

Influence of the urban environment on fox squirrel range overlap

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Keywords

tree squirrel; urban ecology; range overlap; hierarchy; territory; *Sciurus niger*; Texas.

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Editor: Virginia Hayssen

Received 30 December 2010; revised 30 May 2011; accepted 31 May 2011

doi:10.1111/j.1469-7998.2011.00835.x

Abstract

We predicted that features of the urban environment (uneven habitat from buildings, density of conspecifics and scarcity of dead or dying trees) would lead to different patterns of range overlap for urban and rural fox squirrels *Sciurus niger*. During 2003–2005 we captured, tracked and calculated seasonal ranges for 60 individuals at an urban site and 45 individuals on a rural site. Differences in range overlaps were best explained by sex, site and season. We observed a greater amount of seasonal range overlap by squirrels on our rural site. Buildings appeared to form the boundary of squirrels' seasonal ranges. By providing clear demarcations of squirrels' ranges, building might have reduced the costs of delineating territories. During the winter, urban squirrels used fewer [urban $\bar{x} = 1.3$, 95% confidence interval (CI) = 1.0–1.7; rural $\bar{x} = 3.6$, 95% CI = 2.8–4.2] cavities and anthropogenic shelters, suggesting that cavities might be limited on the urban site and worth the cost of defense. Similar population densities on the sites (urban = 1.58 squirrel ha⁻¹, rural = 1.45 squirrel ha⁻¹) did not allow us to examine the influence of densities of conspecifics on seasonal range overlaps. The alternative hypothesis, that reduced seasonal range overlaps were a function of range size had little support (female $F = 1.001$, d.f. = 82, $P = 0.130$); r males $F = 2.33$, d.f. = 118, $P = 0.320$). In summary, squirrels were able to alter their use of space and reduce their range overlap depending on the surrounding environment.

Introduction

The planet's landscapes are increasingly comprised of human-dominated and urban environments (Adams Van Druff & Luniak, 2005; Shochat *et al.*, 2006). Urban environments are characterized by high densities of human populations, buildings, impervious surfaces and high concentrations of food, water, energy, sewage and pollution (McDonnell *et al.*, 1997; Adams Lindsey & Ash, 2006; Shochat *et al.*, 2006). Many natural history studies on wildlife populations in undisturbed settings exist but they do not explain the ecology of populations in urban settings. Wildlife populations in urban landscapes often display different physiology, movements, habitat selection, demography and behaviors than their rural counterparts (VanDruff, Bolen & San Julian, 1996; Adams *et al.*, 2005; Ditchkoff, Saalfeld & Gibson, 2006; Shochat *et al.*, 2006). Some features of the urban environment that may influence animals' behaviors and use of space in the urban environment are: greater densities of conspecifics (Adams, 1994; Gliwicz, Goszczynski & Luniak, 1994; Etter *et al.*, 2002; Prange, Gehrt & Wiggers, 2003; Adams *et al.*, 2006), a complex and uneven environment (Melles, Glenn & Martin, 2003), and reduction in the number of cavities from dead or dying trees which provide nesting sites (Harper *et al.*, 2004; Blewett & Marzluff, 2005).

Hierarchy and territoriality are mechanisms animals use to allocate space (Kaufmann, 1983). Territoriality occurs when an individual (or group) defends a resource within a portion of its range (Kaufmann, 1983). The territory may be small and centered on a nest or valuable resource, or encompass a large portion of an animal's range and may change over time (Kerr & Bull, 2006). Dominance hierarchies occur when individuals mutually recognize a dominant – subordinate relationship, in which the dominant individual has priority access to space or resources (Kaufmann, 1983). Some populations of rodents and other mammals, may simultaneously exhibit both territorial and hierarchical relationships (Davis, 1959; Leyhausen, 1971; Kaufmann, 1983).

