Perception of female reproductive state from vocal cues in a mammal species

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While acoustic signalling by males is known to affect male–male competition, mate attraction and the timing of ovulation, the extent to which sexual selection has shaped the evolution of female acoustic signals is poorly understood. Among mammals, experimental evidence indicates that females attract mating partners by using olfactory and visual signals to advertise their reproductive state. Whether or not males ascertain female reproductive state from vocal signals has, however, never been systematically tested. In this study, we use playbacks of recorded vocalizations to demonstrate that male Barbary macaques, *Macaca sylvanus*, can discriminate between female copulation calls given at different stages of the oestrous cycle, responding more strongly to those given around the time when conception is most likely to occur. Acoustic analysis suggests that the mean dominant frequency of call units and a number of temporal parameters could provide males with the information necessary to discern the proximity of ovulation in this way. Our results provide the first experimental evidence that the calls of female mammals may contain information on reproductive state, which males can perceive and use in such a way as to increase their reproductive success.

Keywords: *Macaca sylvanus*; copulation call; communication; playback; sexual selection; vocalization

1. INTRODUCTION

The importance of sexual selection in shaping the evolution of acoustic signals in insects, anurans, fish, birds and mammals is well established (Andersson 1994). Most work in this area has, however, focused on male signals which are known to influence the outcome of male contests and the timing of ovulation, as well as playing an important role in mate attraction (e.g. Clutton-Brock & Albon 1979; McComb 1987; Hasselquist *et al.* 1996). In contrast, the question of whether acoustic signalling by females has also been affected by sexual selection has tended to be overlooked (Langmore 1998). While the vocal signals of females may have a less obvious role in mate attraction than those of males, they could nonetheless have far-reaching effects on the patterns of mating behaviour that we observe.

A recent study by Langmore *et al.* (1996) highlights the importance of considering the influence of female vocalizations on mate attraction. These authors found that female alpine accentors, *Prunella collaris*, sing only during the time-period when they are fertile and that males approach singing females, who often subsequently solicit copulations from them. This study provided the first indication that female songbirds may produce song to broadcast information about their reproductive state. By varying song output in this way, females could significantly affect the number of matings that they acquire at different stages in their reproductive cycle.

Among mammals, there is no comparable evidence that female vocalizations signal reproductive state and influence patterns of mate attraction. In several species, the occurrence of particular calls has been linked to female fertility, but conclusive experimental evidence that

males respond to these calls and that they influence mate attraction by revealing the caller's reproductive status is lacking. For example, the 50 kHz vocalizations of female brown rats, *Rattus norvegicus*, are most frequently given at pro-oestrus/early-oestrus stages (Matochik *et al.* 1992) and female grey mouse lemurs, *Microcebus murinus*, produce a complex trill call solely on the one day when they are fertile (Buesching *et al.* 1998). In neither of these studies, however, were males' responses to calls experimentally examined.

There is circumstantial evidence that female primates signal reproductive state through copulation calls—loud characteristic vocalizations given just before, during or immediately after copulation (Hauser 1996; Semple 1998a). Observational and experimental studies have indicated that these vocalizations attract males, which compete with each other for subsequent copulations with the calling female (Oda & Masataka 1995; Semple 1998b). Several studies indicate that female copulation calls are longer during the period of time when the sexual swelling is at its peak (Deputte & Goustard 1980; Collins 1981; O'Connell & Cowlishaw 1994). In addition, hormonal studies and controlled mating experiments provide some evidence that the size of the sexual swelling is an indicator of proximity to ovulation (Dixson 1998). The link between parameters of the female copulation call and the size of the sexual swelling suggests that copulation calls could potentially contain information about female reproductive state.

