



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

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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

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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.

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