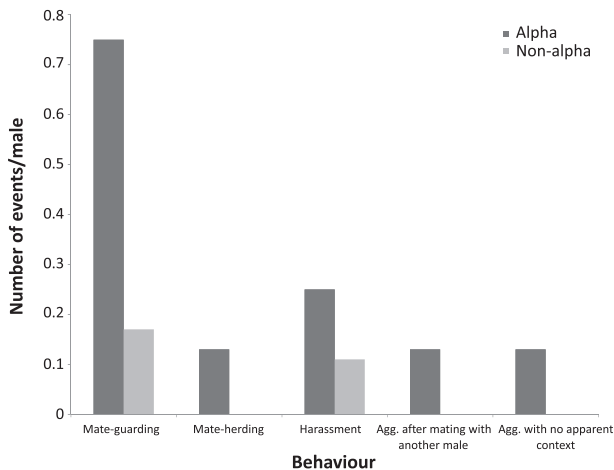

Fig. 5: Aggressive behaviours (n = 16) used by alpha and non-alpha males in four groups to influence the mate choice of cycling females.

influence female mate choice (n = 4 events). When focal-samples and *ad libitum* observations were pooled, we observed 16 aggressive events where males attempted to influence the mate choice of cycling females (mean rate = 0.011 events per hour). These behaviours were used more frequently by alpha males than non-alpha males (Fig. 5). The number of mate-guarding events observed per alpha male was 0.75, while per non-alpha male it was 0.17 (n = 9 events) and in all cases aggression was directed at lower-ranking or extra-group males. Harassment (n = 4) was observed 0.25 times per

alpha male and 0.11 times per non-alpha male. Mate-herding was only done by alpha males (0.13 events per male, n = 1) to prevent a cycling female from approaching another group. Aggression towards cycling females (0.0014 events per hour) was also only done by alpha males (0.25 events per male, n = 2), once after a female had mated with a lower ranking male and once with no apparent context (Fig. 5).

Discussion

We examined the function of male agonistic displays in ursine colobus monkeys in relation to male–male competition, female mate choice and male sexual coercion. The results are most congruent with the male–male competition hypothesis. Male displays seemed to be energetically costly, because the number of roars males' produced during loud calls and the duration of stiff-legs decreased with an increasing number of bouts performed. For jump-displays, which appeared most costly because males were bounding through the trees, durations did not decrease with an increasing number of bouts performed; however, this could be due to the overall short length of these displays. The most common stimulus for loud-calls was other male(s) calling and the presence of extra-group males. Male stiff-legs and jump-displays were overwhelmingly targeted towards other groups and individual males. The overall display output of individual males varied and

correlated with male dominance rank. Male *C. vellerosus* attain their rank by competing individually with other males (Teichroeb & Sicotte 2008b), so high rank is an indication of superior fighting ability in males. High-ranking males display more in this species, suggesting that male displays function to advertise fighting ability. Males that displayed more were also able to evict other males from their group, suggesting that males with greater fighting ability were better able to monopolize females. Male contests in *C. vellerosus* can lead to serious wounding and even death (n = 3, Sicotte et al. 2007; E. Wikberg unpubl. data). Thus, display probably allows males to assess one another and avoid contests and potential injury caused by battling with stronger competitors (Maynard Smith 1982).

We found no differences in display output when individual males changed rank. These males were, in all likelihood, contesting their position with other males before, during, and after their rank change, which probably lead to equal rates of display at both high and low ranks. They also did not show extreme rank changes.

If agonistic displays signal male fighting ability, they could also indicate a male's quality as an infant protector (Wrangham 1979; Watts 1992) or resource defender (Parker 1974; Maynard Smith & Parker 1976). If this is the case, female *C. vellerosus* may benefit by mating with males that display strongly. Thus, male displays may serve the dual functions of informing male-male competition and female mate choice. For *C. vellerosus*, there was some evidence that male displays may also function in female mate choice. Displays appeared energetically costly and where it could be tested, stiff-legs and jump-displays occurred at greater rates when females were cycling compared with when they were not. However, the rates of these displays were far higher in the presence of extra-group males suggesting that they actually function in mate defence rather than mate attraction (Table 3). Nevertheless, displays were often targeted towards other groups, and may have been observed by both extra-group males and females. Thus, they may serve in mate attraction for new females to join a displaying males' group. Our earlier work suggested that females may attempt to enter new groups based on male(s) success in intergroup encounters relative to male(s) in the females' own group (Teichroeb et al. 2009). Thus, females may choose to transfer to certain groups based on male display output. The fact that all males in a group call together in *C. vellerosus*, suggests that groups may also be advertising their overall number

of males and collective fighting ability (e.g. lions, McComb et al. 1994; chimpanzees, Wilson et al. 2001; black howler monkeys, Kitchen 2004).