It is crucial, however, to elucidate whether variation in copulation call characteristics over the course of the oestrous cycle is due to the approach to ovulation *per se*. For example, previous studies have failed to exclude the influence of confounding variables on the length of copulation calls in females. In particular, the average age of mating males and the frequency of complete (i.e. ejaculatory) mounts may increase as a female approaches the

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peak of oestrus (e.g. Collins 1981). As it has been proposed that both these factors can affect the form of female primate copulation calls (Hamilton & Arrowood 1978; Collins 1981; O'Connell & Cowlishaw 1994; Semple 1998a), it could be that they, rather than the female's reproductive state, result in an increase in call length around the time of ovulation. Perhaps more importantly, while variation in female primate copulation calls over the course of the oestrous cycle has been identified, no work has yet demonstrated that males are able to detect such variation, or that they adjust their behaviour in accordance with it.

In this paper, we present the results of a playback experiment carried out on free-ranging Barbary macaques, *Macaca sylvanus*, to test directly whether males respond differentially to female copulation calls given at different stages of the oestrous cycle. If males can assess a female's proximity to ovulation from her copulation calls, we would predict that they should respond more strongly to calls given at times when she is most likely to ovulate. We also analyse the female copulation calls themselves to identify acoustic parameters that males might use to assess reproductive state.

2. METHODS

(a) Study animals

The Barbary macaques involved in this study belong to two habituated troops living in the Upper Rock Nature Reserve, Gibraltar (Semple 1998a). These troops are artificially provisioned, usually being fed daily before 10.00 and again around 14.00. All animals over three years old in the two study troops were individually recognized.

(b) Mating behaviour in Barbary macaques

Barbary macaques live in multi-male, multi-female groups and are seasonal breeders with the majority of matings occurring between November and February. The Barbary macaque has a 'promiscuous' mating system (Small 1990) in which consortships are brief and females rarely mate with the same male twice in succession (Taub 1982; Küster & Paul 1992). Females have between one and five oestrous cycles, during which they develop prominent sexual swellings, and post-conception oestrus is common (Küster & Paul 1984). Females give copulation calls in nearly all matings (Semple 1998a); this call typically begins during pelvic thrusting and ends after dismount. Playback experiments have shown that, by calling, female Barbary macaques increase the number of copulations they receive and also indirectly select for the most dominant males as mating partners (Semple 1998b).

(c) Recording of playback stimuli

We recorded copulation calls from female Barbary macaques between October and December 1997. Calls were recorded *ad libitum* during the first oestrous cycle of each of 12 females (distance from female 2–5 m) using a Sennheiser MKH 416T directional microphone (with Sennheiser windshield and Rycote high-wind cover) in conjunction with a Marantz CP430 cassette recorder.

(d) Selection of playback stimuli

(i) Classification of female reproductive state

The size of the sexual swelling of females was assessed on each day that recording of copulation calls occurred and

Figure 1. Schematic of a typical oestrous cycle of female Barbary macaques, to demonstrate classification of female reproductive state in this study.

regularly throughout the entire study period. Swellings were scored on an absolute scale, according to the distance of protrusion of the swelling from the body (scores for individual females ranged from 0 to 5–9). In this study, we classified a female's calls according to the stage of oestrus at which they were given, defining oestrus as the period of time during which a female copulates (after Hrdy & Whitten 1987). We subdivided the period of oestrus into three parts: 'early oestrus', 'middle of oestrus' and 'late oestrus'. Early oestrus was defined as the period of time that the sexual swelling was the same size as the lowest score at which copulations were observed for each female. Late oestrus was defined as the period at which the sexual swelling of a female was of maximal size for that cycle (the time when ovulation is most likely to occur—see §1). The middle of oestrus was defined as the period of time between early oestrus and late oestrus (i.e. swelling score was above the lowest score at which copulations were seen, but below the maximal score for that cycle). A diagrammatic representation of this classification is given in figure 1.

(ii) Classification of age of the mating male and copulation type

We noted whether males involved in matings were sub-adult or adult, according to the age classification of Fa (1984). Copulations were classified as ejaculatory if the mating male showed a characteristic ejaculatory pause at the end of the mount, and non-ejaculatory if no such pause was observed.