Territorial behavior is explained as a tradeoff between the costs and benefits to the fitness of individuals (Krebs & Davies, 1993). This tradeoff is influenced by interacting ecological factors, including: density and distribution of refugia and nesting sites, density of conspecifics, and habitat features (Maher & Lott, 2000). Territorial behaviors increase at intermediate levels when the benefits of exclusive use (e.g. food, nesting sites) outweigh the costs of defending them (Krebs & Davies, 1993). Similarly, individuals exhibit more territorial behaviors at lower and intermediate densities, while abandoning territorial behaviors at high densities

(Maher & Lott, 2000). Additionally, the complexity of habitats corresponds to more territorial behaviors. Complex habitats may provide clear boundaries, thus reducing the cost of territorial behaviors (Maher & Lott, 2000).

To understand how the urban environment might influence the tradeoff between territorial and hierarchical behaviors, we examined fox squirrels' *Sciurus niger* use of space in urban and rural environments. Most studies of spatial use in fox squirrel and other *Sciurus* spp. (all occurring in rural environments) have concluded that tree squirrels are more hierarchical and characterized by the extensive overlap of ranges (Geeslin, 1970; Benson, 1980; Don, 1983; Kantola & Humphrey, 1990). Under many circumstances, food resources are allocated through a hierarchy based on sex and age (Benson, 1980; Steele & Koprowski, 2001) but some territorial behaviors occur. Females in some fox squirrel populations have exclusive use of small areas around their nests in the winter (Havera & Nixon, 1978).

We examined fox squirrels' use of space by measuring the amount of spatial overlap in squirrel ranges during different seasons. We considered populations with less seasonal range overlap to have more territorial behaviors, and populations with more range overlap to have more hierarchical behaviors. We predicted scarcity of dead or dying trees and uneven habitat in urban environments would correspond to decreased overlap in ranges. We also predicted that the high population densities common in urban squirrel populations would correspond to increased overlap in ranges. To test these predictions, we examined the amount of overlap in ranges by season in an urban and a rural population of fox squirrels. Additionally, we tested whether uneven habitat, density of squirrels and density of tree cavities influenced squirrel behaviors. Finally, we examined an alternative hypothesis that changes in seasonal range overlap were simply an artifact of the size of the individual's ranges.

Methods and materials

Study area

The urban site was the 140 ha main campus of Texas A&M University, College Station, TX, USA. The 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. Dense residential and commercial development surrounded the study site. Dominant tree species on the study site were live oak (*Quercus fusiformis* and *Quercus virginiana*), post oak *Quercus stellata*, Bradford pear *Pryus calleryana*, arborvitae (*Thuja* spp.) and elm (*Ulmus* spp.). Trees with decaying limbs were regularly trimmed and removed from the campus.

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 c. 240 ha of undisturbed

bottomland hardwood forest and meadows with little to no human activity. Fox squirrels had not been hunted or fed on this site for over 20 years. Some of the dominant tree species in the area included post oak, water oak *Quercus nigra*, pecans and hickories (*Carya* spp.) and elms. An abundance of dead and dying trees occurred throughout the site.

Trapping

In an effort to maintain a sample of 20 squirrels (10 males, 10 females) on each study site equipped with functioning radio-telemetry collars, we trapped squirrels periodically from August 2003 to June 2005 on the urban study site and from May 2004 to July 2005 on the rural study site. We strapped >65 Tomahawk wire-cage traps (no. 103, Tomahawk Live Trap Company, Tomahawk, WI, USA) to the limbs of trees (Korschgen, 1981; Adams, 1984) on each study site. Traps were pre-baited with sunflower seeds and pecans 2–3 days before trapping to increase trapping success. Once squirrels were captured they were sexed, aged (Dimmick & Pelton, 1996) and weighed. Each squirrel was ear-tagged (Monel 1005-3, National Band & Tag Company, Newport, KY, USA), given a passive integrated transponder (PIT tag, Biomark, Boise, ID, USA) and adult squirrels (>7 months old, McCloskey & Vohs, 1971) were fitted with a collar and a battery-powered mortality-sensitive radio transmitter (Korschgen, 1981; Samuel & Fuller, 1996; 150–152 MHz, 12 g, model M170 Advanced Telemetry Systems, Isanti, MN, USA or 10 g, model MP-2 AVM Instrument Company, Colfax, CA, USA). All capturing and handling of fox squirrels followed American Society of Mammalogists guidelines (Gannon, Sikes & the Animal Use Care and Use Committee of the American Society of Mammalogists, 2007) and was approved by the Texas Parks and Wildlife Department (Scientific Permit SPR-1101-181), and the Animal Care and Use Committee and Texas A&M University (2001-278T).

