Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job"

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Male eastern gray squirrels (*Sciurus carolinensis*) congregate around and pursue a female on her single day of estrus. The tactics of uniquely marked adult males were monitored during winter mating bouts from 1986 to 1990 to examine variation in male copulatory success. Two tactics were chosen by males: active pursuit or satellite. Active-pursuit males were dominant and defended proximity to females. Satellite males were subordinate and remained dispersed in the female's home range. Active pursuit was used only by males ≥2.75 years old. The switch point between the tactics is about 3 years. Copulations were not distributed evenly among males, with about 30% of all adult males failing to copulate during a breeding season. Active pursuit was the most successful strategy, with male success attributed to the ability to defend access to the female. However, satellite males successfully copulated due to the escape of females from dominant males. Females appear to avoid the overt aggression characteristic of the competition among active-pursuit males by running from the group of males. Male success after a female's breakaway was evenly distributed between the two tactics and accounted for all copulations by satellite males. The active-pursuit and satellite tactics appear to be a conditional evolutionarily stable strategy where young, subordinate males are "making the best of a bad job." *Key words:* active pursuit, alternative reproductive tactics, copulatory success, eastern gray squirrels, satellite males. [*Behav Ecol 4:165–171 (1993)*]

Because female mammals are committed to their progeny through gestation and lactation, female reproductive success usually is more readily quantified than male reproductive success. However, an impressive body of literature has accumulated on the alternative tactics used by individual male vertebrates and invertebrates to gain access to females and to copulate (Cade, 1980; Dunbar, 1982; Rubenstein, 1980). Although alternative tactics may result from genetic polymorphisms or differential developmental constraints acting on similar genotypes, the most common pattern in a variety of taxa is for the tactics to reflect opportunistic, facultative responses to the local social and ecological environment experienced by individual males (Kodric-Brown, 1986). The plasticity of mammalian behavior is well known; however, the alternative reproductive tactics of males have received little attention, and most studies are limited to large mammalian species (Clutton-Brock et al., 1982; Dunbar, 1984; Hogg, 1984; LeBoeuf, 1974).

The polygynous mating systems of many sciurids involve intense combat among males for access to estrous females (Benson, 1980; Farentinos, 1980; Koford, 1982; Michener, 1983). Adult male eastern gray squirrels (*Sciurus carolinensis*) aggressively compete for copulations in conspicuous mating bouts (Thompson, 1977). Female gray squirrels have a 1-day estrus that attracts as many as 34 males (Goodrum, 1961) from as far as 600 m away (Thompson, 1977). Females within local populations typically breed asynchronously (Brown and Yeager, 1945), creating a temporally and spatially limited resource that can be defended by a male (Thompson, 1977). Many (>50%) male tree squirrels that pursue an estrous female are not able to gain access to her (Farentinos, 1972; Koprowski, in press a; Wauters et al., 1990). These observations suggest an interesting question: If so few males mate with a female and mating success is related to dominance (Benson, 1980; Thompson, 1977), then why do subordinate males continue to participate in mating bouts? Evidence from other tree squirrels (Farentinos, 1972; Koprowski, in press a; Wauters et al., 1990) and anecdotal observations on eastern gray squirrels (Bakken, 1959; Thompson, 1977) suggest that subordinates do copulate, perhaps by the use of different tactics to access the female.

Game theory provides a useful tool to examine the adaptive significance of alternative reproductive tactics by modeling the fitness-related consequences of behavioral polymorphisms (Maynard-Smith, 1982). The "biological games" that animals play (Parker, 1984) are divided into contests (pairwise meetings) and scrambles (*n*-player interactions). The nature of tree squirrel mating bouts suggests that scramble games are the most appropriate characterization of adult male mating behavior. Scramble games can be further subdivided into one-option (to gain more of a fitness-related resource an individual can only increase its expenditure beyond that of other competitors) and alternative-option (individuals have more than one option to increase acquisition of a fitness-related commodity) scrambles. Alternative reproductive tactics generally are a form of alternative-option scramble games (Parker, 1984), where the estrous female represents the fitness-limiting resource. Recent studies of male mating tactics of thirteen-lined (*Spermophilus tridecemlineatus*: Schwagmeyer and Parker, 1987), Idaho (*S. brunneus*), and Belding's

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(*S. beldingi*: Sherman, 1989) ground squirrels successfully applied game-theoretical approaches to postcopulatory tactics of males: should the male remain to guard the female or should he search for other estrous females?

