



When males call, females listen: sex differences in responsiveness to rhesus monkey, *Macaca mulatta*, copulation calls

MARC D. HAUSER*†

*Department of Psychology, Organismic & Evolutionary Biology, Harvard University

†Department of Human Evolutionary Biology, Harvard University

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In many species, males and/or females produce advertisement calls before, during or after mating. Responsiveness to these calls may vary by sex because of underlying perceptual, motivational or attentional systems. I conducted playback experiments on free-ranging adult rhesus monkeys to examine whether males and females differentially respond to calls from the same male or to calls from different males. In the within-male condition, subjects were habituated to multiple exemplars from the same male and then tested with a novel exemplar from this male. In the between-male condition, subjects were habituated to multiple exemplars from one male and then tested with a novel exemplar from a different male. For both conditions, females habituated more quickly (i.e. required fewer trials) than males. In the within-male condition, females were significantly more likely to orient towards the speaker in the test trial and to spend more time orienting than males. In the between-male condition, males and females showed no differences either in their probability of responding in the test trial or in their duration of response. Although both males and females used the available acoustic information to discriminate between male callers, females showed a heightened capacity to perceive or a stronger motivation to attend to differences between call exemplars from the same male, suggesting sex differences in the peripheral and/or central mechanisms that enable call discrimination.

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Choosing a mate typically involves first finding members of the opposite sex, then assessing their condition or quality. Since animals do this readily, it is reasonable to assume that individuals are equipped with mechanisms that facilitate discrimination of one sex from the other, as well as high- from low-quality individuals. A central problem in the study of mate choice, therefore, is to determine which characteristics provide honest indicators of quality or condition, the degree to which perceivers can extract such information, and the extent to which they use it in choosing a mate (Zahavi 1975; Andersson 1994; Bradbury & Vehrencamp 1998; Houde 2000; Gerhardt & Huber 2002; Shuster & Wade 2003; Searcy & Nowicki 2005; Phelps et al. 2006). The study of mate choice

therefore involves analyses of the factors underlying the production of mating signals as well as the mechanisms guiding the perception of such signals.

In a wide variety of animals, individuals produce acoustic signals in the context of mating (Hauser 1996; Bradbury & Vehrencamp 1998; Gerhardt & Huber 2002; Shuster & Wade 2003; Searcy & Nowicki 2005). In some cases, such as in most insects, frogs and birds, the acoustic signal is generated by males and designed to attract females. These signals are often referred to as 'advertisement calls' and are associated with the courtship phase of mating (Andersson 1982; Bradbury & Vehrencamp 1998; Gerhardt & Huber 2002; Searcy & Nowicki 2005). In other species, such as in some birds and many primates, acoustic signals are generated during copulation and, sometimes, immediately thereafter (Hauser 1996; Dixon 1998). In terms of our understanding of signal production and perception, we know far more about the adaptive significance and underlying mechanisms of advertisement calls than

Correspondence and present address: M. Hauser, 33 Kirkland Street, William James Hall, Rm 980, Cognitive Evolution Lab, Harvard University, Cambridge, MA 02138, U.S.A. (email: mdh@wjh.harvard.edu).

we do about calls given during or after copulation ('copulation calls' and 'postcopulatory calls', respectively). The following experiments focus on primate copulation calls, and in particular, the mechanisms mediating responsiveness to variation in such calls.

A survey of copulation calls in primates reveals a somewhat puzzling distribution (Hauser 1996). On the one hand, copulation calls are more commonly observed among promiscuous multimale–multifemale species than among monogamous or polygynous species. However, because some promiscuous species (e.g. vervets) lack copulation calls, but in all other respects are like species that do (e.g. macaques), the presence or absence of such calls remains a mystery. On the other hand, among species that do produce copulation calls, in some cases, these calls are restricted to one sex, and in other cases, both sexes call. In parallel with the puzzling relationship between copulation calls and mating patterns, the relationship between copulation calls and sex of the caller is equally confusing. For example, although the different macaque species tend to have highly similar mating and social systems, only males call among rhesus and stump-tail macaques, *Macaca arctoides* (de Waal 1989; Hauser 1993; Manson 1996), whereas only females call among Japanese macaques, *M. fuscata* (Oda & Masataka 1995). This seemingly random distribution of copulation calling behaviour amongst the primates suggests either that different factors influenced its evolution in the different species or that the functional significance of this behaviour is constant across species, but it has manifested itself in different ways. To discern between species-specific differences and general patterns of this behaviour, it is necessary to examine the role of copulation calls in mediating mating behaviour in individual primate species (O'Connell & Cowlshaw 1994; Cowlshaw & O'Connell 1996; Semple 1998; Semple & McComb 2000; Maestripieri & Roney 2004; Maestripieri et al. 2005). An elegant series of studies by Semple (1998, 2001) and Semple & McComb (2000) shows that a better understanding of the proximate and ultimate causes of copulation calls in primates can be achieved through careful behavioural observations and playback experiments.