We calculated seasonal ranges for 60 individuals over a course of seven seasons on the urban site ($n = 16$, autumn 2003; $n = 20$ winter 2003; $n = 18$ spring 2004; $n = 14$ summer 2004, $n = 12$ autumn 2004; $n = 12$ winter 2004; $n = 13$ spring 2005). On the rural site, we calculated seasonal ranges for 45 individuals for five seasons ($n = 20$ autumn 2004; $n = 18$ winter 2004; $n = 22$ spring 2005; $n = 21$ summer 2005, $n = 16$ autumn 2005). We calculated multiple seasonal ranges for >50% of the squirrels on the urban and rural sites.

Radio Telemetry

Once we had ≥ 20 radio-collared squirrels, we collected movement data on the urban site for 21 months (21 September 2003 through 21 May 2005) and on the rural site for 16 months (21 August 2004 through 21 December 2005). We monitored squirrels' locations two to three times per 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). We located fox squirrels via homing (White & Garrott, 1990), noting their

position on geo-referenced maps on the urban site and with a global positioning system (Garmin12, Olathe, KS, USA) on the rural site. Additionally, if the squirrel was not active we recorded the tree species, diameter at breast height of the tree, the nest substrate (i.e. tree cavity, leaf, building, nest box) and where in the tree the nest was located (height and side). In an effort to pinpoint squirrel locations, we often used ladders, accessed rooftops and attic spaces and used mini-digital zoom cameras (model # KPC-S20P, Korea Technology and Communications, Seoul, Korea) and micro-video monitors (Nature Vision Inc., Baxter, MN, USA) attached to telescoping poles as described by Proudfoot (1996). We flagged commonly used nests and all radio-tracking data were placed into a geographic information system (GIS) database.

Ranges and overlap

To determine the sample sizes necessary to calculate ranges, we used the bootstrap analysis tool from the Animal Movement extension in ArcView (Hooge & Eichenlaub, 2000; Kwiatkowski *et al.*, 2008). We calculated average minimum convex polygons for each squirrel by bootstrapping each range 300 times in increments of five points, starting with a sample size of 5 and ending with the sample size for the individual. Then we plotted sample size as a function of the bootstrapped MCP areas and visually inspected the plot to determine the sample size at which no additional increase in range size occurred (Kwiatkowski *et al.*, 2008). Asymptotic seasonal range estimates were achieved in 15 locations (Borger *et al.*, 2006) and we eliminated squirrels with < 15 locations from further analysis.

We calculated seasonal ranges (85%) for each squirrel in ArcView 3.3 (ESRI, Redlands, CA, USA) with a fixed-kernel home-range estimator and a smoothing parameter defined by least-squares cross validation (Worton, 1989; Seaman, Griffith & Powell, 1998; Seaman *et al.*, 1999). We calculated 85% seasonal ranges because using isopleths < 90% (but > 50%) generates less-biased range areas (Borger *et al.*, 2006), and we did not want to exaggerate range overlaps by using traditional 95% ranges that might include dispersal or exploratory movements. We defined seasons as winter (22 December–21 March), spring (22 March–21 June), summer (22 June–21 September), and autumn (22 September–21 December). We chose to examine overlap temporally because of the dramatic difference in squirrel's seasonal movements (Geeslin, 1970; Steele & Koprowski, 2001). Additionally, male and female social systems appear to be separate from each other except during the breeding season (Steele & Koprowski, 2001), so we examined the relative amount of overlap for males and females separately on both study sites. We calculated seasonal range overlap as the average portion of a squirrel's range overlapped by other squirrels of the same sex using the polygon overlapping tool in ArcGIS 9.2 (ESRI).

