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Behavioral tactics, dominance, and copulatory success among male fox squirrels

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The behavioral tactics and mating behavior of male fox squirrels (*Sciurus niger*) were studied in a small population of uniquely marked, free-ranging individuals during the winter breeding season in 1986 to 1990. Twelve mating bouts were observed with an average of 5.83 males. Two alternative male reproductive tactics were active pursuit and satellite. Active-pursuit males were the most dominant squirrels that fought for and defended proximity to the estrous female. Satellite males were subordinates that remained dispersed in the estrous female's home range but avoided interaction with active-pursuit males. Active pursuit accounted for more copulations than the satellite tactic (0.83 vs 0.23 copulations/male/bout) with the copulations distributed more evenly among active-pursuit males (CV = 133.7) than among satellite males (CV = 191.3). Satellite males copulated with a female after she avoided the contest competition among active-pursuit males. Although the tactics were dominance-based, dominance rank was not directly correlated with mating success. However, high-ranking, dominant males gained access to and mounted more females than lower ranking males. The alternative mating tactics of male fox squirrels may be important in mediating intermale mating success.

KEY WORDS: mating behavior, *Sciurus niger*, Sciuridae, alternative mating tactics, copulatory success, dominance rank.

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INTRODUCTION

One hypothesized advantage of intraspecific dominance is increased access to mates in species where estrous females represent a limited resource that can be defended (DEWSBURY 1982). However, alternative male reproductive tactics evidenced in many species appear to have fitness payoffs to subordinates, although the payoffs are usually less than those for dominants (RUBENSTEIN 1980, DUNBAR 1982, HOWARD 1984, KODRIC-BROWN 1986). Such tactics are likely to be a form of a conditional Evolutionary Stable Strategy (ESS) with the rules "when dominant play strategy X; when subordinate play strategy Y"; this ESS is also known as "making the best of a bad job" (PARKER 1984).

The tree squirrels (Sciuridae Sciurinae) are characterized by a mating system of dominance polygyny or promiscuity where numerous males pursue a female on her 1-day estrus; levels of aggression are extremely high (*Sciurus aberti*: FARENTINOS 1972; *S. carolinensis*: BAKKEN 1959, THOMPSON 1977, KOPROWSKI 1993; *S. niger*: BENSON 1980; *S. vulgaris*: WAUTERS et al. 1990). In some species, dominant males copulate more frequently than subordinates (FARENTINOS 1972, THOMPSON 1977, WAUTERS et al. 1990, KOPROWSKI 1993). The observations of BAKKEN (1959), FARENTINOS (1972), THOMPSON (1977) and WAUTERS et al. (1990) suggest that subordinate males may use an alternative tactic by remaining at a distance from the estrous female and the dominant males. I recently documented the existence of the alternative tactics of active-pursuit (which is used by old, dominant males that actively compete for and defend proximity to the estrous female) and satellite (which is used by young, subordinate males that remain peripheral but attentive to the estrous female) among male eastern gray squirrels (*S. carolinensis*: KOPROWSKI 1993).

The tactics of adult male fox squirrels (*S. niger*) during mating bouts are poorly understood. Mating bouts were briefly described by BENSON (1980) who suggested that participation in mating bouts and possibly copulatory success are correlated with dominance. Herein, I report on the mating behavior of a small population of fox squirrels (four to six adult female residents from 1986 to 1990). My objectives were to: (1) describe the mating bouts of the fox squirrel, (2) describe the behavioral tactics used by males, and (3) examine the relationship between dominance rank and the number of mounts and copulations by males.

MATERIALS AND METHODS

Study area

The study area was a 4.2-ha parkland located on the University of Kansas campus, Lawrence, Douglas County, Kansas, USA. University roadways, buildings, and parking lots delineated the boundaries of the area. The canopy of the woodlot was dominated by black walnut (*Juglans nigra*: 18.8% of 319 stems). The ground cover was mowed grass; the absence of a shrub stratum and the habituation of squirrels to humans facilitated observations.

Field methods

Since May 1986, squirrels were trapped in 15 by 15 by 60 cm wire-mesh live traps (Tomahawk Live Trap Company, Tomahawk, WI) baited with peanuts and peanut butter. Squirrels were ear-tagged with uniquely numbered tags (Monel no. 1, National Band and Tag, Newport, KY) and marked for identification at a distance by uniquely coded ear stream-

ers (KOPROWSKI et al. 1988) or patterns of unpigmented pelage by freeze marking (ROOD & NELLIS 1980).

