Response of Fox Squirrels and Gray Squirrels to a Late Spring-Early Summer Food Shortage

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ABSTRACT.—The response of adult and juvenile fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) to a shortage in their two major May–June foods was monitored and compared to a year of typical food abundance. Squirrels foraged more frequently, but less efficiently, during the year of fruit failure than during the typical year. Juvenile survival of both species was reduced during the year of fruit failure, but adult survival remained high. Juvenile losses occurred during late June when weights of adults and juveniles were lower than in the year of typical fruit abundance. By influencing juvenile survival and body condition of adults, late spring–early summer can be a critical period for populations of tree squirrels.

Temporal and spatial variation in the environment are influential factors in the evolution of life-history strategies (Wilbur, 1980). Fox squirrels (*Sciurus niger*) and eastern gray squirrels (*S. carolinensis*) depend heavily on reproductive tissues of deciduous trees for food (Brown and Yeager, 1945; Korschgen, 1981; Nixon et al., 1968). The production of these tissues can be influenced significantly by weather, and mast yields can exhibit great temporal variation (Matthews, 1963; Silvertown, 1980). The two seasons of birth of tree squirrels are well timed with the phenology of deciduous trees; most litters are born during February–March when buds and flowers become abundant and July–August when mast crops ripen (Brown and Yeager, 1945).

Winter can be a critical period for squirrels (Allen, 1943) when energy availability may be less than the energetic requirements of squirrels (Montgomery et al., 1975). Because squirrels rely nearly exclusively on scatterhoarded nuts for food during winter (Korschgen, 1981; Montgomery et al., 1975), overwinter survival may be related to the mast crop of the previous autumn. However, data on the relationship between mast crop and survival of adult squirrels are equivocal; mast crop may influence survival of adults in some populations (Allen, 1954; Nixon and McClain, 1969; Nixon et al., 1975) yet was not correlated with survival of squirrels in other studies (Hansen et al., 1986). The relationship between mast crop and overwinter survival of squirrels is suggestive of a step function (Nixon et al., 1975) with the extremes in size of mast crop the most influential to survivorship (Nixon and McClain, 1969; Nixon et al., 1975; Hansen et al., 1986). However, survival of juveniles may be more sensitive and directly related to food availability (Barkalow et al., 1970; Glanz et al., 1982; Heaney, 1984).

Squirrels may feed on >30 different types of food (Brown and Yeager, 1945; Korschgen, 1981); however, most local populations rely heavily on only a few species (Glanz et al. 1982; Nixon et al., 1968; Packard, 1956) making local populations vulnerable to fluctuations in tree productivity. Herein, I report the response of fox squirrels and gray squirrels to a poor crop of mulberries (*Morus* sp.) and a complete failure of hackberry fruits (*Celtis occidentalis*) resulting in the loss of the two major seasonal food sources for a local population. Squirrels appeared emaciated in May 1987, and this study was initiated to quantify the impact of the shortage of food in late spring by comparing May–June body weights and survival of both juvenile and adult squirrels during a year of fruit failure (1987) and a year of typical fruit abundance (1988).

STUDY AREA AND METHODS

The study area was a 4.2-ha parkland 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 eastern gray squirrels are present with adult densities remaining nearly constant between years (31 adults in 1987 and 34 adults in 1988). The 319 trees consisted of >20 species dominated in size and density by black walnut (*Juglans nigra*; 18.8%). The most heavily used food trees on the site were black walnut, oaks (*Quercus* sp.), hackberry, mulberries, elms (*Ulmus* sp.), pines (*Pinus* sp.), cottonwood (*Populus del-*

toides), and catalpa (*Catalpa bignonioides*). Supplemental feeding of squirrels by humans was never observed. Water was available in several storm drains. Domestic dogs were the principal predators. Weather data were obtained from the University of Kansas Weather Station.

The poor fruit crop followed a week of frosts between 29 March and 4 April 1987, when minimum temperatures were <0°C on 6 days and reached a low of −6.7°C on 30 March. The spring-flowering trees were flowering heavily because of mild March weather (average daily temperature 3.9°C greater than the 9.4°C normal) and frosts severely damaged buds and flowers. Probably as a result, mulberries were scarce and present on only two of three trees and none of 21 hackberry trees possessed fruits. However, in 1988 a more common pattern of fruiting occurred with fruits common on each of three mulberry, and 20 of 21 hackberry trees.

