



Ephemeral temporal partitioning may facilitate coexistence in competing species

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Animals change their daily activity patterns in response to season, food availability and the presence of competitors. Competition may be an important driver of a species' daily activity pattern, as animals manage conflict by avoiding each other temporally. We evaluated how vegetation structure and the presence of competitors changed the daily activity patterns of closely related fox squirrels, *Sciurus niger*, and grey squirrels, *Sciurus carolinensis*. We monitored squirrel activity in north and central Florida using passive game cameras at two spatial scales: local and point. To understand how seasonality and competition interact to drive behaviour, we compared squirrel activity during the leaf-off (1 January – 15 March) and leaf-on (16 March – 1 July) seasons. We tested for a relationship between squirrel activity and canopy cover by fitting a von Mises kernel distribution. To test how season and competition affected squirrel behaviour, we compared activity by computing a kernel density overlap function, ranging from 0 (no overlap: the squirrels are never active at the same time) to 1 (complete overlap: the squirrels have identical activity patterns). We found that daily squirrel behaviour was not influenced by canopy cover ($P = 0.61$). Fox squirrels had a single activity peak occurring around midday. In contrast, grey squirrels had a bimodal activity pattern with peaks shortly after sunrise and before sunset. The intensity of this partitioning existed on a gradient and changed with season and the presence of competitors. Fox and grey squirrel daily patterns overlapped the most when they were allopatric in the leaf-on season (overlap = 0.70, $P < 0.001$) and the least while sympatric in the leaf-on season (overlap = 0.24, $P < 0.08$). This ephemeral response to competition highlights that various axes of resource partitioning can promote coexistence between closely related species.

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Understanding the mechanisms that allow closely related species to coexist is important in explaining patterns of biodiversity and has ramifications for species conservation (Linnell & Strand, 2000). Numerous mechanisms (e.g. niche diversification, resource partitioning, pest pressure and life history differences) allow for the coexistence of species that compete for the same resources (Chesson, 2000; Wilson, 1990). Of these mechanisms, resource partitioning – where species subdivide a niche space – is important in reducing both interference (i.e. antagonistic) and exploitative (i.e. resource use) competition (Schoener, 1974). However, it is unclear at which spatial and temporal scales these mechanisms operate.

Resource partitioning can occur along spatial and/or temporal axes (Kronfeld-Schor & Dayan, 2003). Spatial resource partitioning, in which species divide resources across different locations or along an environmental gradient, is common for promoting coexistence in many mammalian taxa including ungulates (Stewart, Bowyer, Kie, Dick, & Ben-David, 2003), bats (Nicholls & Racey, 2006; Razgour, Korine, & Saltz, 2011) and carnivores (Kozłowski, Gese, & Arjo, 2008). Temporal resource partitioning, where a subordinate species shifts the time when it accesses resources to avoid antagonistic encounters with dominant species, remains poorly understood (Case & Gilpin, 1974; Di Bitetti, Di Blanco, Pereira, Paviolo, & Pérez, 2009; Gutman & Dayan, 2005; Lesmeister, Nielsen, Schaubert, & Hellgren, 2015; Ziv, Abramsky, Kotler, & Subach, 1993). Partitioning resources temporally may be costly because shifting activity to suboptimal times may increase energy demands, predation risk and/or foraging costs (Frey, Fisher, Burton, & Volpe, 2017). Furthermore, closely related species may be

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evolutionarily constrained to being active during the same part of the diel cycle (Gutman & Dayan, 2005). Temporal partitioning may be more common where competition for resources is pronounced, such as at the extremes of species' distributions (Liancourt & Tielbörger, 2009) or when food is restricted seasonally (Kronfeld-Schor & Dayan, 1999). However, species may also use resources at different times because of predation risk (Lima & Bednekoff, 1999), evolutionary history (Case & Gilpin, 1974; Connell, 1980; Kronfeld-Schor & Dayan, 2003), vegetation characteristics (Moreno, Villafuerte, & Delibes, 1996) and morphological restraints (Dahl & Smith, 1985). Separating the effect of competition on species daily activity patterns from other factors can be difficult (Halle, 2000).

Species interactions and sympatry are scale-dependent processes (Bennett, 1990). At larger spatial scales (e.g. within a forest patch), environmental heterogeneity allows species to coexist through habitat specialization, with each species utilizing areas where they are competitively superior (Conner, Landers, & Michener, 1999; Kneitel & Chase, 2004). At smaller scales (e.g. sharing a food patch), species may coexist through temporal partitioning, with each species utilizing times when the other is dormant (Kneitel & Chase, 2004). Finally, food availability may also be an important factor in determining the importance of temporal partitioning (Kneitel & Chase, 2004). Food resources can vary on a daily (i.e. insect availability) or annual (i.e. seasonal changes in

mast) basis. While theory suggests that time of year and spatial scale are critical to understanding how temporal partition plays out between species (Bennett, 1990), we know of few empirical field studies that test the influence of these factors on resource partitioning (Albrecht & Gotelli, 2001).

Coexisting fox squirrels, *Sciurus niger*, and eastern grey squirrels, *Sciurus carolinensis*, are an ideal system for studying temporal partitioning. Fox and grey squirrels are native to the eastern United States (Fig. 1) and are closely related, having diverged relatively recently (late Pleistocene; Pečnerová & Martínková, 2012). Fox and grey squirrels share food resources like pine nuts, hardwood mast, fungi, lichens, flowers and buds (Koprowski, 1994a, 1994b; Weigl, Steele, Sherman, Ha, & Sharpe, 1989). Fox squirrels generally occupy areas with high pine and herbaceous cover while grey squirrels occur in areas with high oak and woody ground cover (Conner et al., 1999; Koprowski, 1994a, 1994b). Despite these patterns, fox and grey squirrels are often found together, especially at the transitions between open and closed canopy forests (Conner et al., 1999; Edwards & Guynn, 1995). Fox and grey squirrels display the same pattern as many sympatric species; where competitive ability and predator vulnerability are traded off (Kneitel & Chase, 2004). Grey squirrels may be more social and aggressive than fox squirrels (Armitage & Harris, 1982; King, 2004; Parker & Nilon, 2008; Thompson, 1978). This aggression combined

