

Research Article

Spatial and temporal partitioning between eastern gray and fox squirrels in a Central Hardwood forest

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Abstract

Congeneric fox squirrels (*Sciurus niger*) and eastern gray squirrels (*S. carolinensis*) compete for resources within North American temperate forests. Both species exhibit regional variation in morphology and behavior—potentially due to differences in geography, community composition, or ecological pressures between forested regions. While many have studied these species in other forested regions of the United States, recent assessments of partitioning between these species in Central Hardwood forests remain scarce. We investigated spatial and temporal partitioning between squirrel species using photographic captures from camera traps at 2 scales (i.e., camera location and camera cluster) across a 16,058-km² region of southern Illinois, United States, during January to April 2008 to 2010. We fitted single-season single-species and co-occurrence occupancy models to assess spatial partitioning at both scales and used kernel density analysis to assess temporal partitioning. We recorded 3,044 photographic captures of focal species ($n = 918$ fox squirrels and 2,126 eastern gray squirrels). Fox Squirrel occupancy was 0.26 ± 0.09 (SE) and 0.50 ± 0.17 at the camera location and camera cluster scales, respectively. Eastern Gray Squirrel occupancy was 0.47 ± 0.07 and 0.84 ± 0.23 at the camera location and camera cluster scales, respectively. Fox Squirrel occupancy increased with more hardwood basal area. Co-occurrence was influenced by distance to road at the camera location scale. We found a moderate level of activity overlap between species ($\Delta = 0.63$, CI = 0.60 to 0.67); however, no evidence of temporal partitioning was observed. Habitat characteristics and spatial scale appear more influential in partitioning eastern gray and fox squirrels in Central Hardwood forests than peak activity.

Key words: niche partitioning, occupancy, *Sciurus carolinensis*, *Sciurus niger*.

Congeneric species may reduce exploitative or interference competition and promote coexistence by differentiating along niche dimensions (Amir 1981); however, species can adopt varying approaches depending on differences in geography, ecological systems, or regional populations (Durrant and Hansen 1954; Weigl et al. 1989; Foster and Cameron 1996). While often arising via partitioning of food resources (Schoener 1974; Wauters et al. 2002), species also coexist through differences in behavior or habitat preferences (Pianka 1974; Hearn et al. 2018). Insights into niche partitioning may be achieved by investigating these differences, even when morphological variations facilitated by character displacement are absent (Dayan and Simerloff 2005) or obscured by regional variation in a species.

Squirrels (Sciuridae) are a rodent family occurring worldwide across myriad ecoregions and include numerous species with distinct behaviors and morphologies (Thorington et al. 2012). Being widespread, many squirrel species have overlapping distributions (Livoreil et al. 1993; Saiful et al. 2001a; Popova et al. 2019; Swati et al. 2023) and rely on niche partitioning to coexist (Emmons 1980;

Saiful et al. 2001b; Sovie et al. 2019). However, geographic variation in resource availability and other ecological or environmental pressures may cause squirrel species to adopt differing behaviors, exploit novel resources, or experience niche shifts (McCleery 2009; Yang et al. 2023). Such differences potentially alter interspecific interactions between sympatric species across their shared distributions as both species adapt to the pressures unique to each geographic region. In particular, fox squirrels (*Sciurus niger*) and eastern gray squirrels (*S. carolinensis*) are sympatric squirrel species capable of thriving in a variety of landcover types (Brown and Yeager 1945; Thorington et al. 2012) and exhibit variation in behaviors (Edwards et al. 1998; Derge and Yahner 2000; Sarno et al. 2015) and morphology (Thorington et al. 2012), making them ideal for examining niche partitioning across a wide array of forested regions.

Eastern gray squirrels are a widespread generalist species (Williams 2011; Amspacher et al. 2019) associated with mature forests and dense undergrowth or woody ground cover (Edwards et al. 1998). Using hardwood mast, fungi, lichens, flowers, and buds as food resources (Koprowski 1994), eastern gray squirrels often

inhabit forested areas containing hardwood stands that provide food and cavities for shelter (Fischer and Holler 1991; Thorington et al. 2012). Common to areas with dense undergrowth (Edwards et al. 1998), eastern gray squirrels are sensitive to fragmentation (Moore and Swihart 2005; Swihart et al. 2007). Ranging throughout the eastern United States and southern Canada, Eastern Gray Squirrel morphology varies across regions with greater size and pelage differences observed in their southern compared to northern ranges (Thorington et al. 2012); however, eastern gray squirrels are typically diurnal with activity peaks at dawn and dusk (Sovie et al. 2019).

