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FORAGING ABILITY, DOMINANCE RELATIONS AND COMPETITION FOR FOOD BY FOX AND GRAY SQUIRRELS

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ABSTRACT

In central Illinois fox squirrels are most common in woodlots, whereas gray squirrels are most common in cities. Several studies have suggested that food is a limited resource during the winter breeding season, therefore we tested the foraging abilities and dominance relations of captive squirrels to assess possible mechanisms of competition between these sympatric species. Female gray squirrels were more efficient at finding buried nuts than female fox squirrels, but female fox squirrels kept female gray squirrels from access to food during breeding seasons. Neither species was dominant during the non-breeding season. These results are consistent with the hypothesis that aggressive behavior of female fox squirrels influences the distribution of gray squirrels in woodlots during the main breeding season (winter) and that this aggression reflects competition for food.

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INTRODUCTION

Woodlots in Champaign County, Illinois contain mostly fox squirrels (*Sciurus niger*), whereas larger cities contain nearly all gray squirrels (*S. carolinensis*) (Nixon et al., 1978). Several studies have indicated that availability of food, particularly mast, often limits the abundance of fox and gray squirrels in woodlots during winter (Barber, 1954; Christisen and Korschgan, 1955; Nixon and McClain, 1969; Nixon et al., 1975), and gray squirrels appear to shift their use of habitat during winter

(Brown, 1984). Thus competition for food may occur (Flyger and Smith, 1980). As part of a study of competition between natural populations of these species (Brown, 1984), we conducted two types of laboratory experiments to explore the role of foraging abilities (exploitation) and dominance relations (aggression) in competition for food.

If food is in fact limiting, then differing foraging abilities of fox and gray squirrels should lead to different abilities to exploit sparse food supplies and would provide a mechanism for competitive exclusion. Smith and Follmer (1972) concluded that fox and gray squirrels had very similar preferences with respect to the five species of naturally occurring foods tested. Fox squirrels consumed nuts faster than did gray squirrels, but their study involved only a few individuals. Some work has been done on recovery of buried nuts by gray (Thompson and Thompson, 1980) and fox squirrels (Cahalane, 1942), but few quantitative or comparative data on the foraging abilities of fox and gray squirrels are available. Therefore our first set of experiments concerned the ability of these two species to find and consume buried nuts. If gray squirrels change their use of woodlots in central Illinois because of exploitative competition for food, we would expect fox squirrels to be more efficient foragers.

Analysis of aggressive interactions in the laboratory can be used to study the mechanisms underlying competitive interactions in nature, as done by Conley (1976) and Koplin and Hoffman (1968) with microtine rodents, Blaustein and Risser (1976) with kangaroo rats; and Sheppard (1971) and Heller (1971) with chipmunks. Ackerman and Weigl (1970) investigated agonistic behavior in captive red (*Tamiasciurus hudsonicus*) and gray squirrels by recording the exclusive or shared use of nest boxes. They concluded that the antagonism between the two species was low, as demonstrated by the frequent sharing of nest boxes. Because we were interested in competition for food, we simulated a food shortage in the laboratory and studied the aggressive behavior of hungry fox and gray squirrels. If gray squirrels change their distribution in woodlots because of interference by fox squirrels, we would expect fox squirrels to win aggressive encounters.

MATERIALS AND METHODS

In April to June of 1981 and 1982 and October of 1983 fox squirrels were live-trapped from oak-hickory and oak maple woods in Champaign and Vermillion Counties, Illinois; gray squirrels were trapped from yards of residences in the cities of Champaign and Urbana. Because we wanted to minimize the confounding effects of sex and age and because aggressive behavior of adult females has been implicated in population regulation of squirrels (Nixon et al., 1975; Havera and Nixon, 1978), only adult females were used. Squirrels were maintained in large outdoor cages (1 × 2 × 2-m) and supplied with nest boxes. English walnuts, a preferred food, supplemented the standard diet of Purina rat chow and water for the first week. All animals were maintained for at least six weeks prior to experimentation in order to acclimate them to laboratory conditions.

