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The function of Barbary macaque copulation calls

Stuart Semple

School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK
(s.a.semple@sussex.ac.uk)

In a wide variety of animal species, females produce vocalizations specific to mating contexts. It has been proposed that these copulation calls function to incite males to compete for access to the calling female. Two separate advantages of inciting male–male competition in this way have been put forward. The first suggests that as a result of calling, females are only mated by the highest ranking male in the vicinity (indirect mate choice hypothesis). The second proposes that copulation calling results in a female being mated by many males, thus promoting competition at the level of sperm (sperm competition hypothesis). In this paper, I give results from the first experimental study to test these hypotheses. Playback was used to examine the function of copulation calls of female Barbary macaques (*Macaca sylvanus*) in Gibraltar. Although rank did not affect lone males' likelihood of approaching copulation calls, when playbacks were given to pairs of males only the higher ranking individual approached. Moreover, females were mated significantly sooner after playback of their copulation call than after playback of a control stimulus. These results suggest that the copulation calls of female Barbary macaques play a key role in affecting patterns of male reproductive behaviour, not only providing an indirect mechanism of female choice, but also promoting sperm competition by reducing the interval between copulations. Potential fitness benefits of inciting male–male competition at these two levels are discussed.

Keywords: copulation call; *Macaca sylvanus*; female choice; sperm competition; indirect mate choice

1. INTRODUCTION

Mating animals give loud, characteristic vocalizations immediately before, during or after copulation in a wide range of animal species. The timing of the call varies between species, as does the sex of the caller. Although in some species only the male produces a copulation call, more commonly it is the female which calls, either alone or in conjunction with the male e.g. elephant seals, *Mirounga angustirostris* (Cox & Le Boeuf 1977), African elephants, *Loxodonta africana* (Poole *et al.* 1988), lions, *Panthera leo* (Schaller 1972), and a variety of birds (Montgomerie & Thornhill 1989). Female copulation calls are particularly common among the primates, e.g. lion-tailed macaques, *Macaca silenus* (Hohmann & Herzog 1985), gibbons, *Hylobates hoolock* (Hamilton & Arrowood 1978), and chimpanzees, *Pan troglodytes* (Hauser 1990; see, also, review by Hauser 1996).

A wide range of hypotheses have been put forward to explain the functional significance of female copulation calling. It has been suggested that the copulation call may function as a signal to the mating male in order to stimulate ejaculation (Todt *et al.* 1995) or coordinate orgasm (Hamilton & Arrowood 1978). Female copulation calls have also been proposed to serve as signals to other females in the group in order to inhibit (Hohmann & Herzog 1985) or promote (Viljoen 1977) breeding synchrony, or to reduce harassment of the caller by other females (O'Connell & Cowlishaw 1994). It is also possible that copulation calls could be self-stimulatory, advancing the date of ovulation in the calling female (Cheng 1992). Most recently, however, attention has focused on the possibility that female copulation calls function as signals to males other than the mating partner (Cox & Le Boeuf 1977; Hauser 1990; O'Connell & Cowlishaw 1994; Oda & Masataka 1995; Hauser 1996). Here, the call is hypothesized to incite competition between males for access to the female. This male–male competition has been proposed to occur at two separate levels—competition between individual males to gain access to a female and prevent the successful mating of others, and competition between their sperm to fertilize her.

At the first level, copulation calling could provide females with a mechanism of indirectly selecting for the strongest males as mates—the indirect mate choice hypothesis (Cox & Le Boeuf 1977; Wiley & Poston 1996). Cox & Le Boeuf (1977) proposed that the copulation calls of female elephant seals incite aggressive competition between males for access to the female, with higher ranking males interrupting and preventing copulatory attempts by subordinates. Several such displacement interactions may occur before the female is successfully mated. As a result, normally only mature, high-ranking males are able to achieve ejaculatory mounts. Copulation calls may also provide a mechanism of indirect mate choice on a longer time scale. Poole *et al.* (1988) proposed that the post-copulatory rumbles of female African elephants incite males to compete for access to the female, with the

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result that low ranking male consorts are displaced over time by higher ranking individuals; these males monopolize the female during the peak of oestrous. Effecting mate choice indirectly may be a more efficient means by which females can assess male quality than active choice, and may also be beneficial in terms of reducing search costs, male aggression or exposure to predation (Manson 1994; Wiley & Poston 1996).