(iii) Selection of copulation calls as playback stimuli

From each of 12 females, two copulation calls were selected as experimental stimuli—one a call given at early oestrus, the other a call given at late oestrus. For each female at each oestrus stage, the call to be used was chosen at random from calls that had been recorded from her during the appropriate time-period. Prior to this random selection, we set out to ensure that any difference between the two calls for a particular female was not due to a difference between the two oestrus stages in the frequency of occurrence of ejaculation or in the ages of the mating males (see §1). In order to control for the potential effect of ejaculation on call form, only copulation calls given by females during non-ejaculatory copulations were considered as potential experimental stimuli. In order to control for the effect of male age on call form, the two calls to be selected for a

particular female came only from copulations with males of one age group (sub-adult or adult).

Analysis of cycle data following call selection indicated that the early oestrus calls used in the experiment were recorded, on average, 19 days (range 13–21 days) before detumescence of the sexual swelling occurred. Late oestrus calls were recorded, on average, three days (range one to seven days) before detumescence.

(e) *Presentation of playback stimuli*

Playbacks were conducted using a Marantz CP430 cassette recorder in conjunction with a NAGRA DSM amplifier–loudspeaker. During all playbacks, the loudspeaker was concealed behind vegetation of sufficient height and thickness to conceal a copulating pair, and at least 30 s were left between concealment of the loudspeaker and commencement of the playback. Playback volumes for all copulation calls were adjusted to produce a standardized peak sound-pressure-level of 65 dB at 5 m from the loudspeaker.

(f) *Experimental protocol*

Playback experiments were conducted between December 1997 and January 1998. To each of 12 sub-adult or adult males, two playback stimuli were presented. One stimulus was the early oestrus copulation call of a female in the male's group; the other was the late oestrus copulation call of the same female. The order of presentation of the two playback stimuli was randomized for each male, and playbacks to one male were separated by one to two days. Each of the 12 males heard the copulation calls of a different female. Importantly, playbacks were presented during the middle of the second oestrous cycle of the female whose calls were being employed as experimental stimuli; thus, neither of the two calls were presented at the oestrus stage at which they were recorded. Playbacks were conducted only when the subject male was at least 20 m from any other sub-adult or adult 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. Playbacks of early oestrus calls were made from a mean of 12 m (range 9–15 m) from the subject male; those of late oestrus calls from a mean of 12 m (range 10–14 m) from the subject male. In order to avoid habituation of the study animals, at least three (and up to seven) days were left between pairs of playbacks in each troop. Males' reactions to playback were recorded using a Sony CCD-TR550E 8 mm video camera and classified according to the criteria given in table 1. In order to compare the responses of each male to playback of the two test stimuli, 'approach' was considered a stronger response than 'look', which in turn was stronger than 'no reaction'. When a male looked following playback of both early and late oestrus calls, the duration of looking was measured from the video of the trial, using a stopwatch; a longer duration of looking was considered a stronger response. We would predict that if males can assess female reproductive state from copulation calls, they should respond more strongly to calls given at late oestrus when ovulation is most likely.

(g) *Acoustic differences between early and late oestrus calls*

Although copulatory vocalizations have generally been referred to in the literature as copulation calls, they could in

Table 1. *Definition of responses of males to playback stimuli*

response	definition
no reaction	male exhibits no visible reaction during the playback stimulus
look	male orientates his head towards the loudspeaker during playback, but does not move towards it either during, or within 5 s of the end of the playback stimulus
approach	male orientates his head towards the loudspeaker during playback and stands and moves at least one step towards it during, or within 5 s of the end of the playback presentation

most cases be termed copulation call bouts as they consist of a rhythmic succession of discrete utterances. However, for consistency, we will employ the more usual terminology, referring to the whole sequence as the call and to the individual components as call units. The 12 pairs of copulation calls used in the playback experiment were analysed using a Kay Elemetrics DSP Sonagraph (Model 5500) to determine whether there were acoustic differences between calls given at late versus early oestrus. Wide band spectrograms, with a frequency range of 0–2 kHz and a time-axis of 8 s, were used for the sound analysis. For each copulation call we assessed the number of call units in the call, copulation call length (in seconds) and rate of call unit delivery (number of call units uttered per second). In addition, we calculated means for the duration of call units contained in the call (in seconds) and for the dominant frequency of these call units (in Hertz); the latter was calculated as the frequency which had the highest relative amplitude when an average power spectrum was taken for the call unit.

