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Management and Conservation Note

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ABSTRACT A number of studies on mammalian species that have adapted to urban areas suggest survival may be higher for urban populations than rural populations. We examined differences in fatalities between an urban and rural population of fox squirrels (*Sciurus niger*). We radiocollared ($n = 50$ rural, $n = 78$ urban) fox squirrels during approximately 2 years. We found monthly survival of rural fox squirrels ($\hat{S} = 0.936$) was lower than urban fox squirrels ($\hat{S} = 0.976$) over the same 12-month period. Nonetheless, when comparing a 24-month period of survival data on urban squirrels with an 18-month period on the rural squirrels (periods overlapped for 12 months), survival rates were more similar between urban ($\hat{S} = 0.938$) and rural squirrels ($\hat{S} = 0.945$). Our data suggest that sex and season may influence survival of urban squirrels and not rural squirrels. We also found that cause of fatalities differed between the urban and rural squirrels, with >60% of fatalities on the rural site caused by predation. In contrast, <5% of the fatalities on the urban site were caused by predation and >60% of urban fox squirrel fatalities were caused by motor vehicle collisions. This study illustrates the need to advance our ability to understand, predict, and mitigate effects of urbanization on wildlife resources. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):133–137; 2008)

KEY WORDS fatalities, fox squirrel, *Sciurus niger*, survival, urban wildlife.

As urbanization increases worldwide wildlife habitats are being altered from forest, prairie, swamp, and desert into areas dominated by buildings, pavement, and exotic plants (Adams et al. 2005). These alterations have adversely affected wildlife populations in and around urbanized areas (Adams et al. 2006). Although urban landscapes vary, urban areas can be defined as places of dense human population, where most land is dedicated to buildings, concrete, grassy lawns, and other human uses (Pickett et al. 2001, Adams et al. 2006). Many wildlife populations have been unable to cope with urban landscapes, whereas other populations have adjusted. The process by which some wildlife populations adjust to urban environments in terms of behavior, habitat selection, and demographics is synurbanization (Adams et al. 2005). In understanding synurbanization, wildlife biologists can better predict and manage wildlife populations as they respond to increased urbanization.

A number of studies on mammalian species that have adapted to urban areas suggest that survival may be higher for urban populations compared with rural populations (Gliwicz et al. 1994, Etter et al. 2002, Lopez et al. 2003, Prange et al. 2004). Differences in survival rates may be due to fewer predators, along with favorable environmental and food conditions found in urban areas (Adams et al. 2005). Survival rates of urban wildlife populations, or even segments of urban populations (by age or sex), that are consistently higher or even different from rural populations could lead to fundamentally different population structures in urban areas. As a result, urban wildlife populations could display differing sex ratios, densities, and age structures in comparison to populations found in rural areas.

We used fox squirrels (*Sciurus niger*), a common tree squirrel found throughout rural and urban areas in midwestern and southeastern United States, to examine differences in survival between urban and rural populations of mammals (Flyger 1974, Adams 1994). Fox squirrels do not exhibit sexual dimorphism; however, male and female fox squirrels differ behaviorally. Male fox squirrels range over greater distances and do not participate in the care and rearing of young (Koprowski 1994). Studies of fox squirrels in rural areas have shown no detectable variation in survival rates between sexes or among seasons (Koprowski 1994, Conner 2001, Steele and Koprowski 2001). Nonetheless, it appears that squirrel survival is influenced by extreme changes in food availability (Steele and Koprowski 2001). To date, no studies have compared survival rates or causes of fatality in an urban fox squirrel population to determine whether they show similar patterns to those seen in rural populations.

We tested the hypothesis that survival and causes of fatalities would differ between a population of fox squirrels found in an urban area and an adjacent population in a rural environment. Specifically, we predicted that fox squirrels would show higher levels of survival in urban areas due to reduced rates of predation. If survival and fatalities differed between urban and rural areas, we wanted to further investigate the assertion that differences would be pronounced by season and we predicted that survival rates would be elevated in urban areas during winter. Additionally, we hypothesized that biological and behavioral differences of males and females would result in different rates of survival and differing causes of fatalities, predicting that males' increased ranges would increase their risk of predation and fatality from roadkill as shown in urban deer (Lopez et al. 2003).

