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Source: Journal of Wildlife Management, 71(4):1149-1157.
Published By: The Wildlife Society
DOI: http://dx.doi.org/10.2193/2006-282
URL: http://www.bioone.org/doi/full/10.2193/2006-282

Research Article

Habitat Use of Fox Squirrels in an Urban Environment

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ABSTRACT Tree squirrels are one of the most familiar mammals found in urban areas and are considered both desirable around homes and, conversely, a pest. We examined fox squirrel (*Sciurus niger*) habitat use in inner city and suburban areas using radiotelemetry. We estimated habitat selection ratios at differing scales by season and fox squirrel activity. Telemetry data suggests that during periods of inactivity radiocollared fox squirrels ($n = 82$) selected 1) areas with greater tree canopy, 2) live oaks (*Quercus fusiromis* and *Q. virginiana*), and 3) trees with larger diameters and canopies. When inactive during the winter and spring, fox squirrels also preferred, within their core areas, to use the inside of buildings, and during periods of activity in the autumn and spring, fox squirrels preferred grassy areas. During periods of activity, fox squirrels avoided using pavement but did not exclude it from their core-area movements. Fox squirrels' ability to use buildings and to tolerate pavement in core-area movements make vast areas of the urban environment available to fox squirrels. In evaluating habitat variables that increased fox squirrel activity in urban areas, we found the number of large and medium trees, amount of pavement and grassy areas, canopy cover, number of oaks, and the area covered by buildings were all important factors in predicting fox squirrel activity in an urban environment. Our data suggests urban planners, animal damage control officials, wildlife managers, and landscapers who want to control urban fox squirrel populations through habitat manipulation should consider the reduction of oaks trees, a reduction of the canopy cover, and restricting the access of fox squirrels to buildings. Alternatively, home owners and squirrel enthusiasts hoping to bolster fox squirrel populations in urban areas should consider increasing the number of large mast–bearing trees and canopy cover and providing nest boxes. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1149–1157; 2007)

DOI: 10.2193/2006-282

KEY WORDS fox squirrel, habitat use, *Sciurus niger,* synurbanization, urban wildlife.

In the twenty-first century, natural landscapes are expected to continue their unprecedented 200-year alteration from rural to urban landscapes (Adams et al. 2006). Wildlife managers and scientists are attempting to prepare for these changes; however, there is only a cursory understanding and limited body of literature available for wildlife in urban areas (Wolch et al. 1995; Vandruff et al. 1996; Adams et al. 2005, 2006). Some wildlife populations, such as deer (*Odocoileus* spp.), squirrels (*Sciurus* spp.), and geese (*Branta* spp.) have managed to adjust to human-dominated landscapes by modifying their basic ecology through a process defined as synurbanization (Adams et al. 2005). Synurbanization usually leads to changes in population size, sex and age structure, survival, behavior, and habitat use (Gliwicz et al. 1994), making it ineffectual to manage urban populations with research conducted on wildlife populations in rural settings. Nonetheless, there is a lack of information even on the basic ecology of common wildlife species inhabiting urban areas. For simplicity, we defined these urban areas as places of relatively dense human population, where most of the land is dedicated to buildings, concrete, grassy lawns, and other human uses (Adams et al. 2006).

Tree squirrels (*Sciurus* spp.) are highly visible in urban areas of North America where some residents consider them desirable around their homes and others, conversely, consider them a pest (Brown et al. 1979, Gilbert 1982, Conover 1997, Adams et al. 2006). Nonetheless, there is still much to be learned (Williamson 1983, Vandruff and Rowse 1986, McPherson and Nilon 1987, Salisbury et al. 2004) about tree squirrels' use of urban habitats, especially by fox squirrels (*S. niger*), a common tree squirrel found in cities throughout the midwest (Adams 1994) and southern (Flyger 1974) United States. We are only aware of one study that has examined urban habitat use by the fox squirrels in fragmented woodlots (Salisbury et al. 2004), and we are unaware of any studies of fox squirrels' usage of the biotic and abiotic substrates commonly found in inner-city and suburban areas. Such habitat information can be used by wildlife managers, urban planners, animal damage control officials, homeowners, and squirrel enthusiasts to attract or manage fox squirrel populations through the manipulation of the urban environment.

Diverging from traditional habitat use studies that look strictly at the biotic environment (e.g., Kantola and Humphrey 1990, Lopez et al. 2004, Perkins and Conner 2004), we evaluated fox squirrels' interactions with the biotic and abiotic features unique to urban environments (e.g., buildings, planted and ornamental trees, concrete, and exotic manicured grasses; Adams 1994). Our study objectives were to 1) understand fox squirrel use of space in relation to the urban substrates, 2) determine tree characteristics selected by fox squirrels during periods of activity and inactivity, and 3) develop a model to understand what features in the urban environment affect levels of fox squirrel activity.

STUDY AREA

We conducted research on the Texas A&M University main campus (140 ha) in College Station, Texas, USA. The campus was comprised of a diversity of urban habitats ranging from inner city areas to more typical suburban areas (Fig. 1). The center of our study area was covered with a

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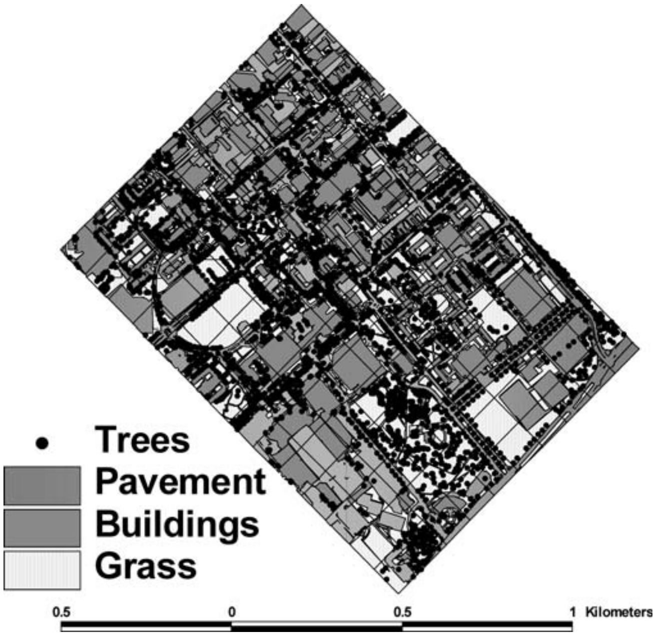