We used an information theoretic approach (Burnham & Anderson, 2002) to determine which factors influenced squirrels' seasonal overlaps. We developed 10 candidate

models, including a null model and models examining the interactive and additive effects of site, sex and season. We determined the fit of each model using a generalized linear model regression (PROC GENMOD, SAS version 9.1), with the average seasonal overlap of each squirrel fitted to a negative binomial distribution. Models were evaluated using ΔAICc , the relative difference to the smallest AICc (Akaike's information criterion, corrected for small sample size), and Akaike weights (w_i) (Burnham & Anderson, 2002). We considered models ≤ 2 AICc units to compete with the best model. We considered models > 2 AICc units and ≤ 4 AICc units from the best model to be plausible and models > 4 AICc units were disregarded as unlikely representations of the data (Burnham & Anderson, 2002). We calculated parameter estimates and 95% confidence intervals (CIs) for all models ≤ 4 AICc of the best model (Burnham & Anderson, 2002), and considered the parameter relevant if their CIs did not include 0 ($\alpha = 0.05$).

Uneven habitat

Buildings add environmental complexity that should reduce the cost of territorial behaviors by simplifying the delineation of territories. If fox squirrel ranges were delineated by buildings, we would predict the perimeter of their ranges to abut buildings. We examined the influence of buildings on the perimeters of squirrel territories by buffering all buildings on the urban study site and determining how much of the perimeter of squirrels' actual ranges landed within building buffers. We compared range borders falling within the buffers for actual and randomly placed ranges of equal shape and size. We used ArcGIS 9.2 to create 10 m buffers around all buildings, and due to the non-normal distribution and unequal variances of the building-range overlap data, we used a nonparametric approach for analysis (Mann–Whitney *U*-test; Ott, 1993).

Density

Populations of urban adapted species, such as squirrels, commonly have higher densities in urban settings than in rural environments (Adams *et al.*, 2005). If high densities were found, we would predict increased seasonal range overlaps due to increased interactions and intruder pressure (Maher & Lott, 2000). To determine whether varying densities corresponded with seasonal range overlap, we calculated density estimates of the two populations. We used ArcGIS 9.1 to randomly assign 28 points on each site. We visited all 28 sites on both study areas for two consecutive mornings four times during the study [August 2004, October 2004, January 2005, and April 2005 (224 point surveys per site)] between 09:00 and 11:00 AM, when fox squirrels are most active (Geeslin, 1970; Koprowski, 1994). After acclimating to the site for 5 min we took a snapshot (Buckland, 2006) of the squirrels visible from the point. We recorded each squirrel's perpendicular distance from the random point. We used DISTANCE, version 5.0, release 2, to analyze our data (Thomas *et al.*, 2005). We fit half-

Table 1 Candidate models comparing range overlap of fox squirrels *Sciurus niger* by sex, season and site on urban and rural populations in College Station, TX, USA

Candidate model	<i>K</i>	$-2\ln L$	AICc	Δ Delta AICc	w_i Akaike weight
Sex \times site	5	-23930.23	-23919.92	0.00	0.617
Sex \times site \times season	17	-23955.45	-23918.13	1.80	0.252
Site	3	-23922.46	-23916.34	3.58	0.103
Sex + site + season	7	-23927.90	-23913.32	6.60	0.023
Season + site	6	-23922.59	-23910.16	9.77	0.005

The table includes the number parameters (*K*) displayed for each model. Negative 2 log-likelihood ($-2\ln L$), Akaike information criteria (AIC), Akaike information criteria adjust for small sample size (AICc), change in AICc from the smallest AICc value (Δ AICc) and Akaike weights (w_i).

normal and uniform detection-function models with ≤ 3 cosine series expansion terms; we fit hazard rate models with ≤ 3 simple polynomial series to all observations (pooled), and selected the model with the smallest AIC value. We then fit the same models independently to data from each study site (i.e. detection function stratified by site) and used AIC values to choose between stratified and pooled models. Additionally, we evaluated goodness-of-fit test statistics to ensure model fit.

