

## Why do male black-tailed prairie dogs (*Cynomys ludovicianus*) give a mating call?

R. MARK GRADY & JOHN L. HOOGLAND\*

Department of Biology, Princeton University, Princeton, New Jersey 08544, U.S.A.

**Abstract.** A colony of black-tailed prairie dogs (Rodentia: Sciuridae: *Cynomys ludovicianus*) is subdivided into harem-polygynous social groups called coteries. The resident male(s) of each coterie often gives a unique mating call before or after copulating. Data on mating calls were available for 367 copulations. Males of one-male coteries were significantly more likely to call than males of multi-male coteries. In cases where a female copulated with more than one male, the first copulating male was significantly more likely to call than subsequent copulating males. A mating call given by the first copulating male did not deter the oestrous female from copulating with additional males. Coterie size varied inversely with calling. Surprisingly, females that copulated with a calling male were significantly less likely to wean a litter.

Black-tailed prairie dogs (Sciuridae: *Cynomys ludovicianus*) are large (700–1500 g), diurnal rodents. They live in large colonies that are subdivided into contiguous, territorial social groups called coteries (King 1955; Hoogland 1979, 1981a, b, 1983). A coterie typically consists of one resident adult male, three or four adult females plus several yearlings and juveniles of both sexes. Coteries sometimes contain two or more resident adult males (multi-male coteries). The black-tail mating system is harem-polygynous, with variance in reproductive success being higher for males than for females (Hoogland & Foltz 1982). As might be expected with such a complex social organization, black-tails display an elaborate system of vocal communication (King 1955; Waring 1970; Smith et al. 1976, 1977). In this report we investigate a unique call given by a male black-tail just before or just after copulating; this call has not been previously described.

In South Dakota, black-tails breed in February and March. Females come into oestrus (sexual receptivity) for only one day of the year. In one-male coteries, a female usually copulates with the single resident adult male (one-male mating). Females in multi-male coteries generally copulate with more than one resident male (multi-male mating). Occasionally a female will copulate with a male from a different coterie (invading male) (Hoogland & Foltz 1982). Even though one-third of all oestrous females in one breeding season may copulate with two or more males, unequivocal

cases of multiple paternity are rare (Hoogland & Foltz 1982). While oestrous females seldom copulate with more than two males, individual males may copulate with as many as nine females during any one breeding season.

Copulation normally takes place underground during an 'underground consortship' (Hoogland 1982; Hoogland & Foltz 1982). An entire mating sequence usually entails a series of underground consortships between which the copulating male and female surface. Sometimes a mating pair will enter a burrow and remain there for the rest of the day.

When a female is in oestrus, a nearby male sometimes emits one or more series of barks. Each series is termed a mating call. These calls may be given prior to the first consortship (a pre-copulatory call), between consortships, or after the last consortship (a post-copulatory call). The timing and cadence of the mating call clearly distinguish it from other black-tail vocalizations. Females never give a mating call. Males also give a unique mating call before or after copulating in Belding's ground squirrels (*Spermophilus beldingi*) (Leger et al. 1984) and white-tailed prairie dogs (*Cynomys leucurus*) (Hoogland, unpublished data), and possibly also in tassel-eared squirrels (*Sciurus aberti*) (Farentinos 1974).

The adaptive significance of the black-tail mating call is not clear. Almost half the copulations occur with no calling. Further, data to this point indicate that calling may be negatively associated with male reproductive success. Because the reason for the mating call is not obvious, several variables were compared with the calling behaviour in hope of finding a possible explanation. Comparisons were made with the following eight variables: time

Present address: Appalachian Environmental Laboratory, The University of Maryland, Gunter Hall, Frostburg, Maryland 21532, U.S.A.

of breeding season, age of male, age of female, coterie size, order of copulation in males, status of the male (resident or invading), number of resident males, and success of the female in weaning a litter (this is equivalent to success of the male in siring a weaned litter). We also tested for a correlation between a male's calling and the oestrous female's subsequent copulation with competing males.

## METHODS

Data for this report were collected by John Hoogland and his field assistants from a black-tail colony in Wind Cave National Park, South Dakota (Hoogland & Foltz 1982). Black-tail matings were observed during six complete breeding seasons from 1978 through 1983; 254 female oestrus periods were observed, involving a total of 367 copulations, 141 different females, and 92 different males. For all copulations, the presence or absence of a mating call was recorded. Other data available for each copulation included age of the copulating male(s), age of the oestrous female, the female's home coterie size (number of adults and yearlings), status of the copulating male(s) (resident or invading), order of copulations in a multi-male mating, and number of resident males within the female's home coterie (one-male or multi-male). Not all matings were observed during each breeding season and not every mating was complete in its data. Copulations which involved a mating pair that remained underground all day were scored as copulations with no calls ( $N=13$ ).