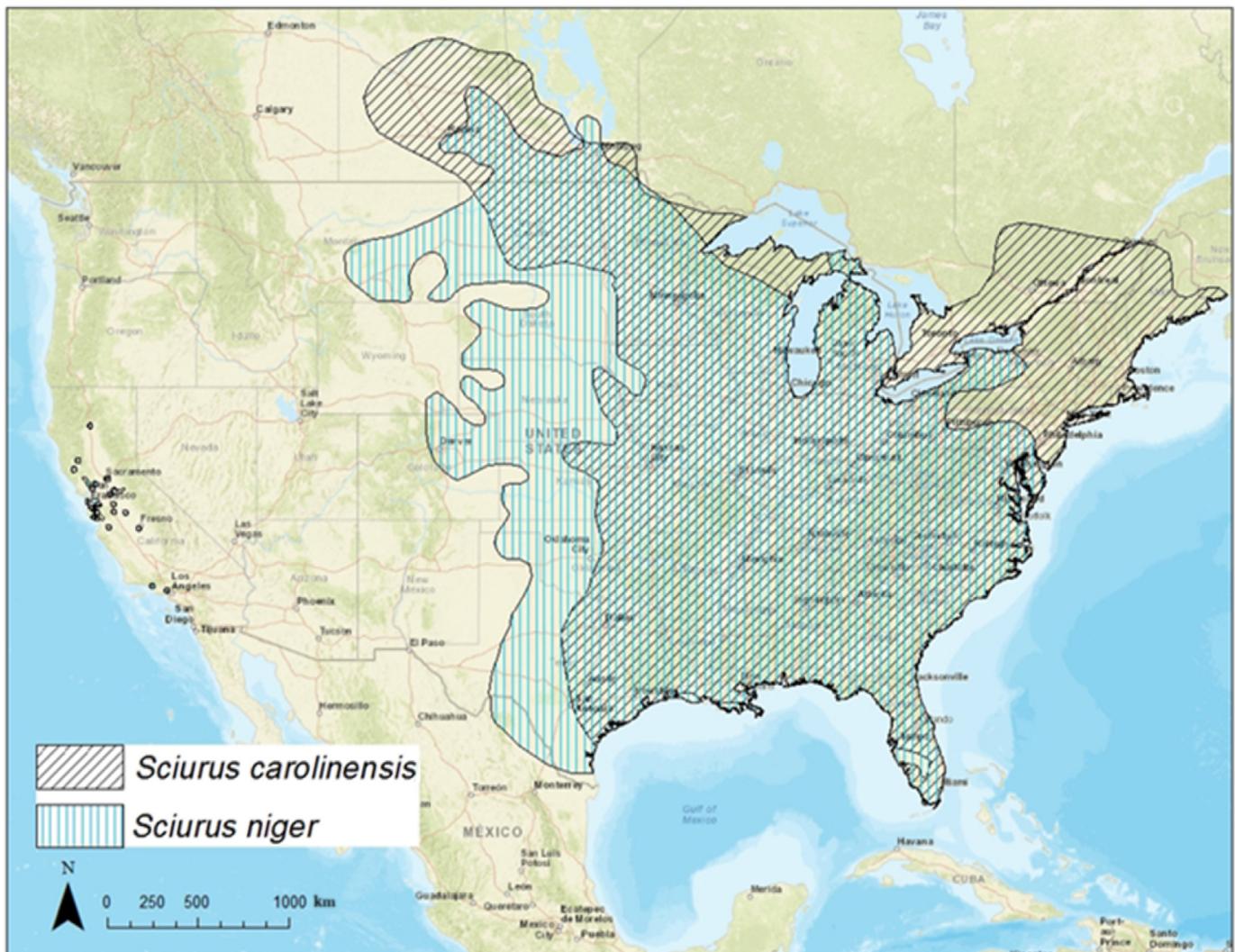


Figure 1. Distribution of grey squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) in North America.

with their superior foraging efficiency leads to the displacement of fox squirrels by grey squirrels as predator densities decline (Sexton, 1990; van der Merwe, Brown, & Jackson, 2005).

Multiple studies have investigated the temporal behaviour patterns of fox and grey squirrels but have reported conflicting results (Derge & Yahner, 2000; Edwards, Heckel, & Guynn, 1998; Edwards & Guynn, 1995; King, 2004). Some studies indicate that both species have similar bimodal activity patterns (Hicks, 1949; Koprowski, 1994a, 1994b) and avoid interaction by habitat specialization (Edwards & Guynn, 1995). However, others suggest that grey squirrels have a bimodal activity pattern and fox squirrels a unimodal activity pattern (Derge & Yahner, 2000). Such contrasting findings may be a result of the spatial and temporal scales of the studies and/or geographical differences (Greene et al., 2017a).

To address this gap in the literature we elucidated the role of vegetation structure, season and competition in determining temporal behaviour. We compared fox and grey squirrel daily activity patterns in north and central Florida. Florida is particularly suited to understand temporal partitioning because of its relatively stable daylength, mild winters that allow year-round squirrel activity, and location at the southern extent of both species' ranges where temporal partitioning should be pronounced (Liancourt & Tielbörger, 2009). In north and central Florida, fox and grey squirrel's shared food resources are limited during the leaf-off season (1 January – 15 March) and become increasingly plentiful during the leaf-on season (16 March – 1 July) (Moore, 1957). We developed the following a priori predictions for the effects of vegetation, competition, seasonality and spatial scale on temporal partitioning between fox and grey squirrels.

Canopy Cover

Vegetation structure, specifically canopy cover, is an important predictor of fox and grey squirrel occupancy (Brown & Batzli, 1985). Visual and flight obstructions (such as dense canopy cover) reduce the ability of diurnal raptors to capture prey (Bechard, 1982; Preston, 1990). We predicted that grey squirrels would use areas with greater canopy cover during midday when raptors are active and use sparse canopy cover areas during the early morning and evening when raptors are inactive (Moreno et al., 1996). In contrast, we did not expect to see a relationship between canopy cover and the daily activity patterns of fox squirrels. Fox squirrels are less susceptible to predation by raptors and regularly use areas of low canopy cover (Steele & Koprowski, 2003).

Competition

In the absence of competition, diurnal species prefer being active early after sunrise and again before dusk (Bednekoff & Houston, 1994; Bonter, Zuckerberg, Sedgwick, & Hochachka, 2013; Farine & Lang, 2013). However, competition may be an important determinant of squirrel daily activity patterns. If competition influences daily activity patterns, we predicted that when facing competition from grey squirrels, fox squirrels would be most active at midday. In contrast, we did not expect the aggressive and dominant grey squirrels to modify their behaviour in the presence of fox squirrels.

Season

Resource availability may modify the competitive behaviour of squirrels. During times of limited resources (leaf-off season), we expected intensified competition and temporal partitioning between grey and fox squirrels. In contrast when resources are

plentiful, during the leaf-on season, we expected to see fewer temporal differences in behaviour.

Spatial Scale

The spatial scale of co-occurrence should modify the influence of competition on the behaviour of squirrels. Within landscapes, we expected grey and fox squirrels to use spatial partitioning to relieve competition (Albrecht & Gotelli, 2001; Bennett, 1990). Whereas at finer scales (i.e. tree or food patch), we expected squirrels to partition temporally to avoid agonistic interactions (Di Bitetti et al., 2009; Parker & Nilon, 2008; Thompson, 1978). To mitigate this conflict, we expected fox squirrels to shift their activity to midday.

Furthermore, we expected that temporal partitioning would exist along a gradient and would be most pronounced when fox and grey squirrels came into direct conflict over limited resources (i.e. sympatric at the point scale during the leaf-off season). We did not expect to detect evidence of temporal partitioning when squirrels were not experiencing competition at large spatial scales when resources were plentiful (i.e. allopatric in a forest patch (grid) in the leaf-on season). We tested these predictions by investigating how grey and fox squirrel activity overlaps under various conditions (Table 1).