Tree cavities

Snags and their associated cavities are scarce in the urban environment because dead and dying trees are often removed (Williamson, 1983; Marzluff, Gehlbach & Manuwal, 1998). For cavity nesting birds, a lack of snags increases competition and decreases densities (Brawn & Balda, 1988; Blewett & Marzluff, 2005). Similarly, squirrel densities decrease when tree cavities are not available for shelter and rearing of young (Nixon, Havera & Greenberg, 1978; Williamson, 1983), especially during winter (Geeslin, 1970; Christisen, 1985). In one instance during winter, female fox squirrels reduced their range overlap and centered their activities on a tree cavity (Havera & Nixon, 1978). Squirrels will also use anthropogenic shelters (attics and eaves) but they do so when tree cavities are not available (Williamson, 1983).

To determine whether cavities were a limiting resource on the urban sites during winter, we compared the average number of nests occupied per squirrel and the average number of nests that were either natural cavities or anthropogenic shelters (nest boxes and buildings) between rural and urban areas. On both sites we assumed nothing limited squirrels' ability to build and use leaf nests. On the rural site, based on the high density of snags, we assumed that tree cavities were unlimited. If squirrels on both sites used the same number of nests and the same proportion of cavity to leaf nests, we would conclude that cavities were not limited on the urban site. If urban squirrels used fewer cavities and proportionally fewer cavities than the rural squirrels, then cavities may be a limited resource. In turn, we predicted that if cavities were limited, we would observe a decrease in seasonal range overlaps. We combined cavities and anthropogenic shelters into one category (cavities) and used *t*-tests (Ott, 1993) to compare the number of leaf, cavity and total

nests used on each site. Additionally, we used a Pearson's χ^2 test (Ott, 1993) to compare the proportion of leaf nests to cavity nests used on each site.

Function of size

As ranges expand, they become more difficult to defend and more susceptible to incursions from conspecifics (Maher & Lott, 2000). Thus overlap maybe a function of range size. To evaluate this possibility, we used a general linear model (PROC GENMOND, SAS version 9.1) to correlate the size of male and female ranges to the average proportion of overlap recorded from neighboring squirrels of the same sex.

Results

Overall, we observed a reduced seasonal range overlap by squirrels on our urban site. This was especially true during the winter, when urban squirrel used fewer cavity nests. Additionally, we found buildings appeared to form the boundary of squirrels' ranges.

To determine which model best explained differences in seasonal range overlap, we used AICc values and selected the interactive model between sex and site as the best model (model 1, Table 1). We also considered the interactive model between sex, site and season (model 2, Table 1) to be a competing model (< 1.80 AICc units of the best model) and the site model (model 3, Table 1, < 3.58 AICc units of the best model) as a plausible model. These three models had a combined w_i of > 0.97 , suggesting a greater than 97% chance that one of these three models yielded the best explanation of the data. CIs of parameter estimates (Table 2) for the sex \times site model indicated that males on the rural site clearly differed from males and females at the urban site. Parameter estimates from the sex \times site \times season model suggested a difference between males in winter on the rural site and females in winter on the urban site, females in spring on the urban site and females in autumn on the urban site. Finally, the Site model parameters showed a decreased overlap on the urban site, compared with the rural site (Table 2, Fig. 1).

Uneven habitats

Randomly placed seasonal squirrel ranges overlapped building buffers far less than observed squirrel ranges (random,

Table 2 Model parameter estimates $\hat{\beta}$ and 95% CI for best competing models comparing range overlap of fox squirrels *Sciurus niger* by sex, season and site on urban and rural populations in College Station, TX, USA

Model	Parameters	$\hat{\beta}$	95% CI	
			Lower	Upper
Sex × site	F urban	-1.3685	-1.9051	-0.8319
	M urban	-0.5767	-1.0738	-0.0797
	M rural	.	.	.
Sex × season × site	F autumn urban	-1.3906	-2.3805	-0.4008
	F spring urban	-1.3709	-2.4003	-0.3415
Site	F winter urban	-4.151	-5.3572	-2.9448
	M winter rural	.	.	.
	Urban	-0.8013	-1.1921	-0.4106
	Rural	.	.	.