STUDY AREA

We conducted our study on 140 ha of the main campus of Texas A&M University, College Station, Texas, USA. Over 45,000 students attended the university during the study and there was a nearly constant flow of pedestrians and vehicles

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on campus during all seasons. The urban site was comprised of a dense cluster of buildings, parking lots, and streets. Extending out from this aggregation of buildings was an area of buildings with opened and sparsely treed lawns of exotic grasses. The site was bisected by roads with varying rates of traffic, creating patches of urban development and landscaping of <10 ha. The areas surrounding the study site were characterized by dense residential and commercial development and heavily trafficked roads. Some of the dominant trees species found on the urban study site were live oak (*Quercus fusiformis* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pyrus calleryana*), arborvitae (*Thuja* spp.), and elm (*Ulmus* spp.). Conversely, the rural study site was on a private ranch 18 km from the main Texas A&M University campus. The area was surrounded by other ranches and bordered by the Navasota River. The study site was approximately 240 ha of undisturbed bottomland hardwood forest and meadows that had little to no human activity. Fox squirrels had not been hunted or fed on this site for >20 years. Some of the dominant trees species in the area included post oak, water oak (*Q. nigra*), pecan (*Carya* spp.), and elm.

METHODS

Trapping

To maintain a sample of 20 squirrels (10 M, 10 F) on each study site equipped with functioning radiotelemetry collars, we trapped squirrels periodically during August 2003–June 2005 on the urban study site and during May 2004–July 2005 on the rural study site. We strapped >65 Tomahawk wire-cage traps (No. 103; Tomahawk Live Trap Company, Tomahawk, WI) to the limbs of trees on each study site (Korschgen 1981). We prebaited traps with sunflower seeds and pecans 2–3 days prior to trapping to increase trapping success. Once we captured squirrels we placed then in a canvas handling bag (Koprowski 2002) and sexed, aged, and weighed them (Dimmick and Pelton 1996). We ear-tagged each squirrel (Monel 1005-3; National Band and Tag Company, Newport, KY) and gave it a passive integrated transponder (PIT tag; Biomark, Boise, ID), and we fitted adult squirrels (>7 months old) with a collar and a battery-powered mortality-sensitive radio transmitter (Samuel and Fuller 1996; Advanced Telemetry Systems, Isanti, MN, or 10-g, model MP-2, AVM Instrument Company, Colfax, CA). All capturing and handling of fox squirrels was approved by Texas Parks and Wildlife (Scientific Permit SPR-1101–181) and the Institutional Animal Care and Use Committee at Texas A&M University (2001-278T).

Radiotelemetry

We tracked radiocollared squirrels on the urban site for the 24 months (21 Sep 2003 through 21 Aug 2005) and on the rural site for the 18 months (21 Jun 2004 through 21 Dec 2005). We monitored squirrels 2–3 times per week at random intervals (16-hr period divided into 8 equal 2-hr segments; we randomly selected one 2-hr segment and located all squirrels during that time). After receiving a mortality signal, we immediately located the collar. We examined collar, squirrel remains, and evidence in the surrounding area to determine cause of death (Adrian 1996). We placed fatalities into 1 of 5 categories: mammalian predation, avian predation, vehicular collision, other (e.g., drowning, poisoning), and unknown.

Data Analysis

We converted radiotelemetry data into encounter histories and used Program MARK (White and Burnham 1999) to generate monthly known-fate survival estimates. Encounter histories consisted of number of squirrels available at the beginning of each month and number of fatalities occurring each month grouped by site and sex. We censored animals during the last month that their radios failed or disappeared (Pollock et al. 1989).