METHODS

We conducted all research under the Florida Fish and Wildlife Conservation Commission's Scientific Collecting Permit (LSSC-11-00026). The University of Florida's Non-Regulatory Animal Research Committee (021-10WEC) approved all research involving live animals and we followed the American Society of Mammalogists guidelines for the care and handling of mammals (Sikes et al., 2011). We did not capture, tag or transport wild animals during this study. To minimize disturbance to wild animals, we did not prebait sites and used only enough natural bait (6–9 cracked, whole pecans and cracked corn) to ensure visits but not habituation. We visited study sites only to set up and take down camera trapping equipment and measure vegetation structure and composition (a maximum of 30 min to complete and sometimes done when setting up or taking down the camera). Our methods did not cause distress or pain to animal subjects.

Study Area

We conducted field surveys on public and private lands throughout north and central Florida (Fig. 2). We surveyed from 1 January to 1 July in 2013 and 2014. Winter/spring is a period of high

Table 1
Predicted temporal partitioning gradient between fox and grey squirrels

Season	Scale	Sympatry	Prediction
Leaf-on	Grid	Allopatric	Bimodal overlap
Leaf-on	Grid	Sympatric	
Leaf-on	Point	Allopatric	↓
Leaf-on	Point	Sympatric	
Leaf-off	Grid	Allopatric	Full partition
Leaf-off	Grid	Sympatric	
Leaf-off	Point	Allopatric	
Leaf-off	Point	Sympatric	

Temporal behaviour is expected to be similar (bimodal overlap) when squirrels occur without competition (allopatric) at large spatial scales (grid) and when resources are plentiful (leaf-on, 16 March – 1 July). We expected temporal partitioning to be pronounced (full partition) when squirrels occurred in the presence of competitors (sympatric) at fine spatial scales (point) and when resources were restricted (leaf-off, 1 January – 15 March).

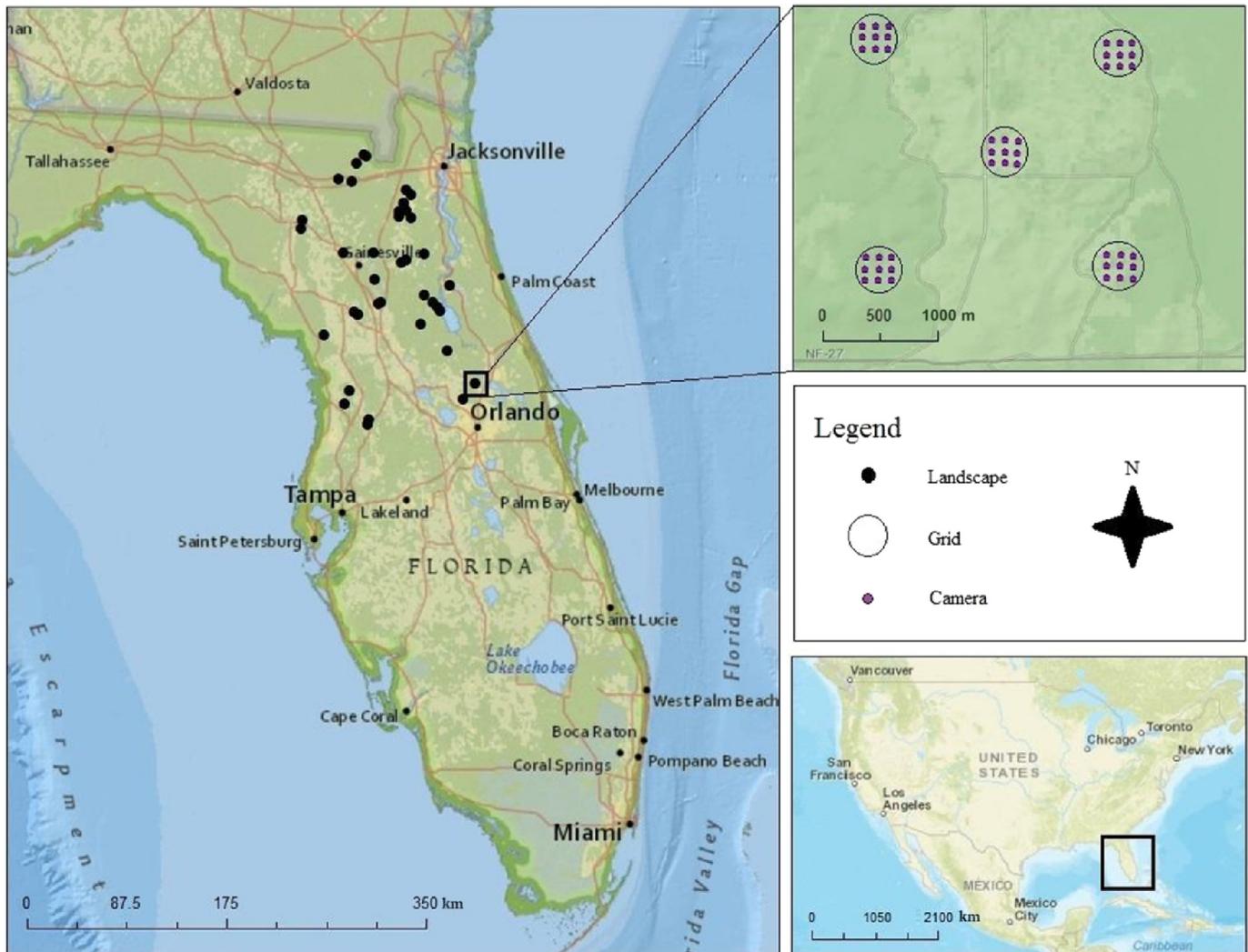


Figure 2. Location of study landscapes in north and central Florida, U.S.A., and an example of camera grid set-up within a landscape.

squirrel activity when food resources are relatively plentiful before midsummer when animals, particularly fox squirrels, become inactive and remain in or near the nest (Moore, 1957; Weigl et al., 1989). The region has a humid, subtropical climate with warm, wet summers (May–October average daily high of 35 °C and 121 cm of rainfall) and dry, mild winters (November–April average high of 25 °C and 25 cm of rainfall). The vegetation communities in north and central Florida included open grasslands, pine-dominated forests, pine-hardwoods, hardwood hammocks, bottomland hardwood forests and pine clear-cuts. The canopy trees included pines and oaks such as longleaf (*Pinus palustris*), slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) and turkey (*Quercus laevis*), live (*Quercus virginiana*), laurel (*Quercus laurifolia*) and water oak (*Quercus nigra*). These hardwood trees start budding in mid-March and reach full leaf-out in April (Moore, 1957). In our study system, fox and grey squirrel's shared food resources are limited during the leaf-off season (1 January – 15 March) and become increasingly plentiful during the leaf-on season (16 March – 1 July).

Study Design

We surveyed 40 landscapes (7.65 km² each) throughout north and central Florida (Greene & McCleery, 2017a). To capture the full suite of landscapes typically occupied by grey and fox squirrels, we

stratified our sampling by land cover type (upland pine/sandhills, mesic/shrubby flatwoods, and other). We randomly selected 10 landscapes in upland pine or sandhills, 10 landscapes in mesic/shrubby flatwoods and 20 landscapes without regard to a land cover type. Within each landscape, we randomly placed five '3 camera × 3 camera' grids (Bushnell Trophy Cam model 119436, Bushnell Outdoor Products, Overland Park, KS, U.S.A.) spaced 115 m apart (Fig. 2). Each grid was a 5.3 ha (230 × 230 m) square containing nine cameras. To maximize grid independence and to reduce spatial autocorrelation, we separated grids by ≥500 m (the mean maximum distance southeastern fox squirrels move; Greene & McCleery, 2017b). We camera-trapped one landscape at a time, running all five grids (45 total cameras) concurrently for 8 days. After 8 days we moved to the next, randomly selected, landscape. We visited each landscape only once over the course of the study. At each camera, we measured percentage of canopy cover using a concave spherical densiometer (Lemmon, 1957; Forestry Suppliers, Inc., Jackson, MS, U.S.A., Model-C). We averaged camera densiometer readings to produce a canopy cover index for each grid.