Due to difficulties in observing copulations during the May-June breeding period because of leaf cover, I focused observations in the winter breeding season. Each morning prior to dawn from mid-December to mid-February 1986-1990, I traversed the study area in search of males congregating in the vicinity of an estrous female's den. Because many males congregate in an estrous female's home range, mating bouts are easily located. Peripheral areas within 500 m of the study area were also explored for mating bouts involving marked males. When a mating bout was detected, the activities and participants were recorded and followed continuously until bout termination. A male was scored as dominant when it chased or aggressively contacted another male. Reversals in the outcome of agonistic encounters were sought; however, none were ever observed within any mating bout. Dominance ranks were assigned based upon the percentage of participating males that each male dominated; the most dominant male won 100% of its encounters with other males and received a rank of 1. Subordinate animals received ranks of 2 to n (where n = number of participants); no tied ranks occurred. The time, location, and fate of all mounts were recorded. Duration of copulation was measured as the time from the first pelvic thrust by the male to the time of dismount. Both sexes groom their own genitalia only after the male's ejaculation (MCCLOSKEY & SHAW 1977) enabling copulations to be distinguished from unsuccessful mounts. Observations on male mating behavior and copulatory plug (KOPROWSKI 1992) formation support the utility and validity of postcopulatory grooming behavior as an indicator of a copulation. Mating bouts terminated when the female was no longer pursued by males.

Statistical analyses

Sample sizes of the mating bout descriptors differ due to difficulties in observing some behaviors or portions of bouts. Frequencies were compared by chi-square contingency techniques or by the Wilcoxon matched-pairs test. Means were tested by Student's one- or two-tailed t dependent on the null hypothesis. Dominance ranks of the males assuming each of the two tactics were compared by the Mann-Whitney U test. All correlational analyses used simple linear correlation techniques (ZAR 1984). Intermale variation in copulatory success was estimated by two commonly used measures: the coefficient of variation, $CV = (SD/\bar{x})*100$, and an intensity of sexual selection index, $I_s = SD^2/\bar{x}^2$ (WADE & ARNOLD 1980). Mean ± 1 SD are presented in the text.

RESULTS

Mating bout descriptors

Twelve winter mating bouts (1986-1987 n = 3, 1987-1988 n = 1, 1988-1989 n = 4, 1989-1990 n = 4) occurred from 17 December to 17 January. Four to seven males participated in each mating bout (5.83 ± 0.58 males/bout) and chased the female over 1.48 ± 0.82 ha (range = 0.33 to 2.79 ha). Bouts were initiated soon after sunrise and continued through mid-afternoon with copulations concentrated near 11 hr 40 ± 126.0 min (n = 22).

Although squirrels copulated on the ground on two occasions, most copulations occurred in trees, frequently high in the canopy (11.78 ± 7.78 m; n = 39), with a mean duration of 18.5 ± 2.5 sec (n = 18). Of 61 mounts attempted by males, 22 (36.6%) resulted in copulation, 19 (31.1%) were terminated by the female pulling away from the male, 19 (31.1%) ended when interrupted by another male, and 1 (1.6%) was terminated by the male. Males attacked a copulating pair upon discovery, and sometimes bit and threw the pair from the tree. Females mated multi-

ply and averaged 2.50 ± 2.07 (range = 0 to 7) copulations/bout. In only one instance did a female copulate with the same male twice in a mating bout. The mean intercopulatory interval was 70.8 ± 54.3 min. No mating occurred less than 12 min after the preceding copulation. Males remained with and tried to guard the female after most copulations (23 of 24; 95.8%).

Adult male alternative tactics

As in eastern gray squirrels (KOPROWSKI 1993), male fox squirrels used two tactics during mating bouts: active pursuit and satellite. Males using the active pursuit tactic fought for and defended proximity to the estrous female. Satellite males remained dispersed either sitting or foraging within the estrous female's home range; however, they remained attentive to the female's activities. Active pursuit was less common among males (45.0% of male participants) than the satellite tactic (2.64 ± 0.71 active-pursuit males/bout vs 3.13 ± 0.48 satellite males/bout: Wilcoxon matched-pairs T+ = 0, T– = 16, df = 9, $P < 0.05$).