Figure 1. Depiction of geo-referenced urban substrates of Texas A&M University, College Station, Texas, USA, divided into 140 1-ha plots, from Geographic Information System database, August 2003.

dense nucleolus of buildings and parking lots. Extending out from this nucleolus was an area comprised of widely spaced buildings interspersed with open fields and sparsely forested openings (no understory), characteristic of many parks and cemeteries in suburban areas (Adams 1994). Dominant tree species on our 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). Most species of trees in our study site were commonly found in urban areas in Texas and throughout the southeastern United States (Gilman 1997). Additionally, a unique aspect of our research was a complete geo-referenced Geographic Information System (GIS) of the substrates (e.g., trees, sidewalks, buildings, etc.) on our study site.

METHODS

Habitat Substrates

We categorized dominant habitat substrates within our study area into 4 major groups: pavement, building, grass, and tree canopy. We classified habitat substrates using 1-m digital orthophoto quarter quadrangles (DOQQs, yr 2001) and an existing GIS database for the campus. For the building classification, there were 163 buildings, ranging from small storage sheds and greenhouses to 15-story buildings. This category accounted for 32 ha of our study area. The pavement classification consisted of all roads, parking lots, paved walkways, courtyards, and building entrances. Pavement was the most dominant feature within the study area and accounted for 54 ha of study area. The grass classification (46 ha) was comprised of all areas with manicured lawns and nonnative grassland areas. Finally, for the tree classification, we obtained a comprehensive GIS tree (>2 m in ht) coverage that included tree species, canopy area, and diameter at breast height for each individual tree on campus. Total tree-canopy area within the study site was 22 ha; however, for data analysis, it is important to note that most of the canopy cover occurred over areas classified as pavement, grass, or buildings. As a result, we measured substrates on multiple planes accounting for >154 ha of total substrate area.

Trapping

We trapped fox squirrels from August 2003 to June 2005 in an effort to maintain ≥20 fox squirrels (10 M, 10 F) with functioning radiocollars. To trap fox squirrels, we strapped >65 Tomahawk wire-cage traps (No. 103; Tomahawk Live Trap Company, Tomahawk, WI) to the limbs of trees (Korschgen 1981, Adams 1984), effectively covering the study area. We prebaited traps with sunflower seeds and pecans 2–3 days prior to trapping to increase trap success. We sexed, aged (Dimmick and Pelton 1996), and weighed captured fox squirrels. For identification, we ear-tagged each fox squirrel (Monel 1005–3; National Band and Tag Company, Newport, KY) and subcutaneously injected a passive integrated transponder (PIT tag; Biomark, Boise, ID) prior to release (Korschgen 1981, Samuel and Fuller 1996). We fitted with a collar and battery-powered mortality-sensitive radiotransmitter (150–152 MHz, 12 g, model M170; Advanced Telemetry Systems, Isanti, MN, or 10 g, model MP-2; AVM Instrument Company, Colfax, CA) captured adult fox squirrels with the potential for reproductive activity (>7 months old; McCloskey and Vohs 1971).

Radiotelemetry

We tracked radiocollared fox squirrels from September 2003 to August 2005. We located fox squirrels 2–3 times per week at random intervals (16-hr periods divided into 8 equal 2-hr segments; we randomly selected 1 2-hr segment and located all fox squirrels during that time). We located fox squirrels via homing (White and Garrott 1990), noting their position on geo-referenced maps and recording the habitat substrate (i.e., tree, grass, pavement, or building) occupied by the fox squirrel. If we located a fox squirrel in a tree, we recorded the tree's unique identification number. We also recorded the fox squirrel's activity to differentiate between the fox squirrel's selection of daytime refugia (e.g., areas used for shelter) and selection of habitat features during activity periods (e.g., foraging, mating, grooming, etc.; McCloskey 1975). We entered all locations and information into the GIS database.

Data Analysis

We evaluated fox squirrel habitat use at multiple spatial and temporal scales. Evaluating habitat use at different spatial scales can help reduce the biases introduced by defining what habitats are available to individual animals or animal populations (Porter and Church 1987). In total, we evaluated fox squirrel habitat selection on 5 spatial scales during different times of the year and distinct behavioral states. We used habitat selection ratios (the obs portion of habitat used divided by the portion of habitat expected to be used; Manly et al. 2000, Lopez et al. 2004), for the first 3 spatial scales, which analyzed fox squirrel use of urban substrates. We calculated habitat selection ratios by season (autumn = 22 Sep–21 Dec, winter = 22 Dec–21 Mar, spring = 22 Mar–21 Jun, summer = 22 Jun–21 Sep) to reduce the temporal biases (Anderson and Gutzwiller 1996). We combined male and female estimates by season, due to small sample sizes and because previous studies have reported fox squirrels do not differentially use habitat by sex (Perkins and Conner 2004). Finally, we incorporated a behavioral component, or scale, to our analysis. Fox squirrels can be inactive for large portions of the day (Hicks 1949), especially during summer and winter. Separating our analysis of fox squirrel substrate use by activity and inactivity minimized potential biases due to fox squirrel behavior. We provide a description of each of the scales we used below.