Since May 1986, fox squirrels and gray squirrels were trapped in 15- by 15- by 60-cm wire-mesh live traps (Tomahawk Live Trap Co., Tomahawk, WI) baited with peanuts or peanut butter. Traps were attended constantly when set and trapping efforts were restricted to vacations in the academic year or early mornings to avoid human disturbance of traps. Trapping to gain data on the initial effects of food shortage was conducted 26 May–7 June 1987 and 16 May–3 June 1988. To obtain data on weight change of juveniles, trapping also occurred 3–4 July 1987 and 25–29 June 1988. Birth dates of juveniles probably were similar each year; the mean date of mating was 9 January in both 1987 (range, 27 December 1986–22 January 1987) and 1988 (range, 5–21 January). Squirrels were ear-tagged with uniquely numbered tags (Monel no. 1, National Band and Tag, Newport, KY) and freeze-marked for identification at a distance (Rood and Nellis, 1980).

Age of squirrels was estimated by the appearance of external genitalia and characteristics of the tail pelage upon first capture (Larson and Taber, 1980; McCloskey, 1977). Squirrels were weighed with a spring scale while restrained in a cloth handling cone. Observations were conducted almost daily through June 1989 by use of 35-mm binoculars to scan the area while walking the same route at 20-min intervals. The absence of a shrub stratum and the habituation of squirrels to humans facilitated observation. Survival was calculated as the percentage of individuals alive on the study area during the May–June trapping period and subsequently confirmed alive by trapping or observation during or after the late June–early July trapping period. This period was selected because the nut crop became readily available in early July, thereby ending the food shortage. Only juvenile offspring of resident adult females nesting on the study area were used in calculating survival. Because of traditionally poor trapping success in summer (Brown and Batzli, 1985), only sample sizes of gray squirrels were sufficient to permit mean weights to be tested for differences between years by use of Student's *t*-tests. Frequencies of surviving and disappearing squirrels of both species, frequencies of squirrels feeding on or foraging under mulberries, hackberries, and other species, frequencies of foraging, feeding, and other behaviors were compared using chi-square contingency techniques (Zar, 1984).

RESULTS

The failure of seed crops of mulberry and hackberry in 1987 had a significant impact on the foraging ecology of marked squirrels. Mulberries and hackberries were the major component of the diet of squirrels in the year of typical abundance, but declined from 78.7% of 61 identified food items in 1988 to 8.3% of 36 identified food items in the fruit failure of 1987 ($\chi^2 = 47.98$, $P < 0.01$). In 1987, no mulberries or hackberries were observed to be eaten after 12 June and squirrels scavenged fragments of walnuts and acorns from autumn 1986. Squirrels foraged solely under canopies of mulberries or hackberries during 42.8% of 290 foraging bouts in 1988, but used these areas during only 9.4% of 615 foraging bouts following the fruit failure of 1987 ($\chi^2 = 136.25$, $P < 0.01$). During the food shortage, squirrels foraged more frequently (60.6% of 1,189 observations were of squirrels feeding or foraging) than in the year of typical fruit abundance (39.3% of 872 observations were of squirrels feeding or foraging; $\chi^2 = 91.43$, $P < 0.01$). Foraging efficiency as indicated by the ratio of foraging observations: feeding observations was 3.1:1 during 1987 and only 2.1:1 in 1988.

Survival of squirrels generally was high during June except for juveniles in 1987 when only 39% remained at the beginning of July (Table 1). Sex-specific survival was not different in either juvenile ($\chi^2 = 0.3$, $P > 0.50$) or adult ($\chi^2 = 1.7$, $P > 0.10$) age classes permitting sex-specific data to be combined. Similarly, survival rates did not differ significantly between juveniles of *S. niger* and *S. carolinensis* during 1987 ($\chi^2 = 3.6$, $P > 0.05$) or 1988 ($\chi^2 = 0.9$, $P > 0.20$) or in adults during 1987 ($\chi^2 = 0.1$, $P > 0.50$) or 1988 ($\chi^2 = 1.6$, $P > 0.20$); therefore, species-specific data were combined. Adult survival was high (>85%) and did not differ significantly between

TABLE 1.—*Survival rates for adult and juvenile fox squirrels and gray squirrels during June 1987 and June 1988 in Lawrence, Kansas.*

Year	Age-class	Species	n^a	Survival (%)	Combined-species survival (%)
1987	Juvenile	Gray	9	56	
		Fox	4		39
	Adult	Gray	19	95	
		Fox	12	92	94
1988	Juvenile	Gray	24	92	
		Fox	10	100	94
	Adult	Gray	23	87	
		Fox	11	100	91

[a] Initial sample size.

the year of failure of the fruit crop and the year of typical food abundance for gray squirrels ($\chi^2 = 0.7$, $P > 0.20$), fox squirrels ($\chi^2 = 1.0$, $P > 0.20$), or after combining the data for both species ($\chi^2 = 0.2$, $P > 0.50$).