We did find some evidence against the female mate choice hypothesis. Female *C. vellerosus* did not appear to choose mates based on their display output; they mated promiscuously, possibly as a counter-strategy to the relatively high rates of infanticide in this species (Hrdy 1977; Teichroeb & Sicotte 2008a). However, we could not fully test the female mate choice hypothesis with the current data set. Female *C. vellerosus* may still be preferentially selecting males that display strongly, while mating promiscuously. Indeed, observed mating success is not always a good predictor of paternity success (e.g. Curie-Cohen et al. 1983). In chimpanzees (Stumpf & Boesch 2005; Pieta 2008; Stumpf et al. 2008), orangutans (Stumpf et al. 2008), tufted capuchins (Janson 1984), and white-faced capuchins (Carnegie 2004; Carnegie et al. 2006; Jack & Fedigan 2006), females use a mixed reproductive strategy in which they are selective of their mates during the periovulatory phase (POP) when conception is probable, but are promiscuous in non-POP, when conception is unlikely or impossible. Therefore, hormonal data is needed to determine the timing of mate selection in *C. vellerosus* females. Although males that displayed strongly did not mate more often in this population, they may achieve greater paternity success if females choose them during POP.

As male display correlated with dominance rank, female *C. vellerosus* also did not appear to choose mates based on high dominance rank. Although, in mammals (Ellis 1995), and more specifically in primates (Cowlishaw & Dunbar 1991), high male dominance rank tends to correlate with mating success and paternity (Di Fiore 2003), this is not always the case (Fedigan 1983; Cowlishaw & Dunbar 1991; Dixson 1998). Alpha male *C. vellerosus* tried to monopolize cycling females more than non-alpha males by following them and using aggressive behaviours to influence female choice. These behaviours (mate-guarding, mate-herding, harassment and aggression to cycling females) are usually considered sexually coercive (see: Smuts & Smuts 1993:2; Clutton-Brock & Parker 1995); although, it needs to be determined whether they are directed more often to the most fecund females, if they generate increased mating success for coercive males, and if they are physiologically costly to females (e.g. Muller et al. 2007).

Because of the presence of behaviours that appeared sexually coercive, we also investigated whether the function of male display behaviours

could be intimidation of cycling females to make them more likely to mate with the male. This hypothesis received little support, since males that displayed more did not copulate more frequently and displays were very rarely directed at females. Jump-displays were never targeted to individual females and only a small proportion of stiff-legs (3.9%) were directed towards females. Stiff-legs that were aimed at females were often done so in a mating context (n = 8). Of these, half (n = 4) were given to a proceptive, pregnant female that was harassing a male to mate, three were given in the midst of mating, and one was given to a female when she left during mating. These stiff-legs did appear to be threats to the female but were not followed by any more intense aggression and did not appear to make the female more likely to mate with the male. The vast majority of male displays were not given in a context that could be deemed as sexual coercion, thus this does not seem to be a main function of male displays for *C. vellerosus*.

Higher-ranking males are more sexually coercive than lower-ranking males in several primate species (e.g. Japanese macaques, Matsubara 2003; mandrills, Setchell et al. 2005; grey-cheeked mangabeys, Arlet et al. 2008; chimpanzees, Muller et al. 2009). The level of monopolization that an alpha male can achieve over mating opportunities depends on the degree of overlap among females' cycling periods (Paul 1997). Although they did not mate seasonally, cycling periods for female *C. vellerosus* often over-lapped, given that male takeovers and subsequent infanticide often lead to the synchronization of female reproductive cycles within a group (Teichroeb & Sicotte 2008b). Thus, alpha males had to target a specific female to mate-guard, leaving lower-ranking males with the opportunity to guard other females (i.e. as in the priority-of-access model, Altmann 1962) and unguarded females more liberty to exercise mate choice. As female *C. vellerosus* lack external signals of ovulation, they may be able to conceal the timing of the fertile phase from males. This characteristic has been suggested to be a female counter-strategy to infanticide to thwart male mate-guarding and achieve more freedom in mate selection (van Schaik et al. 2000).

In conclusion, male agonistic displays in ursine colobus monkeys (*C. vellerosus*) appear to be sexually selected signals according to the criteria presented by Snowdon (2004). They were sexually dimorphic, being performed almost exclusively by males and there was variation among males in their display output. While we do not have direct evidence that highly displaying males had better reproductive success, male displays appeared to indicate fighting ability. Between males, these signals correlated with high rank and male ability to monopolize cycling females, although actual copulation rates and rates of proceptive behaviours did not differ between males.

Acknowledgements

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