In this study, my objectives were to (1) describe the mating bouts and alternative reproductive tactics of adult male eastern gray squirrels, (2) determine the intermale and intertactic variability in copulatory success, and (3) apply a game-theoretical approach to examine the adaptive significance of the alternative male reproductive tactics.

Study animal

Eastern gray squirrels are medium-sized (adult mass = 500 to 750 g), long-lived (maximum male longevity = 9.0 years; Barkalow and Soots, 1975) rodents inhabiting deciduous and mixed forests of the eastern United States and southern Canada (for a review see Brown and Yeager, 1945). Gray squirrels rely heavily on the reproductive tissues of trees for food, especially the winter-storable seeds of nut-bearing trees such as oaks (*Quercus*), hickories (*Carya*), walnuts (*Juglans*), and beech (*Fagus*). Nuts are scatter hoarded and buried beneath the soil surface. Tree squirrels do not hibernate, and cached reserves are the primary food source during winter, which represents a critical period for squirrels when available energy may be less than maintenance needs. Most mating takes place during December–February and May–June; gestation is 45 days. The two major peaks in births are well timed with the spring emergence of buds in February and March and the ripening of nut crops in July and August. Individual females are in estrus for less than 1 day; two females are rarely in estrus simultaneously in a local population ($n = 1$, this study). Paternal care does not occur.

MATERIALS AND METHODS

The study area was a 4.2-ha parkland located on the University of Kansas campus, Lawrence, Kansas, USA (38°57.8′ N, 95°14.3′ W). University roadways, buildings, and parking lots delineated the boundaries. The canopy 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. From May 1986 to May 1990, I trapped squirrels in 15 × 15 × 60-cm wire-mesh live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanuts and peanut butter. I attended traps constantly, and most traps were set during recesses in the academic schedule to avoid human disturbance of traps. Squirrels were ear-tagged with uniquely numbered tags (Monel no. 1, National Band and Tag, Newport, Kentucky) and marked for visual identification at a distance by uniquely coded ear streamers (Koprowski et al., 1988) or patterns of unpigmented pelage induced by freeze marking (Rood and Nellis, 1980). The number of resident adult females remained nearly constant (10–13 squirrels) and 20 or 21 adult males participated in mating bouts during the study.

Upon first capture, I assigned males to one of three age classes (juvenile, <6 months; subadult, 6–12 months; adult, >1 year) by the appearance of external genitalia and characteristics of tail pelage (Larson and Taber, 1980; McCloskey, 1977). I estimated ages of juvenile and subadult males based on March 1 as the birth date of spring-born young and July 1 as the birth date for summer litters (Brown and Yeager, 1945; Koprowski JL, personal observation). I used these same birth dates to assign the minimum age required for a squirrel to be recognized as an adult on the date of first capture.

Because leaf cover obscured copulations during the May–June breeding period, 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. The tendency of males to follow females in the 5 days before estrus (Thompson, 1977) was useful in locating estrous females. Because many males congregate in an estrous female's home range, mating bouts are easily located. No females bred in winter 1988–1989; therefore, the data presented here are from 1986–1987, 1987–1988, and 1989–1990. I also explored areas peripheral to the study site for mating bouts involving marked males. When a mating bout was detected, the activities and participants were recorded and followed continuously until bout termination. Dominance relations were scored when a male chased or aggressively contacted another individual. Reversals in the outcome of agonistic encounters were sought; however, none were ever observed within any mating bout. I assigned dominance ranks, with the most dominant male receiving a rank of 1. The time, location, and fate of all attempted mounts were recorded. Duration of copulation was measured as the time from the first pelvic thrust to the time of dismount by the male. Female and male gray squirrels groom their genitalia following the male's ejaculation (Horwich, 1972). Observations of male mating behavior and copulatory plug formation (Koprowski, 1992) support the validity of this criterion. Mating bouts were considered to terminate when the female was not pursued by males.