Point-study area.—We examined fox squirrel habitat selection on a point-study area scale (comparable to Johnson's [1980] first-order selection). We calculated habitat selection ratios (S) for each fox squirrel by dividing observed use by expected use for each substrate and season. We calculated selection ratios as $S = \mathrm{u}/(\mathrm{nx} \times \mathrm{ph})$, where u = the number of radio locations on a substrate for an individual, nx = total number of radio locations for an individual, and ph = portion of substrate for our entire study area (Aebischer et al. 1993, Lopez et al. 2004).

Range-study area.—We evaluated range selection of fox squirrels by comparing the proportions of substrates within a given fox squirrel's range to the proportions of substrates on our study area (comparable to Johnson's [1980] second-order selection). We calculated habitat selection ratios for each fox squirrel as $S = \mathrm{pr}/\mathrm{ph}$, where pr = the portion of substrate inside an individual's range and ph = portion of substrate for our entire study area.

Point-range.—We evaluated fox squirrel habitat selection within an animal's range (comparable to Johnson's [1980] third-order selection). We compared the number of fox squirrel locations on a given substrate to the proportional amount of that substrate available within each fox squirrel's range. More specifically, we determined habitat selection ratios as $S = \mathrm{ur}/(\mathrm{nt} \times \mathrm{pr})$, where ur = the number of radio locations on a substrate for an individual within its range, nt = an individual's total number of radio locations inside its range, and pr = portion of substrate inside an individual's range.

When calculating range-study area and point-range selection, it is common to represent animal ranges using 95% or 100% minimum convex polygons (MCPs; e.g., Lopez et al. 2004, Perkins and Conner 2004). We chose to represent fox squirrel ranges using 50% kernels (Seaman et al. 1998) to yield a more precise estimate of the areas used by fox squirrels (i.e., 50% core area, hereafter range). Fox squirrels are not territorial and can have expansive MCP ranges (>40 ha; Koprowski 1994) that encompass long-distance travels (Kantola and Humphrey 1990). We calculated seasonal core areas as 50% kernels using animal movements extension (Hooge and Eichenlaub 1999) in ArcView 3.2. We only used fox squirrels with ≥30 telemetry locations per season (Seaman et al. 1999) in the calculation of range areas. Although the fox squirrel is one of the least arboreal tree squirrels (Conner and Godbois 2003), they still spend a considerable portion of their time in the tree canopy (Geeslin 1970). To adjust for this, we calculated the total area of ranges and our study site as a 2-planed total area (total area = the 2-dimensional area on the ground + 2-dimensional area encompassed by the tree canopy). We calculated proportions of study site and range substrate areas as the area of the substrate divided by the 2-planed total area. In the calculation of selection ratios, we avoided zeros in the numerator or denominator by adding 0.01 to observed and expected values ($S = [\mathrm{U} + 0.01]/[\mathrm{E} + 0.01]$; Aebishcher et al. 1993, Lopez et al. 2004). Selection ratios >1 suggest that animals used (i.e., preferred, selected; Litvaitus et al. 1996) the substrate greater than expected, whereas ratios <1 suggest avoidance of substrate (Manly et al. 2000).

Tree selection.—For our fourth spatial scale, we examined fox squirrel use of trees in urban areas. Similar to our examination of urban substrates, we partitioned fox squirrel telemetry data into periods of activity and inactivity. This microlevel habitat analysis was comparable to Johnson's (1980) fourth-order selection. We were in a unique position to conduct an analysis of tree-level selection because of our comprehensive GIS tree database for the campus. From the database we could compare the species, canopy, and diameter at breast height of all trees where we found a squirrel to the species, canopy, and diameter at breast height of all trees on the study site in which we did not find a squirrel. Due to the diversity of trees (>60 species) and a minimal number of some tree species, we analyzed fox squirrel selection of only major tree groups within the study area. The 10 most numerous species or groups (>40 individuals) were live oak, post oak, other oaks (*Quercus* spp.), pines (*Pinus* spp.), elms, Chinese pistachio (*Pistacia chinensis*), bald cypress (*Taxodium distichum*), arborvitae, Bradford pear (dominant large tree species), and other fruit trees (*Malus* spp. and *Prunus* spp., less dominant smaller fruit trees).

To describe fox squirrels' use of trees by species, we compared the proportion of fox squirrel locations expected to be found in a particular species of tree (or group of trees) to the 95% confidence interval of the proportion of fox squirrel locations observed in each species of tree. We calculated expected proportions ($E = \mathrm{T}/\mathrm{W}$, where E = exp fox squirrel use of a tree species) as the number of trees of a particular species (T) divided by the total number of trees on the study area (W). We calculated the proportion of observed fox squirrels ($O = \mathrm{L}/\mathrm{T}$, where O = obs use) as the number of fox squirrel locations recorded on each species of tree (L) divided by the total number of times fox squirrels were located in trees (T). We compared observed and expected proportions with Wald binomial confidence intervals (Simonoff 2003) and compared the mean and 95% confidence intervals of the diameter at breast height and tree canopy between trees with fox squirrel locations

Table 1. Urban fox squirrel observed versus expected use of tree by species groups during period periods of activity and inactivity with 95% confidence interval and average canopy area (2-dimensional area cover by tree braches and leaves) and diameter at breast height measurements with 95% confidence intervals for trees with active squirrel, inactive squirrels, and no squirrels recorded (absent) by trees species group, College Station, Texas, USA, September 2003–August 2005.[a]

