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Reproduction, juvenile survival and retention in an urban fox squirrel population

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Abstract Fox squirrels in an urban environment had an average litter size of 2.83 (95% CI 2.5, 3.16) which was similar to rural populations. Nonetheless, the proportion of squirrels reproductively active during the summer/fall breeding season (0.73) and annually (spring + summer/fall) was higher (1.23) than previously recorded for non-manipulated rural populations. The average monthly survival rate ($\hat{S} = 0.960$) of urban juvenile fox squirrels during the first 14 weeks of life was higher than reported for adult populations in the area. High rates of reproduction and juvenile survival yielded high juvenile to adult ratios (juveniles/adults) averaging 0.44. Retention of juveniles after 6 months (15%) was significantly less (χ^2=7.24, p=0.0071) than adults/subadults (40%). Results suggest that the urban environment provides quality habitat for fox squirrels and fox squirrels in urban environments have the potential to be a source population for surrounding suburban and rural environments.

Keywords Fox squirrel · Urban · Reproduction · Source · *Sciurus niger*

The global trend of urbanization (Adams et al. 2006) has led researchers to examine the influence of human dominated landscapes on wildlife populations (see Adams et al. 2005). While many native species have been unable to thrive in urban landscapes, other generalist species have shown an ability to adapt to the urban environment (Nilon and Pais 1997; Adams et al. 2005). Urban adapted mammals such as raccoons (*Procyon lotor*), white-tailed deer (*Odocoileus virginianus*) and striped field mice (*Apodemus agrarius*) have shown different population dynamics than their rural counterparts (Adams et al. 2005). Urban adapted mammal populations often display increased densities (Adams 1994; Gliwicz et al. 1994; Etter et al. 2002; Prange et al. 2003; Adams et al. 2006) and rates of adult (Gliwicz et al. 1994; Etter et al. 2002; Lopez et al. 2003; Prange et al. 2003) and juvenile survival (Peterson et al. 2004). Urban adapted mammals have also shown increased reproductive

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rates, including: maternity (Beckman and Berger 2003), litter size (Beckman and Berger 2003), juvenile to adult female ratios (Prange et al. 2003) and breeding season length (Gliwicz et al. 1994). Increased rates of reproduction and juvenile survival in urban mammal populations should lead to a surplus of juveniles. This surplus of juveniles in turn could either be recruited into the population or disperse into other populations. The dispersal of individuals out of urban populations could make urban areas a source of urban adapted native fauna for surrounding suburban areas, and rural areas.

This project examined fox squirrels (*Sciurus niger*) to determine the reproductive rates, juvenile survival and juvenile retention of an urban adapted species. Fox squirrels are a common tree squirrel found throughout rural and urban areas in the mid-western and southeastern United States (Flyger 1974; Adams 1994). Reproductive intensity in fox squirrel populations varies by litter size (Harnishfeger et al. 1978) and the portion of females producing two litters during the year (Brown and Yeager 1945; McCloskey and Vohs 1971; Koprowski 1994). Fox squirrel populations typically have litters during the spring and to a lesser extent in the late summer and early fall; however, it is rare for an individual squirrel to produce two litters in a given year (Steele and Koprowski 2001).

In general, juvenile mammals have an increased risk of mortality. A compilation of tree squirrel research suggests that juvenile squirrels have mortality rates of >50% higher than adults (Steele and Koprowski 2001). A study of gray squirrels (*S. carolinensis)*, considered similar to fox squirrels in terms of demographics due to similar size and life spans (Steele and Koprowski 2001), found high rates of juvenile mortality during the first 3 month of life (Thompson 1978). This period was followed by periods of juvenile dispersal and rates of survival similar to those of adults (Thompson 1978). However, to my knowledge, no studies have measured juvenile survival of fox squirrels or other *Sciurus sp*. in an urban environment.

One method biologists have used to infer rates of dispersal is to use retention rates or lengths of residence as a proxy (Nixon et al. 1975; Thompson 1978; Hansen and Nixon 1985; Hansen et al. 1986). Using mark and recapture data to determine the length of time that an individual or age-classes of individuals can be found in a particular area has one notable drawback. It is not possible to determine if mortality or dispersal was the reason for an individual leaving the area. Juvenile survival data was used to evaluate the assumption that the rates of mortality of all weaned squirrels were similar. Under this assumption, it was hypothesized that squirrels captured as juveniles (<5 months) would show shorter residency times on the study site than subadult/adult squirrels (>5 months).

The purpose of this paper was to understand the influence of the urban environment on the reproductive rates and juveniles of a fox squirrel population. Specifically, the goals of the study were to (1) estimate reproductive rates of an urban fox squirrel population and to compare the results to reproductive rates found in rural populations (2) estimate juvenile survival of an urban fox squirrel population prior to dispersal and (3) compare the retention rates of adults and urban juvenile fox squirrels to determine if dispersal was likely.