The following experiments, focused on proximate causation, were designed to better understand the mechanisms mediating responses to the copulation calls of male rhesus macaques. In this species, only the male calls, the call is individually distinctive, given during thrusting and ejaculation, and sometimes suppressed as a result of intense mating competition (Hauser 1993). Results from one study suggested that the male's call functions as an honest indicator of quality, as indicated by the higher mating success of callers than noncallers, and the greater costs incurred by callers as a result of attacks by other males (Hauser 1993). In a second study, however, observations failed to find support for this hypothesis (Manson 1996). Copulation calls are one of the loudest signals within the male's repertoire and they typically cause orienting responses by both males and females. When males respond, they often approach the mating pair, and depending upon the dominance relationships, may instigate an aggressive attack. Given that both males and

females attend to these calls, but that females may have been preferentially selected to pick up on subtle variation in call morphology that predicts male quality, I designed and implemented a set of playback experiments to explore sex differences in response to male copulation calls. In particular, based on the fact that the call is loud, that it indicates clear success in terms of mating access, and is individually distinctive, all common features of fitness-related mating calls, I predicted that female rhesus macaques would show greater responsiveness to variation in call morphology than male rhesus macaques.

METHODS

Subjects

Observations and experiments were conducted on adult male and female rhesus macaques living on the 38-acre island of Cayo Santiago, Puerto Rico. This population has been under intensive observation since 1938 (Rawlins & Kessler 1987), including natural observations of their social, reproductive and ecological behaviour. During the period of investigation, there were 10–15 social groups, encompassing approximately 968–1187 individuals. The Cayo population subsists on a diet of monkey chow, grass, flowers, fruits and soil. Water is provided ad libitum, both in natural ponds as well as in artificially supported drinking wells. There are no predators on the island and there is no medical intervention. Mortality arises from feeding competition, aggression and old age. All individuals over the age of 2 years are tattooed on the inner thigh and chest, and also marked with notches on each ear. Owing to the long history of research on the island, all subjects are well habituated to the presence of human observers and are accustomed to researchers recording vocalizations at close range (1–3 m) and conducting playback experiments by broadcasting natural and synthetic acoustic signals from concealed speakers (Gouzoules et al. 1984; Hauser 1991, 1998; Rendall et al. 1996, 1998). The mating season occurs approximately during June–October, with males siring their first offspring at approximately 6 years and females giving birth at approximately 4 years. When females come into oestrus, they either show no visual signs or show slight swelling and reddening around the vagina. Females may not conceive on the first cycle, and thus, often have multiple consort partners over the mating season.

Observational Data

To supplement the playback data, several assistants and I conducted focal follows on 10 adult males from a large high-ranking group (Group F). Within each group, half of the males were high ranking and half were low ranking. We selected focal males that we observed in consort with one female and we followed the pair throughout the consorting and mating period. In addition, we obtained opportunistic data, both vocal and behavioural, from males and females in Group F as well as from other social groups.

Recordings

We recorded copulation calls opportunistically and during focal follows of consorting pairs. Vocalizations were recorded using a Sony TCD-5M stereo-cassette recorder and a Sennheiser MKH816 (with K3U power module) directional microphone. This recording system, used in previous studies (Gouzoules et al. 1984; Hauser 1991; Hauser & Marler 1993a, b), is sufficient to capture the full range of calls in the rhesus monkey's repertoire.

Playback Design and Method

Playback experiments were conducted using digitized vocalizations, played out over a CD player or from a Macintosh Powerbook. Either the CD player or the Powerbook were connected to Advent Powered Partner speakers (with a ± 2 dB flat response from 80 Hz to 18 kHz); this system accurately covers the bandwidth of male copulation calls and has been used in previous experiments with this call (Hauser & Andersson 1994; Hauser 1998).