			Obs frequency			Dbh		Canopy area	
Species group	Squirrels activity	*n*	%	95% CI	% exp	$\bar{x}$	95% CI	$\bar{x}$	95% CI
Live oak	Active	211	8.8	6.78–8.8	7.69	20.0	19.1–20.9 b	38.4	36.6–40.2 b
	Inactive	319	13	10.57–13.0	10.14 p	20.4	19.7–21.1 b	40.1	38.6–41.6 b
	Absent	1,097				15.8	15.4–16.9	31.3	30.6–32.1
Post oak	Active	34	1.67	0.84–1.67	1.44	20.7	18.6–22.8	33.0	29.2–36.8
	Inactive	58	2.69	1.68–2.69	1.89	20.9	19.6–22.2 b	36.0	33.4–38.6
	Absent	211				18.6	17.8–19.4	32.0	30.3–33.7
Other oaks	Active	17	0.93	0.33–0.93	0.52	12.4	8.0–16.8	31.0	22.3–39.7
	Inactive	12	0.77	0.23–0.77	0.69	19.0	12.7–25.4 b	35.0	23.5–46.6
	Absent	79				8.4	7.5–9.3	22.5	20.5–24.5
Chinese pistachio	Active	10	0.6	0.14–0.60	0.29	10.9	6.9–14.9	27.6	19.7–35.5
	Inactive	9	0.55	0.12–0.55	0.39	18.1	14.0–22.2 b	37.1	30.4–43.4 b
	Absent	43				10.0	8.3–1.7	26.2	22.5–29.9
Pines	Active	2	0.18	0–0.18	0.21 a	8.5	7.5–9.5	20.5	17.7–23.3
	Inactive	5	0.35	0.02–0.35	0.28	12.0	8.4–15.6	28.6	20.7–36.5
	Absent	37				10.9	9.5–12.3	24.0	20.7–27.3
Bald cypress	Active	4	0.29	0–0.29	0.33	13.5	11.2–15.8 b	29.0	27.5–30.5 b
	Inactive	3	0.24	0–0.24	0.44 a	14.0	11.7–16.3 b	30.0	27.7–32.3 b
	Absent	62				6.5	5.5–7.5	15.9	13.2–18.2
Arborvitae	Active	6	0.4	0.04–0.40	0.47 a	11.3	6.4–16.2	12.0	7.1–16.9
	Inactive	7	0.45	0.01–0.45	0.61 a	10.1	4.5–15.7	19.4	8.8–30.0
	Absent	82				8.8	7.5–10.1	17.7	15.8–19.6
Bradford pear	Active	20	1.06	0.42–1.06	0.67	8.2	6.9–9.5	21.3	17.6–25.0
	Inactive	8	0.5	0.09–0.50	0.88 a	8.1	5.7–10.5	22.0	16.1–27.9
	Absent	135				7.0	6.4–7.6	16.7	15.4–18.1
Elms	Active	28	1.33	0.61–1.33	1.03	11.4	9.7–13.1	26.2	23.7–28.7
	Inactive	33	1.63	0.81–1.63	1.37	11.5	10.3–12.8 b	28.3	25.5–31.1 b
	Absent	156				9.1	8.3–9.9	23.8	22.2–5.4
Fruit trees	Active	9	0.55	0.12–0.55	0.42	6.0	3.9–8.1	15.3	10.4–20.2
	Inactive	6	0.45	0.01–0.45	0.55 a	7.3	5.1–9.5	22.0	16.2–27.7
	Absent	70				5.9	5.2–6.6	17.1	15.4–18.8

[a] p = preferred, obs values > exp value; a = avoided, obs value < exp value; b = > trees without squirrels (absent).

(active and inactive) and trees with no squirrel locations recorded.

Squirrel activity.—To understand what habitat components of the urban environment increased or decreased fox squirrel activity, we divided the study site in 140 1-ha grids and recorded every fox squirrel location within that grid over the 2-year period. Within each grid, we quantified 8 habitat components that we believed would affect fox squirrel activity: 1) the number of trees (ntrees), 2) the area of grass (grass), 3) the area of buildings (build), 4) the area of concrete, asphalt, and brick on the ground (pave), 5) the number of medium-sized trees (dbh 14–20 cm [medium]), 6) the number of large-sized trees (dbh >20 cm [large]), 7) the number of oaks (oaks), and 8) the area covered by canopy (canopy; we used the natural log of this value to better fit the model). We limited the number of a priori models to minimize overfitting our data (Norman et al. 2004). Our a priori models were generated from the limited urban tree squirrel habitat literature and field observations. We ran general linear model regressions of these models against the number of fox squirrel locations per grid fitted to a negative binomial distribution using SAS (PROC GENMOD, SAS version 9.1; SAS Institute, Inc., Cary, NC). First, we evaluated 8 a priori models, a global model containing all 8 variables (Model 10; Table 1), and an intercept-only model (Model 1) using Akaike's Information Criterion corrected for small sample size (AIC_c, Simonoff 2003). From the evaluation of the a priori models, we generated a second set of a posteriori models (Norman et al. 2004, models 11–16). We tested the second set of models and used the relative difference to the smallest AIC value in the entire set of models (ΔAIC_c) and Akaike weights (w_i) to select the best approximating models (Burnham and Anderson 1998). We considered models ≤ 4 AIC_c units to compete with the best model and we disregarded models >4 AIC_c units as an unlikely representation of the data (Burnham and Anderson 1998, Norman et al. 2004). To deal with the possibility of model uncertainty caused by competing models ≤ 4 AIC_c units from the model with the lowest AIC_c, we presented averaged model parameters and averaged 95% confidence intervals (Burnham and Anderson 1998).