I followed all mating bouts within 500 m of the study area in 1987–1988 and 1989–1990; the well-documented copulatory success of males during these years permitted analysis of intermale and intertactic variability in copulatory success. I estimated intermale variation in copulatory success from two common 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 and Arnold, 1980). Sample sizes of mating bout descriptors may differ due to difficulties in observing some behaviors or portions of a mating bout. Frequencies were compared with chi-square contingency techniques, and the Yates' correction for continuity was applied if any cell contained a frequency ≤ 5. I tested means by one- or two-tailed Mann-Whitney U or Student's t tests, depending on the null hypothesis. Dominance ranks of the males adopting each tactic were compared using the Mann-Whitney U test; because some males used more than one tactic during a breeding season, I compared the ranks of males using the two tactics within each mating bout. To examine the correlation between dominance rank and age, I pooled the interactions between males within a breeding season to determine ranks. All correlational analyses used simple linear correlation or regression techniques (Zar, 1984). Means ± 1 SD are presented in the text.

RESULTS

Mating bout descriptors

Winter mating bouts ($n = 22$) occurred from 27 December to 28 January during the study. From 4 to 18 (10.6 ± 5.2) males participated in each bout. Bouts started soon after sunrise and continued through mid-afternoon; however, most copulations occurred in late morning (1120 h ± 95.5 min, $n = 57$). Copulations were always in trees, frequently high in the canopy (8.20 ± 4.74 m, $n = 57$), with a mean duration of 21.8 ± 3.1 s ($n = 42$). Of 128 mounts attempted by males, 50 (39.1%) resulted in copulation, 51 (39.8%) were terminated by the female pulling away from the male, and 27 (21.1%) ended when interrupted by another male. Whenever a male detected a copulating pair, he attacked, bit, and sometimes knocked the male and female from the tree. Females mated with one to eight (3.47 ± 2.12, $n = 22$) males/bout; in only four instances did a female copulate with the same male twice in a mating bout. The mean intercopulatory interval was 54.8 ± 38.0 min ($n = 26$) for females that mated with > 1 male. Copulations were separated by at least 11 min, apparently due to the female's unwillingness to mate, although the activity of all male participants also slowed in the postcopulatory period. Following most copulations (49 of 50; 98%), males remained with and attempted to guard the female; however, subordinate males were quickly displaced by dominant males.

Adult male alternative tactics

Male squirrels used two tactics during mating bouts; however, individuals only used a single tactic within a mating bout. Some males continually fought for and defended proximity to the estrous female; I call this tactic "active pursuit." The remainder of males were dispersed, either sitting or foraging within the estrous female's home range; however, the males remained attentive to the female's activities. These males do not actively attempt to sneak copulations; as a result, I call this tactic "satellite." Active pursuit was less common among males (30.3% ± 8.8% of male participants in 22 chases) than the satellite tactic.

Dominance rank and age differed between males using the two tactics. Active-pursuit males were always dominant over satellite males; active pursuit was used by the higher ranking males (mating bout $n = 22$; range in median dominance rank = 1.5–4.0), whereas satellite males were subordinates (range in median dominance rank = 5.0–14.5; range in Mann-Whitney $U = 3.0–28.0$; $.08 < p < .0005$; 75% of p-values $< .05$). The tactics were age dependent, with active pursuit used only by the oldest males. The mean minimum age of active-pursuit males was greater than that of satellites in both 1987–1988 (2.75 ± 0.00 years versus 1.80 ± 0.61 years; $t = 5.40$, $p < .05$) and 1989–1990 (3.96 ± 0.70 years versus 1.95 ± 0.75 years; $t = 5.67$, $p < .01$). The lack of variability in the minimum ages of active-pursuit males in 1987–1988 is an artifact of the length of study. The maximum known age of adult males during winter 1987–1988 observations was 2.75 years, the minimum age of males captured as adults in the first year of study (1986).