Once we located a subject who was alone or in proximity (≤ 3 m) to no more than two other individuals, we set up the speaker. One experimenter placed the cable and speaker approximately 10–15 m away from the subject, at a 90-degree angle; the positioning of the speaker was designed to facilitate coding a response, and especially an unambiguous orientation towards the speaker. The second experimenter moved within 3–5 m of the test subject and prepared for filming; the cameraperson noted the relative position of the speaker, and thus the direction required for an orienting response. Once the test subject was sitting on the ground, resting, the cameraperson gave a subtle hand wave indicating the start of a trial and then began filming. Following 10 s of filming, the other experimenter played the designated signal and recorded written notes of all other possibly relevant events, including other individuals approaching, calling or engaging the focal subject in an interaction; filming then continued for an additional 10 s. Intertrial interval was kept at 10–60 s. Thus, no playback started earlier than 10 s after the previous playback ended, and no later than 60 s after. We calibrated the sound pressure level of the playback to the intensity level of a naturally occurring copulation call heard 10–15 m away using a Radio Shack sound level meter (68–72 dB).

For each playback session, there was a habituation phase followed by a test discrimination phase. During the habituation phase, exemplars from one class were repeatedly played back until the subject failed to orient towards the speaker on two consecutive trials. The test discrimination phase followed immediately and entailed one playback of an exemplar from a different class. The experimenter responsible for delivering the playback waited until the subject was oriented away from the speaker, and then played it back. If the subject oriented towards the speaker before the 60-s intertrial interval had elapsed, the next playback was initiated to maintain a relatively constant pace of playback delivery. If this occurred during the habituation phase, we conservatively

labelled the response as a 'yes', even if the response was ambiguous; the logic here was to assume that a response had been given to guarantee that once we moved into the test discrimination phase, subjects were clearly habituated based on the criterion of two consecutive 'no' responses. If a subject was oriented towards the speaker during the test discrimination phase, we initiated the playback; this only occurred twice, and in both cases, resulted in an uninterpretable response, forcing us to remove these data from the final analyses.

Following habituation, if a subject failed to respond in the test trial, we ran a post-test playback, using the rhesus monkey's 'shrill bark', a call given during alarm. The reason for the post-test was to distinguish between a general habituation to the test situation as opposed to the perceptual, similarity clustering of the habituation material with the test material; only the latter is conceptually interesting because it suggests that the habituation and test material are treated as the same. If a subject failed to respond to the test trial and also failed to respond to an alarm call, we assumed that the subject had habituated to the test situation and we kept this session out of the final analyses. In contrast, if any of the subjects failed to respond in the test trial, but they responded to the alarm call in the post-test trial, we assumed that they had classified habituation and test materials as the same, and thus, we included these data in the final analyses.

Experiments were aborted under the following criteria: if a fight broke out between rhesus monkeys nearby, if a copulation call was heard within 5 min of the intended initiation of the playback, or if the target subject moved during the 10-s preplayback period and failed to sit down before the playback.

There were two experimental conditions. The first condition involved a within-male design in which we repeatedly played back different exemplars of one male's copulation calls until the target subject failed to orient towards the speaker on two consecutive trials, and then we played back a novel exemplar from the same male's repertoire of copulation calls. Given prior evidence from acoustic analyses that male copulation calls are individually distinctive (Hauser 1993), the statistics reveal that the variation within a given male's calls is less than that between the calls of different males (Fig. 1). That said, there is variation within the male's calls, and the within-male design sought evidence that such variation is perceptually meaningful. We used the copulation calls from four adult males of different dominance rank from the target focal group F. For each of these males, we used up to 10 exemplars in the habituation phase and two exemplars in the test phase; we presented an approximately equal number of sessions with each of these male's calls. During habituation, we presented the exemplars in a randomized order; if a subject required more than 10 trials to habituate, we cycled back through the 10 exemplars in a randomized order. In the test phase, we played back only one of the two exemplars. We originally tested 20 adult females and 20 adult males, but data for 12 subjects were omitted using the criteria discussed above, so the final data set included 13 adult females and 15 adult males. None of the subjects were in consort, and none of the females