RESULTS

We collected 3,467 radio locations on 82 fox squirrels (42 M, 40 F) between August 2003–2005. We calculated seasonal core-area ranges for 61 different fox squirrels with >30 locations per season; some fox squirrels had ranges

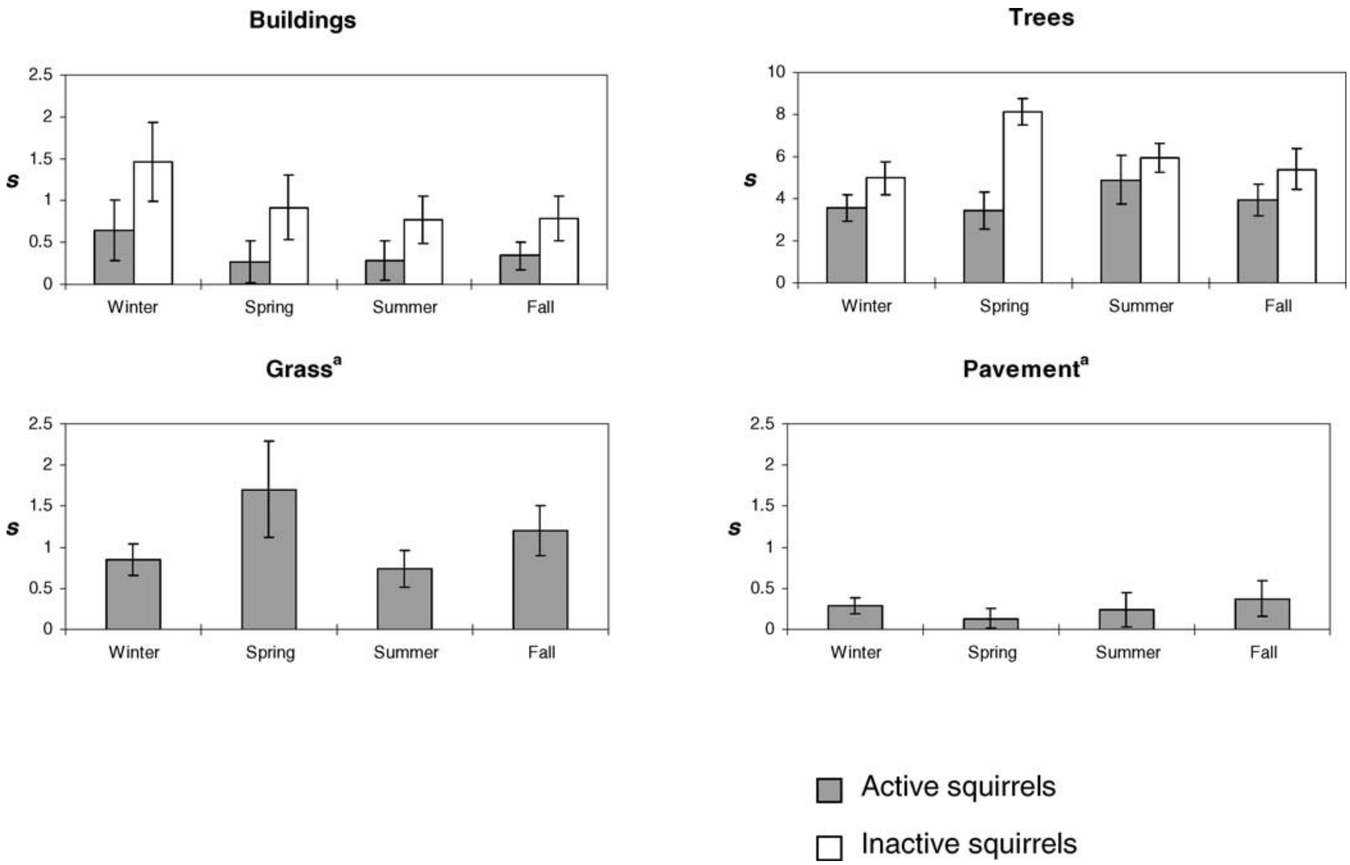

Figure 2. Fox squirrels averaged point-study area selection ratios of urban substrates (buildings; tree = tree canopy; pavement = concrete asphalt, brick; and grass = manipulated grass areas) and 95% confidence interval error bars by season and activity (active and inactive), in College Station, Texas, USA, September 2003–August 2005. Squirrels were not recorded on grass or pavement during periods of inactivity.

calculated during multiple seasons (winter = 32, spring = 13, summer = 13, autumn = 17). Fox squirrels overwhelmingly selected for tree canopy at all scales and during all seasons while active and inactive (Figs. 2, 3, and 4). Fox squirrels showed differential use of the other 3 substrates (pavement, grass, and buildings) based on temporal (seasonal), spatial (point-study area, range-study area, and point range) and behavioral (active and inactive) scales. We did not observe fox squirrels using grass or pavement during periods of inactivity (Figs. 2 and 4); however, fox squirrels did select to use buildings within their core areas as a substrate and daytime refugia (inactive) during the winter ($S = 1.96$) and spring ($S = 1.12$; Fig. 4). Active fox squirrels avoided buildings in their core areas during the spring ($S = 0.53$), summer ($S = 0.45$), and autumn ($S = 0.54$; Fig. 4). Fox squirrels showed a clear pattern of avoiding pavement as a substrate (Figs. 2 and 4) but did not appear to exclude pavement from their core areas (Fig. 3). Fox squirrels selected grass in their core areas during activity periods, especially in the spring ($S = 1.83$; Fig. 4); however, they disproportionately excluded grass from their core areas during the winter ($S = 0.68$) and summer ($S = 0.73$; Fig. 3).

In our analysis of tree selection, active fox squirrels avoided pines, bald cypress, and arborvitae (Table 1). During these periods of activity fox squirrels selected to use live oaks with a greater canopy area (95% CI = 36.6–40.2 m) and diameter at breast height (95% CI = 19.1–20.9 cm). During periods of inactivity fox squirrels used live oaks more than expected and bald cypress, Bradford pear, and arborvitae less than expected (Table 1). When taking refuge (inactivity) fox squirrels selected elms (95% CI = 25.5–31.1 m), Chinese pistachio (95% CI = 30.4–43.4 m), bald cypress (95% CI = 27.7–32.3 m), and live oaks (95% CI = 38.6–41.6 m) with greater canopy than trees of the same species (Table 1). Similarly, fox squirrels used live oaks (95% CI = 19.7–21.1 cm), post oaks (95% CI = 19.6–22.2 cm), other oaks (95% CI = 12.7–25.4 cm), Chinese pistachio (95% CI = 14.0–22.2 cm), bald cypress (95% CI = 11.7–16.3 cm), and elm (95% CI = 10.3–12.8 cm) with larger diameters at breast height during periods of inactivity (Table 1).