At each point on the grid, we attached a camera to a tree or stake 50 cm above the ground and angled it towards a bait pile of pecans and cracked corn. Each camera covered a field of detection ~25 m in front of it. We did not prebait camera sets. Using the normal sensitivity setting, we set cameras to take three photos every time

the sensor was tripped and to rest for 10 s between bursts. We defined squirrel observations to be independent if ≥ 20 min had elapsed between detections (Greene, McCleery, Wagner, & Garrison, 2016). We treated camera failure as missing data (Foster & Harmsen, 2012) and assumed failures were randomly distributed and do not affect our analysis (Little & Rubin, 2014).

Data Analysis

We extracted date and time information from the metadata of each picture. To account for Daylight Savings Time and daylength, we created a 'day unit'. We calculated the time since sunrise for each observation and applied a time correction such that for all observations dawn = 0 and sunset = 837 (see Appendix).

Vegetation

First, we tested for a relationship between the density of squirrel observations throughout the day (squirrel activity) and canopy cover. We used directional regression by fitting a von Mises kernel distribution to squirrel observations. The von Mises describes a linear variable (e.g. canopy cover) as a function of a circular predictor (e.g. time) (Xu & Schoenberg, 2011). We fitted the function using 'lincircKern' in package 'Activity' in R v.3.4.3 (Rowcliffe, 2016). We calculated confidence intervals by resampling using the 'fitlincirc' function in package 'Activity'. 'Fitlincirc' randomly assigns an activity time to each observation by sampling with replacement from the empirical distribution of activity times. We repeated this procedure 999 times and 'fitlincirc' generated a confidence band by connecting the 0.025 and 0.975 quantiles. The resulting 95% confidence bounds represent the range within which observations would be expected to fall, assuming no relationship between time of day and squirrel activity exists (Xu & Schoenberg, 2011).

Competition

To understand how competition affects the timing of squirrel activity, we investigated the behaviour of squirrels in the presence (sympatry) or absence (allopatry) of their primary competitors. We assumed that differences between allopatric and sympatric behaviour were a result of competition (Colwell & Futuyma, 1971; Klawinski, Vaughan, Saenz, & Godwin, 1994; Monceau, Hager, Bonnard, & Thiery, 2015). We analysed the presence or absence of competitors at two spatial scales, local (grid) and fine (point). We did not analyse temporal partitioning at the landscape scale, as co-occurrence at this scale was common. For our grid analysis, we categorized observations as sympatric if we observed both squirrel species anywhere on the grid during the 8-day sampling period. For our point analysis, we categorized observations as sympatric if we observed both squirrel species at the same camera during the 8-day sampling period.

We tested for differences in activity patterns between squirrels by comparing the overlap of smoothed curves of activity. For each set of observations (Table 1), we used kernel density functions to produce a smoothed curve of the density of data points across time. Kernel density functions treat observations as a random sample from an underlying continuous distribution (Frey et al., 2017; Worton, 1989). To fit the circular kernel density function, we used the 'fitact' function in R v.3.2.2. We used the Dhat1 ($\hat{\Delta}_1$) estimator of Schmid and Schmidt (2006) to estimate the coefficient of overlap of two estimated kernel functions $\hat{f}_1()$ and $\hat{g}_1()$. Dhat1 is calculated from vectors of densities estimated at T equally spaced times, t , between 0 and 2π , and takes the form:

$$\hat{\Delta}_1 = \frac{2\pi}{T} \sum_{i=1}^T \min \left\{ \hat{f}_1(t_i), \hat{g}_1(t_i) \right\}$$

We used the 'OverlapEst' function in package 'Overlap' (Meredith & Ridout, 2014) to calculate the Dhat1 coefficient of overlap. The coefficient of overlap represents the area under the curve where the two curves intersect and ranges from 0 (no overlap) to 1 (complete overlap). A high coefficient of overlap between sympatric populations indicates that competition is not driving temporal behaviour. However, a low overlap coefficient indicates temporal avoidance. We used bootstrapping to estimate a 95% confidence interval (CI) and the 'compareCkern' function in the R package 'Activity' (Rowcliffe, 2016) to test for significance. 'CompareCkern' creates a null distribution from the combined data and uses it to estimate the probability ($P < 0.05$) that the observed overlap arose by chance (Ridout & Linkie, 2009). To test whether estimates across different spatial scales and seasons differed from one another with 95% confidence, we used the method of Payton, Greenstone, and Schenker (2003) to compare intercepting confidence intervals (CI_{Payton}).

Activity peak and proportion of day

To identify differences in the time(s) of peak activity between squirrels, we plotted a density function for each set (Table 1) of observations and identified the value of the highest peaks (0–837 day units, 0 = sunrise, 837 = sunset).

RESULTS

We collected a total of 1692 independent squirrel observations (see Appendix, Table A1). At both spatial scales, fox squirrels used intermediate canopy cover (grid: mean = 62.09% canopy cover, CI = 60.03–63.9; point: mean = 65.09% canopy cover, CI = 62.88–67.30), while grey squirrels used high canopy cover (grid: mean = 89.01% canopy cover, CI = 88.01–89.93; point: mean = 93.11% canopy cover, CI = 92.29–93.93). Generally, fox and grey squirrels either did not use canopy cover differently over the course of the day, or used lower canopy cover during midday (however these changes were subtle: 0.01–0.1% below the mean; Fig. 3, Fig. 4). There were two notable exceptions: grey squirrels at the grid and point scale in the leaf-off season appeared to use higher canopy cover during midday (82.60% canopy cover, $P < 0.01$ –90.30% canopy cover, $P < 0.01$; Figs 3d and 4d).