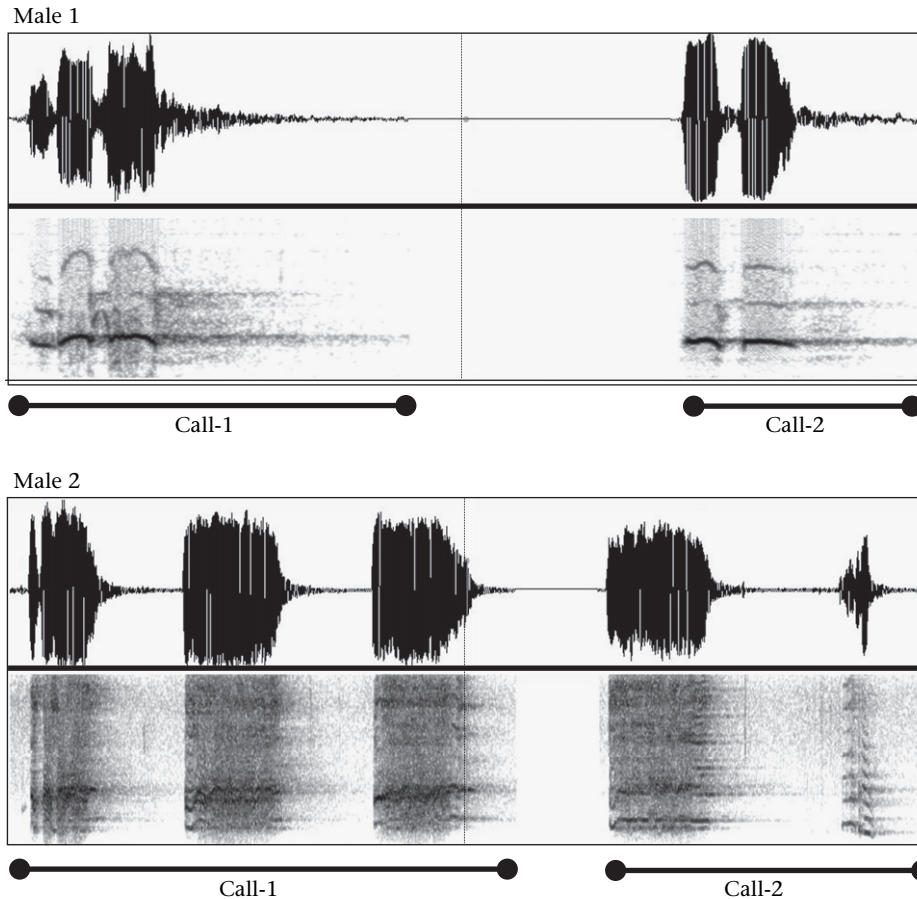


Figure 1. Exemplars of rhesus monkey copulation calls, revealing both within- and between-male variation in acoustic morphology. The upper panel of each row is the time–amplitude waveform (Y axis is amplitude, X axis is time), and the bottom panel is a 256-point FFT spectrogram (Y axis is frequency, X axis is time, greyscale is amplitude). The time axis is 2 s.

showed clear signs of being in oestrus; as noted above, and in other work on rhesus mating, reddening and swelling does not occur in all females. Although there was variation in dominance rank between our subjects, both among males and among females, the sample size was too small to look at rank as an independent variable. That said, none of the subjects were at the top or bottom end of the hierarchy within their group.

The between-male condition implemented a design that was largely the same as that used for the within-male condition, with the following exceptions. The habituation phase involved playing back multiple exemplars from one male's repertoire of copulation calls, followed by a test discrimination phase in which we played back a copulation call exemplar from a different male. In this condition, we tested 20 adult females and 20 adult males, but the final data set included 16 adult females and 14 adult males. We used the copulation calls from the same four adult males, pairing them up with each other for the habituation test phases, and providing an approximately comparable number of each pairing overall and for males and females separately.

All video records were digitized on a Macintosh computer (30 frames/s) and then analysed with Adobe Premiere. Each trial was coded blind to condition by two

independent observers. All files were analysed in terms of whether the subject oriented towards the speaker, and if so, the length of this response. Interobserver reliability for 30 independently scored trials was 100% for the dichotomous yes/no response and 93% for the duration of response.

RESULTS

The Within-male Condition

Of 28 completed habituation–discrimination sessions, the mean \pm SD number of trials to habituation was 9.1 ± 3.1 . Subjects responded on 20 of the test trials. With a sign test, this represents a statistically significant level of discrimination ($P = 0.04$). The mean \pm SD duration of response in the test trial was 2.15 ± 1.82 s.