Materials and methods

Study area

Urban ecosystems have high densities of people and a landscape covered by built infrastructure (Pickett et al. 1989). This study occurred on 140 ha of the main campus of Texas A&M University, College Station, Texas, USA. There were over 45,000 students,

faculty, staff and visitors on the study site daily and >9,000 students in residence. The study site was dominated by buildings (29%), pavement (39%) and manicured exotic grasses (32%). On the center of the site was a dense cluster of buildings, parking lots and streets. Extending out from this aggregation of buildings was an area of buildings with open and sparsely treed lawns of exotic grasses. The areas surrounding the study site were characterized by dense residential and commercial development. Some of the dominant tree species found along roads and in front of buildings on the study site were live oak (*Quercus fusiforms* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pryus calleryana*), arborvitae (*Thuja* spp.) and elm (*Ulmus* spp). Forty squirrel nest-boxes (Weigl et al. 1989) were placed on trees around the study area to aid in the monitoring of squirrel reproductive activities.

Trapping

Approximately every 3 months from August 2003 through August 2005, squirrels were trapped for three consecutive days. To trap squirrels >65 Tomahawk wire-cage traps (No. 103, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) were tied to the limbs of trees (Korschgen 1981; Adams 1984), effectively covering the study area with traps. Traps were pre-baited with sunflower seeds and pecans 2–3 days prior to trapping to increase trapping success. Once squirrels were captured, they were sexed, weighed, and aged using tail pelage and nipple and scrotal characteristics (McCloskey and Vohs 1977). For the purpose of this study, squirrels were classified into two age groups (>5 subadult/adult, <5 juvenile). Each squirrel was ear-tagged (Monel 1005-3, National Band and Tag Company, Newport, Kentucky, USA) and given a passive integrated transponder (PIT tag, Biomark, Boise, Idaho, USA; Korschgen 1981; Samuel and Fuller 1996). Adult females were fitted with a collar and a battery-powered mortality-sensitive radio transmitter (150–152 MHz, 12 g, model M170 Advanced Telemetry Systems, Isanti, Minnesota, USA or 10 g, model MP-2 AVM Instrument Company, Colfax, California, USA). Occasionally, supplemental trapping was used to maintain ten radio-collared females on the study site. All capturing and handling of fox squirrels was performed in a humane manner under the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). In addition, the project was approved by the Texas Parks and Wildlife Department (Scientific Permit SPR-1101-181) and the Animal Care and Use Committee at Texas A&M University (2001-278T).

Reproductive intensity

To measure reproductive intensity of an urban fox squirrel population, both the portion of females producing young and litter sizes were estimated during spring and summer/fall breeding seasons. These two estimates were then compared to published estimates made of rural fox squirrel populations.

Radio-collared squirrels were tracked on the study site for a 24-month period (January 2004 to December 2005). Squirrel locations were monitored two–three times/week at random intervals (16-h period divided into eight equal 2-h segments; one 2-h segment was randomly selected and during that time all squirrels were located). Fox squirrels were located via homing (White and Garrott 1990), their position was noted on geo-referenced maps and they were classified into one of three categories: active, inactive or in a nest. Nesting locations were transferred to a Geographic Information System (GIS) database of the study site used to track female squirrels.

Nests attributed to female squirrels were examined for the presence of new born squirrels once a week during periods of minimal reproductive activity, and two times a week during peak birthing and weaning periods (1 August–15 October, and 1 February–30 March). Nest locations of radio-collared squirrels in nest boxes, trees and on buildings were examined using a mini-digital zoom camera (model # KPC-S20P, Korea Technology and Communications, Seoul, Korea) and micro-video monitors (Nature Vision INC., Baxter, MN) attached to a telescoping pole as described by Proudfoot (1996). Squirrels with nests that were out of the reach of the telescoping pole or that could not be viewed (inside a building) were omitted from the study. Nests were monitored for a 2 year period (January 2004 to December 2005), including four breeding seasons (Spring 04, Fall 04, Spring 05, Fall 05). Radio-collared females with young present in their nests were classified as reproductively successful and radio-collared squirrels without young in their nests were classified as reproductively unsuccessful. The portion of squirrels reproducing was estimated for each of the four breeding periods during the study. Differences between the spring and summer/fall seasons were examined using a Pearson's Chi-squared test (Simonoff 2003). The results were compared to other studies that examined fox squirrel reproduction in rural environments.