Fox and grey squirrels displayed different temporal behaviour (Fig. 5). Grey squirrels displayed a bimodal activity pattern with peaks in midmorning and shortly before sunset, while fox squirrels displayed a unimodal activity pattern with a single peak at midday (Fig. 5). We found that this dual pattern was generally consistent across spatial and temporal scales and regardless of sympatry. We found evidence that temporal partitioning between grey and fox squirrel occurred on a gradient. Estimates of overlap ranged from 0.70 (CI = 0.64–0.76, $P < 0.001$; Fig. 5a) for allopatric squirrels during the leaf-on season at the grid scale to 0.24 (CI = 0.02–0.46, $P = 0.08$; Fig. 5h) for sympatric squirrels during the leaf-off season at the point scale. These estimates of overlap were significantly different from one another ($CI_{\text{Payton}} = 0.65$ –0.74; $CI_{\text{Payton}} = 0.08$ –0.39, respectively). While point estimates of overlap ranged along a gradient, the other various combinations of season, scale and sympatry did not produce significantly different overlap estimates from one another. Leaf-on grid scale sympatric (overlap = 0.57, $CI_{\text{Payton}} = 0.51$ –0.63), leaf-on point scale allopatric (overlap = 0.66, $CI_{\text{Payton}} = 0.62$ –0.70), leaf-on point scale sympatric (overlap = 0.65, $CI_{\text{Payton}} = 0.53$ –0.78), leaf-off grid scale sympatric (overlap = 0.64, $CI_{\text{Payton}} = 0.53$ –0.74) and leaf-off point scale allopatric (overlap = 0.60, $CI_{\text{Payton}} = 0.54$ –0.66) squirrels all had overlapping CIs. Leaf-off grid scale allopatric squirrels (overlap = 0.53, $CI_{\text{Payton}} = 0.45$ –0.61) had a similar overlap coefficient to the other estimates except for

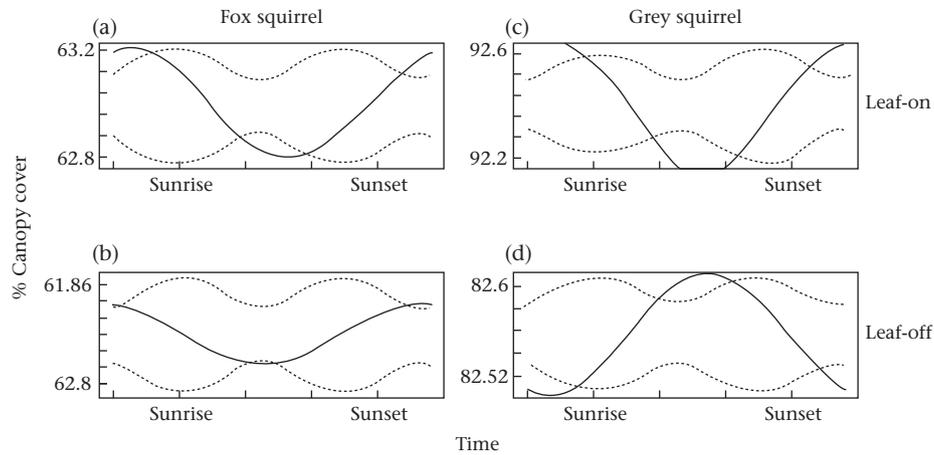


Figure 3. Fitted von Mises relationship between grid-average percentage of canopy cover and timing of squirrel activity (solid line) with 95% confidence intervals (CI; dotted line) for (a, b) fox squirrels and (c, d) grey squirrels in north and central Florida, U.S.A. during leaf-on (16 March – 1 July) and leaf-off (1 January – 15 March) seasons, respectively. Deviation from the 95% CI indicates a significant ($P < 0.05$) relationship between time of day and percentage of canopy cover used by squirrels.

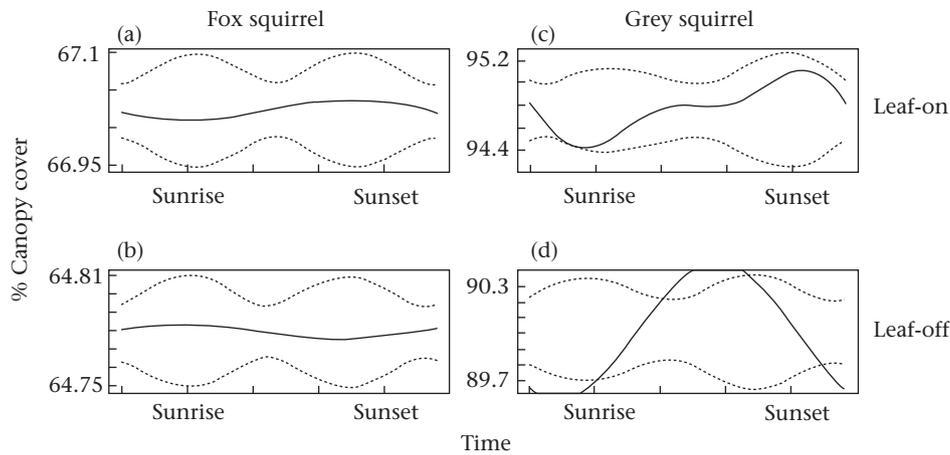


Figure 4. Fitted von Mises relationship between point percentage of canopy cover and timing of squirrel activity (solid line) with 95% confidence intervals (CI; dotted line) for (a, b) fox squirrels and (c, d) grey squirrels in north and central Florida, U.S.A. during leaf-on (16 March – 1 July) and leaf-off (1 January – 15 March) seasons, respectively. Deviation from the 95% CI indicates a significant ($P < 0.05$) relationship between time of day and percentage of canopy cover used by squirrels.

leaf-on point scale allopatric squirrels (overlap = 0.66, $CI_{\text{Payton}} = 0.62\text{--}0.70$).

At both spatial scales of co-occurrence, grey squirrel allopatric behaviour changed with season. During the leaf-off season, grey squirrels concentrated activity peaks shortly after sunrise and shortly before sunset (Fig. 5e, f, g, h). However, during the leaf-on season, grey squirrels showed a distinct activity peak after sunrise and a broad distribution of activity in the afternoon (Fig. 5a, b, c, d). Fox squirrel local scale sympatric behaviour changed by season (Fig. 5). During the leaf-off season, fox squirrels displayed a mildly bimodal activity pattern with peaks before and after midday; this behaviour changed during the leaf-on season when fox squirrels concentrated their activity to midday (Fig. 5a, b, c, d).

DISCUSSION

We found that incorporating temporal and spatial scales was critical to understanding how competition affected the activity of fox and grey squirrels. The importance of competition as a driver of squirrel activity was highly context dependent. The varied results of past studies of fox and grey squirrel temporal behaviour (Brown & Yeager, 1945; Derge & Yahner, 2000; Flyger & Smith, 1980; Healy &

Welsh, 1992; King, 2004; Koprowski, 1994a, 1994b) may be partially explained as differences in the chosen scale of study. Greene et al. (2017a, 2017b) showed that fox squirrel habitat associations differed depending on the chosen scale of study. Our study found similar trends in temporal behaviour. Focusing on a single scale or season could lead to inaccurate conclusions about the importance of competition in driving animal behaviour.

Contrary to our prediction, we found that canopy cover had little influence on the temporal behaviour of either species. While we found statistically significant relationships between canopy cover and activity, these relationships were weak and not a likely driver of the large scale partitioning we observed (Fig. 3 and 4). Consistent with other research on fox and grey squirrels in the southeastern United States (Conner et al., 1999; Greene & McCleery, 2017a, 2017b), we found that grey squirrels were associated with dense canopy cover (>80%) and fox squirrels with intermediate canopy cover (~60%). Despite this habitat specialization, we found that co-occurrence on multiple scales was common in our study area (Table A1).

