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NATAL PHILOPATRY, COMMUNAL NESTING, AND KINSHIP IN FOX SQUIRRELS AND GRAY SQUIRRELS

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Tree squirrels (Sciuridae: Sciurini) are considered to be asocial; however, communal nesting is reported for most species. I examined the sociality of uniquely marked fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) to investigate interspecific patterns of natal philopatry, communal nesting, and kinship. Natal philopatry was female-biased in gray squirrels, resulting in the formation of kin clusters, but no fox squirrels remained in their natal areas. Adult male and female squirrels interacted less than expected, suggesting that the social systems of the sexes are separate. Communal nesting occurred in all seasons, but was most frequent in winter. Unrelated adult males commonly nested together in both species. However, adult female fox squirrels rarely nested in groups, although communal nests were common among female gray squirrels. Amicable behaviors were directed only toward closely related females ($r = 0.5$) within kin groups of gray squirrels; aggression was directed primarily at unrelated females. The female-female bond was important in the formation of groups in gray squirrels.

Key words: *Sciurus carolinensis*, *Sciurus niger*, sociality, relatedness, recruitment

Agonistic interactions play an important role in the regulation of populations of squirrels (Sciuridae; Armitage, 1986; Thompson, 1978a, 1978b). Adults may be particularly important in determining patterns of recruitment by directing aggression toward immature animals (Boutin and Schweiger, 1988; Downhower and Armitage, 1981; Thompson, 1978a, 1978b) and toward nonresident adults that ingress (Thompson, 1978a, 1978b). However, juvenile residents also direct considerable aggression toward other juveniles (Boutin and Schweiger, 1988; Koprowski, 1993a), and the most aggressive juveniles are successful in establishing residence within a local population (Pasitschniak-Arts and Bendell, 1990). Furthermore, kinship can influence agonistic and amicable interactions, spatial overlap, and success of recruitment into populations (Armitage, 1987; Koprowski, 1993a; Thompson, 1978a).

The female-female dyad is the fundamental subunit of the societies of ground-dwelling squirrels (Armitage, 1981; Mich-

ener, 1983). Increased levels of sociality result from the retention of females in or near the natal area; the most social species are characterized by female-biased natal philopatry that results in matrilineal, nest sharing, and cooperative behavior (Armitage, 1981, 1987; Michener, 1983). Kin groups present the opportunity for kin-directed amicable behaviors, which suggests the potential for kin selection to contribute to a female's inclusive fitness (Armitage, 1987). Several species of ground-dwelling squirrels demonstrate kin-directed behaviors within kin groups (Armitage, 1986, 1987; Hoogland, 1986; Sherman, 1981). However, the way that kinship influences the distribution of social behaviors is controversial. Are individuals treated differentially in direct proportion to their level of relatedness, or are only close kin treated preferentially (Armitage, 1987; Bennett, 1987)?

Among tree squirrels (tribe Sciurini), sociality is poorly known (Koprowski, in press). Adult *Tamiasciurus* defend exclusive territories in coniferous forests, while

mixed-forest populations of *Tamiasciurus* and *Sciurus* are not territorial, and their home ranges overlap extensively (Heaney, 1984; Wauters and Dhondt, 1992). Natal philopatry occurs in gray squirrels, *Sciurus carolinensis* (Cordes and Barkalow, 1972; Thompson, 1978b). Adult gray squirrels, fox squirrels (*S. niger*), Arizona gray squirrels (*S. arizonensis*), tassel-eared squirrels (*S. aberti*), European red squirrels (*S. vulgaris*), and Mexican fox squirrels (*S. nay-aritensis*) occasionally share nests (Koprowski, in press). Unfortunately, the relatedness of individuals in nesting groups is rarely known, but some evidence suggests that nesting groups consist of relatives (Taylor, 1969). My objectives were to describe the social interactions of fox squirrels and gray squirrels, examine species-specific tendencies for natal philopatry and communal nesting, and investigate whether amicable and agonistic interactions vary with levels of relatedness.