Litter sizes of all reproductively successful radio-collared females were recorded. In addition, litter sizes of newborn squirrels (<1 week, Allen 1942) from 40 nest boxes were recorded. Nestboxes were monitored with the same camera system and protocol described in the previous section. Differences in litter sizes between the spring and summer/fall breeding seasons were evaluated using the nonparametric Mann–Whitney U test (Ott 1993). The combined average litter size was compared with other studies of rural fox squirrel populations.

Juveniles

Preliminary data suggested that young squirrels stayed in close proximity to their nests for at least 14 weeks. Any reduction in the number of young in or around a radio-collared squirrel's nest during the 14 week period was considered a mortality. Only the young of radio-collared squirrel were used in the analysis of survival (young in nestboxes were excluded) because female squirrels and their young are known to move nests (Steele and Koprowski 2001). A Kaplan–Meier estimator modified for staggered entry (Pollock et al. 1989) was used to calculate monthly and annual survival ($\hat{S}$) rates for squirrels during the first 14 weeks of life.

The proportion of juvenile and subadult/adult squirrels recaptured on the study site ≥6 months was determined from mark and recapture data collected during trapping. The respective proportions were compared using a Pearson's Chi-squared test (Simonoff 2003). Additionally, the squirrel population was surveyed twice annually on six 4 km transects traversing the study site. Transects were walked in November and April, when juveniles were clearly distinguishable from adults. Survey results were used to calculate the ratio of juveniles to adults (juveniles/adults) in the population. SAS statistical software (SAS version 9.1, SAS Institute Inc., Cary, North Carolina) was used to perform all statistical analysis for this project.

Results

Sixteen female fox squirrels were tracked during the springs of 2004 (n=9) and 2005 (n=7), eight of which produced liters. Seventeen female fox squirrels were tracked during summer/

fall of 2004 (n=10) and 2005 (n=7). However, two squirrels that nested inside buildings in the fall/summer of 2004 could not be observed, reducing the sample size to eight for that season. Eleven of the 15 remaining fox squirrels produced liters during the summer/fall season. No significant difference was found between the portion of squirrels that were reproductively successful during the spring and fall seasons (χ^2=1.77, p=0.183). The proportion of reproductively successful squirrels during the summer/fall birthing period was higher than previously documented rates for squirrels in rural areas (Table 1). In addition, the overall annual proportion (spring summer/fall) of the population reproducing (1.23) over the course of 2 years was again higher than recorded for the rural populations of squirrels (Table 1).

Thirty squirrel-nests (19 radio-tracked squirrels nests and 11 nestboxes) recorded new born squirrels (Spring '04 n=5, Fall '04 n=8, Spring '05 n=8, Fall '05=9). The average litter size was 2.83 (95% CI 2.5, 3.16). No difference was found in litter size between seasons (p=0.441). The average litter size recorded in this study was comparable to other studies in rural environments (Table 2). The average litter size of seven previous studies was 2.83.

Fifty-three young from 19 radio collared squirrels were used to estimate juvenile survival for the first 14 weeks of their lives. Seven squirrels were considered as mortalities. The estimated rate of survival over the first 14 weeks of life was $\hat{S} = 0.868$ (95% CI 0.777, 0.959). This estimate was equivalent to a monthly survival rate of $\hat{S} = 0.960$ (95% CI 0.930, 0.988) and an annual survival rate of $\hat{S} = 0.591$ (95% CI 0.391, 0.856).

Six of 40 (15%) squirrels captured as juveniles during the first 18 months of the 2 year study were recaptured ≥6 months after their initial capture, while 27 of 68 adult/sub adult squirrels (40%) captured during the first 18 months were recaptured ≥6 months after their initial capture. The proportion of juveniles recaptured on the study site was significantly less that the proportion of subadult/adults (χ^2=7.24, p=0.0071). Transect surveys yielded juveniles to adults ratios (juveniles/adults) averaging 0.44 (Spring '04=0.39, Fall '04=0.55, Spring '05=0.57, Fall '05=0.25).

Discussion

Urban fox squirrels showed a clear pattern of bimodal reproduction (two distinct breading seasons annually). This was not unique (Koprowski 1994), but the portion of the females

Table 1 Comparison of average seasonal and annual proportion of reproductive female reported for studies in published literature on urban and rural fox squirrel populations

Study	Years	Landscape	Spring	Summer/fall	Annual
McCleery 2008[a]	2004–2005	Urban	0.5	0.73	1.23
McCloskey and Vohs 1971	1966–1967	Rural	–	–	0.25
Hansen and Nixon 1985[b]	1979–1981	Rural	0.64	0.25	0.89
Hansen and Nixon 1985[c]	1979–1981	Rural	0.83	0.5	1.33
Weigl et al. 1989	1985–1986	Rural	–	–	0.10–0.88
Herkert et al. 1992	1984–1986	Rural	–	–	0.58
Harnishfeger et al. 1978	1968–1976	Rural	0.38	0.12	0.50