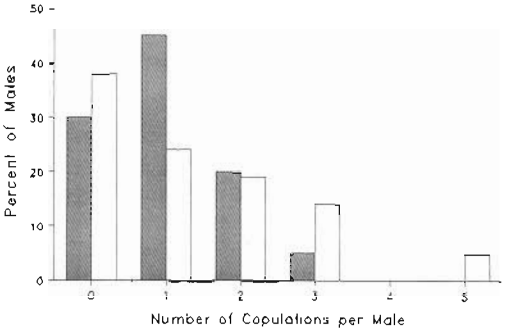

Figure 1
Distribution of copulatory success of male eastern gray squirrels during the winters of 1987–1988 (shaded bars; $n = 20$ males) and 1989–1990 (open bars; $n = 21$ males) breeding seasons.

Copulatory success

Twenty-two copulations were observed in 1987–1988 and 29 in 1989–1990. These copulations were not distributed evenly among males; among reproductively active males, only 14 of 20 in 1987–1988 (70.0%; 1.00 ± 0.86 copulations/male; CV = 85.8; $I_s = 0.74$) and 13 of 21 in 1989–1990 (61.9%; 1.38 ± 1.69 copulations/male; CV = 122.5; $I_s = 1.50$) copulated in each winter breeding season (Figure 1).

Both active-pursuit and satellite males copulated. Although active pursuit and satellite accounted for an equal percentage of copulations (Table 1), active pursuit conferred more copulations per male per mating bout than the satellite tactic in 1987–1988 (one-tailed $t = 1.62$, $p < .06$), 1989–1990 (one-tailed $t = 2.38$, $p < .03$), and both years combined (one-tailed $t = 2.87$, $p < .01$). The relative variability in intermale copulatory success was greater for satellite males than for active-pursuit males in each year (Table 1); in other words, copulatory success was more variable among satellite males.

Active-pursuit males and satellite males participated in an equal number of mating bouts during 1987–1988 (median = 5; Mann-Whitney $U = 55.5$, $p > .20$) and 1989–1990 (median = 5; Mann-Whitney $U = 93.0$, $p > .20$). Neither tactic consistently copulated first or last within a mating bout; first copulations (active pursuit = 10, satellite = 12; $\chi^2 = 1.68$, $p > .20$) and last copulations (active pursuit = 10, satellite = 10; $\chi^2 = 2.73$, $p > .20$) were distributed in a fashion similar to the tactics (30.3% of males adopt active pursuit). Furthermore, the median order of mating did not differ between the two tactics (active-pursuit median = 2.0; satellite median = 3.0; Mann-Whitney $U = 767.5$, $p > .20$).

The dependence of alternative tactics on dominance and age suggests a relationship between these characters. Dominance rank (where low ranks equal high dominance) was highly correlated with age in 1987–1988 ($r = -.78$, $p < .01$; df = 12) and 1989–1990 ($r = -.87$, $p < .01$, df = 10). Similarly, dominance rank was highly correlated with the average copulatory success of males during a bout (copulations/male/bout) in 1987–1988 ($r = -.55$, $p < .05$, df = 12) and 1989–1990 ($r = -.72$, $p < .01$, df = 10). The absolute success of males over the course of a breeding season (number of copulations/male/breeding season) also tends to be great-

Table 1

Measures of intertactic variation in copulatory success for adult male gray squirrels

Measure of copulatory success	Year	Tactic	
		Active pursuit	Satellite
Number of copulations	1987–88	10	12
	1989–90	15	13
Mean number of copulations per male per bout (SD)	1987–88	0.32 (0.47)	0.16 (0.37)
	1989–90	0.62 (0.71)	0.25 (0.44)
Coefficient of variation	1987–88	146.9	231.3
	1989–90	114.5	176.0

er in the most dominant males (1987–1988: $r = -.42$, $p < .20$, df = 12; 1989–1990: $r = -.69$, $p < .05$, df = 10).