Fox squirrels are edge specialists (Amspacher et al. 2019) associated with open hardwood associations (Weigl et al. 1989; Edwards et al. 1998), savannas (Thorington et al. 2012), and forest edges, including fencerows and farmland borders (Derge and Yahner 2000). Fox squirrels favor areas with little woody understory and ground cover (Greene and McCleery 2017) that improve sightlines (Potash et al. 2019) as they forage on the ground for herbaceous food, nuts, fungi, and seeds (Allen 1982; Weigl et al. 1989; Pynne et al. 2020). However, this species appears to be highly adaptable to habitat loss and fragmentation (Greene and McCleery 2017), often preferring heterogeneous landscapes and tolerating anthropogenic disturbance (McCleery 2009; Lewis et al. 2021). Ranging across the Midwestern United States, southern Canada, and northern border of Mexico, Fox Squirrel morphology is more variable in southern compared to northern regions with multiple, distinct subspecies found throughout Florida, Alabama, and Texas (Thorington et al. 2012). Further highlighting the variability of the species, fox squirrels have exhibited varying activity patterns with differing activity peaks (Edwards et al. 1998; Derge and Yahner 2000).

The ecological mechanisms and interspecific interactions between such sympatric species are often complex (Case et al. 2004; Poisot et al. 2014), and to better study these relationships, co-occurrence modeling approaches and extensions were developed (MacKenzie et al. 2006; Bailey et al. 2009). Recent advancements and extensions to co-occurrence occupancy modeling have allowed researchers to investigate the influence of interspecific interactions and environmental factors on occupancy of multiple species at once and without needing to assume or know ecological relationships between the study species (Rota et al. 2016; Fidino et al. 2019). Utilizing detection/nondetection data collected simultaneously on focal species, this approach incorporates sampling schemes similar to the single-species approach (MacKenzie et al. 2006) with data collected from multiple surveys during a single season (i.e., multiple survey sessions where the system is assumed closed; MacKenzie et al. 2003). The detections/nondetections of focal species at a given site during a survey are assumed to be a Bernoulli random variable that is a function of the latent occupancy state and conditional detection probability (Rota et al. 2016). Such approaches allow researchers to gain insights into occupancy dynamics.

Although eastern gray and fox squirrels are common (Brown and Yeager 1945), application of novel approaches for studying these species, particularly across large geographic regions in Central Hardwood forests, remains scarce. Multiple researchers have investigated habitat preferences and behavioral differences between these species (Derge and Yahner 2000; Van Der Merwe et al. 2005; Sovie et al. 2021), with many recent studies concentrated in the southern or western United States (Edwards et al. 1998; Greene and McCleery 2017; Amspacher et al. 2019; Sovie et al. 2019, 2020). However, forest composition varies between regions with pine-dominated forest communities prevalent in southern regions (Mickler 1996), western forest compositions shifting toward fire-sensitive shade-tolerant species such as fir (*Abies* spp.;

Hanberry 2014), and hardwood associations common in Midwestern forests (Ma et al. 2016). Leaf-on and leaf-off seasons can also differ between regions due to varying latitudes, elevations, or climatic conditions (Gill et al. 2015), potentially influencing resource availability for squirrel species (Sovie et al. 2019). Moreover, the regional morphological variation exhibited by both species (Thorington et al. 2012) warrants additional research in understudied regions and systems. Researchers reported conflicting results for Fox Squirrel activity patterns (e.g., unimodal or bimodal activity patterns) and spatial partitioning between these 2 species (Edwards et al. 1998; Derge and Yahner 2000), potentially arising from temporal or spatial differences among studies (Greene and McCleery 2017; Sovie et al. 2019). Although studies have used occupancy modeling extensions to investigate niche partitioning of these squirrel species (Greene and McCleery 2017), few were conducted on study sites >10,000 km² in area or investigated interspecific interactions across such large geographic regions (Sovie et al. 2020). Furthermore, as keystone seed dispersers (Steele et al. 2004), understanding habitat preferences and interspecific interactions influencing the occupancy of squirrel species is of conservation interest in the Midwest (Nupp and Swihart 2001; Goheen and Swihart 2003; Palmer et al. 2007).

To address these gaps in literature, we used photographic captures from camera trapping surveys, occupancy modeling, and kernel density analyses to investigate spatial and temporal partitioning between eastern gray and fox squirrels in a >16,000-km² forested landscape in southern Illinois, United States. We predicted that Fox Squirrel activity would peak at midday with a unimodal activity pattern, and Eastern Gray Squirrel activity would peak near dawn and dusk in a bimodal activity pattern (Sovie et al. 2019). We further predicted that activity patterns of 1 species would vary depending on detection or nondetection of the other species due to potential temporal partitioning to avoid competition (Larson and Sander 2022). Additionally, we hypothesized that Eastern Gray Squirrel occupancy would be positively associated with dense forest structures and increased groundcover, as these sites contain more food resources and nesting cavities (Fischer and Holler 1991; Edwards et al. 1998) while providing potential cover from predators. Given that eastern gray squirrels are somewhat sensitive to forest fragmentation and disturbances that reduce groundcover (Amspacher et al. 2019), we predicted that Eastern Gray Squirrel occupancy would be negatively associated with anthropogenic influences that can disrupt forest structures (e.g., roads, structures). Conversely, we hypothesized that as edge specialists (Allen 1982; Edwards et al. 1998) Fox Squirrel occupancy would be positively associated with habitat variables related to forest edges and open forest structures where they have the competitive advantage and can more efficiently exploit resources (Sovie et al. 2021). Furthermore, we predicted that anthropogenic influences causing such fragmentation would not influence Fox Squirrel occupancy given their ability to adapt and resilience to such disturbances (Amspacher et al. 2019). Considering the differences in habitat preferences and associations, we also predicted that eastern gray and fox squirrels would be less likely to occupy the same site due to spatial partitioning (Weigl et al. 1989; Edwards et al. 1998; Moore and Swihart 2007).