In the initial evaluation of fox squirrel activity on a 1-ha-resolution spatial scale, we found the ΔAIC_c and w_i values from a priori Models 4 and 5 and the global model (10) to be the best-approximating of the data and used them to generate a posteriori models (Table 2). Comparing all models, again using ΔAIC_c and w_i values, we selected the global model and Model 11 as competing best-approximating models (Table 2). They had a combined $w_i \geq 0.84$, suggesting there is $\geq$84% probability that one of these 2 models yielded the best explanation of the data. Our examination of individual parameters showed that only the parameter estimate and 95% confidence interval of ntrees

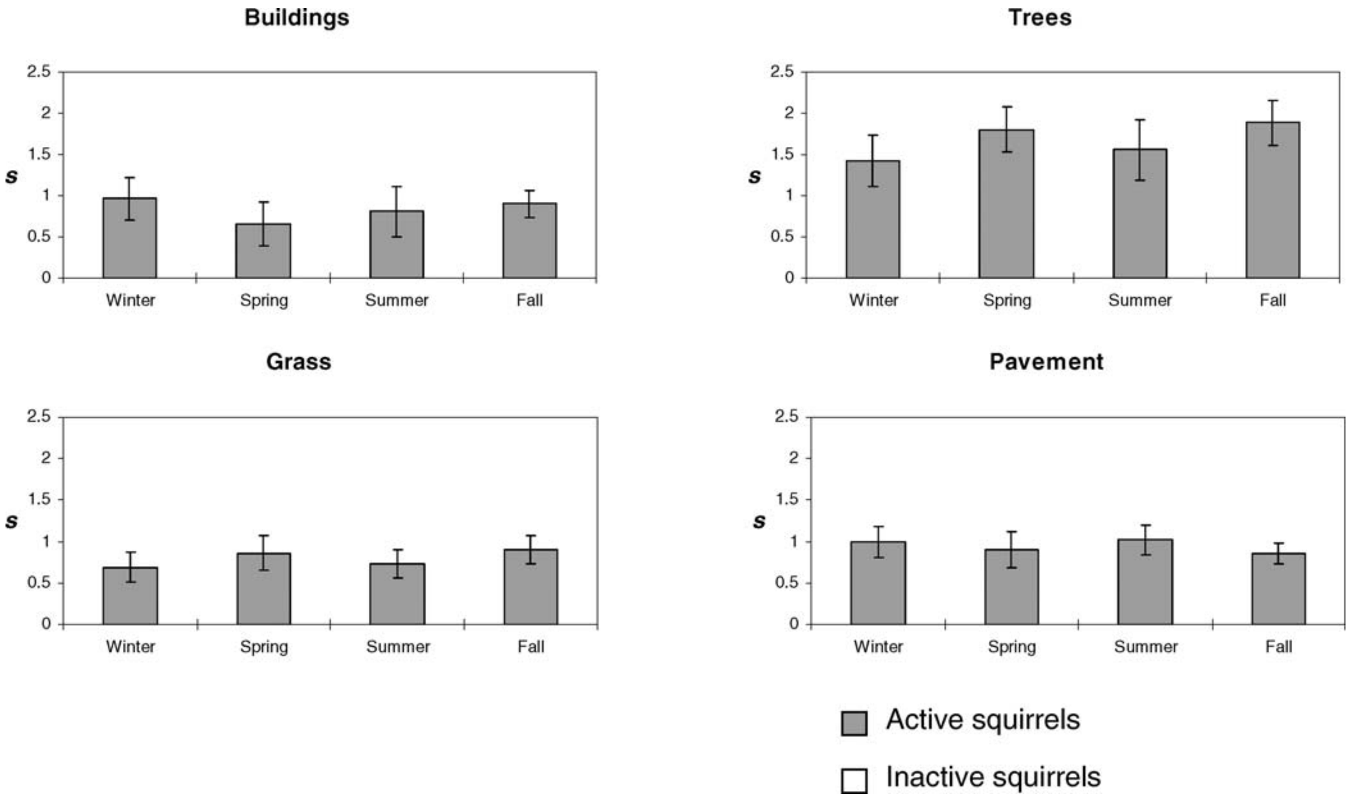

Figure 3. Fox squirrels averaged range-study area selection ratios of urban substrates (buildings; tree = tree canopy; pavement = concrete, asphalt, brick; and grass = manipulated grass areas) and 95% confidence interval error bars by season, in College Station, Texas, USA, September 2003–August 2005.