We used an information-theoretic approach to evaluate monthly survival and survival by site, sex, season, and year (Burnham and Anderson 1998). This commonly used approach for analysis of survival data allows researchers to evaluate relative fit of a suite of potential models (see Leberton et al. 1992, Burnham and Anderson 1998). We used Program MARK to evaluate 3 sets of a priori models. For the urban study site ("urban"), we generated 8 models to evaluate the influence of sex and season. We defined seasons ("season") as 4 3-month periods resembling commonly defined calendar seasons with fall beginning on 21 September, and we defined 2 yearly periods ("year") beginning on 21 September 2003 and 21 September 2004. For the rural site ("rural"), we evaluated 5 models, comparing survival by sex, season of the year ("season"), and each of the 6 seasons we tracked squirrels ("season year"). To compare survival between the study sites ("combined"), we evaluated seasonal and site specific models, pooling the data by sex. We compared survival between sites for the 12 months the sites simultaneously had >19 radiotagged squirrels (21 Jul 2004–20 Jul 2005). All 3 sets of models contained a constant model representing no fluctuation in survival rates. We evaluated models using the differences in Akaike's Information Criterion (ΔAIC_c), the relative difference to the smallest AIC corrected for small sample size (AIC_c), and Akaike weights (w_i; Burnham and Anderson 1998). We considered models ≤ 2 AIC_c units to compete with the best model, models >2 but ≤ 4 AIC_c units from the best model plausible, and disregarded models >4 AIC_c units as an unlikely representation of the data (Burnham and Anderson 1998). We calculated model-averaged 95% confidence intervals for monthly survival rates with a logit transformation and presented parameter estimates of all models ≤ 4 AIC_c of the best model and a lower AIC_c value than the constant model (Burnham et al. 1987).

We examined differences in 3 categories of cause-specific fatalities (avian and mammalian predation, vehicular collision, and we pooled unknown and other) between sites, between sexes on both sites, and among season on the urban site using contingency tables and a Pearson chi-square test (Simonoff 2003). We calculated observed values as number of fatalities occurring for sex, season, or site. We determined expected values by multiplying the total number of fatalities

Table 1. A priori models used to analyze the influence of season, year, sex, and site on the survival of fox squirrels from September 2003–September 2005 in College Station, Texas, USA.

Model sets[a]	Model[b]	K[c]	AIC_c[d]	ΔAIC_c[e]	w_i[f]
Combined	1. {site}	2	140.54	0	0.690
	2. {constant}	1	142.48	1.94	0.261
	3. {season}	4	145.85	5.31	0.049
Urban	4. {year}	2	193.14	0	0.450
	5. {year sex}	4	194.27	1.13	0.256
	6. {season}	4	196.19	3.05	0.098
	7. {constant}	1	196.91	3.77	0.068
	8. {season year}	8	197.15	4.01	0.061
	9. {season year sex}	12	198.03	4.89	0.039
	10. {sex}	2	198.93	5.79	0.025
	11. {season sex}	8	203.40	10.26	0.003
Rural	12. {constant}	1	118.33	0	0.546
	13. {sex}	2	119.94	1.61	0.244
	14. {season sex}	7	121.42	3.09	0.116
	15. {season}	4	123.14	4.81	0.049
	16. {season year}	6	123.35	5.02	0.044

[a] Model sets: combined = survival on urban and rural sites from 21 Jul 2004–20 Jul 2005; urban = survival on urban site 21 Sep 2003–21 Aug 2005; rural = survival on rural site 21 Jun 2004–21 Dec 2005.
[b] Variables: constant = constant survival; sex = M and F; year = (yr 1 = 21 Sep 2003–20 Sep 2004, and yr 2 = 21 Sep 2004–20 Sep 2005); season = (winter = 21 Dec–20 Mar, spring = 21 Mar–20 Jun, summer = 21 Jun–20 Sep, fall = 21 Sep–20 Dec); season year in the rural model set considers each of the 6 seasons from 21 Jun 2004–21 Dec 2005 independently.
[c] No. of parameters in each model.
[d] Akaike's Information Criterion adjusted for small sample size.
[e] Difference between AIC_c of the model and the best model.
[f] Akaike wt.

by the proportion of months that squirrels were available for season, sex, or site. Due to only one recorded occurrence of predation on the urban site, we did not include predation in analysis of the urban study.