MATERIALS AND METHODS

The study area was a 4.2-ha parkland, dominated by black walnut (*Juglans nigra*), located on the University of Kansas campus, Lawrence, Douglas Co., Kansas. University buildings, roadways, and parking lots surround the study area. Both fox squirrels and gray squirrels were present, with abundances of adults remaining nearly constant between years (22–27 adult gray squirrels, 12–13 adult fox squirrels). The woodlot represents a high-quality habitat that supports high densities of fox squirrels and gray squirrels (Koprowski, 1994a, 1994b) on a diversity of mature seed-producing trees, including *J. nigra*, *Quercus palustris*, *Q. velutina*, *Q. rubra*, *Morus rubra*, *M. alba*, *Celtis occidentalis*, *Ulmus rubra*, *U. americana*, *Populus deltoides*, *Cornus florida*, *Catalpa bignonioides*, *Crataegus*, and *Gymnocladus dioica* (Koprowski, 1991).

From May 1986 to May 1990, I trapped squirrels and temporarily restrained them in a cloth handling cone. I weighed squirrels with a spring scale and estimated their age class from the appearance of external genitalia and characteristics of pelage of the tail upon first capture (Larson and Taber, 1980). Unique patterns of pelage induced by freeze-marking (5 s for gray squirrels,

7 s for fox squirrels—Rood and Nellis, 1980) enabled me to identify individuals at a distance. While walking a circular route at 20-min intervals, I scanned the study area during 1,265 h of observation to record interactions ad lib. (Altmann, 1974) and note the locations of individuals on a map of the area. The absence of a shrub stratum and the habituation of squirrels to humans facilitated observation.

Amicable interactions included: allogrooming—the licking, mouthing, and grooming with the forepaws of another squirrel's pelage; greeting—oral-nasal contact between two squirrels; playing—amicable wrestling and forelimb boxing between individuals; nest sharing—two or more animals simultaneously inhabiting a single nest. Agonistic behaviors included: chasing—one individual leaps at or runs after another; aggressive contact—a continuum of behaviors from swatting with the forepaws to wrestling and biting. The individual amicable and agonistic behaviors were combined for analyses of the two general classes of behavior.

I considered squirrels to be philopatric if continuous residence was maintained within any portion of the natal area until an age of ≥ 1.25 years, the age at which adult body size and reproduction may be achieved (Heaney, 1984). In actuality, philopatric individuals used the same dens and home range before and after maturation. Maternity of juveniles was determined easily because females den with and nurse litters in isolation; however, paternity could not be determined because females mate with several males (Koprowski, 1993b, 1993c). All coefficients of relatedness (r —Krebs and Davies, 1993) in the text refer to relative relatedness based upon maternal genealogy.

I used χ^2 contingency techniques to compare frequencies unless otherwise noted. Expected rates of amicable and agonistic interactions among age and sex classes were calculated using equation 7 of Altmann and Altmann (1977) that accounts for differences in composition of groups and observation efforts. Observed frequencies of social behaviors were compared to expected values and the summed deviations compared to the χ^2 distribution. Only nesting groups in which I identified the entrance and exit of all nest occupants were included in analyses. Females with young < 1.0 year of age were eliminated from the analysis. I conducted a one-way analysis of variance to determine seasonality in

size of nesting group (spring, March–May; summer, June–August; autumn, September–November; winter, December–February) and compared means using Tukey's post hoc test. The Bonferroni Z-test method (Marcum and Loftsgaarden, 1980) enabled me to examine the influence of relatedness on the distribution of social behaviors. This method first tests for the independence of amicable and agonistic behaviors from levels of relatedness by use of the χ^2 test of homogeneity, and then determines by use of a Z-test which classes are proportionally more common or depauperate than expected. The confidence intervals are used to determine if the proportion of amicable interactions includes the proportion of agonistic interactions (i.e., these proportions are not significantly different). If the confidence interval includes 0, then the proportions are not considered to be different. Confidence intervals that do not include 0 suggest that a significant difference exists between the proportions.

RESULTS

Trapping efficacy.—I captured and uniquely marked 151 gray squirrels (80 males, 71 females) and 44 fox squirrels (24 males, 20 females). Fox squirrels were more difficult to capture; however, on any day after December 1986, >84% of the fox squirrels and >95% of the gray squirrels that I observed were animals I had marked. Furthermore, all resident adult female squirrels were captured and marked. Most unmarked squirrels that I observed were either transients or residents from peripheral areas that moved quickly through the study area.