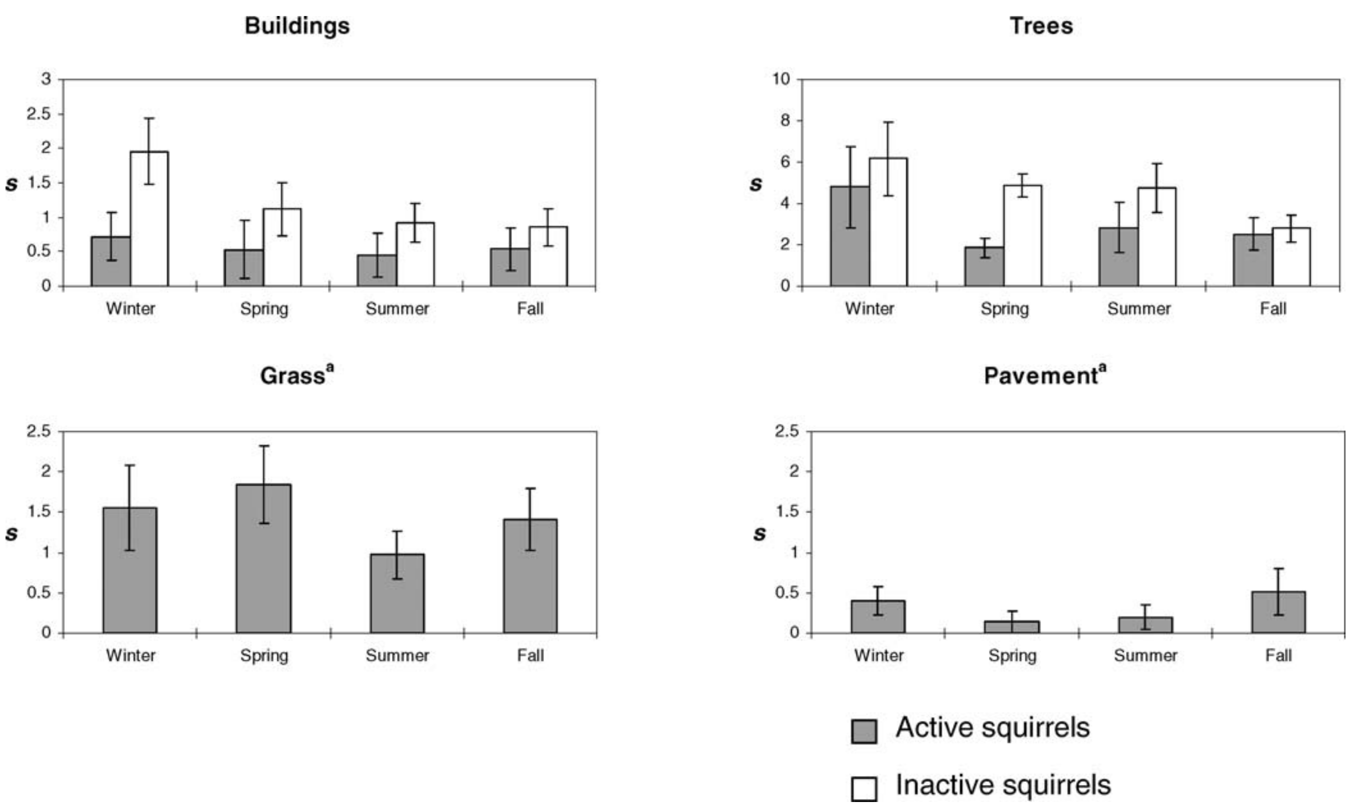

Figure 4. Fox squirrels averaged point-range selection ratios of urban substrates (buildings; tree = tree canopy; pavement = concrete asphalt, brick; and grass = manipulated grass areas) and 95% confidence interval error bars by season and activity (active and inactive), in College Station, Texas, USA, September 2003–August 2005. Squirrels were not recorded on grass or pavement during periods of inactivity.

Table 2. A priori and a posteriori models relating squirrel activity (the no. of squirrel locations in 1-ha blocks) to urban habitat components in College Station, Texas, USA, September 2003–August 2005. We display the Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), Akaike weights (w_i), and the number parameters (K) for each model.

	Model [a]	K	AIC_c	ΔAIC_c	w_i
a priori models					
1	None	2	−18,409	67.1	0.000
2	Ntrees + canopy + oaks + large	6	−18,458	18.2	0.000
3	Grass + oaks + ntrees	5	−18,427	49.7	0.000
4	Pave + grass + large	5	−18,464	12.8	0.001
5	Build + large + canopy	5	−18,471	5.3	0.039
6	Medium + large	4	−18,447	29.5	0.000
7	Large + oaks	4	−18,449	27.6	0.000
8	Oaks + grass	4	−18,423	53.8	0.000
9	Canopy + oaks	4	−18,442	34.7	0.000
10	Ntrees + grass + canopy + build + pave + medium + large + oaks	10	−18,475	1.3	0.285
a posteriori models					
11	Large + build + canopy + pave + grass	7	−18,477	0.0	0.559
12	Large + build + canopy + pave + oaks	7	−18,469	7.1	0.016
13	Large + build + canopy + pave	6	−18,469	7.3	0.014
14	Large + build + canopy + grass	6	−18,470	6.8	0.018
15	Large + build + canopy + oaks	6	−18,471	5.1	0.044
16	Large + build + canopy + oaks + grass	7	−18,470	6.5	0.022

[a] Variable notation for habitat components of 1-ha blocks: none = intercept only, ntrees = total no. of trees, grass = area of grass, canopy = ln (canopy area), build = area of buildings, pave = area of pavement, concrete, and asphalt, medium = no. of trees with dbh >14 but <20 cm, large = no. of trees with dbh >20 cm, oaks = no. of oaks.

contained zero, suggesting that the number of trees was the only variable that was not a relevant predictor of fox squirrel activity (Table 3).

DISCUSSION

Fox squirrels in our study preferred live oaks and trees with a greater diameter at breast height and canopy cover. They also selected tree canopy as a preferred substrate during active and inactive periods, and they concentrated movements in areas with proportionally greater tree canopy. These findings are congruent with research on fox squirrels in forested areas showing that large trees and hardwoods are preferred for daytime refugia, presumably because of the shelter and protection from predators that larger trees provide (Conner and Godbois 2003).

Our study and findings differed from studies in nonurban areas by examining fox squirrels use of exotic and introduced trees commonly found in urban environments. A microanalysis of tree selection indicated fox squirrels avoided introduced pines and other conifers (Table 1), suggesting urban fox squirrels were not using pine seeds and other conifer fruit as food sources, as observed in other studies (Baker 1944, Kantola and Humphrey 1990, Steele and Koprowski 2001). For daytime refuge trees, fox squirrels also avoided pines, along with bald cypress, arborvitae, Bradford pear, and fruit trees (Table 1), all of which were prevalent on our study site and common in urban areas in the southeastern United States (Gilman 1997).