Several pieces of information suggest that the switch point between tactics is between 2.75 and 3.25 years of age. The youngest male to use the active-pursuit tactic was 2.75 years old and the oldest male to use the satellite tactic was 3.75 years old. Five males used both the satellite and active-pursuit tactic during the same breeding season, although in different chases; all of these males were 2.75–3.75 years old. A crude estimate of the switch point is obtained by regressing copulatory success on age for each tactic and determining the point at which the regression lines intersect. The intersection at 3.13 years represents the age when the copulatory success of males is equivalent for each tactic; at ages >3.13 years, the copulatory success of males is greater for active-pursuit than satellite tactics (Figure 2). Although the copulatory success of males using each tactic was negatively related to the proportion of males using the tactic, the frequency dependence was not significant (satellites, $r = -.20$, $p > .20$; active pursuit, $r = -.10$, $p > .50$).

The dominance of active-pursuit males over satellite males raises the question of how satellite males gain access to females. The female is not a passive element of the mating bout (Koprowski, in press b). After being confined on the end of a tree limb or in a tree cavity by the group of active-pursuit males, the female frequently bolts from and avoids contact with the males. She then remains motionless, usually low on the trunk of a tree; the first male to relocate the female following one of these breakaways always mated with her ($n = 49$). The form of competition changes from contest competition, where males can defend the female to mate, to scramble competition, where matings are attributed to the ability of males to locate the female (Schwagmeyer and Woontner, 1986).

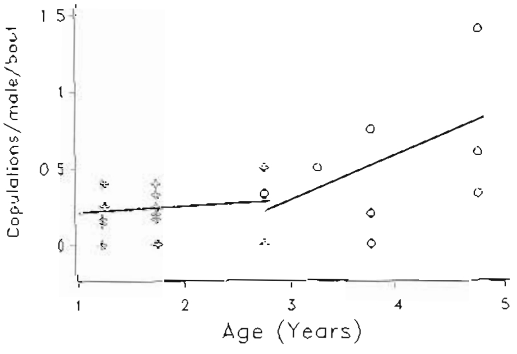

Figure 2
The copulatory success and age of male eastern gray squirrels using the alternative reproductive tactics. Copulatory success (Y = number of copulations/male/bout) was regressed upon the age of males (X = years) in each tactic. The equations for the regression lines are: satellites (+), $Y = 0.15 + 0.03X$, $F = 0.16$, $p = .70$, $R^2 = .01$; active pursuit (O), $Y = -0.59 + 0.27X$, $F = 1.61$, $p = .25$, $R^2 = 0.19$.

Thirty-four of 49 copulations (69.4%) followed a breakaway by the female. Active-pursuit males accounted for all copulations occurring in the contest competition when the female was defended and surrounded by active-pursuit males (15 copulations); however, following a female's breakaway and the ensuing scramble competition to relocate her, satellite males accounted for 25 of 34 copulations (73.5%). The success of satellites was attributed entirely to their ability to locate the female during the scramble competition after a breakaway; all 25 satellite male copulations followed breakaways. Conversely, only 37.5% of the copulatory success (9 of 24 copulations) of active-pursuit males accrued from their success in relocating a female following her breakaway. The distribution of copulations among the tactics following breakaways (9 copulations by active-pursuit males, 25 copulations by satellite males) did not differ from the distribution of males in each tactic (30.3% of participants are active-pursuit males, $\chi^2 = 0.24$, $p > .50$, df = 1). Therefore, copulations following a breakaway were randomly distributed among males regardless of tactic.

Females apparently avoid the overt aggression and vulnerable locations of copulations that characterize mating bouts. Copulations following breakaways were lower in the canopy (6.2 ± 4.1 m aboveground) than copulations where the female was confined and surrounded (11.2 ± 2.8 m aboveground; $t = -4.81$, $p < .01$, df = 30). Also, the likelihood of a female being attacked by males while copulating decreased (although not significantly) from 0.375 ($n = 24$) when confined by males to 0.245 ($n = 49$) after a breakaway ($\chi^2 = 1.34$, $p < .25$, df = 1). One female died from an infected eye and facial wound apparently inflicted during her mating bout.