A mating was termed successful only if the female weaned offspring. Accurate data on reproductive success prior to weaning were not available because juveniles are born underground and do not appear above ground until they are approximately 6 weeks old (at or near weaning). A successful male therefore was one that copulated with a female that weaned a litter. In multi-male matings, the identity of the true father was often unknown (Hoogland & Foltz 1982); consequently, the test of calling versus male reproductive success was done using only data from one-male matings.

The time of breeding season in which a mating took place was determined from the median of all mating dates for the entire colony for that particular year. Copulations observed before the median date were labelled early; copulations observed after the median date were labelled late. Females within a coterie usually breed synchronously and females

of one coterie may breed as much as 2 weeks before or after females of an adjacent coterie (Hoogland 1981a). Accordingly, the oestrous females within each coterie were also divided into early or late categories; the first half of the females to copulate within the coterie was labelled early while the second half of the females to copulate was labelled late. The female oestrus periods for a coterie were used only if more than half the adult females of that coterie were observed to copulate; data were available for 64 coterie involving 204 oestrus periods. In coterie with an odd number of oestrous females, the 'late' group was made the larger.

Data were analysed by either the  $2 \times 2$  chi-squared test or the Mann-Whitney  $U$ -test. All significance levels are from two-tailed tests. Data from the same individual during different matings were considered independent.

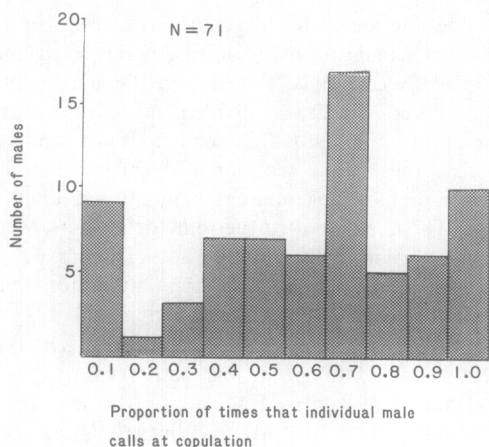
## RESULTS

Of the 254 periods of oestrus, 177 (70%) involved at least one mating call; 77 (30%) had none. One-male matings occurred with 167 (66%) of the oestrous females; 87 (34%) of the females mated with two or more males. No female ever mated with more than four males. Matings with at least one invading male occurred with 36 (14%) of the females. Only four (2%) females mated solely with an invading male. Of the 254 periods of oestrus, 121 (48%) led to weaned young while 133 (52%) did not.

The 254 oestrus periods involved a total of 367 copulations; 167 (46%) of the copulations were part of one-male matings while 200 (54%) were part of multi-male matings. The male called at least once in 200 (54%) of the 367 copulations; 167 (46%) copulations involved no calling. Of the 367 copulations, 38 (10%) involved invading males.

One mating call consists of a series of barks. For copulations involving at least one mating call ( $N=200$ ), there is extreme variation in (a) the number of mating calls (mean  $\pm$  SD =  $5.3 \pm 6.1$ , range = 1–28) and (b) the cumulative length of calling time (mean  $\pm$  SD =  $11.0 \pm 20.1$  min, range = 0.1–136 min). Individual males also show a high variability in their tendency to give a mating call (Fig. 1). With only three or four exceptions, a mating call was never heard unless a nearby female was in oestrus. The exceptions occurred on the day before or the day after a female's oestrus.

Regarding the colony as a whole, 111 of 198 early



**Figure 1.** Proportion of times that an individual male calls at copulation. Only data from males that copulated two or more times were used. The mean  $\pm$  SD number of copulations for each male was  $4.9 \pm 2.7$  (range = 2–14). If a male copulated in more than one year, then data from all years were combined so that there was a single proportion for each male.

copulations (56%) and 89 of 169 late copulations (53%) involved at least one mating call. This difference is not significant ( $\chi^2 = 0.42$ ,  $P > 0.40$ ). Regarding individual coterie, 61 of 94 early copulations (65%) and 74 of 110 late copulations (67%) involved at least one mating call. This difference is also not significant ( $\chi^2 = 0.13$ ,  $P > 0.25$ ).