O'Connell & Cowlishaw (1994) proposed that the function of copulation calling in the chacma baboon, *Papio ursinus*, is to promote competition between males at a second level—that of sperm competition (sperm competition hypothesis). Female chacma baboons in oestrous are usually consorted by males who maintain sole mating access. Females call at the end of copulation, following ejaculation when it occurs. Males attending to calls are unable to prevent the insemination event and can compete only by subsequently displacing the consort male and copulating with the female. O'Connell & Cowlishaw (1994) proposed that copulation calls in this species incite males to compete for the consort, such that the rate of consort takeover is increased and sperm competition occurs. However, Henzi (1996) disputed this suggestion, arguing that in this species aggressive consort takeovers are rare, and that there is little evidence of sperm competition occurring. This finding may result, however, from the unusual demography of study populations considered by Henzi (Cowlishaw & O'Connell 1996). O'Connell & Cowlishaw (1994) suggested that by inciting sperm competition by copulation calling, females may gain an indirect (genetic) and a direct benefit. First, if sperm quality is heritable, females may benefit through the increased reproductive success of their sons. Second, the reduced paternity certainty of males in the group may lead to an increase in male care of infants and a reduced likelihood of infanticidal attacks.

The evidence put forward in support of both the indirect mate choice and sperm competition hypotheses is inconclusive. Copulations are announced by a complex of signals—vocal, visual and also possibly olfactory—and consequently, observational methods cannot reliably be used to elucidate the function of one signalling modality alone, such as the copulation call. Despite this, very little experimental work has been carried out to explicitly test the hypotheses of the function of female copulation calling. Todt & Pohl (1984) found that male Barbary macaques, *Macaca sylvanus*, approached loudspeakers from which female copulation calls were played but failed to examine the key issue of whether these calls affected males' subsequent reproductive behaviour. Here, I report the results of playback experiments conducted on free-ranging Barbary macaques to test the indirect mate choice and sperm competition hypotheses of the function of female copulation calls.

2. MATERIALS AND METHODS

(a) *Study animals*

The Barbary macaques involved in this study belonged to two habituated troops—Middle Hill and Rock Gun (Ming 1996)—living in the Upper Rock Nature Reserve, Gibraltar. The demography of these troops is given in table 1. These troops are artificially provisioned, usually being fed daily before 10:00 h. The two troops typically have minimal contact with humans outside of the provisioning time. All individuals over 3 years old were individually recognizable.

Table 1. *Demography of the two study troops*

	male		female		
	adult	subadult	adult	subadult	juveniles[a]
Middle Hill	10	4	11	2	26
Rock Gun	7	4	10	4	22

[a] Number of juveniles assessed by counts as animals descended from sleeping areas; these animals were not individually recognized.

Barbary macaques live in multi-male, multi-female groups and are seasonal breeders; in Gibraltar, the majority of matings occur between November and February. Females develop prominent sexual swellings during oestrous. Females have between one and five oestrous periods, and post-conception oestrous is common (Küster & Paul 1984). All subadult and adult females in this study had at least one oestrous cycle, and up to five (Middle Hill) or six (Rock Gun) females were simultaneously at peak oestrous in one troop. Male rank is positively correlated with mating success (Paul *et al.* 1993), with high ranking males often peripheralizing lower ranked individuals during the mating season. As a result, the latter often mate at night or attempt to attract females away from the group to mate (Paul 1989). Females commonly mate with several different males each day while in oestrous, and consortships are typically brief (Taub 1982; Kuester & Paul 1992). The most common mount pattern seen is the single mount to ejaculation. Females give copulation calls in nearly all matings (Paul 1989); this call consists of a rhythmic succession of low frequency grunts, and typically begins during pelvic thrusting and ends after dismount. Acoustic analysis has shown that this vocalization contains sufficient cues for individual identification (Todt *et al.* 1995).

(b) *Recording and playback of experimental stimuli*

Playback experiments were conducted between December 1996 and February 1997. Copulation calls from oestrous females were recorded (distance from female 2–4 m) *ad libitum* before and during this experimental period using a Sennheiser MKH 416T directional microphone (with Sennheiser windshield and Rycote high wind cover), in conjunction with a Sony TCD-D7 digital audio tape recorder or a Marantz CP230 cassette recorder. Recordings of copulation calls given by females at the peak of oestrous during ejaculatory copulations with adult males were selected as experimental stimuli; peak oestrous was identified as the period at which the sexual swelling of a female was maximal. A 5 s duration of white noise was recorded and used as the control stimulus in experiment 3. Playbacks were conducted using a Marantz CP230 cassette recorder in conjunction with a NAGRA DSM amplifier-loudspeaker. Playbacks of all copulation calls and the control stimulus were equalized to reach a peak sound pressure level of 65 dB at 5 m in the field, with no vegetation between the speaker and sound pressure level meter. In order to avoid habituation of the study animals, at least three (and up to seven) days were left between the days (or pairs of days in experiment 3) on which playbacks occurred in one troop.