Foraging studies were conducted during the morning hours from 13 June 1981 to 22 July 1981 and from 14 July 1982 to 10 September 1982. Eight adult female gray squirrels and seven adult female fox squirrels were tested for their foraging abilities in a 3 × 3 × 2.5-m experimental enclosure that was constructed of 2-cm wire mesh and had a dirt floor. The soil was maintained in a friable and moist con-

dition during foraging trials. Commercial walnuts were used in these trials rather than native mast (black walnuts or acorns) to insure a low incidence of wormy or moldy nuts, which could have affected results because squirrels often avoid unsound nuts (Dennis, 1930; Lloyd, 1968). English walnuts may be more difficult for squirrels to find than native mast because commercial walnuts are cleaned and washed. However, flotation methods that are often recommended to sort out sound from unsound nuts proved to be unreliable with acorns and walnuts (26% of 250 nuts tested were classified incorrectly).

Six small, unshelled English walnuts were placed in the enclosure just prior to the introduction of a squirrel that had been starved for 48 hours. One nut was placed on the surface of the soil (surface nut), one just under the surface (subsurface nut) and the remainder with one, two, three and four cm of soil above the top of each nut, respectively. The positions of the nuts on a 0.3-m grid were determined using a random number table. The surface of the soil was raked after the nuts were buried to eliminate any visual cues of their location. Weather conditions, squirrel activity and movements within the enclosure, the amount of time spent foraging, the time required to open the nuts (gnawing time) and the time required to consume the meats (eating time) were recorded for each trial.

An experiment was terminated when the squirrel found all six nuts, remained at one spot for more than 20 minutes, or went more than 30 minutes without finding an additional nut. The last two criteria were established after repeated observations which showed that additional time in the enclosure did not produce different results. After each experiment undetected and uneaten nuts were checked for soundness. Each squirrel was given five opportunities to forage at one-week intervals. Data for the number of nuts found was based on the best three trials for each squirrel because some learning was involved in the initial trials and because the foraging of squirrels was sometimes disturbed by other animals or bad weather.

Dominance relationships were established by using all possible pairwise combinations of interspecific encounters between three fox and three gray squirrels during the non-breeding season (September 1981) and the winter breeding season (January 1984) and between four of each species during the summer breeding season (July and early August 1982). Different animals were used each year. Squirrels were starved for 48 hours prior to being placed into the enclosure (described above) and rested one week between encounters. Vaginal smears were taken during the trials conducted in 1982 and 1984 to determine if any of the animals were in estrus, since these studies were conducted during breeding seasons.

A small metal feeder that allowed squirrels to feed on English walnut meats was attached to the enclosure wall at ground level. Behavior of the paired fox and gray squirrels was observed with binoculars from a blind 15 m from the enclosure. Dominance was determined by the ability of one squirrel to maintain possession of the feeder in spite of efforts of the other squirrel to feed. Possession was established by displacing and/or chasing off the other squirrel. Most encounters were short in duration and aggressive behaviors occurred almost exclusively at the feeder. In all but one of the 34 trials conducted, a dominant animal was determined by its aggressive behavior at the feeder; the other trial was scored as a draw. Experiments were terminated when the dominant squirrel relinquished the feeder.

RESULTS

Both species of squirrels examined, opened and ate walnuts in a very similar manner during the foraging trials. Occasionally, the nut was eaten where it was found, but more often the squirrel opened and consumed the nut elsewhere. After each successive nut was found it was taken to the same spot and eaten. Squirrels that consumed all six nuts in the enclosure were still hungry; they continued to forage and consumed an additional introduced nut. Successful squirrels usually found and consumed the nut on the surface first (19 of 24 trials). The incidence of wormy and moldy nuts was low (<1%) and created no complications. The time taken to find or to consume nuts did not change significantly during a trial for gray squirrels that found all 6 nuts. (one-way ANOVA; $F = 0.87$; 5, 48 d.f.; $P > 0.1$ and $F = 2.05$; 5, 60 d.f.; $P > 0.05$, respectively). However, there was a significant positive correlation between the order in which nuts were found by gray squirrels and the depth at which they were buried, deeper nuts being found later in the trial ($r = 0.57$, d.f. $= 64$, $P < 0.001$). Fox squirrels did not find enough nuts to allow a similar analysis.

Although the larger fox squirrels consumed English walnuts significantly faster than gray squirrels, gray squirrels found significantly more nuts (Table 1). None of the seven fox squirrels found all six nuts, although some individuals spent up to 25 minutes foraging without success. Conversely, five of the eight gray squirrels found all six nuts during one or more of their foraging trials.