Natal philopatry.—More female than male gray squirrels remained in their natal area. Of 43 females captured as juveniles, 16 (37%) remained in their natal area until at least 1.25 years of age while only two of 34 (6%) males remained in their natal area ($\chi^2 = 10.42$, $P < 0.05$). The only philopatric males ($n = 2$) remained in the natal area after their mothers' death immediately after weaning.

I located eight adults (seven males, one female) that had dispersed from their natal area. Males moved an average of 1.10 km

(range = 0.38–3.23 km) while the only female established residence 0.32 km from her birthsite. The 16 females that remained in their natal areas were not simply delaying dispersal from the natal area, for 12 (75.0%) mated (Koprowski 1993b) and eight (50.0%) produced at least one litter in their natal area.

Unlike gray squirrels, no juvenile fox squirrels demonstrated natal philopatry and all juvenile females and males disappeared from their natal areas. I never resighted as adults any of the 21 (10 males, 11 females) juvenile fox squirrels that were born on the study area. Only two carcasses of juveniles (one male, one female) were recovered. The female apparently died at 10 weeks of age after entering a large honey bee (*Apis mellifera*) nest at the base of her den tree, while the male died of a granuloma on the liver at 6 months of age.

Social interactions.—Both amicable and agonistic interactions were infrequent among adults. I observed 900 interactions (0.711 interactions/h of observation) between marked adult gray squirrels and 315 interactions (0.249 interactions/h of observation) between marked adult fox squirrels. Amicable interactions accounted for 38.2% of interactions of adult gray squirrels and 33.7% of interactions of adult fox squirrels.

Adult-adult chases were the most common agonistic interaction between gray squirrels (0.449 chases/h of observation), with only 18 of 568 (3.2%) chases between adults escalating into interindividual contact and fighting. Adult males and females aggressively chased each other less frequently than expected; adult males chased each other nearly as often as expected while adult females chased other adult females more frequently than expected (Table 1).

The frequency of amicable behaviors by adult gray squirrels differed between sexes (Table 1). Adult males and adult females interacted amicably much less frequently than expected. Adult males behaved amicably toward other adult males more frequently than expected, whereas adult fe-

TABLE 1.—Social interactions between adults in gray squirrels and fox squirrels, 1987–1990. The populations remained nearly constant (10–13 female and 12–14 male gray squirrels, 5–6 female and 6–7 male fox squirrels). Observed values that contribute a large portion of the chi-square test statistic are considered to be biologically significant; ^a indicates observed value contributed 25–50% of the chi-square statistic; ^b indicates observed value contributed >50% of the chi-square statistic.

Interaction group	Gray squirrels				Fox squirrels			
	Amicable		Agonistic		Amicable		Agonistic	
	Ex-pected	Observed	Ex-pected	Observed	Ex-pected	Observed	Ex-pected	Observed
Male-female	179	103 ^a	289	202 ^a	57	23 ^b	113	72 ^a
Male-male	92	144 ^a	149	170	57	78	55	94 ^b
Female-female	73	97	119	184 ^a	21	5 ^a	41	43
χ^2		69.2		65.3		40.1		42.2
<i>P</i>		<0.01		<0.01		<0.01		<0.01

males demonstrated only a slight tendency to be amicable with other adult females.

During the 4 months following weaning of juvenile gray squirrels (from ca. 10–26 weeks of age), adult females did not differentially chase juvenile males or females. However, adult males tended to chase juvenile males more frequently than juvenile females (Table 2). Amicable interactions between adult males and juveniles were too infrequent for analysis; however, adult females did not differentially apportion amicable behaviors between juveniles of each sex (Table 2).

Chases involving two adults were the most common agonistic interaction between

fox squirrels (0.165 chases/h of observation), and only three of 209 (1.4%) chases between adults escalated into combat. As in gray squirrels, the sexes behaved agonistically toward each other less frequently than expected (Table 1). Adult males chased each other more frequently than expected, while chases between adult females were observed as frequently as expected.

Amicable behavior also differed among male and female fox squirrels (Table 1). Again, adult males and adult females interacted much less frequently than expected. The frequency of amicable behavior between same-sex individuals differed between adult males and females. Amicable

TABLE 2.—Social interactions between adults and juveniles in gray squirrels and fox squirrels, 1987–1990. The data include all interactions during the 4 months after juveniles were weaned. χ^2 test could not be performed where sample sizes were less than three.

