SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF ADULT FOX SQUIRRELS IN SOUTHWESTERN GEORGIA

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Abstract: Survival estimates are important for understanding and managing wildlife populations. I used radiotelemetry to estimate survival and cause-specific mortality of a non-harvested fox squirrel (*Sciurus niger*) population in southwestern Georgia, United States. Adult fox squirrels ($n = 101$) were monitored continuously from March 1998 to December 1999. I determined the cause of death to be predation in 7 cases, disease in 5 cases, and unknown in 12 cases. Sex and season-specific mortalities were independent of the cause of mortality; therefore, I omitted cause of mortality from subsequent analyses. I did not detect differences in seasonal survival between males and females ($P = 0.27$) or among seasons ($P = 0.52$). When sexes were pooled, seasonal survival (± SE) ranged from 0.86 ± 0.07 to 0.92 ± 0.02. Annual survival of males (0.73 ± 0.07) and females (0.66 ± 0.07) was similar ($P = 0.60$). When sexes were pooled, annual survival was 0.69 ± 0.07. High fox squirrel survivorship, relative to gray squirrels (*S. carolinensis*), challenges the paradigm that similar strategies should be used to manage harvest of fox squirrels and gray squirrels.

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Fox squirrel populations in the Midwest appear to be expanding in number and geographic range (Swihart and Nupp 1998), and relative to eastern populations, more research has been conducted on fox squirrels in this region (Weigl et al. 1989, Loeb and Moncrief 1993). In contrast, many eastern fox squirrel populations are declining in number, presumably as a function of habitat loss (Taylor 1973, Weigl et al. 1989). Three (Delmarva fox squirrel [*S. n. cinereus*], big cypress fox squirrel [*S. n. avicennia*], and Sherman's fox squirrel [*S. n. shermani*]) of the 8 recognized subspecies of fox squirrels are afforded special conservation status (Loeb and Moncrief 1993, Whitaker and Hamilton 1998); all 3 are found only in the eastern United States. One of these subspecies, the Delmarva fox squirrel, is federally endangered.

Survival estimates are needed to appropriately manage a population of wild vertebrates. To date, studies of fox squirrel survival have been restricted to capture–recapture studies in relatively small (<100 ha) woodlots and thus were complicated by emigration of study animals (Nixon et al. 1974, 1975; Hansen et al. 1986; Herkert et al. 1992). Moreover, each of these studies took place in the midwestern United States. Because differences in morphology (Kiltie 1989; Weigl et al. 1989, 1998), habitat preference (Edwards et al. 1989, Weigl et al. 1989), diet (Nixon et al. 1968, Kantola and Humphrey 1990), and home range size (Weigl et al. 1989, Kantola and Humphrey 1990) exist between midwestern and eastern fox squirrel populations, extrapolation of survival estimates from midwestern studies to eastern populations may not be appropriate.

My primary objective was to estimate survival rates of a non-harvested population of fox squirrels and to compare these estimates to survival rates reported elsewhere for this species. I also determined whether cause-specific mortality differed between sexes and among seasons to test the hypothesis that temporal phenomena (e.g., food availability, reproduction) predisposed squirrels to specific mortality agents. I predicted that larger male home ranges (Conner 2000) would result in reduced survival of males. Because food availability is lowest and females experience increased energetic demands associated with lactation and neonatal care during summer, I predicted that survival rates would be lowest then.

METHODS

Study Area

The study took place at Ichauway, the former hunting plantation of Robert W. Woodruff and current research site of the Joseph W. Jones Ecological Research Center. Ichauway is located about 20 km south of Newton, Georgia. The 12,000-ha research site relied heavily on prescribed fire to maintain a 2-layered forest dominated by

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longleaf pine (*Pinus palustris*) in the overstory, herbaceous vegetation in the understory, and an open midstory. Scattered individual hardwoods and hardwood patches existed within the longleaf matrix. Additionally, management for northern bobwhites (*Colinus virginianus*) resulted in a diverse habitat mosaic of interspersed food plots and small weedy openings within the forested matrix. Rainfall averaged 132 cm/year, and average daily temperature was 11°C during winter and 27°C during summer. Although fox squirrels and gray squirrels were sympatric on the study site, gray squirrels were generally restricted to hardwood-dominated sites, and the 2 species were seldom found together (Conner et al. 1999).