(c) *Experiment 1: does male rank affect reaction to female copulation calls?*

Adult and subadult males in the two study troops were ranked into a dominance hierarchy by creating a dominance matrix based on the outcome of clear dyadic dominance interactions observed *ad libitum* between October 1996 and February 1997. Males were arranged in the hierarchy such that the number of interactions below the diagonal of the matrix was as low as possible (Martin & Bateson 1993). A clear linear dominance hierarchy was present among males in both troops. In the Middle Hill troop, the top-ranking 7 out of the 14 males in the hierarchy were designated as high-ranking, the bottom seven as low-ranking. In the Rock Gun troop, the middle male in the dominance hierarchy (6th of 11) was not used as an experimental subject, due to the odd number of males in this troop. Males ranked 1–5 were designated high-ranking, those ranked 7–11 as low-ranking.

In this experiment, the copulation call of a female at the peak of oestrous was presented on the same day to each of two males, one high and one low-ranking, in one troop. The order of presentation of playbacks to high and low-ranking males was randomized. Playbacks were made from a concealed loudspeaker an average of 13.4 m (range 8–17 m) from the subject male. Playbacks were carried out when this male was sitting, facing away from the speaker, either resting or self-grooming. Playbacks were conducted only when the subject male was at least 20 m from any other male, and 10 m from any oestrous female (though not necessarily out of sight of such animals), and when the female, whose call was being used was out of sight, had not been in contact with the male for at least 10 min and had not mated with the male for at least 1 h. One playback was made to each of the 24 males in this experiment. The call of a different oestrous female was used as the playback stimulus for each of the 12 test pairs of high and low-ranking males. Males' reactions to playback were classified as: *look*, the male orients his head towards the speaker during playback, but does not move towards it, and *approach*, during, or within 5 s of the end of the playback stimulus, the male stands and moves at least one step towards the speaker.

(d) *Experiment 2: does rank relative to that of nearby individuals affect males' reaction to female copulation calls?*

In each of 14 trials, the copulation call of a female in peak oestrous was played from a concealed loudspeaker to a pair of males, sitting close together (mean 4.3 m; range 1–10 m) and in view of each other. The loudspeaker was placed at a point judged to be equidistant from both males (mean 17.4 m; range 13–25 m). Playbacks were conducted only when no male was within 20 m, and no oestrous female within 10 m of the experimental subjects and when the female, whose call was being used was out of sight, and had not been in contact with either male for at least 15 min. The higher-ranking male of the test pair was designated the dominant animal, the lower-ranking the subordinate (the difference in rank between males in test pairs was 2–7). No combination of males was used in more than one test pair, and no male was used in more than two pairs. Seven males appeared in two pairs; these males had a different role (i.e. subordinate in one, dominant in the other), and were presented with the playback of the call of a different female in each of the two pairs. Fourteen different copulation calls, from ten females, were used as experimental stimuli in this experiment. The males' response to playbacks was assessed as in experiment 1.

(e) *Experiment 3: do copulation calls incite sperm competition?*

In this experiment, playbacks were made when a chosen subject female at peak oestrous was out of sight of all subadult and adult males in the troop, at least 10 m (mean 15.8 m; range 10–30 m) from the nearest such male, and not in a consort. The playback stimulus was broadcast from a loudspeaker concealed from, but within 5 m of, the female, and at least 12 m from the nearest male. For each subject female, two playbacks were carried out on consecutive days. On each day, one of two stimuli—the subject female's copulation call or a white noise control—was used. The order of presentation of the two stimuli for each subject female was randomized. The identity of any males which approached the speaker during, or within the 5 s period following, the playback stimulus, was noted. Following playback, the subject female was followed and the time (to the nearest second) from the beginning of the playback to her next copulation was noted. Ten different females were used as subjects in this experiment.

(f) *Statistical analysis*

Simple non-parametric statistics were used in all comparisons. All tests were two-tailed.

3. RESULTS

(a) *Experiment 1*

When individual males were presented with playbacks of female copulation calls, all males looked toward the loudspeaker on playback of the copulation call, and some subsequently approached it (see table 2). High-ranking males were no more likely to approach the speaker than low-ranking males (Yates' corrected $\chi^2_1 = 0$, d.f. $= 1$, $n = 24$, n.s.).

(b) *Experiment 2*

When playbacks were given to pairs of males, only the dominant animals in the pair approached the loudspeaker following playback (see table 3). The difference between dominants and subordinates in probability of approaching the speaker was significant (Fisher's exact probability test: $n = 14$ pairs, $p < 0.01$).

(c) *Experiment 3*

An approach by at least one male occurred following playback of a copulation call in 5 out of 10 trials, and in none out of 10 trials following playback of the control stimulus. Subject females were mated after a significantly shorter time following playback of their copulation call than following playback of the control stimulus (table 4) (Wilcoxon matched pairs signed-ranks test $t = 3$, $n = 10$ pairs, $p < 0.01$).

