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Why do male Columbian ground squirrels give a mating call?

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Male Columbian ground squirrels, *Spermophilus columbianus*, give a repetitive vocalization after copulation. This 'mating call' sounds similar to certain alarm calls that are given during attacks by terrestrial predators. During 2005–2006, we investigated (1) the acoustic structure and similarity of mating calls and alarm calls; (2) the environmental context when mating calls occur; (3) whether males that are likely to benefit from mate guarding (viz., males that have sperm precedence because they are the first to copulate in a female's series of matings) give mating calls to guard oestrous females; and (4) whether mating calls advertise the caller to females that have not yet mated. Our approach was to observe mating behaviour in the field and quantify reactions of squirrels to mating calls and alarm calls, both in and out of their normal context, with playback experiments. Males that were the first to copulate with an oestrous female called during mate guarding, and guarded females experienced delays before subsequent copulations. Although sound characteristics of mating calls and alarm calls did not differ, squirrels became vigilant and sought protection upon hearing alarm calls, but continued feeding during mating calls. However, when we played recorded mating calls to squirrels after breeding season, they usually reacted as if an alarm call had been given. We conclude that (1) the male mating call is an intrasexual or intersexual signal that announces postcopulatory mate guarding, and (2) contextual information is important for assessing the message of mating calls.

Keywords: alarm call; Columbian ground squirrel; communication; competition; context; mate guarding; mating call; postcopulatory; *Spermophilus columbianus*; vocalization

Mating interactions often involve an exchange of auditory signals. The pioneering description of a postejaculatory vocalization given by male brown rats, *Rattus norvegicus* (Barfield & Geyer 1972) led to studies that considered some consequences of male 'mating calls' on which sexual selection could act to favour call expression. Precopulatory calling can expedite ovulation (McComb 1987), coordinate mating interactions (Lobel 1992; Palombit et al. 1999), or increase female sexual receptivity by reducing female aggression (e.g. Nyby & Whitney 1978; Pomerantz et al. 1983; Heth et al. 1988). Mated females are hindered from extrapair copulations if males give intrasexual or intersexual threat calls that announce postcopulatory mate guarding (Tamura 1995; McElligott & Hayden 2001; Grafe et al. 2004). Calling males can also attract the attention of prospective mates or entice nearby females to copy the mate choice of earlier-copulating females (e.g. Mobley et al. 1988; Clutton-Brock et al. 1989; Hoglund et al. 1990; Gibson et al. 1991; Møller 1991; Kelley 2004; Velez & Brockmann 2006).

For species such as black-tailed prairie dogs, *Cynomys ludovicianus*, mating calls are acoustically unique vocalizations (Grady & Hoogland 1986; Hoogland 1995). But

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other animals such as Formosan squirrels, *Callosciurus erythraeus thaiwanensis*, give mating calls that are acoustically similar to antipredator alarm calls, thus manipulating listeners through a dishonest 'cry of wolf' (Tamura 1995). These deceptive calls may occupy the attention of male rivals or prolong lordosis of a mated female, thereby ensuring that the caller's sperm reach the female's uterus (Barfield & Geyer 1972; Cherry 1989; Tamura 1995). However, listeners can sometimes differentiate between similar calls by extracting information from subtle changes in the rate and duration of the calls (Leger et al. 1984; Cherry 1989), or individual differences in the acoustic characteristics (Shipley et al. 1981; Gyger & Marler 1988). Furthermore, incidental contextual cues may be available from the circumstances surrounding calls, rather than from the structure or pattern of the calls per se (Smith 1977, 1991; Leger 1993).