Whereas 184 of 329 copulations by a resident male (56%) involved at least one mating call, only 16 of 38 copulations by an invading male (42%) involved at least one mating call. Although this difference is not significant ( $\chi^2 = 2.62$ ,  $P > 0.10$ ), possibly owing to the small number of invading males, it does indicate a trend for resident males to call more than invading males.

In one-male coterie, 91 of 131 copulations (69%) involved at least one mating call; in multi-male coterie, only 93 of 198 copulations (47%) involved at least one mating call. This difference is highly significant ( $\chi^2 = 16.2$ ,  $P < 0.001$ ). Data from invading males were excluded from this analysis.

Whereas 59 of 87 first copulations (68%) in a multi-male mating involved at least one mating call, only 31 of 113 subsequent (second, third or fourth) copulations (27%) involved at least one mating call. This difference is highly significant ( $\chi^2 = 32.4$ ,  $P < 0.001$ ).

In one-male matings with no mating calls, 33 of

57 copulations (58%) resulted in a weaned litter; in one-male matings with at least one mating call, only 44 of 110 (40%) resulted in a weaned litter. This difference is significant ( $\chi^2 = 4.84$ ,  $P < 0.05$ ), indicating that a male is more likely to call with an oestrous female who subsequently fails to wean a litter.

Of 169 matings in which the first copulating male called, 59 involved copulations with subsequent males (35%); of 85 matings in which the first copulating male did not call, 28 involved copulations with subsequent males (33%). This difference is not significant ( $\chi^2 = 0.10$ ,  $P > 0.20$ ), indicating that calling by the first copulating male does not inhibit subsequent copulations by the oestrous female with other males.

The mean  $\pm$  SD age (in years) of females whose oestrus involved a mating call was  $2.8 \pm 1.4$  ( $N = 140$ ); the mean  $\pm$  SD age of females whose oestrus did not involve a mating call was  $2.7 \pm 1.4$  ( $N = 62$ ). The mean  $\pm$  SD age (years) of copulating males that gave a mating call was  $2.6 \pm 0.8$  ( $N = 184$ ); the mean  $\pm$  SD age of copulating males that did not give a mating call was  $2.4 \pm 0.8$  ( $N = 160$ ). These differences are not significant for either sex (Mann–Whitney  $U$ -test,  $P > 0.10$ ).

For copulations involving at least one mating call, the mean  $\pm$  SD coterie size was  $8.2 \pm 5.5$  ( $N = 200$ ); for copulations that did not involve any mating calls, the mean  $\pm$  SD coterie size was  $9.1 \pm 5.5$  ( $N = 167$ ). This difference was significant (Mann–Whitney  $U$ -test,  $P = 0.025$ ), and may result because small coterie are more likely than larger coterie to be one-male rather than multi-male (Hoogland 1981b; Hoogland & Foltz 1982).

## DISCUSSION

Individual male black-tails show tremendous variation in their calling behaviour. A particular male may call for one oestrous female on one day but may not call for another oestrous female on another day (Fig. 1). Also, a male may call with an oestrous female one year but the same male (or a different male) may not call with the same female when she is in oestrus the next year. Further, a male may call before or after copulating or he may call both before and after. In general, whereas some calls can be accurately categorized as coming before or after a copulation, the majority cannot be so easily categorized. An additional problem is

that, in most calling situations, it is difficult to tell, from field observations, where the call is actually directed. As discussed below, the male may be calling to the oestrous female, to competing males, or to females who have not yet come into oestrus.

A male usually calls when the oestrous female is nearby, suggesting that he is calling directly to her. Studies of myomorphic rodents have shown that, in many species, a male reduces a female's aggressiveness and stimulates sexual contact by emitting an ultrasonic pre-copulatory call (Nyby & Whitney 1978; Barfield et al. 1979). In black-tails, the oestrous female generally behaves antagonistically towards a male's sexual advances (Hoogland, unpublished data); therefore, it is possible that the mating call functions to reduce her aggressiveness (see also Farentinos 1974). If the mating call does act to increase a female's receptivity, then the male should only call before copulating. However, since males frequently call after copulating, it is doubtful that the call functions solely to increase female receptivity. Further, males sometimes call while the oestrous female is still underground where she may not hear the call very well.