(h) *Statistical analyses*

Simple non-parametric tests were used for all statistical comparisons (Zar 1996); all probability values quoted are two-tailed.

3. RESULTS

(a) *Playback experiment*

Males responded more strongly to copulation calls given at late oestrus than to those given at early oestrus (table 2). When presented with playbacks of copulation calls given at early oestrus by the 12 different females, five males looked toward the loudspeaker while seven showed no reaction. When the males were presented with playbacks of copulation calls from the same females at late oestrus, all males looked towards the loudspeaker and six subsequently approached it. Considering the response of each of the 12 males in the study to their matched pair of playback stimuli, the response type to playback of the late oestrus call was stronger than that to playback of the early oestrus call for ten males and the same for two males. The two males whose response type was the same for the two playbacks both looked towards the loudspeaker on presentation of early and late oestrus calls, but did not subsequently approach it. For one of these males, the duration of looking at the loudspeaker was longer for the playback of the early oestrus call than for the

Table 2. *The response of male Barbary macaques to playback of female copulation calls given at early and late oestrus*

(Where necessary, the duration of looking, in seconds, is given.)

male	response	
	early oestrus call	late oestrus call
RIC	look	approach
PIX	no reaction	look
TRI	no reaction	look
BAD	look	approach
BOS	no reaction	approach
GRO	look	approach
VAD	no reaction	look
NEI	look (0.8)	look (4.6)
TER	no reaction	approach
SIX	look (1.3)	look (0.8)
DEX	look	approach
PUL	no reaction	look

playback of the late oestrus call; for the other, the duration of looking was longer following playback of the late oestrus call. Male response was therefore stronger following playback of the late oestrus call for 11 out of the 12 males in this experiment (see table 2; sign test: $n=12$, $x=1$, $p < 0.01$).

(b) *Acoustic analysis*

Our acoustic analysis revealed significant differences between calls given at late versus early oestrus in all the parameters that we measured (table 3). Compared with calls given at early oestrus, late oestrus calls had a higher number of call units per call (Wilcoxon matched-pairs signed-ranks test: $n=12$, $t=0$, $p < 0.001$) and were of greater length (Wilcoxon matched-pairs signed-ranks test: $n=12$, $t=0$, $p < 0.001$). In addition, calls given at late oestrus contained units that had greater mean durations (Wilcoxon matched-pairs signed-ranks test: $n=12$, $t=7$, $p < 0.01$) and higher mean dominant frequencies (Wilcoxon matched-pairs signed-ranks test: $n=12$, $t=0$, $p < 0.001$) but a lower rate of delivery (Wilcoxon matched-pairs signed-ranks test: $n=12$, $t=12$, $p < 0.05$) than early oestrus calls.

4. DISCUSSION

Our playback experiments indicate that male Barbary macaques are able to perceive differences in female copulation calls that allow them to assess female reproductive state. To our knowledge, this is the first experimental demonstration that male mammals can discern female reproductive state from acoustic signals, responding more strongly to calls uttered around the time when conception is most likely to occur. The criteria which we used to select calls as playback stimuli ensured that this differential male response did not result from the potentially confounding effects of male age and copulation type on call form.