[a] Averages were from the present study

[b] Averages from this portion of the study were from non-manipulated grids

[c] Averages from this portion of the study were from girds which experimentally removed females

Table 2 Comparison of average litter sizes reported for studies in published literature on urban and rural fox squirrel populations

Study	Landscape	Years	Litter size
McCleery 2008[a]	Urban	2004–2005	2.81
Allen 1942	Rural	1937–1939	2.92
Weigl et al. 1989	Rural	1979–1986	2.50
McCloskey and Vohs 1971	Rural	1966–1967	3.35
Brown and Yeager 1945	Rural	1941–1942	2.51
Goodrum 1967	Rural	1966	2.54
Packard 1956	Rural	1953–54	2.83
Baumgartner 1940	Rural	1937–1939	3.19

[a] Averages were from the present study

reproducing annually (1.23) and during the summer/fall (0.73) was exceptional when compared with studies of rural populations (Table 1). With the exception of one study showing compensatory reproduction after the removal of females (Hansen and Nixon 1985) no study has ever shown annually reproductive success >1.0.

Litter sizes of urban fox squirrels were comparable to rural fox squirrels. Nonetheless, when average litter sizes were combined with the inflated portion of reproductive females, urban fox squirrels showed high reproductive productivity over the 2 years of the study. Reproduction is one of the best indicators of habitat suitability (Krebs 2001). Reproductive rates of fox squirrels and other urban adapted species (Gliwicz et al. 1994; Beckman and Berger 2003; Prange et al. 2003) suggest the urban environment provides them with favorable habitats. However, the influence of high reproductive rates on a population would be minimal if newborns did not survive to be recruited into the population.

The average monthly survival rate ($\hat{S} = 0.960$) for juvenile squirrels during the first 14 weeks of life was higher than adults in the same population ($\hat{S} = 0.938$; McCleery et al. 2008) and a nearby rural population ($\hat{S} = 0.945$; McCleery et al. 2008). This finding contradicts previous literature suggesting tree squirrel mortality is elevated during the first 3 to 4 months of life (Thompson 1978). However, similar patterns have been recorded for other urban adapted mammals, which have shown higher rates of juvenile survival than their rural counterparts (Peterson et al. 2004). A likely explanation for the increased survival rates observed during the first 14 weeks for the juvenile urban fox squirrels was a reduced risk of predation. Predation has been shown to be limited in urban fox squirrels and specifically on this study site (McCleery et al. 2008).

Urban fox squirrels also displayed average juvenile/adult ratios (0.44) higher than previously published reports from non-manipulated rural fox squirrel populations (0.21, Hansen and Nixon 1985). Considering urban fox squirrels high reproductive rates, survival during the first 14 weeks and juvenile to adult ratios, the urban environment appeared to be producing a surplus of juvenile squirrels that could either disperse or be recruited into the population.

Data supported the hypothesis that juveniles had reduced lengths of residence on the study site. This in turn suggested that a surplus of juveniles were dispersing. After 6 months, only six of 40 juvenile squirrels were recaptured on the study site. Fox squirrels have been shown to regulate population levels through dispersal (Nixon et al. 1975; Thompson 1978; Steele and Koprowski 2001).

Retention estimates were predicated on the assumption that squirrels age >14 <22 weeks had survival rates equal or greater than squirrel >22 weeks (>than 5 months when they were

classified as sub adults). There is no reason to believe squirrels >14 <22 weeks were at a higher risk of death by vehicular collision (the largest cause of mortality on the study site; McCleery et al. 2008). Additionally, urban squirrels <14 weeks had already shown higher rates of survival at an age when the survival rate should have been less than adults (Thompson 1978). A plausible alternative is that dispersing juvenile squirrels had a higher risk of mortality as they dispersed over roads and highways in search of suitable habitats. A pattern similar to this was described for urban black bear (*Ursus americanus*), which showed higher rates of reproduction and higher mortality of dispersing juveniles, mainly due to road kill (Beckman and Berger 2003).

The urban environment provides a high quality habitat for a number of generalist mammals. The urban environment also appears to create a barrier to movements and dispersal for some urban adapted mammals (Gliwicz et al. 1994; Etter et al. 2002; Gehrt 2004) which can lead to inflated population densities (Prange et al. 2003). Yet, urban fox squirrel movements do not appear to be limited by concrete and pavement (McCleery et al. 2007), allowing fox squirrels to readily disperse across the urban landscape. The findings from this study suggested that urban fox squirrels have the potential to be a source population for surrounding suburban and rural environments. Whether or not juveniles can reach these surrounding areas depends on their ability to avoid mortalities due to road kill, something that adult urban squirrels appear to have difficulty doing (McCleery et al. 2008).

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