Interaction group		Gray squirrels				Fox squirrels			
		Amicable		Agonistic		Amicable		Agonistic	
		Ex-pected	Observed	Ex-pected	Observed	Ex-pected	Observed	Ex-pected	Observed
Adults	Juveniles								
Male	Male		0	14	19		1	7	12
Male	Female		2	17	12		0	8	3
χ^2					3.62				6.80
<i>P</i>					<0.10				<0.05
Female	Male	18	20	39	37	16	19	7	10
Female	Female	22	20	49	51	19	16	9	6
χ^2			0.41		0.28		0.79		1.58
<i>P</i>			>0.20		>0.20		>0.20		>0.20

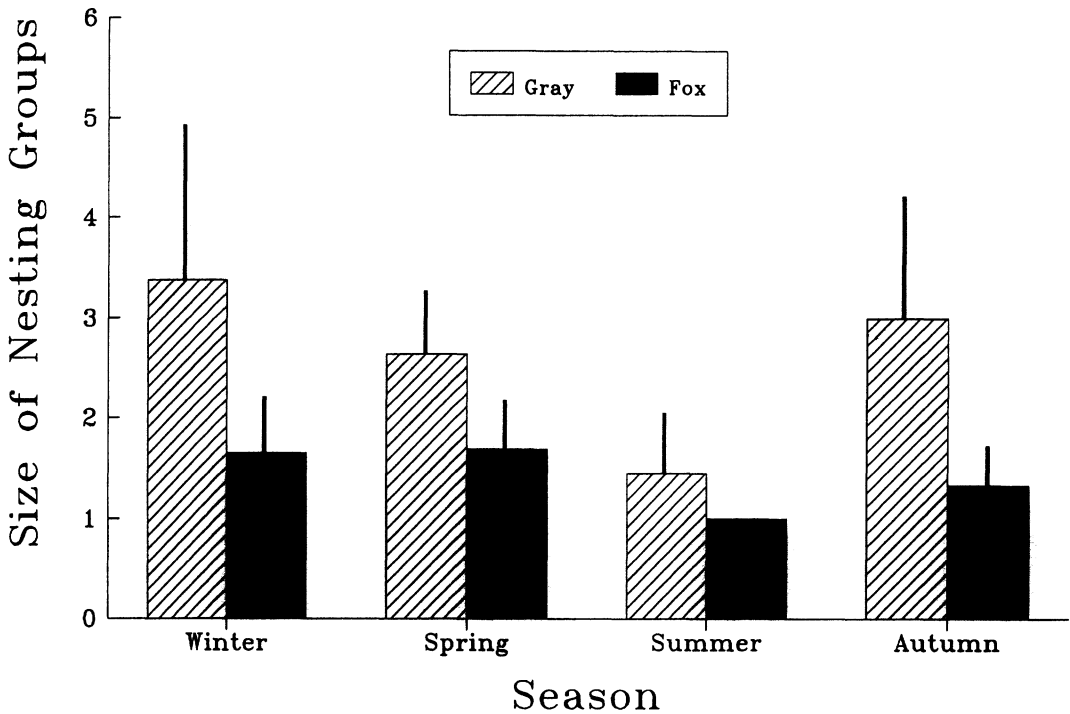


FIG. 1.—Seasonality of the size of nesting groups (mean + 1 SD) for gray squirrels and fox squirrels.

behaviors were less common than expected among adult females, while adult males were amicable more frequently than expected.

Although samples were limited ($n = 15$), adult male fox squirrels chased juvenile males more frequently than they chased juvenile females during the 4 months after juveniles were weaned (Table 2). Adult females did not differentially chase juvenile males and juvenile females. Amicable behavior between adult males and juveniles was too infrequent for analysis; however, as in gray squirrels, adult female fox squirrels did not treat the sexes differently (Table 2).