For some mammals, a male's call, given in the presence of an oestrous female, announces his competitive status and warns other males of his willingness to defend the oestrous female (Tembrock 1963; Anisko et al. 1978; Peters 1980). The fact that male black-tails sometimes attempt to interrupt another male's copulation (Hoogland, unpublished data) might justify a call directed to competing males. A male black-tail usually herds and defends the female with whom he has just copulated; a post-copulatory call would perhaps aid his defence. If a black-tail female copulates with only one male, then that male is guaranteed paternity; when a female copulates with two or more males, paternity is not assured for any of the copulating males (Hoogland & Foltz 1982). Thus, the first male to copulate has more to lose genetically than subsequent copulating males; this might explain why first copulating males are more likely to call in a multi-male copulation than any of the subsequent copulating males. On the other hand, if the first copulating male calls to warn off competing males, then the oestrous female should be less likely to copulate with subsequent males when the first copulating male calls. However, data show that calling by the first copulating male does not significantly decrease the probability of the female copulating with additional males. Additionally,

although multi-male coterie have more competing males than one-male coterie, males of multi-male coterie are significantly less likely to call than males of one-male coterie.

Lastly, a male's mating call may be directed to females who have not yet come into oestrus. If a male is calling to non-oestrous females, then he should call more often early in the breeding season, rather than late, since the number of females who have not yet come into oestrus declines with time. However, time of mating for the entire colony showed no significant correlation with whether a male called. Further, time of mating within coterie versus calling also showed no significance. These tests both imply that males are not calling solely to females who have not yet come into oestrus.

It seems surprising that calling males sire fewer weaned offspring than do males that do not call. Since mating calls are more likely in small, one-male coterie and since weaning success varies inversely with coterie size (Hoogland 1981b), it seems that calling would be positively associated with weaning success. Perhaps oestrous females that are unlikely to wean a litter are less sexually receptive and therefore are more likely to require a mating call for successful copulation. More data are clearly needed for a better understanding of the black-tail mating call. In view of the black-tail's complex social organization and the extreme individual variation reported here, it seems unlikely that any one function will explain the significance of the male black-tail's mating call.

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## REFERENCES

- Anisko, J. J., Suer, S. F., McClintock, M. K. & Adler N. T. 1978. Relation between 22 kilohertz ultrasonic signals and socio-sexual behavior in rats. *J. comp. physiol. Psychol.*, **92**, 821–829.
- Barfield, R. H., Auerbach, P., Geyer, L. A. & McIntosh, T. K. 1979. Ultrasonic vocalizations in rat sexual behavior. *Am. Zool.*, **19**, 469–480.
- Farentinos, R. C. 1974. Social communication of the tassel-eared squirrel (*Sciurus aberti*). A descriptive analysis. *Z. Tierpsychol.*, **34**, 441–458.
- Hoogland, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. *Behaviour*, **69**, 1–35.
- Hoogland, J. L. 1981a. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology*, **62**, 252–272.
- Hoogland, J. L. 1981b. Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 283–310. New York: Chiron Press.
- Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. *Science, N.Y.*, **215**, 1639–1641.
- Hoogland, J. L. 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Anim. Behav.*, **31**, 472–479.
- Hoogland, J. L. & Foltz, D. W. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behav. Ecol. Sociobiol.*, **11**, 155–163.
- King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib. Lab. Vertebr. Biol. Univ. Mich.*, **67**, 1–123.
- Leger, D. W., Berney-Key, S. D., & Sherman, P. W. 1984. Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). *Anim. Behav.*, **32**, 753–764.
- Nyby, J. & Whitney, G. 1978. Ultrasonic communication of adult myomorph rodents. *Neurosci. Biobehav. Rev.*, **2**, 1–14.
- Peters, R. 1980. *Mammalian Communication: A Behavioral Analysis of Meaning*. Monterey, California: Brooks/Cole.
- Smith, W. J., Smith, S. L., DeVilla, J. G. & Oppenheimer, E. C. 1976. The jump-yip display of the black-tailed prairie dog, *Cynomys ludovicianus*. *Anim. Behav.*, **24**, 609–621.
- Smith, W. J., Smith, S. L., Oppenheimer, E. C. & DeVilla, J. G. 1977. Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. *Anim. Behav.*, **25**, 152–164.
- Tembrock, G. 1963. Acoustic behaviour of mammals. In: *Acoustic Behavior of Animals* (Ed. by R. G. Bushel), pp. 751–786. New York: Elsevier.
- Waring, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *Am. Midl. Nat.*, **83**, 167–185.

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