Consistent with our second prediction, we found that temporal partitioning appears to exist on a gradient, mediated by competition and resource availability. The most pronounced differences

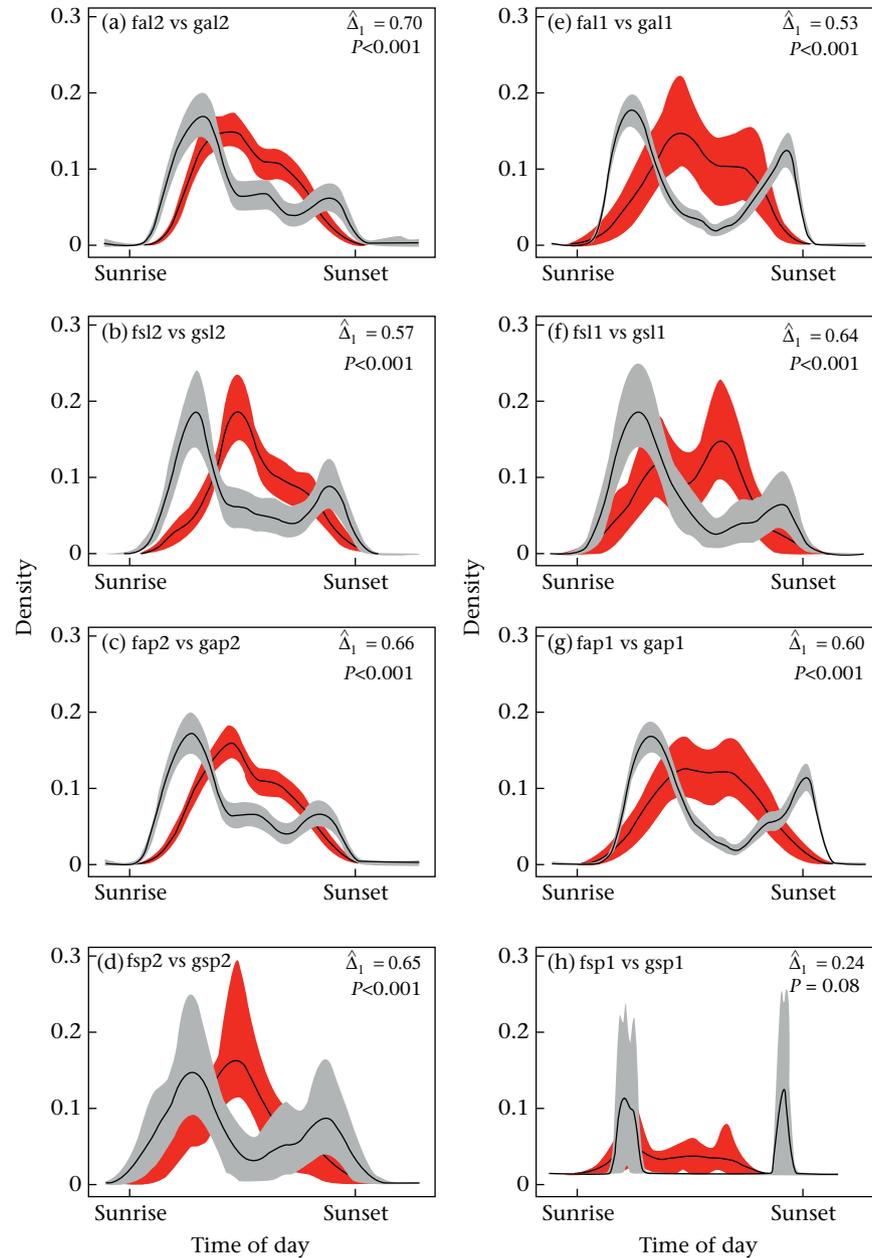


Figure 5. Smoothed kernel density functions of daily activity for grey squirrels (grey shading) and fox squirrels (red shading) in 2013 and 2014 in north and central Florida with estimated activity overlap ($\hat{\Delta}_1$, or Dhat1). Dhat1 can be thought of as the shared area under the curve of both functions (Schmid & Schmidt, 2006). Dhat1 ranges from 0 (indicating that the two species were never active at the same time) to 1 (indicating that the two species shared identical activity patterns). Species (fox squirrel = f; grey squirrel = g), sympatry (*s* = sympatric; *a* = allopatric), spatial scale (*p* = point, *l* = grid) and season (1 = leaf-off, 1 January – 15 March; 2 = leaf-on, 16 March – 1 July) are presented in the predicted order of Dhat1. With high expected overlap, gal2 (grey, allopatric, grid, leaf-on) versus fal2 (fox, allopatric, grid, leaf-on) presented first, and with low expected overlap, gsp1 (grey, sympatric, point, leaf-off) versus fsp1 (fox, sympatric, point, leaf-off) presented last. *P* represents the probability that the observed density functions come from the same distribution.

between activity patterns occurred when the squirrels were sympatric during the leaf-off season at fine scales of sympatry (Fig. 5h). This is consistent with our prediction that sharing the same space and limited resources would increase temporal partitioning. We found that temporal partitioning may facilitate the coexistence of fox and grey squirrels, but only during certain times of year and at certain spatial scales. When allopatric at local scales during the leaf-on season, both species concentrated their activity in the morning (Fig. 5a). Fox squirrels, however, changed their behaviour in the presence of grey squirrels, moving their activity peak to midday (Fig. 5b, d). Potentially, sympatric fox squirrels were shifting their activity later in the morning to avoid agonistic interactions

with grey squirrels. This pattern of a temporarily partitioned species relaxing to similar activity times when the competitor is excluded has been observed in other mammals including foxes (Di Bitetti et al., 2009) and other rodents (Gutman & Dayan, 2005).

Our results did not support our prediction that competition is a major mechanism determining the timing of species activity (Di Bitetti et al., 2009). Contrary to our prediction, we found that intermediate combinations of season and spatial scale did not produce different patterns of temporal partitioning. Regardless of spatial scale or season (leaf-on or leaf-off), fox squirrels were more active closer to midday compared to grey squirrels. Although some subtlety existed, we found that fox and grey squirrels generally

maintained separate activity. These activity patterns may not be a result of present-day competition between squirrels, but past competition (Connell, 1980; Rosenzweig, 1979). Activity patterns have genetic components (Ben-Shlomo, Ritte, & Nevo, 1995), and past competition may result in genetic changes that do not respond to short-term changes in competition pressure. Macroevolutionary processes can occur in as few as 200 generations (Gingerich, 2001), and fox and grey squirrels became sympatric in Florida approximately 5000 generations ago, after the last glacial maximum (15 000–10 000 BP, Koprowski, 1994b; Pečnerová & Martínková, 2012).

Differences in grey and fox squirrel activity patterns may be influenced by morphology (Di Bitetti, De Angelo, Di Blanco, & Paviolo, 2010; Smith & Follmer, 1972). In our study region, grey squirrels' small body size may make them more susceptible to diurnal avian predators (Steele & Koprowski, 2003). Thus, grey squirrels are likely to maintain bimodal activity patterns and avoid times of day when they are most visible and vulnerable to birds of prey. The larger fox squirrels are likely not as susceptible to avian predators, and thus may not face increased predation costs to forage at midday. Finally, body size greatly affects mammal thermoregulation and can affect activity budgets and timing (Aschoff, 1981; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). The smaller grey squirrel may need to restrict activity to cooler times to effectively thermoregulate whereas the larger-bodied fox squirrel, which has a large tail for shading (Muchlinski & Shump, 1979), can withstand heat stress better. However, the degree of temporal partitioning between grey and fox squirrels may be different in the northern extent of their ranges where they are most morphologically similar (Koprowski, 1994a, 1994b). Investigating these patterns across a range of convergent morphologies may help us better understand if and how size mediates competition and partitioning between sympatric species.