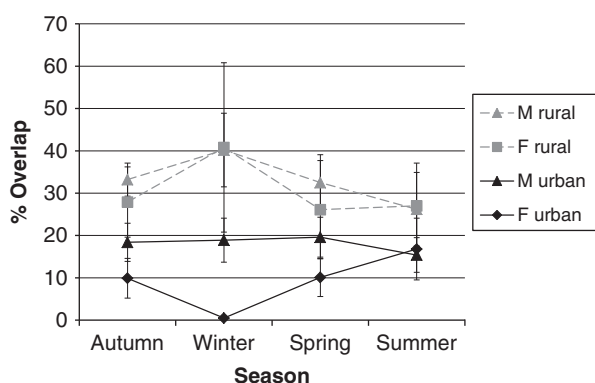


Figure 1 Average range overlap and error bars (standard error) by season of male and female squirrels on an urban and a rural site in College Station, TX, USA.

$N = 789$; actual, $N = 1179$). The mean length of random building-range overlaps ($\bar{x} = 272.8$ m) and actual building-range overlaps ($\bar{x} = 1460.3$ m) differed significantly from each other when summed across all seasons ($Z = -33.9$, $P < 0.001$), and for each season (winter, $Z = -11.8$, $P < 0.001$; spring, $Z = -20.0$, $P < 0.001$; summer, $Z = -18.3$, $P < 0.001$; autumn, $Z = -16.1$, $P < 0.001$) and yearly (2003, $Z = -15.5$, $P < 0.001$; 2004, $Z = -27.2$, $P < 0.001$; 2005, $Z = -11.7$, $P < 0.001$).

Density

From 448 point samples we recorded 113 fox squirrel observations. Using AIC values we selected a model with a detection function fitted to uniform key distribution with 1 cosine adjustment that did not vary between sites. The model appeared to fit the data well ($\chi^2 = 8.29$, d.f. = 11, $P = 0.687$). Fox squirrel densities differed little between the urban site (1.58 squirrels per ha, % CV = 21.8) and the rural site (1.45 ha squirrels per ha, % CV = 19.6).

Tree cavities

Squirrels on the urban site used significantly fewer nests ($t = 3.58$, $P = 0.001$) during winter than rural squirrels (urban $\bar{x} = 2.6$, 95% CI = 2.1–3.1; rural $\bar{x} = 4.0$, 95% CI = 3.4–4.6). Urban squirrels also used fewer ($t = 5.83$, $P < 0.001$) cavities and shelters (urban $\bar{x} = 1.3$, 95% CI = 1.0–1.7; rural $\bar{x} = 3.6$, 95% CI = 2.8–4.2) and used cavities and shelters proportionally less than leaf nests when compared to their rural counter parts ($\chi^2 = 25.57$, d.f. = 11, $P = 0.008$).

Function of size

Average seasonal ranges were smaller on the urban site (female $\bar{x} = 18$ ha, 95% CI 8–28 ha; male $\bar{x} = 53$ ha, 95% CI 39–67 ha) than on the rural site (female $\bar{x} = 40$ ha, 95% CI 22–60 ha; male $\bar{x} = 139$ ha, 95% CI, 50–229 ha) for males and females. However, no significant correlation occurred between range size and average seasonal overlap from neighboring squirrels of the same sex for females ($F = 1.001$, d.f. = 82, $P = 0.130$) or males ($F = 2.33$, d.f. = 118, $P = 0.320$).

Discussion

Based on these two populations we saw a clear increase in the amount of seasonal range overlap displayed by rural squirrels compared to urban squirrels. Thus, squirrels adjust their behavior to use space based on particular conditions. On the urban site, squirrel ranges were smaller, showed considerably less overlap than the rural site, and range overlap varied by sex and season. We examined a number of features of the urban environment that could explain the reduced rates of overlap. Several of our predictions appeared to be consistent with the data.

First, the perimeters of actual squirrels' seasonal ranges bordered buildings more than randomly placed squirrel ranges. Thus, range boundaries might be influenced by buildings and the increased habitat unevenness may increase the ease of delineating ranges. Compared with the more homogenous rural landscape, the structural complexity that buildings bring to the urban environments might allow a shift toward more territorial behaviors. To our knowledge, this is the first documentation of buildings influencing the seasonal ranges and movements of a mammalian population.