Nesting associations.—The most common amicable behavior occurring between adults was simultaneous nest sharing, which accounted for 85.5% of 344 amicable interactions. Gray squirrels commonly nested in groups of two to nine squirrels per den (Fig. 1) and size of group varied with season (ANOVA; $F = 15.7$, $d.f. = 189$, P

< 0.001); the largest groups occurred in autumn and winter. Although summer nesting groups were smaller than groups in all other seasons (Tukey's $q > 5.14$, $P < 0.05$), some adults nested in groups during each season. The sexes tended to nest separately; single-sex groups (35.2% all-male nesting groups and 20.0% all-female nesting groups) were the most common assemblage of the 245 communal nesting groups that I observed among gray squirrels.

Kinship influenced the composition of nesting groups of female gray squirrels. Of 52 nesting groups that included more than one adult female, related females ($r > 0.25$) exclusively were together in 82.7% of the nests. I observed only nine nesting assemblages that contained unrelated adult females. In two instances, an adult female and her young-of-the-year joined another nesting assemblage of females, while on seven occasions a yearling female with no known

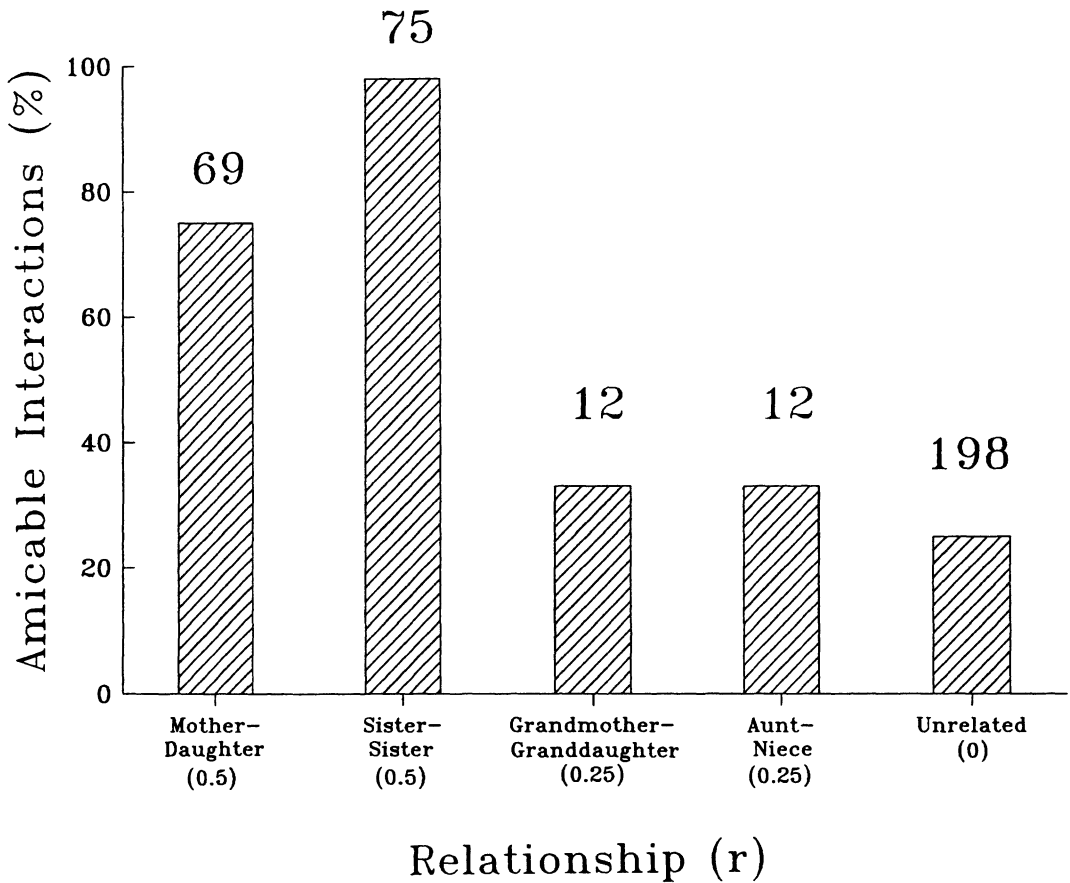


FIG. 2.—The percentage of social interactions among adult female gray squirrels that were amicable, for each relatedness dyad. All pairs of sisters were littermates. The number of interactions is shown above each bar.

relatives joined a nesting group of adult females that were sisters.