Females habituated significantly faster than males (Student's t test: $t_{26} = 2.96$, $P = 0.008$; Fig. 2a). Following habituation, females were also more likely to respond to a novel exemplar from the habituating male's copulation call repertoire (chi-square test: $\chi_1^2 = 5.18$, $P = 0.02$). Furthermore, females spent more time oriented towards the speaker than males (Student's t test: $t_{26} = 68.58$, $P = 0.002$; Fig. 2b). Females showed a statistically significant

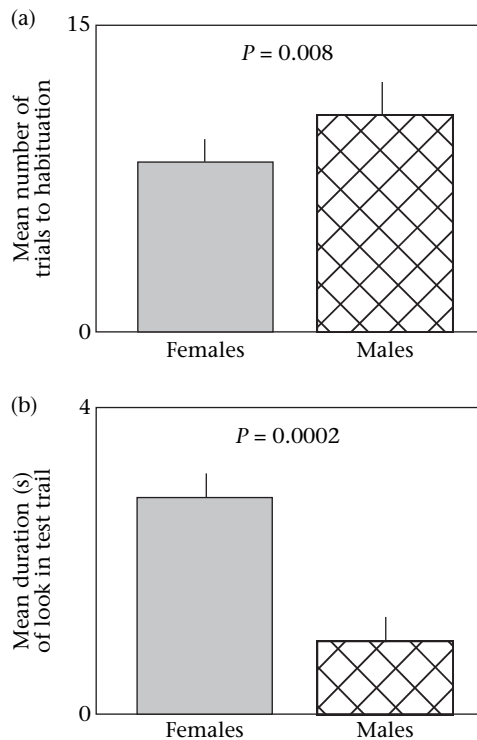


Figure 2. Response to playbacks in the within-male condition. (a) Mean + SE number of trials to habituation for adult female and male subjects. (b) Mean + SE duration (s) of look in test trial for adult female and male subjects.

level of discrimination (12 of 13; binomial test: $P = 0.003$), whereas males did not (8 of 15; $P = 0.99$).

The identity of the caller used in the playback did not affect the mean number of trials to habituation (repeated measures ANOVA: $F_{3,26} = 0.72$, $P = 0.93$), or the mean duration of response ($F_{3,26} = 1.04$, $P = 0.85$). That is, although there was acoustic variation among exemplars of a male's calls and differences between males, these differences did not generate significant differences either in the length of the habituation period or in the duration of response to the test trial.

The Between-male Condition

Of 30 completed habituation–discrimination sessions, the mean \pm SD number of trials to habituation was 9.0 ± 3.12 . Subjects responded on 26 test trials. With a sign test, this represents a statistically significant level of discrimination ($P = 0.0006$). The mean \pm SD duration of response in the test trial was 3.29 ± 1.6 s.

Females habituated significantly faster than males (Student's t test: $t_{28} = 3.14$, $P = 0.004$; Fig. 3a). Following habituation, females were no more likely than males to respond to the new male's call (chi-square test: $\chi^2_1 = 0.02$, $P = 0.89$). Furthermore, the duration of the response did not differ between females and males ($t_{28} = 0.64$, $P = 0.53$; Fig. 3b). Individuals of both sexes showed a statistically significant level of discrimination (binomial test: females: 14 of 16, $P = 0.004$; males: 12 of 14, $P = 0.01$) (Fig. 3).

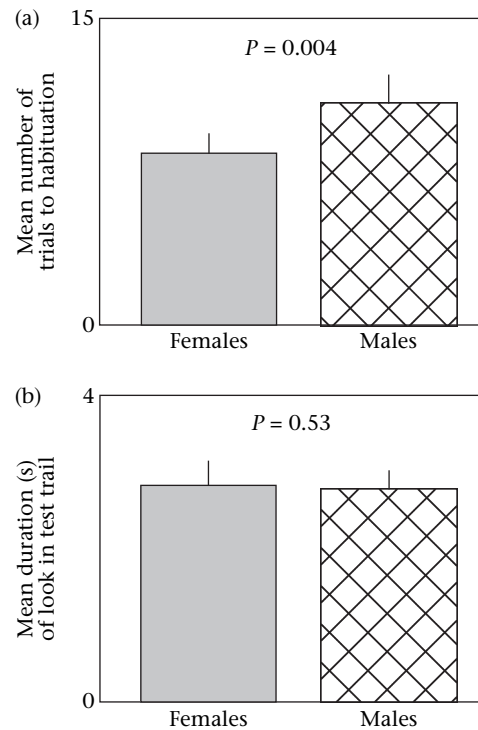


Figure 3. Response to playbacks in the between-male condition. (a) Mean + SE number of trials to habituation for adult female and male subjects. (b) Mean + SE duration (s) of look in test trial for adult female and male subjects.