Table 3. Averaged model parameter estimates and 95% confidence interval relating squirrel activity to urban habitat components in College Station, Texas, USA, September 2003–August 2005.

Urban habitat components[a]	$\hat{\beta}$	95% CI
Large	0.140	0.081 to 0.199
Build	−5.949	−11.718 to −0.181
Canopy	0.334	0.147 to 0.522
Grass	−2.866	−5.924 to −0.0245
Medium	−7.645	−12.621 to −2.689
Pave	−8.006	−13.267 to −2.745
Ntrees	0.004	−0.027 to 0.035
Oaks	−0.050	−0.097 to −0.003

[a] Variable notation for habitat components of 1-ha blocks: large = no. of trees with dbh >20 cm; build = area of buildings; canopy = ln (canopy area); grass = area of grass; ntrees = total no. of trees; medium = no. of trees with dbh >14 but <20 cm; pave = area of pavement, concrete, and asphalt; oaks = no. of oaks.

Our examination of fox squirrel use of urban substrate on various scales also illuminated the fox squirrels' ability to use an environment that is uninhabitable to many other mammal species (Adams et al. 2006). In our study, fox squirrels selected buildings within their ranges (point-range scale; Fig. 3) during the winter and spring, likely providing safe, warm refugia. We noted female fox squirrels used buildings in the late winter and early spring to raise their young. The use of buildings might be more pronounced in northern urban areas where the numbers of nest cavities are a limiting factor for many fox squirrel populations (Nixon et al. 1984, Kantola and Humphrey 1990) and could provide a warm refuge from colder temperatures.

Much of the urban environment consists of concrete, pavement, and asphalt (Adams 1994, Adams et al. 2006), which fox squirrels clearly avoided on both the point-study area and point-range scales. Nonetheless, range-study area analysis showed fox squirrels proportionally included pavement in their core-area ranges (Fig. 3). This suggests that although fox squirrels were not spending time on pavement, they did not let this seemingly biologically useless substrate limit their movements and areas of activity. The ability to tolerate pavement in core-area movements and to use buildings makes vast areas of the urban environment available for fox squirrels to exploit. Considering that pavement and buildings typically can comprise up to 80% of the inner-city environment (Adams et al. 2006) and that squirrels are not restricted to parks, forest fragments, and green areas may help explain their success in urban environments. This ability to adapt and tolerate altered environments seems to correspond with their high tolerance to disturbed areas (Salisbury et al. 2004).

Fox squirrels spend considerably more time on the ground than other tree squirrels (Whitaker and Hamilton 1998) and appeared during certain times of the year to use open grassy areas common in many urban areas. Fox squirrels appeared to select or avoid the manicured grassy areas common in urban areas depending on the season. Fox squirrels selected grassy areas within the study area and their core areas during the autumn and spring and within their core areas during the winter (Figs. 2 and 4). These are times when fox squirrels are most active, burying and retrieving their caches (Baker 1944, Whitaker and Hamilton 1998). Conversely, fox squirrels established core areas that appeared to avoid grass during the summer and winter (Fig. 3). One possible explanation for these movements is that the squirrels reduced their time in risky environments (open grassy areas; Lima and Dill 1989) when they were not using them for food storage and recovery.

Results from our analysis of fox squirrel activity models suggest that not only large trees but multiple features of the urban environment including number of buildings, pavement, tree canopy cover, number of oaks, and number of medium-size trees (>14 cm and ≤20 cm dbh) were all important factors in determining fox squirrel activity. Interestingly, the number of trees present was not a relevant predictor of squirrel activity in addition to the features previously listed. Our data suggest that tree size, species, and canopy cover were more important than tree numbers alone. Our effort to simplify and explain fox squirrel activity with a few variables failed as fox squirrel activity appears to be influenced by numerous features (buildings, pavement, canopy, tree composition) of the urban landscape.

In conclusion, our study suggests urban fox squirrels have been able, through the process of synurbanization, to adapt to urban areas. They made the most of the large mast–bearing trees that mimicked the habitats they have been shown to prefer in nonurban areas, and managed to use, tolerate, or avoid the numerous nonnative and man-made features of the urban environment.

MANAGEMENT IMPLICATIONS

Urban landscapes with large trees (Flyger 1974, Adams 1994), buildings, and manicured grass may provide an excellent habitat for fox squirrels. This increases the possibility of fox squirrel damage in some urban areas (Flyger 1974). Nonetheless, planners and landscapers who want to control fox squirrel populations through habitat manipulation (McComb 1984) may have options. Our data suggests that removal or reduction of oaks and other large trees and the reduction of canopy may be one way to address the problem. Removed trees may be replaced with pines, bald cypress, arborvitae, Bradford pear, and fruit trees, which urban fox squirrels appeared to avoid. Additionally, our data indicate that fox squirrels in urban areas may be controlled by restricting access of fox squirrels to buildings. Alternatively, to bolster fox squirrel populations in urban areas, large mast–bearing trees such as oaks and canopy cover should be increased, along with sufficient grassy areas for the caching of mast. In addition, those trying to encourage fox squirrel populations without inviting squirrels into buildings might want to consider the use of nest boxes (Nixon et al. 1984).

ACKNOWLEDGMENTS

We thank anonymous reviewers for their constructive criticism and editing suggestions and D. McCleery for her editing of the manuscript. Special thanks are extended to the undergraduate students whose hard work and dedication made this project possible. We also want to make a special note of the contribution of L. Gallant and T. Catanach, whose countless hours trapping and tracking fox squirrels were invaluable. Funding and support was provided by the Ed Rachel Foundation and the Texas Agricultural Experiment Station. The project was approved by the Texas Parks and Wildlife (Scientific Permit SPR-1101-181) and the Animal Use Committee and Texas A&M University (2001-278T).

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Associate Editor: Block.