Fox squirrels also nested in groups of two to five squirrels per den (Fig. 1). Communal nests occurred during all seasons except summer, when all adults nested alone (ANOVA; $F = 3.8$, $d.f. = 113$, $P < 0.01$); the largest nesting groups were in winter and spring (Tukey's $q > 4.14$, $P < 0.05$). Most (35 of 48; 72.9%) group nesting consisted of adult males; females were solitary and only nested with another unrelated adult female on five occasions. Because all juvenile males and females disappeared from their natal areas, kinship did not influence the composition of nesting aggregations.

Social interactions and kinship.—Because some female gray squirrels remain in their natal area, the potential exists for kinship to influence patterns of amicable and agonistic behaviors. Such kin-directed behaviors were not seen in adult fox squirrels and male gray squirrels because of the absence of natal philopatry. The frequencies of amicable and agonistic behaviors among adult females varied with the level of relatedness (Fig. 2; $\chi^2 = 157.3$, $P < 0.001$). Among mother-daughter ($r = 0.5$) and littermate sister-sister ($r = 0.5$) dyads, the proportion of amicable interactions was significantly greater than that of agonistic behaviors (Bonferroni Z-test, 90% confidence intervals; mother-daughter, -0.31 , -0.12 ;

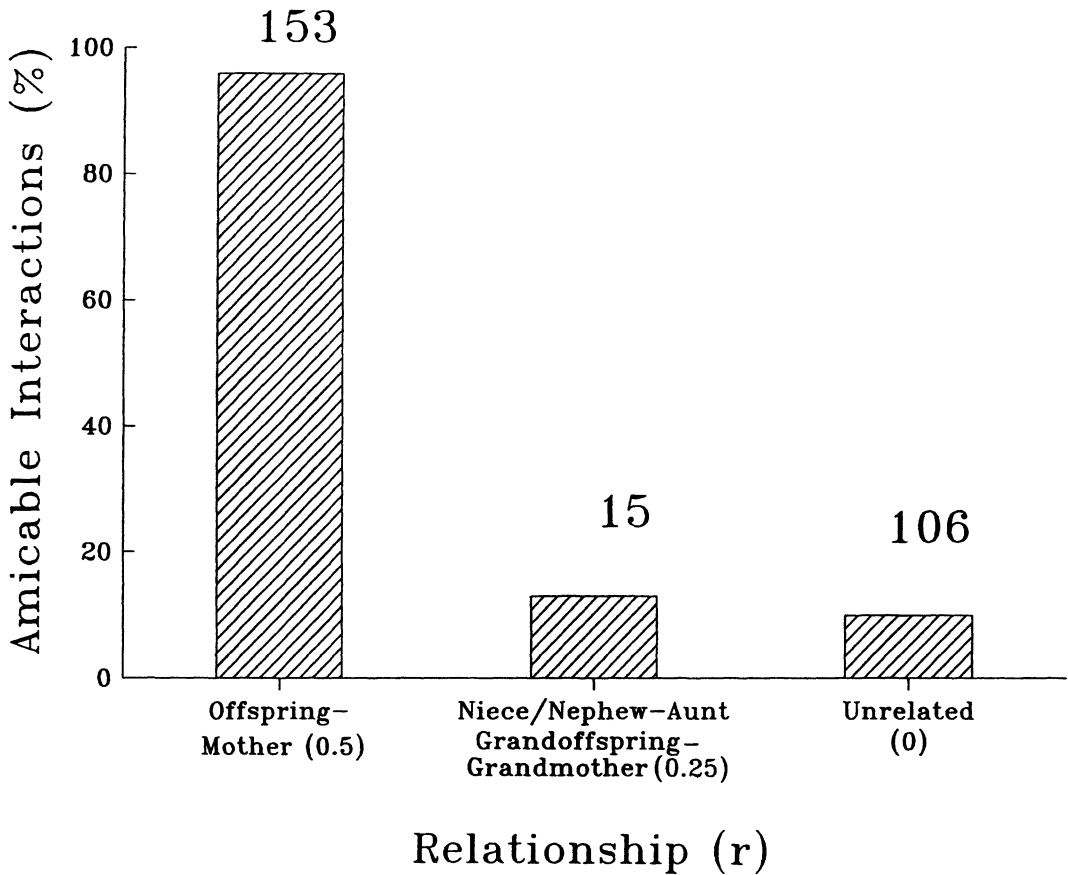


FIG. 3.—The percentage of social interactions between adult female and juvenile gray squirrels that were amicable for each relatedness dyad. The sexes of juveniles were not treated differently by adults, and so are combined here. The categories for niece/nephew–aunt and grandoffspring–grandmother (both $r = 0.25$) are combined because of small samples. The number of interactions is shown above each bar.