4. DISCUSSION

The results of the first two experiments demonstrate that although male rank does not seem to affect lone males' propensity to approach female copulation calls, the proximity of a higher-ranking male will prevent subordinates from approaching. The results of the third experiment support the hypothesis that copulation calls serve to reduce inter-copulation intervals, and consequently promote sperm competition among males. This

Table 2. *The response of low and high-ranking males to playback of female copulation calls*

	low-ranking	high-ranking
look	4	5
approach	8	7

Table 3. *The response of subordinate and dominant males of a test pair to playback of female copulation calls*

	subordinate	dominant
look	14	7
approach	0	7

Table 4. *Time in seconds to copulation of the subject female following playback of the control stimulus or the female's copulation call*

female	control	copulation call	difference[a]
Sca	300	79	+221
Eve	807	804	+3
Lew	1102	85	+1017
Ear	786	92	+694
Len	288	410	−122
Pix	1740	47	+1693
Sun	217	36	+181
Haw	122	46	+76
Qua	471	312	+159
Sho	900	180	+720

[a] Time to next copulation after playback of the control stimulus minus time to next copulation after playback of the copulation call.

study therefore supports both the indirect mate choice and sperm competition hypotheses, and demonstrates that copulation calling by female Barbary macaques has a dual function.

First, copulation calling provides an indirect mechanism of mate choice, by which females increase their likelihood of being mated by strong males, and acquiring 'good genes' for their offspring (Andersson 1994). The reluctance of males to approach copulation calls in the presence of higher-ranking animals may well be due to the possibility of harassment or punishment (Hauser 1990). This mechanism of indirect mate choice by copulation calling could be at least partially responsible for the correlation between male social rank and relative mating and reproductive success found in this species (Paul *et al.* 1993).

This study also demonstrates that copulation calling by female Barbary macaques incites males to gain subsequent copulations with the calling female. In this way, females promote sperm competition between the males in the group. Behavioural observations of the Barbary macaque suggest that sperm competition is an important determinant of male reproductive success; in addition to copulation calling, females may actively incite sperm competition by terminating mating contacts and moving towards other males in the troop (Kuester & Paul 1992). Although there is as yet no clear evidence of an indirect (genetic) benefit to female Barbary macaques of inciting sperm competition, there is some evidence for a direct benefit as a result of paternity uncertainty of males. Infanticide is rare in this species (Angst & Thommen 1977). In addition, adult male–infant interactions are common, but paternity determination has demonstrated that males do not preferentially interact with their own progeny (Paul *et al.* 1996). However, it is not clear that adult male–infant interactions should be considered as male care; male carrying of infants can result in infant fatality (Kuester & Paul 1986), and males appear to use infants as 'agonistic buffers' (Paul *et al.* 1996). Females may also gain two further direct advantages of reducing inter-copulation intervals—by increasing their number of copulations and/or partners, they may improve their chance of conception (Dunbar & Sharman 1983; Sommer *et al.* 1992), and, in addition, the presence of a mating partner may reduce the amount of harassment suffered (O'Connell & Cowlishaw 1994).

Although copulation calls attract other males, mating males appear to combat the threat of sperm competition by maintaining contact with the female after dismount. Todt *et al.* (1995) found that male Barbary macaques remain in close proximity to a female for a longer period of time following copulations marked by female calls than following those in which no call was given; this post-mating contact is often characterized by prolonged grooming by males, and may serve a mate-guarding function. That males maintain contact for longer periods after copulations in which the female vocalizes, than after 'silent' matings supports the evidence provided here that female copulation calls attract nearby males and incite sperm competition.

It should be noted that this study has addressed only two of the hypotheses of female copulation calling. However, these vocalizations may also have further functions to those demonstrated in this work. Further work is required to examine whether other hypotheses, such as those that that suggest the call is a signal to the mating male (Todt *et al.* 1995; Hamilton & Arrowood 1978), a signal to other females (e.g. Viljoen 1977; Hohmann & Herzog 1985), or self-stimulatory (Cheng 1992), are valid. Previous attempts to examine the function of female copulation calling have been limited by the use of observational data, and the equivocal nature of the findings. The use of experimental techniques, such as playbacks, is critical if the function of vocalizations such as female copulation calls is to be systematically examined (Cheney & Seyfarth 1990).

The findings of this study have important implications for the many other primate and non-primate species in which females give copulation calls. Previous studies have proposed single functions for female copulation calls (Hamilton & Arrowood 1978; O'Connell & Cowlishaw 1994), but few have considered the potential for multiple functions, nor how these functions might interact. This work suggests that female copulation calling can indeed function at more than one level, and that these vocalizations play a key role in affecting patterns of male reproductive behaviour.

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