Dominance rank (most dominant male's rank = 1) differed between males using the two tactics. Active-pursuit males were always dominant over satellite males; active pursuit was used by the higher ranking (median dominance rank = 2) males while satellite males were subordinates (median dominance rank = 5; Mann-Whitney U = 396.0, $P < 0.01$, $n_1 = 27$, $n_2 = 26$). Unfortunately, adult male fox squirrels were exceptionally difficult to capture, which precludes analysis of the relationship between individual characteristics and dominance.

Copulatory success

All mating bouts within 500 m of the study area were well-documented in the winter breeding season of 1988-1989; therefore, the variability of mating success among males and between tactics was analyzed. The 10 observed copulations were not distributed evenly; only 4 of 7 (57.1%; 1.67 ± 1.37 copulations/male; CV = 82.0; $I_s = 0.67$) reproductively active males copulated.

Males adopting each tactic copulated. Active pursuit was the more successful tactic over the duration of study and accounted for 62.5% (15 of 24) of the observed copulations while the satellite tactic accounted for 37.5% (9 of 24) of the copulations ($\chi^2 = 2.87$, df = 1, $P > 0.10$). During 1988-1989, individual active-pursuit males (0.83 ± 1.11 copulations/male/bout) were more successful than individual satellite males (0.23 ± 0.44 copulations/male/bout: one-tailed t = 1.75, $P = 0.05$, df = 14). Copulations were also spread more evenly among active-pursuit males (CV = 133.7) than among satellites (CV = 191.3).

Females frequently are confined on the end of a tree limb or in a tree cavity by pursuing males and may bolt from confinement, sometimes losing contact with the males. The first male to relocate the female mates with her. Thirteen of 24 copulations (54.2%) occurred after a 'breakaway' by the female. The success of the tactics differed markedly before and after a breakaway. Active pursuit was most successful before a breakaway and accounted for all of the 11 copulations while the female was confined by males; however, success declined to only 4 of 13 (30.8%) of the copulations after a breakaway. Satellite male success increased from 0% of the copulations before a breakaway to 69.2% of the post-breakaway copulations. The distribution of copulations among the tactics following breakaways (four copulations by active-pursuit males, nine copulations by satellite males) was not different from the distribution of males in each tactic (45.0% of participants are

active-pursuit males, $\chi^2 = 1.06$, $P < 0.25$, df = 1). While all of the copulatory success of satellite males (n = 9) was due to their success in the post-breakaway competition to relocate the female, only 26.7% of the 15 copulations by active-pursuit males followed a breakaway.

Females may avoid the vulnerable locations of copulations that are characteristic of mating bouts. Copulations following breakaways were lower in the canopy (4.2 ± 5.3 m aboveground) than copulations where the female was confined (13.7 ± 6.3 m aboveground; $t = -4.74$, $P < 0.01$). The likelihood of a female being attacked by males while copulating was identical (42.9%; 9 of 21 copulation attempts) before and after a breakaway.

Dominance rank (where low numerical ranks are assigned to the most dominant males) was not related to the copulatory success of males (number of copulations/number of mating bouts) in 1988-1989 ($r = -0.49$, $P > 0.20$, df = 6). However, dominance rank was highly correlated with the number of mounts/mating bout, a measure of access to the estrous female ($r = -0.82$, $P < 0.05$, df = 6).

Intermale variance in reproduction

Intermale variance in mating success of fox squirrels is intermediate to those reported for other squirrels (Table 1). *Spermophilus beldingi*, *Sciurus niger*, and *S. carolinensis* are characterized by high levels of combat in competition for estrous females and possess slightly higher estimates of intermale variation in mating success.

DISCUSSION

The tactics chosen by adult male fox squirrels during mating bouts are similar to the tactics of active pursuit and satellite used by male gray squirrels (Koprowski 1993) and red squirrels, *S. vulgaris* (Wauters et al. 1990). Three tactics were employed by male *S. vulgaris*: "protective leader" and "persistent male", which appear similar to the active pursuit tactic of fox squirrels except that the dominant male fox squirrel never abandons a bout as observed in red squirrels, and "sneaker", in which young subordinate males copulated with the female while dominant males were distracted.