Analysis of calls employed as playback stimuli to represent late versus early oestrus stages suggests that males could have based their assessment of female reproductive state on a number of temporal parameters of the

Table 3. *Acoustic differences between the 12 pairs of calls used in the playback experiment*(Values indicate mean $\pm$ standard deviation.)

	early oestrus calls	late oestrus calls
number of call units in the call	4.083 ± 0.941	24.750 ± 2.107
copulation call length (seconds)	1.098 ± 0.316	6.162 ± 0.663
mean duration of call units (seconds)	0.070 ± 0.003	0.086 ± 0.009
mean dominant frequency of call units (Hertz)	145 ± 17	300 ± 31
rate of call unit delivery (call units per second)	6.787 ± 1.198	4.214 ± 0.223

call and/or the distribution of energy in the frequency spectra of the call units. Not only were the calls given at late oestrus longer than those given at early oestrus but they also contained more call units, which themselves had greater mean durations; the overall rate of delivery of call units was lower at late compared with early oestrus. Moreover, in addition to these temporal differences we found that the mean dominant frequency of call units was significantly higher in late than in early oestrus calls.

The differences between early and late oestrus copulation calls in total duration, and in the number and duration of call units, are likely to have rendered the late oestrus calls more conspicuous to listeners. Indeed, this difference in overall acoustic energy could have provided the basis for the discrimination which males performed in playback experiments. However, the significant difference between early and late oestrus calls in mean dominant frequency of call units suggests that features of the frequency spectrum (and hence qualitative rather than quantitative variation) may also be important in this respect. Irrespective of the discriminatory mechanism involved, what is important is that in this species female copulation calls do contain information relating to their reproductive state, which males can perceive and use in such a way as to increase their reproductive success.

Previous experimental work has indicated that female mammals signal reproductive state by visual and olfactory means. Work on visual signals has focused in particular on the information provided by the sexual swellings that females of many primate species exhibit during oestrus. Bielert & Van der Walt (1982), for example, found that the masturbatory behaviour and serum testosterone concentration of male chacma baboons, *Papio ursinus*, exposed to visual contact with females were linked to sexual swelling size, being greatest at the time when the swelling was at its peak. Further work, in which artificial swellings were attached to ovariectomized females, produced evidence that this relationship is due to the visual stimulus of the swelling itself and not to other potentially confounding variables, such as vocal or olfactory signals (Bielert *et al.* 1989).

There is experimental evidence from a number of mammal species that olfactory stimuli may also provide

accurate information on female reproductive state. Huck & Banks (1984) demonstrated that male collared lemmings, *Dicrostonyx groenlandicus*, exposed to the odour of conspecific females in an olfactometer, were able to discriminate between oestrous and anoestrous females. In domestic sheep, *Ovis aries*, Blissitt *et al.* (1994) have shown that rams are sensitive to olfactory cues in the urine of ewes, which broadcast information on the date of ovulation. Olfactory cues to female reproductive state have also been documented in primates (Dixon 1998). Converse *et al.* (1995), for example, demonstrated that although the rate of female scent marking in pygmy marmosets, *Cebuella pygmaea*, did not vary across the oestrous cycle, males responded more strongly to such scent marks during the females peri-ovulatory period.

Our study emphasizes that it is important to evaluate the full range of signalling modalities through which information on reproductive state may be provided when considering female signalling strategies. Several authors have proposed that the lack of a sexual swelling in females of some primate species indicates that ovulation in these species is concealed from distant receivers (e.g. Sillén-Tullberg & Möller 1993). However, loud female copulation calls are found in a number of the primate species where no obvious visual signal of ovulation occurs (e.g. cotton-top tamarin, *Saguinus oedipus*; orang-utan, *Pongo pygmaeus*; Semple 1998a). It is possible that although ovulation is concealed visually in these species, receivers may nonetheless be sensitive to information on female reproductive state that is broadcast acoustically.

As well as suggesting that the potential for vocal signalling of female reproductive state should be examined in other mammal species, our results focus attention on the possibility that females may indicate their sexual receptivity using multiple signals. Female Barbary macaques have an obvious sexual swelling, which varies in relation to oestrus state, yet still produce vocalizations which contain information about their reproductive state. Recent theoretical work has concentrated on how sexual selection may have led to the evolution of multiple signals that provide information on the same aspect of the signaller (e.g. Iwasa & Pomiankowski 1994; Johnstone 1996), but this work has focused almost exclusively on traits exhibited by males. Our study indicates that the influence of sexual selection on the evolution of multiple signals in female traits should now be given serious consideration.

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