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References

Albrecht, M., & Gotelli, N. J. (2001). Spatial and temporal niche partitioning in grassland ants. *Oecologia*, 126(1), 134–141.
 Armitage, K. B., & Harris, K. S. (1982). Spatial patterning in sympatric populations of fox and gray squirrels. *American Midland Naturalist*, 108, 389–397.

Aschoff, J. (1981). Thermal conductance in mammals and birds: Its dependence on body size and circadian phase. *Comparative Biochemistry and Physiology Part A: Physiology*, 69, 611–619.
 Bechard, M. J. (1982). Effect of vegetative cover on foraging site selection by Swainson's hawk. *Condor: Ornithological Applications*, 84(2), 153–159.
 Bednekoff, P. A., & Houston, A. I. (1994). Avian daily foraging patterns: Effects of digestive constraints and variability. *Evolutionary Ecology*, 8(1), 36–52.
 Ben-Shlomo, R., Ritte, U., & Nevo, E. (1995). Activity pattern and rhythm in the subterranean mole rat superspecies *Spalax ehrenbergi*. *Behavior Genetics*, 25(3), 239–245.
 Bennett, W. A. (1990). Scale of investigation and the detection of competition: An example from the house sparrow and house finch introductions in North America. *American Naturalist*, 135(6), 725–747.
 Bonter, D. N., Zuckerberg, B., Sedgwick, C. W., & Hochachka, W. M. (2013). Daily foraging patterns in free-living birds: Exploring the predation–starvation trade-off. *Proceedings of the Royal Society B*, 280(1760), 20123087.
 Brown, B. W., & Batzli, G. O. (1985). Field manipulations of fox and gray squirrel populations: How important is interspecific competition? *Canadian Journal of Zoology*, 63, 2134–2140.
 Brown, L. G., & Yeager, L. E. (1945). Fox squirrels and gray squirrels in Illinois. *Natural History Survey Division*, 23, 454–460.
 Case, T. J., & Gilpin, M. E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America*, 71(8), 3073–3077.
 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
 Colwell, R. K., & Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology*, 52(4), 567–576.
 Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35(2), 131–138.
 Conner, L. M., Landers, J. L., & Michener, W. K. (1999). Fox squirrel and gray squirrel associations within minimally disturbed longleaf pine forests. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies*, 53, 364–374.
 Dahl, J. F., & Smith, E. O. (1985). Assessing variation in the social behavior of stump-tail macaques using thermal criteria. *American Journal of Physical Anthropology*, 68(4), 467–477.
 Derge, K. L., & Yahner, R. H. (2000). Ecology of sympatric fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) at forest–farmland interfaces of Pennsylvania. *American Midland Naturalist*, 143(2), 355–369.
 Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E., & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36, 403–412.
 Di Bitetti, M. S., Di Blanco, Y. E., Pereira, J. A., Paviolo, A., & Pérez, I. J. (2009). Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cercopithecus thous*) and pampas foxes (*Lycalopex gymnocercus*). *Journal of Mammalogy*, 90(2), 479–490.
 Edwards, J. W., & Guynn, D. C. (1995). Nest characteristics of sympatric populations of fox and gray squirrels. *Journal of Wildlife Management*, 59(1), 103–110.
 Edwards, J. W., Heckel, D., & Guynn, D. C. (1998). Niche overlap in sympatric populations of fox and gray squirrels. *Journal of Wildlife Management*, 62(1), 354–363.
 Farine, D. R., & Lang, S. D. J. (2013). The early bird gets the worm: Foraging strategies of wild songbirds lead to the early discovery of food sources. *Biology Letters*, 9(6), 20130578.
 Flyger, V., & Smith, D. A. (1980). A comparison of Delmarva fox squirrel and gray squirrel habitats and home range. *Transactions of the Northeast Section of the Wildlife Society*, 37(1), 19–22.
 Foster, R. J., & Harnsen, B. J. (2012). A critique of density estimation from camera-trap data. *Journal of Wildlife Management*, 7(2), 224–236.
 Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, 3(3), 123–132.
 Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–291.
 Gingerich, P. D. (2001). Rates of evolution on the time scale of the evolutionary process. *Genetica*, 113(1), 127–144.
 Greene, D. U., & McCleery, R. A. (2017a). Multi-scale responses of fox squirrels to land-use changes in Florida: Utilization mimics historic pine savannas. *Forest Ecology and Management*, 391, 42–51.
 Greene, D. U., & McCleery, R. A. (2017b). Reevaluating fox squirrel (*Sciurus niger*) population declines in the southeastern United States. *Journal of Mammalogy*, 98(2), 502–512.
 Greene, D. U., McCleery, R. A., Wagner, L. M., & Garrison, E. P. (2016). A comparison of four survey methods for detecting fox squirrels in the southeastern U.S. *Journal of Fish and Wildlife Management*, 7(1), 99–106.
 Gutman, R., & Dayan, T. (2005). Temporal partitioning: An experiment with two species of spiny mice. *Ecology*, 86, 161–173.
 Halle, S. (2000). Ecological relevance of daily activity patterns. In S. Halle, & N. C. Stenseth (Eds.), *Activity patterns in small mammals. Ecological studies (analysis and synthesis)* (Vol. 141, pp. 67–90). Berlin, Germany: Springer.
 Healy, W. M., & Welsh, C. J. E. (1992). Evaluating line transects to monitor gray squirrel populations. *Wildlife Society Bulletin*, 20, 83–90.