sister-sister; -0.50 , -0.32). The proportion of amicable behaviors among unrelated females ($r = 0$) was significantly less than that of agonistic behaviors (Bonferroni Z-test, 90% confidence intervals: 0.49 , 0.69). Amicable and agonistic interactions were distributed similarly among distant kin ($r = 0.25$) and unrelated females ($\chi^2 = 2.16$, $P > 0.10$). Relatives with $r = 0.5$ were treated differently than individuals with $r < 0.25$ (distant kin and unrelated combined: $\chi^2 = 148.71$, $P < 0.001$).

Amicable behavior between adult females and juveniles also is kin-directed (Fig. 3; $\chi^2 = 203.0$, $P < 0.001$). Because

the frequency of amicable and agonistic interactions did not differ between juvenile males and females in any relatedness class (χ^2 contingency tests, $P > 0.10$), I combined data for juvenile males and females. The proportion of amicable interactions was significantly greater than that of agonistic behaviors among mother-offspring dyads ($r = 0.5$; Bonferroni Z-test, 91% confidence intervals: -0.93 , -0.80). Interactions between adult females and unrelated juveniles were decidedly depauperate of amicable interactions in proportion to the frequent agonistic behavior (Bonferroni Z-test, 91% confidence intervals: 0.68 , 0.85). Amicable

and agonistic interactions were not different between distant kin ($r = 0.25$) and unrelated juveniles ($\chi^2 = 0.11$, $P > 0.50$). Juveniles with $r = 0.5$ received lower levels of agonistic behavior than juveniles with $r < 0.5$ ($\chi^2 = 202.5$, $P < 0.001$).

Kinship also appeared to influence recruitment patterns of female gray squirrels. Of the 18 adult female gray squirrels that were recruited into the population (i.e., became resident for >1.0 year), only two females were not related to resident females ($r < 0.25$). In fox squirrels, only four females were recruited into the population, and all were unrelated to resident females. Due to the efficacy of trapping and marking, unmarked animals were considered non-residents and likely distantly or not related to residents. Unmarked and presumably unrelated adult gray squirrels and fox squirrels lost more chases than expected (gray: wins = 11, losses = 29; fox: wins = 16, losses = 51; Goodness-of-fit $\chi^2 > 3.84$, $P < 0.05$, assuming a 50:50 distribution of wins and losses), which suggests ingressing squirrels would have had difficulty in establishing residence in the population.

DISCUSSION

Although the level of sociality differed between fox squirrels and gray squirrels, a similarity in the patterns of interaction within each species was the separation of the social systems of the adult males and females. Male squirrels do not exhibit paternal care, and the mating system is one of dominance polygyny/prosmiscuity where males actively compete for access to a female on her single day of estrus (Koprowski, 1993b, 1993c; Thompson, 1977). Males and females compete for food and dens throughout the year. Because all males disperse, adult males and females are unrelated; therefore, indirect fitness gains through cooperation are not possible. The reproductive goals of males and females can differ and conflict (Armitage, 1986; Downhower and Armitage, 1971), and direct conflict between sexes of tree squirrels is evident dur-

ing mating bouts in evasive behavior, selectivity of mating sites, and removal of the copulatory plug by the female (Koprowski, 1993b, 1993c, in press).

Although rates of interaction were low among adult squirrels, a well-defined and relatively complex social system was evidenced especially in gray squirrels. Amicable behaviors were associated with dens. Winter is a critical period when available energy may be limited (Montgomery et al., 1975) at a time when ambient temperatures are low. The prevalence of nesting aggregations in the coldest months relative to the warmest months suggests that communal nesting has a significant thermoregulatory function, as in a variety of small mammals inhabiting temperate environments (Andrews et al., 1987; Madison, 1984). Although dens occupied in winter by a single adult fox squirrel have temperatures that are nearly 30°C above ambient (Havera, 1979), the energetic benefits of communal nests are unknown but may be significant.