The identity of the caller used in the playback did not affect the mean number of trials to habituation (repeated measures ANOVA: $F_{3,28} = 0.86$, $P = 0.96$), or the duration of response ($F_{3,28} = 1.43$, $P = 0.36$). That is, although there was acoustic variation among exemplars of a male's calls and differences between males, these differences did not generate significant differences either in the length of the habituation period or in the duration of response to the test trial.

Contrasting the two conditions with an ANOVA, there were no statistically significant differences in the mean number of trials to habituation ($F_{1,56} = 1.26$, $P = 0.26$), the number of responses in the test trial ($F_{1,56} = 0.93$, $P = 0.73$), or the mean duration of response in the test trials ($F_{1,56} = 1.08$, $P = 0.48$).

DISCUSSION

Previous studies showed that male rhesus monkeys produce loud, individually distinctive copulation calls during mating, and sometimes suppress these calls when mating competition is intense. When males produce copulation calls, they attract the attention of other males and females, and in some cases, receive physical attacks from males. Although there is current controversy concerning the adaptive function of these calls, with one study suggesting that they are handicaps (Hauser 1993), and another rejecting this account (Manson 1996), the present study provides a test of the hypothesis that selection has led to sex differences in the perception of copulation calls.

Given that these calls may provide some indication of mate quality, I predicted that females would be either more motivated or perceptually sensitive to acoustic variation than males. To test this hypothesis, I contrasted male and female responses to copulation calls in two discrimination tasks. In condition 1, I explored whether individuals would discriminate among exemplars of a single male's calls, and in condition 2, I explored whether they would discriminate between exemplars from two callers. Prior acoustic analyses revealed distinctive individual signatures, suggesting that discrimination among exemplars within a male's repertoire might be harder than discrimination among exemplars between males. Results provided support for this hypothesis. In the within-male condition, females habituated faster than males (i.e. required less input to pick up on the variation within the class), and they also responded on significantly more test trials and with longer durations. In contrast, although females habituated faster in the between-male condition, they showed the same level and duration of response in the test trial. Although there were no sex differences in the between-male condition, both males and females readily discriminated between callers.

There are at least two possible interpretations of the current results. The sex difference is mediated either by differences in motivation or by differences in perception. On the motivational account, females and males have similar perceptual abilities (i.e. on a psychophysical level, they would be equally capable of discriminating between exemplars of a single male's repertoire), but they have significantly different motivational systems, with females showing heightened interest and attention to male copulation calls, possibly because these calls encode information about the quality of the caller. This claim is, in part, driven by the nature of the experimental method used. By its nature, habituation–discrimination paradigms can only extract just-meaningful differences as opposed to just-noticeable differences (Nelson & Marler 1990). That is, when a subject responds in the test trial, this shows that it not only perceives a difference, but also finds it functionally relevant. In contrast, when a subject fails to respond in the test trial, we cannot conclude that it has failed to perceive a difference; rather, we can only conclude that whatever difference may be present, it is insufficiently salient to trigger a response. For the present studies, therefore, we can conclude that whatever difference is present among the exemplars of a male's copulation calls, it is sufficiently salient to females to warrant a response, and insufficiently salient to males. In contrast, even with sex differences in motivation, the acoustic differences between two male callers is sufficient to trigger comparable levels of responses between males and females.

The alternative account is that males and females have different perceptual capacities, with females showing a heightened ability to extract subtle differences in copulation calls from a single male. On this account, males and females are equally motivated to respond, but females perceive differences in call structure that males do not.

At present it is not possible to distinguish between these accounts, and it is, of course, possible that both are important. Psychophysical and neurophysiological tests

would provide one wedge into this problem, enabling a clear test of the perceptual account. That said, the combination of results from both conditions tilts the interpretation towards the motivational account. In the between-male condition, there was no evidence for a sex difference; both males and females showed statistically significant levels of response in the test trials, suggesting that males and females are comparably motivated to respond, as long as there are sufficient acoustic differences.

What remains for future research, therefore, is to disentangle the differences between motivation and perceptual processing, and furthermore, to better understand how acoustic variation in the male's call maps onto differences in male quality. In this sense, work on male copulation calls lags far behind that on female copulation calls, where acoustic variation is closely correlated with sexual receptivity and the probability of conception (O'Connell & Cowlshaw 1994; Oda & Masataka 1995; Cowlshaw & O'Connell 1996; Semple 1998; Semple & McComb 2000; Maestriperieri & Roney 2004; Maestriperieri et al. 2005).

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