- Hicks, E. A. (1949). Ecological factors affecting the activity of the western fox squirrel, *Sciurus niger rufiventer* (Geoffroy). *Ecological Monographs*, 19(4), 287–302.
- Keane, E. M., & O'Halloran, J. (1992). The behaviour of a wintering flock of mute swans *Cygnus olor* in southern Ireland. *Wildfowl*, 43, 12–19.
- King, J. L. (2004). *The current distribution of the introduced fox squirrel (Sciurus niger) in the greater Los Angeles metropolitan area and its behavioral interaction with the native western gray squirrel (Sciurus griseus)*. M.Sc. thesis. Los Angeles: California State University.
- Klawinski, P. D., Vaughan, R. K., Saenz, D., & Godwin, W. (1994). Comparison of dietary overlap between allopatric and sympatric geckos. *Journal of Herpetology*, 28(2), 225–230.
- Kneitel, J. M., & Chase, J. M. (2004). Tradeoffs in community ecology: Linking spatial scales and species coexistence. *Ecology Letters*, 7(1), 69–80.
- Koprowski, J. L. (1994a). *Sciurus carolinensis*. *Mammalian Species*, 480, 1–9.
- Koprowski, J. L. (1994b). *Sciurus Niger*. *Mammalian Species*, 479, 1–9.
- Kozłowski, A. J., Gese, E. M., & Arjo, W. M. (2008). Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of Western Utah. *The American Midland Naturalist*, 160, 191–208.
- Kronfeld-Schor, N., & Dayan, T. (1999). The dietary basis for temporal partitioning: Food habits of coexisting *Acomys* species. *Oecologia*, 121(1), 123–128.
- Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution and Systematics*, 34, 153–181.
- Lemmon, P. E. (1957). A new instrument for measuring forest overstorey density. *Journal of Forestry*, 55(9), 667–669.
- Lesmeister, D. B., Nielsen, C. K., Schaubert, E. M., & Hellgren, E. C. (2015). Spatial and temporal structure of a mesocarnivore guild in Midwestern North America. *Wildlife Monographs*, 191(1), 1–61.
- Liancourt, P., & Tielbörger, K. (2009). Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. *Functional Ecology*, 23(2), 397–404.
- Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives anti-predator behavior: The predation risk allocation hypothesis. *American Naturalist*, 153(6), 649–659.
- Linnell, J. D., & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, 6(4), 169–176.
- Little, R. J., & Rubin, D. B. (2014). *Statistical analysis with missing data* (2nd ed.). Hoboken, NJ: John Wiley.
- Meredith, M., & Ridout, M. (2014). Overview of the overlap package. (*R. Project*, 23:1–9). <https://CRAN.R-project.org/package=overlap>.
- van der Merwe, M., Brown, J. S., & Jackson, W. M. (2005). The coexistence of fox (*Sciurus niger*) and gray (*S. carolinensis*) squirrels in the Chicago metropolitan area. *Urban Ecosystems*, 8(1), 335–347.
- Monceau, K., Hager, N., Bonnard, O., & Thiery, D. (2015). Evaluation of competition between a native and an invasive hornet species: Do seasonal phenologies overlap? *Bulletin of Entomological Research*, 105(4), 462–469.
- Moore, J. C. (1957). The natural history of the fox squirrel, *Sciurus niger shermani*. *Bulletin of the American Museum of Natural History*, 113, 1–71.
- Moreno, S., Villafuerte, R., & Delibes, M. (1996). Cover is safe during the day but dangerous at night: The use of vegetation by European wild rabbits. *Canadian Journal of Zoology*, 74, 1656–1660.
- Muchlinski, A. E., & Shump, K. A. (1979). The sciurid tail: A possible thermoregulatory mechanism. *Journal of Mammalogy*, 60(3), 652–654.
- Nicholls, B., & Racey, P. A. (2006). Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. *Behavioral Ecology and Sociobiology*, 61(1), 131–142.
- Parker, T. S., & Nilon, C. H. (2008). Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems*, 11(3), 243–255.
- Payton, M. E., Greenstone, M. H., & Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science*, 3, 34. insectscience.org/3.34.
- Pečnerová, P., & Martinková, N. (2012). Evolutionary history of tree squirrels (Rodentia, Sciurini) based on multilocus phylogeny reconstruction. *Zoologica Scripta*, 41(3), 211–219.
- Preston, C. R. (1990). Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor: Ornithological Applications*, 92(1), 107–112.
- Razgour, O., Korine, C., & Saltz, D. (2011). Does interspecific competition drive patterns of habitat use in desert bat communities? *Oecologia*, 167(2), 493–502.
- Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337.
- Rosenzweig, M. L. (1979). Optimal habitat selection in two-species competitive systems. *Fortschritte der Zoologie*, 25, 283–293.
- Rowcliffe, M. (2016). *Activity: Animal Activity Statistics (R package version 1.1)*. <https://CRAN.R-project.org/package=activity>.
- Schmid, F., & Schmidt, A. (2006). Nonparametric estimation of the coefficient of overlapping: Theory and empirical application. *Computational Statistics & Data Analysis*, 50(6), 1583–1596.
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39.
- Sexton, O. J. (1990). Replacement of fox squirrels by gray squirrels in a suburban habitat. *American Midland Naturalist*, 124, 198–205.
- Sikes, R. S., & Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92(1), 235–253.
- Smith, C. C., & Follmer, D. (1972). Food preferences of squirrels. *Ecology*, 53, 82–91.
- Steele, M. A., & Koprowski, J. L. (2003). *North American tree squirrels*. Washington, D.C.: Smithsonian Institution Press.
- Stewart, K. M., Bowyer, R. T., Kie, J., Dick, B. L., & Ben-David, M. (2003). Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? *Ecoscience*, 10(3), 297–302.
- Thompson, D. C. (1978). The social system of the grey squirrel. *Behaviour*, 64(3), 305–328.
- Weigl, P. D., Steele, M. A., Sherman, L. J., Ha, J. C., & Sharpe, T. L. (1989). The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: Implications for survival in the southeast. *Bulletin of Tall Timbers Research Station*, 28, 1–93.
- Wilson, J. B. (1990). Mechanisms of species coexistence: Twelve explanations for Hutchinson's 'Paradox of the Plankton': Evidence from New Zealand plant communities'. *New Zealand Journal of Ecology*, 13, 17–42.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.
- Xu, H., & Schoenberg, F. P. (2011). Point process modeling of wildfire hazard in Los Angeles County, California. *Annals of Applied Statistics*, 1, 684–704.
- Ziv, Y., Abramsky, Z., Kotler, B. P., & Subach, A. (1993). Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, 66, 237–246.

Appendix

Time Correction for Daylength

Because grey squirrels and fox squirrels showed different daily activity patterns (bimodal versus unimodal, respectively), we chose to derive our own method for adjusting daylength. Using time since dawn (Keane, 1992) would not adequately adjust the evening mode of grey squirrel activity (i.e. the evening mode naturally drifts later in the day as daylength increases) and using time since twilight (either dawn or dusk) would artificially suppress the midday fox squirrel activity peak. Thus, to account for Daylight Savings Time and daylength, we calculated the time since sunrise for each observation and applied a time correction. For each day of our study we calculated the number of daylight minutes between sunrise and sunset at the geographical centre of our study area (<https://www.esrl.noaa.gov/gmd/grad/solcalc/azel.html>). The longest day of our study had 837 min of sunlight and the shortest 624 min. We calculated the ratio between the number of minutes in each day and the longest day (e.g. the shortest day had a ratio of $837/624 = 1.34$) such that each minute of the shortest day represented 1.34 min of the longest day. For each observation we calculated the time since dawn and then multiplied the difference by the ratio (e.g. an observation at sunset on the longest and shortest day had a value of $837 (624 \times 1.34 = 837)$).

Table A1

Sample sizes of fox squirrels and grey squirrels during the 6-month study period, leaf-off (1 January– 15 March) and leaf-on (16 March– 1 July), at two spatial scales of co-occurrence (fine = point; local = grid), and without regard to co-occurrence (no scale)

		<i>N</i> Grey	<i>N</i> Fox	<i>N</i> Total
Leaf-off				
Grid	Sympatric	69	60	129
	Allopatric	687	80	767
Point	Sympatric	6	15	21
	Allopatric	750	125	875
Total		756	140	896
Leaf-on				
Grid	Sympatric	124	142	266
	Allopatric	250	280	530
Point	Sympatric	31	23	54
	Allopatric	343	399	742
Total		374	422	796
6 months				
Grid	Sympatric	193	202	395
	Allopatric	937	360	1297
Point	Sympatric	37	38	75
	Allopatric	1093	524	1617
Total		1130	562	1692