Second, the most pronounced differences in overlap came during winter when fox squirrels prefer to den in cavities (Geeslin, 1970; Christisen, 1985). During winter, urban squirrels used fewer nests overall and fewer cavities and anthropogenic shelters than squirrels on the rural site. Thus, cavities might have been a limited resource on the urban site and worth the cost of maintaining exclusive use. This would be especially true for females that are pregnant, birthing and nursing young during winter. Accordingly, females on the urban site maintained almost exclusive territories with minimal overlap (0.5%), while rural squirrels with apparently ample nesting cavities showed heightened levels of overlap

(40%). Prior research has suggested that communal nesting of fox squirrels is most prevalent during the winter and that this behavior might be beneficial for thermoregulation (Koprowski, 1996). An alternative explanation for the patterns is that where cavities are available, fox squirrels benefit by overlapping seasonal ranges and sharing dens. However, sharing leaf nests may not be as feasible or beneficial as sharing cavities; thus, urban squirrels which used more leaf nests showed less overlap.

Our results did not support the influence of other aspects of the urban environment on range overlap. With only a minimal difference in the densities of the two populations of squirrels (urban = 1.58 squirrel ha⁻¹, rural = 1.45 squirrel ha⁻¹), testing our prediction that increased density of conspecifics would increase range overlaps was difficult. Also, the alternative hypothesis that territorial behaviors were a function of range size had little support. Although seasonal range sizes were larger on the rural site, the size of a squirrel's seasonal range and the proportional amount of overlap from neighboring individuals of the same sex were not correlated.

One factor that we did not explore that could have explained differences in overlap was the availability and quality of food resources. Quantifying food resources on both sites would have been extremely challenging, because fox squirrels consume parts of over 100 different plants, along with insects, eggs and anthropogenic food (Koprowski 1994). Nonetheless, in natural areas, fox squirrel food resources peak in the spring and fall and decline in the summer and winter (Steele & Koprowski, 2001). Conversely, the presence of vast amounts of human food throughout the year (Adams *et al.*, 2005) and stabilized production in the parks and yards of urban areas (Imhoff *et al.*, 2000) should mitigate the seasonal peaks and declines of the food resources available to urban squirrels. If food resources influenced seasonal range overlap, we would have expected more pronounced changes in range overlaps from season to season in rural environments compared with urban environment. In a *post hoc* analysis, we compared the average seasonal change in the range overlap of squirrels between sites using an ANOVA test (Ott, 1993) and found no difference ($F = 0.002$, $P = 0.965$) between the urban site ($\bar{x} = 0.087$, 95% CI = 0.033–0.14) and rural site ($\bar{x} = 0.086$, 95% CI = 0.057–0.11). Thus, food resources likely did not influence the amount of seasonal range overlap found in each population or the peaks in food resources on both sites were similar.

Historically, squirrel movements have been characterized by extensive range overlap (Geeslin, 1970; Benson, 1980; Don, 1983; Kantola & Humphrey, 1990). In our study, squirrels were able to alter their use of space and reduce their range overlap depending on the surrounding environment. Thus behaviors, movements and dynamics of wildlife living in urban environments cannot be predicted by observations made in remote locations. Urban environments are dominated by features that were created and altered by humans and are unlikely to have been experienced in the species' evolutionary history. Thus, wildlife using urban

areas must have the mechanisms and plasticity to adjust to this novel environment. Understanding these mechanisms and what triggers them can help provide researchers and managers with valuable insights into the interplay between the manmade environment and animal ecology.

Acknowledgments

We would like to thank Roel R. Lopez and Nova J. Silvy for their support during this project. We are grateful to Kyle Kacal for allowing us to work on Tonkaway Ranch and always lending a helping hand when it was needed. We would also like to thank the anonymous reviewers of this manuscript whose constructive criticism and editing suggestions greatly improved it. 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 contributions of S. Kahlich and L. Gallant, whose countless hours trapping and tracking fox squirrels were invaluable.

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