Animal Capture and Monitoring

Squirrels were captured in wooden box traps (Baumgartner 1940) baited with dried corn. I placed traps in areas known to have fox squirrels and trapped squirrels periodically during January 1998–November 1999 (i.e., there were no defined trapping seasons).

I transferred captured squirrels into a nylon mesh bag, where they were then sedated using either inhalation of Methoxyflorane or intramuscular injection of Ketamine hydrocloride (10 mg/kg). While squirrels were sedated, I determined sex, collected standard measurements, affixed ear tags (Monel 1005-3, National Band and Tag Company, Newport, Kentucky, USA), and determined whether squirrels were juveniles or adults (i.e., sexually mature) following Weigl et al. (1989). Finally, I attached a 25-g radiotransmitter collar (Telemetry Solutions, Walnut Creek, California, USA) to all captured adults that weighed >850 g (i.e., transmitter weight ≤ 3% of squirrel body weight). I maintained sample sizes of radiotagged squirrels at ≥ 30 animals throughout the study. All squirrels were released at the capture site after they completely recovered from anesthesia. Trapping and handling followed guidelines of the Animal Care and Use Committee (1998).

Radiotagged squirrels were located ≥ 2 times/week using triangulation from known reference points. To ensure that mortalities were detected quickly, I visually located each animal ≥ 2 times/month. If a squirrel did not appear to move between consecutive locations, a special effort was made to visually locate the animal. Mortalities were confirmed when squirrel remains were located in the area of the transmitter or when signs of a struggle were apparent in the vicinity of the transmitter (e.g., torn ground, canine or talon marks on the transmitter). When mortality was detected, I examined squirrel remains in an attempt to determine the cause of death. Mortality events were placed into 1 of 3 classes: predation, natural causes (i.e., other than predation), and unknown.

Data Analysis

Animals entered the analysis the day following capture. I censored animals upon loss of the radio signal or when a transmitter was found with no sign of mortality. Additionally, squirrels were censored for 1 day on the day of recapture because squirrels in traps or recovering from anesthesia were not at risk in the population. Deaths that occurred within 7 days of capture were assumed to be capture-related, and these squirrels were not included in the analysis. I assumed squirrels were randomly sampled; survival times for individuals were independent; survival of right-censored animals was equal to animals remaining in the monitored population; and capture, handling, and monitoring did not affect survival rates (Pollock et al. 1989, White and Garrott 1990). Analysis of cause-specific mortality required that I also assume that daily survival rates did not vary within seasons and date of death was precisely estimated (Heisey and Fuller 1985). However, the procedure is robust to imprecise estimates of mortality date (Heisey and Fuller 1985).

I considered cause-specific mortality to represent probability of an animal of a given sex dying during a set interval (i.e., season) from a specific factor in the presence of other competing mortality factors (Heisey and Fuller 1985). I developed cause-specific mortality rate models and used a model reduction approach to determine whether cause-specific mortality was independent of sex and season. I developed a full model using 2 sexes, 7 seasons, and 3 causes of mortality. I then created a reduced model by pooling sources of mortality and used a likelihood-ratio goodness-of-fit test to compare models.