Broadcasting the presence of an oestrous female might compromise a male's opportunity to sire progeny, owing to the increased possibility of subsequent copulations with the oestrous female by nearby males. So, why give a mating call? And what sources of information do listeners use to interpret mating calls? To address these questions, we report a postcopulatory vocalization given by male Columbian ground squirrels, *Spermophilus columbianus*, that has not been described previously. Columbian ground squirrels are diurnal, herbivorous, and colonial rodents (Betts 1976; Elliott & Flinders 1991). When a predator attacks, they run to a burrow and assume a vigilant posture, and may give an alarm call at any time (Harris et al. 1983; Lickley 1984; MacWhirter 1992). Females live adjacently in philopatric kin clusters and with a few nonreproductive animals of both sexes (King & Murie 1985). During a 3-week mating period, a territorial reproductive male (usually $\geq$3 years old) overlaps the ranges of one or a few females (Murie & Harris 1978, 1988). Young subordinate males (2–3 years old) usually do not maintain a territory, but are physically able to reproduce and sometimes obtain copulations (F. S. Dobson, T. G. Manno, P. H. Jones & A. P. Nesterova, unpublished data). Females are highly promiscuous during their annual day of oestrus, which occurs 2–12 days after emergence from hibernation in April (Betts 1976; Murie 1995). Females may solicit courtship or copulate with their territorial male, adjacent territory holders, and subordinate young males. Litter size is 2–4, and males that copulate first in a female's series of matings (viz., usually the nearest territorial male) have sperm precedence (Murie 1995; J. O. Murie, personal communication).

We examined (1) the acoustic structure and similarity of mating calls and alarm calls; (2) the environmental context when mating calls occur; (3) whether males that are likely to benefit from mate guarding (viz., males that copulate first in a female's series of matings) give mating calls to guard oestrous females; and (4) whether mating calls advertise the caller to females that have not yet mated. Our approach was to observe mating behaviour in the field and quantify reactions of squirrels to mating calls and alarm calls, both in and out of their normal context, with playback experiments (after Hoogland 1995; Tamura 1995).

METHODS

Oestrus and Copulation

From April to July in 2005 and 2006, we observed wild, free-ranging Columbian ground squirrels of known age and matrilineal genealogy at two colonies (Meadow B and DOT) in Sheep River Provincial Park, Alberta, Canada (50°38′N, 114°38′W, elevation 1500 m) from 4-m-high observation towers. Squirrels were trapped 1–2 days after they emerged from hibernation, ushered into a cloth bag, restrained by hand, weighed, and fitted with numbered metal fingerling eartags for long-term identification (National Band & Tag Co., Newport, KY, U.S.A.). For visual identification from a distance, we painted each animal with a unique symbol using black dye (Lady Clairol Hydrience; Proctor and Gamble, Stamford, CT, U.S.A.). We considered males with a pigmented scrotum and large descended testes at the time of trapping to be reproductive. We also trapped females several additional times during the 3-week breeding period and examined their vulvar condition to determine whether they were in oestrus (viz., had a fully opened vulva).

We watched squirrels at both colonies from dawn until dusk every day during breeding. This observation period extended from the third week of April to the first or second week of May. Each reproductive female was sexually receptive for a few hours on a single day during this period, and we easily observed the copulations that occasionally occurred aboveground. We also used the methods of Hoogland (1995) and Murie (1995) to infer underground copulations of individuals from aboveground diagnostic behaviours: (1) submergence of both partners into the same burrow, where they remained for at least several minutes; (2) self-licking of genitals by both partners upon later emergence, which was sometimes accompanied by dustbathing; and (3) behaviours indicating that males were mate guarding, such as chasing the female into a burrow, sitting on that burrow, and fighting with other males. We considered males to be territorial if there was an established area in which they were victorious in hostile interactions with other males (other males were considered subordinate; Dobson 1983). We scored the territoriality level of males based on the proportion of the breeding season during which they were territorial.

Recording of Vocalizations and Vigilance

Males sometimes give a series of 'chirps' shortly after copulating with an oestrous female. During our observations of oestrus and copulation, we noted every time this occurred; each series of chirps was termed a 'mating call' (after Grady & Hoogland 1986; Hoogland 1995). In 2006, three of us (T.G.M., L.M.D., K.S.W.) also made audio recordings of mating calls as they occurred during breeding at colony DOT ($N = 33$ calls). We recorded the calls from our towers, which were about 20–30 m away from the calling males, so as to not interfere with courtships. During the recordings, we simultaneously noted the behaviours of individuals that were within 10 m of calling males in four ways. First, we noted the maximum vigilant