The results from the non-breeding season showed no trend in dominance relations, but those from the breeding seasons showed significantly more wins by fox squirrels than expected if wins were distributed evenly (Table 2). Low sample sizes from the non-breeding season may lead to a Type II error, which might indicate a difference between breeding and non-breeding season behavior even if none existed. A Fisher exact test was applied to the dominance data from all three periods to determine if a difference did occur. A highly significant difference resulted ($P = 0.007$, $N = 33$). The adult female fox squirrels weighed more than the grays, which is normal for these two species (Brown and Yeager, 1945). Vaginal smears taken during the 1982 and 1984 trials indicated that none of the squirrels had been or was in estrus, even though these trials were done during normal breeding seasons.

DISCUSSION

Fox and gray squirrels foraged in similar ways in our experiments, and in nature there is almost complete overlap in food preferences and food habits of these species (Nixon et al., 1968, Smith and Follmer, 1972). Winter food consists largely of mast. Fox and gray squirrels may respond differently to English walnuts than they would to native mast owing to differences in scent. Thus native foods may be easier to find than English walnuts, and use of native mast in foraging trials might reduce the differences we saw between foraging abilities of fox and gray squirrels. Fox and gray squirrels find buried nuts using olfactory stimuli (Cahalane, 1942; Thompson and Thompson, 1980) and consequently nuts buried more deeply may be more difficult to find. The positive correlation between the order in which nuts were found and the depth at which they were buried supports this idea. Although neither squirrel species normally buries nuts deeper than 1 to 2 cm (Cahalane, 1942; Thompson and Thompson, 1980), these animals are often forced to forage for food covered by snow. The superior ability of gray squirrels to find buried nuts should be of great competitive advantage during these times, and during periods of food shortage they should be able to displace fox squirrels if only exploitative competition were important.

Little is known about the behavioral relationships between fox and gray squirrels in natural populations but our results indicate that fox squirrels should win aggressive encounters during breeding seasons. Bakken (1952) observed aggressive interactions in fox and gray squirrels and noted that fox squirrels were more aggressive as food supplies declined over the winter. Berry et al. (1978) reported that dominance hierarchies of gray squirrels within an enclosure may change with the addition of more animals and a different size enclosure. Although our procedures differed, the size of our test enclosure may have affected squirrel behavior.

The difference in our results for breeding and non-breeding seasons (Table 2) reflects seasonal changes in aggressive behavior. Although none of our animals were in estrus during the encounters, aggressive behavior in females generally increases during the breeding season (Bakken, 1952; Taylor, 1966; Nixon et al., 1975). The 1981 encounters were carried out during the early fall, after the summer breeding season, when adult females might be less aggressive. The overall dominance of fox squirrels is consistent with Grant's (1972) finding that the larger of two otherwise similar rodent species is usually the dominant one.

While the results of our laboratory experiments may not reflect precisely the relationship between squirrels in nature, they are consistent with the hypothesis that aggressive behavior of fox squirrels causes the change in habitat use by gray squirrels during winter. Female fox squirrels may need to displace gray squirrels in woodlots during the winter breeding season because gray squirrels are more efficent foragers. Thus gray squirrels may reduce the availability of stored mast below levels that will support breeding fox squirrels.

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Table 1. Comparative foraging abilities of fox and gray squirrels. Values are $\bar{X} \pm 1$ SE.

	n	Gnawing time (sec)	Eating time (sec)[a]	No. nuts found[b]
Fox	7	35.8 ± 13.3	160.0 ± 12.2	1.6 ± 0.5
Gray	8	76.8 ± 23.7	262.0 ± 43.0	4.1 ± 0.8

[a]Student's t-test, $P < 0.05$ for comparison between species.
[b]Student's t-test, $P < 0.025$ for comparison between species.

Table 2. Results of round-robin aggressive encounters between adult female fox and gray squirrels.

	Mean Body Mass (N)		Observed Number of Wins (Expected)		
	fox	gray	fox	gray	draws
Winter breeding Season, 1984[a]	877 (3)	490 (3)	9 (4.5)	0 (4.5)	0
Summer breeding Season, 1982[b]	725 (4)	475 (4)	13 (7.5)	2 (7.5)	1
Non-breeding Season, 1981[c]	813 (3)	603 (3)	4 (4.5)	5 (4.5)	0

[a]$P = 0.004$, binomial exact test
[b]$P = 0.006$, binomial exact test
[c]$P = 0.49$, binomial exact test