The tactics of male fox squirrels appear to represent opportunistic, facultative behavioral responses to social environments (Kodric-Brown 1986) where subordinate animals assume a non-territorial or satellite tactic that is commonly called "making the best of a bad job" (Parker 1984). Alternative tactics of subordinates are less successful in obtaining matings than the tactics of dominants but generally yield some matings (Kodric-Brown 1986) as in the gray squirrel (Koprowski 1993). Fox squirrels add to a growing list of vertebrates in which males use alternative mating tactics that are likely opportunistic responses to local social conditions (LeBoeuf 1974; Howard 1978, 1984; Clutton-Brock et al. 1982; Hogg 1984; Kodric-Brown 1986).

The high levels of aggression characteristic of tree squirrel mating bouts (Farentinos 1972, Thompson 1977, Benson 1980, Wauters et al. 1990) suggest that the ability to defend a resource (the estrous female) is likely a strong correlate of copulatory success. Because the most dominant males choose the more successful active-pursuit tactic, a crude positive relationship between dominance and copula-

tory success was expected. Furthermore, the dominance rank of males participating in the mating bouts should represent resource holding potential and be correlated with copulatory success during contest competition for the female. Although copulatory success increased with dominance, dominance rank was not related significantly to the copulatory success of male fox squirrels. However, the opportunity to mount the female was related to dominance status. Dominance was useful in accessing the female; yet, due to the frequent attacks experienced by copulating pairs and the escape behavior of the female, copulatory success was not an obvious benefit of dominance in the fox squirrel.

The mating bouts of the fox squirrel were similar to those of the eastern gray squirrel including the levels of aggression, copulatory behavior, copulatory success, and behavioral tactics of males (HORWICH 1972, THOMPSON 1977, KOPROWSKI 1993). The behavior of the female plays an important role in the copulatory success of participating males (FARENTINOS 1980, KOPROWSKI 1993). Male success depends on the ability to compete in two phases of a mating bout. Prior to breakaways, competition is based on resource holding potential skills useful in contest competition while a breakaway results in a scramble competition to relocate the female. Satellite males exploit the escape behavior of females and copulate.

SCHWAGMEYER & WOONTNER (1986) state that, although combat levels differ among several ground-dwelling squirrels, the question of whether combat generates significant variability in male mating success remains open. Intermale combat is an important component of the mating system of tree squirrels (FARENTINOS 1972, THOMPSON 1977, BENSON 1980). Intermale variation in mating success of tree squirrels is equal to or greater than that of ground squirrels characterized by considerably less combat for mates (Table 1). For instance, intermale variation in copulatory success of fox squirrels is similar to the intermale variation of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), a species in which intermale combat is reduced and males display a queuing convention to mate with females (SCHWAGMEYER & WOONTNER 1986). Although combat might generate increased levels of variation in copulatory success because many subordinate males would be unable to mate, the alternative tactic used by subordinate males mediates intermale variation in copulatory success.

Table 1.

Variances in the copulatory success of male sciurids indicated by two measures: the coefficient of variation (CV) and an intensity of selection index (I_s). Species are ranked from lowest to highest I_s. Data for *Spermophilus* and *Cynomys* are from SCHWAGMEYER & WOONTNER (1986) while results for *Sciurus carolinensis* are from KOPROWSKI (1993).

Species	Mating system	Range of	
		CV	I_s
Cynomys ludovicianus	harem polygyny	55.8	0.31
Spermophilus tridecemlineatus	scramble competition polygyny	61.3-86.5	0.38-0.75
Sciurus niger	dominance polygyny	82.0	0.67
Sciurus carolinensis	dominance polygyny	85.8-122.5	0.74-1.50
Spermophilus beldingi	lek/dominance polygyny	109.8-113.8	1.20-1.30

Alternative reproductive tactics appear to constrain the levels of variation in mating success among male tree squirrels. Subordinate males are successful via a component to reproductive success that is not related to combat but is due to the escape behavior of the female. If alternative tactics actually are the result of opportunistic, facultative responses to social and/or ecological environments (KODRIC-BROWN 1986) then alternative tactics are expected to mediate intermale variance in male copulatory success as individual males attempt to maximize their fitness. The alternative tactics of male eastern gray squirrels (and possibly fox squirrels) likely are facultative (KOPROWSKI 1993). Future research must focus on the experimental manipulation of local social and ecological conditions (see PERRILL et al. 1982, KODRIC-BROWN 1986) to further investigate the plasticity of alternative tactics as well as the their role in mediating intermale variation in reproductive success.

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