The fundamental social unit of ground squirrels is the female-female dyad that extends from the prolonged association of mother and daughters (Armitage, 1981; Michener, 1983). In ground squirrels characterized by high levels of sociality, retention of daughters in the natal area increases the probability of producing descendants, and therefore increases the fitness of both mother and daughter (Armitage, 1986, 1988). Female gray squirrels were organized into interactive social units that formed as a result of natal philopatry and were characterized by high levels of relatedness among group members. However, female fox squirrels did not form groups, perhaps because juveniles did not remain in their natal areas.

The differences in the sociality of fox squirrels and gray squirrels within a local area are perplexing. Both species have similar food preferences and digestive efficiencies (Smith and Follmer, 1972), which suggests that the habitat likely is equally attractive to both species. Furthermore, the

study area was characterized by a diversity of high-quality food trees, and observations on the growth and survival of young suggest that differential mortality between the species does not occur (Koprowski, 1991). If communal nesting in winter is an energy saving strategy, then why do adult female fox squirrels not nest in groups while female gray squirrels form sex-biased nesting assemblages? Future analyses of sociality in tree squirrels must attempt to delineate differential fitness costs and benefits of retaining daughters in gray squirrels and fox squirrels. Fox squirrels are ca. 20% larger than gray squirrels (Koprowski, 1994a, 1994b); energetic differences associated with body size, including resistance to starvation (Millar and Hickling, 1990), may permit adult female fox squirrels to nest alone and forego any potential costs associated with group nesting. Additionally, juvenile fox squirrels are born on average 2–4 weeks earlier in the year than gray squirrels (Brown and Yeager, 1945). Perhaps the slight headstart permits fox squirrels to reach a critical body mass and independence earlier in the year than juvenile gray squirrels, thereby enabling natal dispersal without adverse effects to survival and the direct fitness of mothers. Such trade-offs might resemble the strategies of ground squirrels (Koprowski, in press). The more social ground squirrels do not reach adult size during the first year of life and are philopatric, while asocial ground squirrels mature in the first year and disperse (Armitage, 1981). This potential linkage suggests that the ecological constraints that influence the evolution of sociality may be similar in ground and tree squirrels (Koprowski, in press).

Kinship clearly influenced the apportioning of behaviors among adult and juvenile female gray squirrels (Koprowski, 1993a, this study). Female gray squirrels did not distribute their social behaviors in proportion to relatedness levels as a proportional-altruism model would suggest, but rather preferentially directed these behaviors only

toward close kin ($r = 0.5$; Armitage, 1989; Bennett, 1987). This pattern of kin-biased behaviors also was reflected in the pattern of recruitment of females into the population; unrelated females were chased by residents and rarely recruited into the population. Unmarked and presumably transient squirrels are frequently chased in populations of gray squirrels (Taylor, 1969; Thompson, 1978a, 1978b; this study).

Female gray squirrels demonstrate a pattern that appears common in the social ground squirrels; close relatives receive more amicable behavior than distant relatives (Armitage, 1986, 1987; Hoogland, 1986; Sherman, 1981), which are treated in a manner similar to unrelated females (Armitage, 1987). Adult females behave in a manner consistent with a strategy to maximize the direct fitness component of their inclusive fitness by behaving amicably toward adult female progeny and sharing nests, almost exclusively, with them. The rarity of agonism among littermate sisters suggests the potential for kin selection to occur; however, before kin selection is assumed to occur, it must be demonstrated that sisters gain indirect fitness via collateral kin. Sister-sister groups originate from a mother that recruits daughters, as in the matriline of yellow-bellied marmots (*Marmota flaviventris*; Armitage, 1987), and sisters may gain direct fitness if communal nesting increases the probability of survival, reproduction, or inheritance of a nest (Van Vuren and Armitage, 1994). The frequent nest sharing by both sexes, increase in communal nests in winter, and the difficulty of establishing residence suggests that natal philopatry and communal nesting have survival value for gray squirrels. Sharing space and nests with descendant kin appears to be a strategy to maximize direct fitness, while indirect fitness gains are a coincidental benefit that results from the direct fitness strategies of other squirrels.

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