Juvenile survival contrasted markedly with adult survival (Table 1). Juvenile survival for the species combined was significantly lower during the year of fruit failure than during the year of fruit abundance ($\chi^2 = 17.3$, $P < 0.01$). Although samples were small, both juvenile gray squirrels ($\chi^2 = 5.7$, $P < 0.05$) and juvenile fox squirrels ($\chi^2 = 14.0$, $P < 0.01$) exhibited lower survival in 1987 than in 1988. A within-year comparison of juvenile and adult age-classes after combining species, suggests that the age-classes exhibited differential survival during June 1987, but not in June 1988. In 1987, juvenile survival (39%) was lower than adult survival (94%; $\chi^2 = 15.9$, $P < 0.01$); however, juvenile (94%) and adult survival (91%) were similar during 1988 ($\chi^2 = 0.2$, $P > 0.30$).

Juvenile mortality in June 1987 occurred in a 2-week period in late June when the two entire litters of fox squirrels disappeared and some members of each of three litters of gray squirrels disappeared. On 25 June 1987, I observed a juvenile male gray squirrel that appeared extremely emaciated. The squirrel experienced difficulty walking and fell to its side when attempting to sit upright. The juvenile was chased and bitten several times by an adult female gray squirrel as it approached a water source; it was never resighted. This observation suggests that poor physical condition contributed to the death of some juveniles.

Body weights differed for both juvenile and adult gray squirrels in late May–early June between 1987 and 1988. Weights did not differ between juvenile males and females in either 1987 ($t = 0.6$, $d.f. = 6$, $P > 0.10$) or 1988 ($t = 0.9$, $d.f. = 37$, $P > 0.10$) or adult males and females in either 1987 ($t = 0.4$, $d.f. = 11$, $P > 0.10$) or 1988 ($t = 0.2$, $d.f. = 16$, $P > 0.10$). Sex-specific weights were combined yielding age-class-specific weights. Weights of adults were significantly less (-10.6%) during the fruit failure in 1987 compared with 1988 (1987: 547.2 ± 42.0 g, $n = 18$; 1988: 612.3 ± 54.3 g, $n = 13$; $t = 3.6$, $d.f. = 29$, $P < 0.05$). Similarly, weights of juveniles were significantly less (-20.7%) in 1987 compared with 1988 (1987: 245.0 ± 29.3 g, $n = 8$; 1988: 309.0 ± 39.2 g, $n = 39$; $t = 4.8$, $d.f. = 45$, $P < 0.05$).

Trapping success in late June–early July was poor and only three juvenile gray squirrels were captured in each year; two juveniles in each year were captured previously in May–early June. Mean weight ($\pm SD$) of the three juveniles captured in 1987 was 256.7 ± 38.2 g representing only a 4.8% weight increase during June. The weight of a juvenile female increased 11.5%, whereas a juvenile male lost 10.4% of its body weight during June. The juveniles captured in 1988 averaged 453.3 ± 20.8 g, representing a substantial increase of 47.7% during June. Two recaptured juvenile females gained 48.4% and 104.3% during June.

DISCUSSION

The potential for an early summer critical period for squirrel populations was recognized >40 years ago (Allen, 1943; Brown and Yeager, 1945). More recently, the vulnerability of juveniles

to shortage of food in late spring and the greater contribution of supplemental foods such as insects has been espoused (Nixon, 1970). Furthermore, the late spring–early summer period is thought to be crucial in the annual cycle of the eastern gray squirrel in England (Kenward and Parish, 1986) and the European red squirrel, *S. vulgaris* (Wauters and Dhondt, 1989). However, the critical period in winter has been emphasized in research on North American *Sciurus* sp. (Havera and Nixon, 1980; Merson et al., 1978; Montgomery et al., 1975). For instance, habitat suitability index models for *S. niger* and *S. carolinensis* only directly incorporate measures of sources of winter food (nut-producing trees, proximity to corn) and include the assumption that spring and summer foods always contribute less than winter foods (Allen, 1982a, 1982b).