I used the staggered entry modification (Pollock et al. 1989) of the Kaplan-Meier product limit survival estimator (Kaplan and Meier 1958) to estimate survival rates. Survival rates were calculated separately for each sex during each calendar season. Initially, I planned to calculate seasonal survivorship for each season of the 2 years of study, but too few squirrels were captured before March 1998 to allow for meaningful analysis. Therefore, I began the survival study on 21 March 1998, and I calculated sex-specific, seasonal survival rates for 7 calendar seasons (i.e., spring 1998–fall 1999). I determined whether seasonal survival rates differed between sexes and whether survival rates differed among seasons using a generalized chi-square hypothesis testing procedure because this procedure permits an omnibus test of homogeneity for multiple survival rates (Sauer and Williams 1989). I used a log-rank test (Pollock et al. 1989) to compare sex-specific survival distributions from 21 March–31 December 1998 to the same period during 1999 to determine whether pooling data from different years to derive annual survivorship curves was justified. Similarly, I used a log-rank test to compare annual survival distributions between sexes.

RESULTS

I monitored 101 fox squirrels and detected 24 mortalities. Evidence in the vicinity of squirrel remains indicated that predators (i.e., raptors and mammalian carnivores) killed 7 squirrels. Because 5 intact carcasses were recovered with no signs of predation (e.g., no puncture wounds or sign of struggle), natural causes other than predation contributed to 5 deaths. Cause of mortality could not be determined in 12 deaths due to scarcity of remains. However, all of the 12 unclassified carcasses were extensively fed upon, and it is likely that most of the unclassified mortalities were the result of predation. I detected no difference (χ^2_{14} = 1.04, P = 0.99) between full and reduced models, indicating that the distribution of mortality by sex or season was independent of the cause of mortality. Therefore, I pooled across mortality causes for subsequent analyses.

Seasonal survival rates did not differ (χ^2_1 = 1.21, P = 0.27) between sexes; therefore, sexes were pooled to determine if survival rates differed among seasons. When sexes were pooled, seasonal survival rates were homogeneous (χ^2_6 = 5.15, P = 0.52), indicating a relatively constant risk of mortality (Table 1).

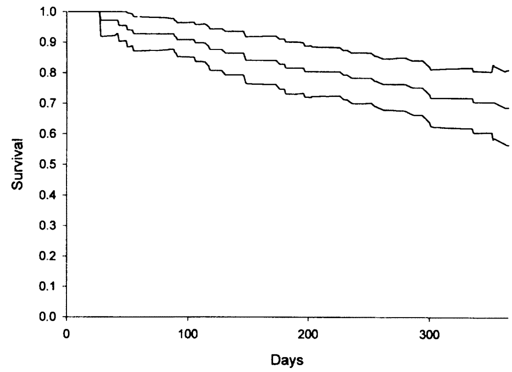

Fig. 1. Annual fox squirrel (*Sciurus niger*) survival in southwestern Georgia, 21 March 1998–20 December 1999. Upper and lower lines represent 95% confidence intervals. Data were pooled into a single calendar year.

Sex-specific survival distributions from 21 March 1998–31 December 1998 were similar to survival distributions from 21 March 1999–31 December 1999 (males, χ^2_1 = 0.024, P = 0.88; females, χ^2_1 = 1.51, P = 0.22). Therefore, I combined data from 1998 and 1999 to create sex-specific annual survival distributions.

Annual survival (±SE) of female fox squirrels was 0.66 ± 0.07, and annual survival of males was 0.73 ± 0.07. Sex-specific survival distributions were similar (χ^2_1 = 0.28, P = 0.60). When sexes were pooled, annual survival was 0.69 ± 0.06 (Fig. 1).

DISCUSSION

The majority of mortalities were not classified. If the true cause of unclassified mortalities varied

Table 1. Seasonal survival rates ($\hat{S}$) of adult fox squirrels (*Sciurus niger*) in southwestern Georgia, 1998–99.

	Males			Females			Combined		
Season[a]	n[b]	$\hat{S}$	SE	n	$\hat{S}$	SE	n	$\hat{S}$	SE
Spring 1998	19	0.85	0.08	23	0.96	0.04	42	0.91	0.04
Summer 1998	17	0.94	0.06	22	0.88	0.06	39	0.90	0.04
Fall 1998	17	1.00	0.00	25	0.96	0.04	42	0.92	0.02
Winter 1998–99	16	0.93	0.07	25	0.89	0.05	41	0.90	0.04
Spring 1999	14	0.95	0.06	29	0.88	0.07	43	0.91	0.05
Summer 1999	12	1.00	0.00	18	0.84	0.08	30	0.91	0.05
Fall 1999	18	0.87	0.09	16	0.86	0.11	34	0.86	0.07

[a] Calendar seasons.