RESULTS

We captured, radiocollared, and tracked 128 fox squirrels, 50 (30 M, 20 F) on the rural site and 78 (41 M, 37 F) on the urban site, for an average of 5.4 months per squirrel (range = 0.5–14.3 months). We compared rates of survival between the rural and urban site and found the best approximating model for the combined model set to be a model that separated data by site (Table 1). The site model (model 1) had an Akaike weight ($w_i = 0.690$) >2 times larger than a constant model ($w_i = 0.261$), suggesting it was at least twice as likely to reflect the data. We found monthly survival of rural fox squirrels ($\hat{S} = 0.936$) was lower than urban fox squirrels ($\hat{S} = 0.976$) over the same 12-month period (Table 2). Models, including year, year sex, and season, and a constant value (models 4, 5, 6, 7) were all plausible (≤ 4 AIC_c units from the best model) for explaining variation on the urban study site. Nonetheless, models with year and year and sex (models 4, 5) were considered as competing best approximating models with a combined Akaike weight >0.70 (Table 1). On the urban study site, survival was lower during year 1 ($\hat{S} = 0.913$) and higher during year 2 ($\hat{S} = 0.968$), whereas survival for males was lower than females during year 1 ($\hat{S} = 0.904$) and higher than females during year 2 ($\hat{S} = 0.989$; Table 2). Models including sex and season

Table 2. Monthly averaged survival ($\hat{S}$) estimates, standard error, and 95% confidence interval for parameters of best approximating models of fox squirrel survival from September 2003 to September 2005 in College Station, Texas, USA. Best approximating models were ≤ 4 Akaike's Information Criterion adjusted for small sample size (AIC_c) units of lowest AIC_c valued model with a lower AIC_c than a constant survival model.

Model sets[a]	Parameter[b]	$\hat{S}$	SE	95% CI Lower	95% CI Upper
Combined	Urban	0.976	0.011	0.944	0.990
	Rural	0.936	0.018	0.891	0.963
	Constant	0.957	0.010	0.932	0.973
Urban	Yr 1	0.913	0.019	0.869	0.943
	Yr 2	0.968	0.013	0.931	0.986
	M yr 1	0.904	0.025	0.842	0.944
	F yr 1	0.926	0.027	0.852	0.964
	M yr 2	0.989	0.011	0.925	0.998
	F yr 2	0.949	0.022	0.884	0.979
	Fall	0.941	0.022	0.882	0.972
	Winter	0.974	0.015	0.922	0.991
	Spring	0.887	0.032	0.807	0.936
	Summer	0.944	0.024	0.872	0.976
	Constant	0.938	0.012	0.910	0.957
Rural	Constant	0.945	0.014	0.911	0.967

[a] Model sets: combined = survival on urban and rural sites from 21 Jul 2004–20 Jul 2005; urban = survival on urban site 21 Sep 2003–21 Aug 2005; rural = survival on rural site 21 Jun 2004–21 Dec 2005.
[b] Parameters: constant = constant survival, yr 1 = 21 Sep 2003–20 Sep 2004, yr 2 = 21 Sep 2004–20 Sep 2005, winter = 21 Dec–20 Mar, spring = 21 Mar–20 Jun, summer = 21 Jun–20 Sep, fall = 21 Sep–20 Dec.

(models 13, 14) were plausible models for survival on the rural site; however, the model with a constant survival rate (model 12) had the lowest AIC_c value and an Akaike weight ($w_i = 0.546$) more than double the next closest model ($w_i = 0.244$; Table 1).