DISCUSSION

Making the best of a bad job: tactics of males

Active-pursuit and satellite tactics represent alternative mating tactics among male eastern gray squirrels. Previous researchers hinted at the existence of distinct tactics in gray squirrels: Bakken (1959) noted two groups of male participants, and Thompson (1977) documented an age difference between the dominant and subordinate squirrels. Similar reproductive tactics recently were described for European red squirrels, where dominant males pursue the female and subordinates avoid the conflict (Wauters et al., 1990).

The age relatedness of the tactics and switching point suggest that the tactics of gray squirrels are correlated with phenotype. The existence of phenotype-correlated, alternative male reproductive tactics in gray squirrels is similar to the pattern occurring in a variety of other vertebrates where dominant males with the greatest resource-holding potential assume a territorial or aggressive pursuit tactic and subordinates exploit a nonterritorial, satellite, or sneaker strategy (Clutton-Brock et al., 1982; Hogg, 1984; LeBoeuf, 1974). The tactics do not appear to be a consequence of fixed genetic polymorphisms nor of different developmental constraints acting on similar genotypes (see Kodric-Brown, 1986). The use of both tactics during a breeding season by some males with an age near the switching point suggests the plasticity of individual decision making and implies that males act opportunistically and respond to local social conditions (Kodric-Brown, 1986).

The payoffs to the two tactics are related to the success of males in two distinctly different forms of competition: contest versus scramble. Most of the success of active-pursuit males results from these males' success in contest competition, where dominance rank is important in gaining access to a limited resource. The principal determinant of dominance among male gray squirrels is age; dominance status increases with age (Allen and Aspey, 1986; Pack et al., 1967; Thompson, 1977). However, dominance rank is not related to body size (Allen and Aspey, 1986). Asymmetries in resource-holding potential apparently lead to different tactics in gaining access to the estrous female. Sequestering the female, thereby restricting access and maintaining a contest competition, maximizes the copulatory success of active-pursuit males. If the female escapes confinement, scramble competition ensues, in which copulatory success is randomly distributed between the tactics. Success in scramble competition is related to the ability of males to locate the female; asymmetries in resource-holding potential that permit active-pursuit males to retain access to the female in contest competition are likely of little importance following breakaways, and copulations are distributed randomly among males. Scramble competition was the only means by which satellite males mated.

The relationships between age, dominance status, and copulatory success suggest that the tactics may be a form of the producer–scrounger game (Barnard and Sibly, 1981), where the older dominant animals choose the "producer" role (P = active pursuit) and defend the female, thereby limiting access to the resource, and the younger subordinate animals assume the "scrounger" role (S = satellite). Parker (1984) outlines the conditions for phenotype-limited, conditional evolutionarily stable strategies: (1) competitive ability of P increases with age; (2) payoffs in P and S are negatively related to the frequencies of the strategies; (3) the age at the switch point (T) conveys an equal number of copulations to either strategy P or S; (4) if age is < T, then fitness (i.e., copulatory success) of the phenotype in S is greater than in P; and (5) if age is > T, then fitness of the phenotype in P is greater than that in S.

The mating behavior of gray squirrels appears to partially or completely satisfy these conditions. The most difficult conditions to verify are 4 and 5, which examine the fitness of males in tactics that the phenotypes normally do not assume. However, because much of the success of active pursuit is related to the ability to maintain proximity to the female, the success of young subordinate males assuming the active-pursuit tactic is likely to approach 0 and satisfy condition 4. Because success following breakaways is randomly distributed between active pursuit and satellite and because satellites achieve lower overall success than active-pursuit males, the older animals should achieve more copulations in active pursuit than as satellites, which satisfies condition 5. Given these conditions, the tactics of active pursuit and satellite cannot be invaded by other tactics. The alternative reproductive tactics of male eastern gray squirrels appear to be a conditional pure strategy with the rules "when younger than 3 years, play satellite; when older than 3 years, play active pursuit." Therefore, young males are "making the best of a bad job" (their age) and obtain some copulations while waiting until they are older and more successful in contest competition.