[b] Number at risk on first day of the season.

among seasons or sexes, then the cause-specific portion of the analysis is biased (Heisey and Fuller 1985). However, this potential bias in cause-specific mortality does not impact survival estimates or hypothesis tests based on the Kaplan and Meier (1958) procedure because that estimator does not incorporate cause-specific mortality into the analysis.

Pregnancy and lactation place increased energetic demands on female fox squirrels (Havera 1979) and may decrease female survival. Unfortunately, captures occurred sporadically and were insufficient to adequately assess reproduction. However, if female fox squirrels experienced increased energetic demands associated with reproduction, these demands did not alter female survival during the reproductive season.

Home ranges of male fox squirrels were about 2 times larger than female home ranges on the study area (Conner 2000). Weigl et al. (1989) observed males to be more active than females during the breeding season while searching for mates. However, larger home range sizes and increased seasonal activity of males did not affect male survival.

Fox squirrel survival was relatively stable among seasons (sexes combined, range = 0.86–0.92). In the absence of harvest, about 10% of the adult population died each season (Table 1, Fig. 1). Therefore, differential survival associated with seasonal food availability (Nixon et al. 1975, Koprowski 1991) or other temporal phenomena did not occur during this study.

Despite obvious differences in study design, harvested populations of fox squirrels had much lower annual survival (10%, Ohio, Nixon et al. 1974; 21%, Illinois, Herkert et al. 1992) than observed in this study, and harvest is most likely responsible for these differences. Fox squirrel survival during this study was similar to retention rates reported for a non-hunted Illinois population (about 65%; Hansen et al. 1986), but survival was somewhat higher than rates reported for 2 other non-hunted Illinois fox squirrel populations (55% and 56%; Herkert et al. 1992). Because earlier work (Nixon et al. 1974, Hansen et al. 1986, Herkert et al. 1992) was based on disappearance rates derived from recaptures, emigration and mortality events were inseparable. Had these studies estimated emigration rates, the differences between the current study and previous studies may have been reduced.

Flyger and Gates (1982) stated that it is reasonable to assume fox and gray squirrel mortality rates would be similar. Indeed, fox squirrel longevity (Koprowski et al. 1988) and gray squirrel longevity (Barkalow and Soots 1975) records are similar (12.6 years and 12.5 years, respectively). Barkalow et al. (1970) reported an annual survival rate for nonhunted gray squirrels of 0.52, a rate similar to that previously reported for nonharvested fox squirrels (Hansen et al. 1986, Herkert et al. 1992) but less than estimates reported in the present study.

MANAGEMENT IMPLICATIONS

Survival rates estimated during this study indicate that fox squirrels may have higher survival rates in the southeastern United States than in the midwestern United States. This indicates that eastern subspecies of fox squirrels should not be managed using information derived from midwestern studies. Because eastern fox squirrels appear to be declining, yet adult survival rates are high, estimates of reproductive rates and juvenile survival for eastern subspecies are critical for effective management.

Survival of non-harvested fox squirrels is high relative to gray squirrels, yet fox and gray squirrel harvests are often similarly managed. In many states, fox and gray squirrels are not differentiated in terms of bag limits (Loeb and Moncrief 1993, Tappe and Guynn 1998), and some states do not report estimated squirrel harvest by species. Fox squirrels may be more appropriately managed as a relatively K-selected species, and harvest guidelines of southeastern fox squirrels should be reevaluated (Tappe and Guynn 1998). A controlled study of the effects of harvest on fox squirrels is needed before realistic harvest guidelines, based on biological parameters, can be established.

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