A shortage of food during late spring–early summer is frequently implicated to explain differential levels of reproduction between spring and summer birth seasons. Although litter sizes in spring and summer are equivalent or larger during the summer season (Brown and Yeager, 1945; Harnishfeger et al., 1978; Nixon et al., 1975), the percentage of adult females lactating may be considerably lower in the summer season (Brown and Yeager, 1945; Harnishfeger et al., 1978; McCloskey and Vohs, 1971). The reproductive pulse in summer also may vary greatly (0–75% of female fox squirrels per season), presumably in response to the spring supply of food (Harnishfeger et al., 1978). Similarly, the Neotropical red-tailed squirrel (*S. granatensis*) appears to have only one litter closely timed with the annual cycle of the one major food source, whereas a population on Barro Colorado Island (30 km away) has 2–3 litters/year with three primary food sources that fruit successively (Glanz et al., 1982). Although lower reproduction in summer may be related to reduced food sources in late spring–early summer, experimental studies including manipulations of food levels are lacking.

The reduced survival rates and lower body weights of juvenile squirrels during the year of fruit failure suggest that early summer can be a critical period for both fox squirrels and gray squirrels in North America. Because natal dispersal in gray squirrels does not occur until autumn when squirrels are 8–12 months old (Cordes and Barkalow, 1972; Horwich, 1972; Thompson, 1978), juvenile mortality was probably related to starvation as indicated by low weights of juveniles and the lack of weight gain by juveniles during June. Weights of squirrels captured at the beginning of July 1987 represent a biased sample of the original cohort of spring 1987. These squirrels had survived the food shortage with a minimal weight gain; the juveniles not surviving likely lost weight during this period.

Spring-born gray squirrels are 110–120 days old by late June. Weights of captive and wild-reared juveniles range from 350 to 400 g at this age (Shorten, 1951; Uhlig, 1955). During 1987, squirrels were in poor condition at nearly 100 g below the usual range, whereas in 1988, juveniles were in good condition exceeding the usual range by 50 g. Juveniles 80–90 days old weigh 250–300 g (Shorten, 1951; Uhlig, 1955); thus, the late May–early June weights were slightly below average in 1987, and slightly above average in 1988. Both mulberries and hackberries are good sources of crude protein (8–12% of dry weight); hackberries are extremely high in calcium content (10–12% of dry weight—Halls, 1977). Deficiencies in these nutrients may have contributed to the low weights. The differences in mean weights existing between juveniles in 1987 and 1988 probably were magnified by the end of June because of continued food shortage.

Juveniles are weaned by 10 weeks of age (Shorten, 1951) suggesting squirrels are not fully weaned until mid-May in Kansas. In Kansas, mast of oak and black walnut does not ripen sufficiently to be eaten by squirrels until July. As a result, squirrels feed almost exclusively on mulberries and hackberry fruits during May and June. Reichard (1976) reported that fox squirrels in Michigan fed exclusively on samaras of red maple (*Acer rubrum*) and silver maple (*A. saccharinum*) during late May and June demonstrating a similar dependence of squirrels on only a few species of trees. The dependence of squirrels on a limited number of food sources creates a vulnerability to crop failure. Although considered as only supplemental in the annual diet, some species of trees can be of critical seasonal importance. The low weights of juveniles and high mortality in 1987 can be attributed to the dependence of squirrels on mulberry and hackberry. Mulberries were exhausted or decaying by mid-June and no substantial food source

was available until the oak and walnut mast began to ripen. Squirrels foraged more frequently and less time-efficiently on carry-over mast fragments during food shortage.

Adult gray squirrels exposed to cold and deprived of food were able to withstand weight losses of 36% before death, probably by relying on fat stores (Merson et al., 1978); therefore, an 11% weight loss probably was not sufficient to influence survival of adults in early summer. Only under extreme shortage of food would adult survival be affected. However, juveniles probably lack fat stores comparable to adults and possess average daily metabolic rates nearly double that of adults (0.176 and 0.096 kJ g^{-1} day^{-1}, respectively—Knee, 1983). Juvenile squirrels learn to locate and process food items (Fox, 1982; Weigl and Hanson, 1980). Inexperience in locating and processing scarce food items, and the low social rank of juveniles (Allen and Aspey, 1986) may further increase the vulnerability of juveniles to food shortage. I hypothesize that late spring–early summer before the ripening of mast is a critical period for spring-born juveniles and can have significant consequences to populations. Future models of the ecology of tree squirrels should incorporate late spring–early summer sources of food to reflect more precisely the energetic limitations experienced by squirrels during their annual cycle.

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