We recorded 40 fatalities on the 2 sites (Table 3). Of the 26 fatalities on the urban site, 15 were caused by vehicular collisions and we recorded only one predation event in the fall of 2004. Additionally, on the urban site we found 3 dead squirrels in open drainage pipes and 2 squirrels dead within 20 m of rodent poison; we placed all 5 in the other category to represent anthropogenic causes of fatality. On the rural site, we classified 9 of 14 fatalities as predations. We listed the other 5 fatalities on the rural site as unknown because we were unable to determine the cause of death. Fatalities differed between study sites ($\chi^2_5 = 22.26$, $P < 0.001$) but we did not detect a difference by sex on the urban ($\chi^2_3 = 0.28$, $P = 0.961$) or rural site ($\chi^2_3 = 0.07$, $P = 0.994$) or by season on the urban site ($\chi^2_7 = 5.57$, $P = 0.594$).

DISCUSSION

During the same 12-month period, survival of rural squirrels was lower than urban squirrels, as we hypothesized. Nonetheless, an examination of all the data appeared to yield contrary results; comparing the 24-month period on the urban site with the 18-month period on the rural site suggested survival rates did not differ. Survival in the urban population was influenced by year and season whereas the rural population appeared to have a constant rate of survival, a result consistent with other research on rural squirrels (Conner 2001).

Table 3. Fox squirrel fatalities from September 2003 to September 2005 on an urban and rural site in College Station, Texas, USA.

Site	Sex	n	Months at risk	Predation Avian	Predation Mammal	Vehicle collision	Unknown	Other[a]	Total
Rural	M	30	168	2	3	0	3	0	8
	F	20	111	1	3	0	2	0	6
Urban	M	41	226	0	0	9	2	3	14
	F	37	193	1	0	6	3	2	12

[a] Other included suspected drowning and poisoning.

Sex and season had a greater influence on survival rates on the urban site than on the rural site. In support of our hypothesis and in correspondence with other research on small mammals, survival of urban squirrels increased during winter (Gliwicz et al. 1994; Table 2). Sex was a variable in a competing best approximating model for urban squirrels, but the relation between sex and survival was vague because male survival was high during the first year and considerably decreased during the second (Table 2).

We found fatalities differed between urban and rural areas. Additionally, our data supported the belief that higher survival rates in urban areas are in part due to a reduced risk of predation (Adams et al. 2005). At least 60% of the fatalities on the rural site were caused by predation, whereas <5% of the fatalities on the urban site were caused by predation, despite a large feral cat population on the urban site (Ash and Adams 2003). Fatalities differed considerably between the sites but not by sex as we had hypothesized. Greater movements by male fox squirrels did not appear to correspond with higher rates of predation or roadkill (Koprowski 1994).

Our data suggest that urban squirrels may have higher survival rates or at least show survival rates that fluctuate seasonally and annually unlike rural fox squirrels. Research conducted on other highly urbanized mammals living in urban and rural environments, such as raccoons (*Procyon lotor*; Prange et al. 2004), white-tailed deer (*Odocoileus virginianus*; Etter et al. 2002, Lopez et al. 2003) and striped field mice (*Apodemus agrarius*; Gliwicz et al. 1994), have shown higher survival in urban areas compared to rural areas. Raccoons, white-tailed deer, and striped field mice (see Adams 1994, Gliwicz et al. 1994, Prange et al. 2003), along with gray squirrels (*S. carolinensis*; Adams 1994) and most other mammals (Adams et al. 2006) that live in both urban and rural environments also show increased densities, fecundity, and recruitment in urban areas (Gliwicz et al. 1994, Beckman and Berger 2003, Prange et al. 2003, Peterson et al. 2004). We advocate an exploration of the relationship between survival, densities, dispersal, and recruitment in urban fox squirrels and other urban wildlife to develop a body of literature on synurbanization and advance our ability to understand, predict, and mitigate effects of urbanization on wildlife resources.

Management Implications

Broad scale management efforts should not assume demographic rates of rural wildlife populations are applicable in the management of urban populations (e.g., nuisance species). Wildlife managers should attempt to determine appropriate demographic parameter estimates prior to implementation of population management activities.

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