Copulatory success is only an indicator of potential fitness and the benefits of each tactic. Unfortunately, the costs of each tactic are unknown and remain a potentially important component for understanding the actual payoffs of the alternative tactics (Caro and Bateson, 1986). Some obvious potential costs incurred by active-pursuit males during contest competition are physical wounding, the energetic costs of combat (satellite males feed and remain motionless, whereas active-pursuit males do so only rarely) and reduced survivorship that might decrease future reproductive effort (likely common in other sciurids: Michener, 1989; Michener and Locklear, 1990; Sherman and Morton, 1984). By not participating in active pursuit, satellites also could incur a cost as the loss of current reproduction, especially if survival until future breeding seasons is low. However, gray squirrels are long lived, and the survivorship of adults is high with the mean expectation of life (e_x) for 1-, 2-, and 3-year-old squirrels estimated at 1.8 years, 2.4 years, and 2.1 years, respectively (Barkalow et al., 1970); the average satellite male will participate in three to five additional breeding seasons. Measurement of fitness costs will be necessary over the course of individual lifetimes to assess more accurately the actual benefits of alternative tactics in male gray squirrels.

Avoiding males: a reproductive tactic of females?

Conflict between the sexes during mating bouts is evidenced in the behavior of females. Although males try to restrict access to the female by guarding after copulation, females mate with multiple males. Multiple mating is common among both sexes of sciurids (Farentinos, 1972; Schwagmeyer, 1984; Sherman, 1989), and the order of mating can significantly influence the success of male copulations in producing offspring. In thirteen-lined and Belding's ground squirrels, a first-male advantage in fertilization exists (Foltz and Schwagmeyer, 1989; Sherman, 1989), while a last-male advantage was documented for the Idaho ground squirrel, although the influence of mating order and frequency of copulation are confounded (Sherman, 1989). Unfortunately, the influence of order of copulation on paternity is unknown for any tree squirrel.

The behavior of females likely plays an integral role in the maintenance of two tactics. Because females frequently break from the aggressive confinement of active-pursuit males, the satellite strategy offers some success to young subordinates. Why do females avoid the dominant, active-pursuit males? At least two possibilities exist. The avoidance behavior may result from active female mate choice. Female tassel-eared squirrels appear to actively solicit matings by subordinate males (Farentinos, 1980). Because a copulating pair is at risk of being attacked, a more proximate and parsimonious explanation is that females avoid the intense aggression associated with male intrasexual contest competition.

Several points support the avoidance-of-risk hypothesis. First, females copulate at sites closer to the ground and with a somewhat lower probability of being attacked after breaking away from active-pursuit males. Female eastern chipmunks (*Tamias striatus*), which are pursued in much the same manner as female gray squirrels, also appear to mate preferentially with males that locate them in seclusion (Yahner, 1978). Second, the copulations are randomly distributed between the active-pursuit and satellite tactics after a breakaway, which is not consistent with female choice. An additional point suggests the influential role of overt aggression on mating behavior in gray squirrels. The duration of copulations is only 21 s in gray squirrels, whereas ground squirrels with queuing conventions and lower levels of aggression have longer copulations (>1 min; Schwagmeyer and Woontner, 1986); the intensity of aggression may lead to selection for short copulation duration.

Conclusions

Two factors appear to influence the origin and maintenance of alternative reproductive tactics in male eastern gray squirrels. Asymmetries in resource-holding potential between young and old squirrels result in some individuals foregoing participation in overt combat for access to a female. The escalated aggression characteristic of tree squirrel mating bouts yields measures of variance in mating success that are intermediate to high among the few ground squirrel species reported to date (Koprowski, in press a; Schwagmeyer and Woontner, 1986). A second major influence is the conflict between male and female reproductive interests during the mating bout (Koprowski, 1992, in press b). The avoidance behavior of females creates mating opportunities that are exploited by subordinates. These results further emphasize the importance of examining the influence of resources and environment (Caro and Bateson, 1986) on the ontogeny of alternative tactics.

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