Materials and methods.

Study area.

We studied eastern gray and fox squirrels in the 16 southernmost counties of Illinois, United States (Fig. 1; 16,058 km²; Lesmeister et al. 2015). The study area included 6 of the 14 natural land divisions in Illinois (Southern Till Plain, Wabash Border, Shawnee Hills, Ozarks, Lower Mississippi Bottomlands, and Coastal Plain; Schwegman

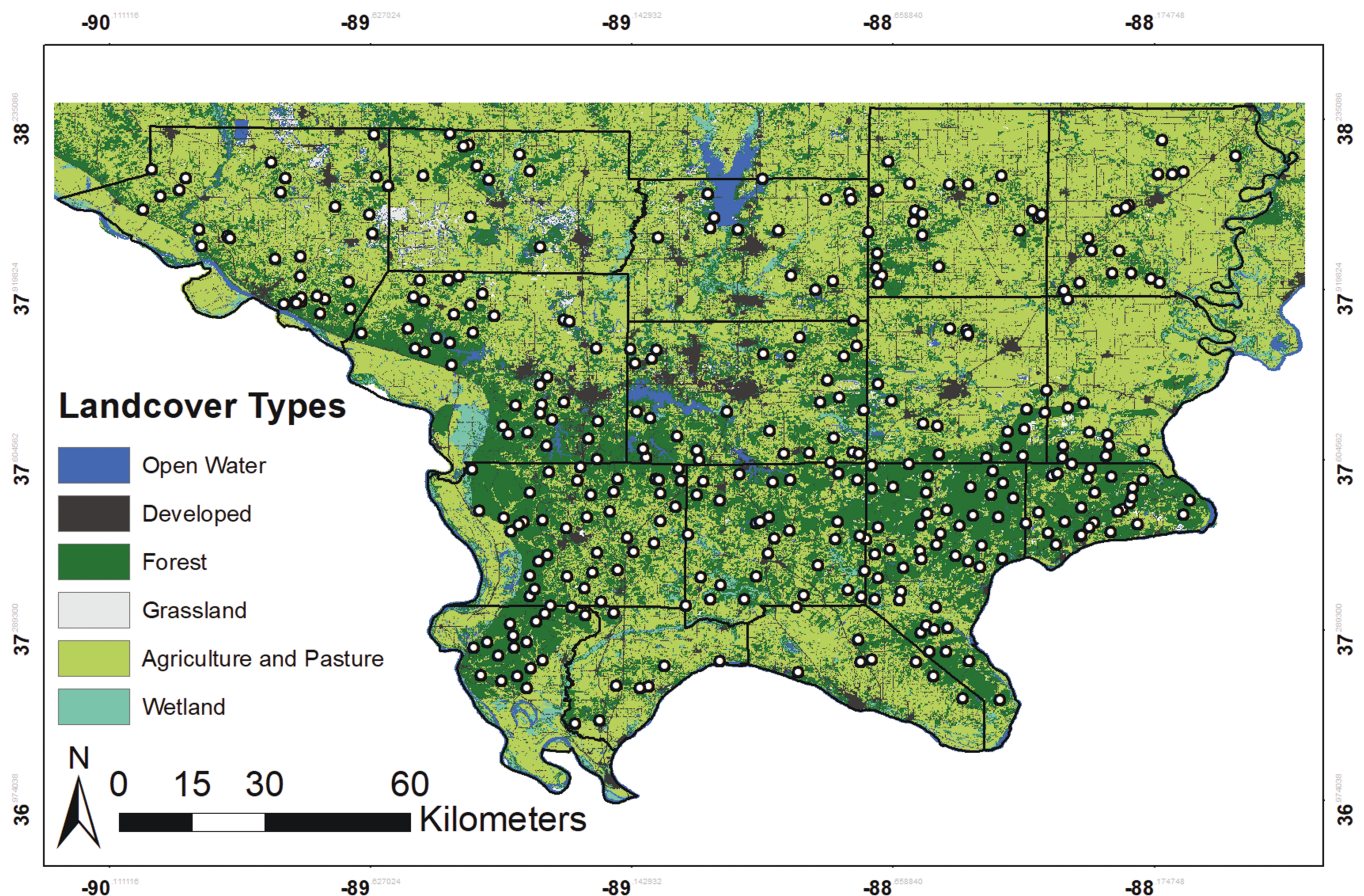


Fig. 1. Map of study area with landcover types and locations of the 357 political sections (2.6 km²) surveyed using camera traps in the 16 southernmost counties of Illinois, United States, during January to April 2008 to 2010.

1973; Neely and Heister 1987). Light-colored Alfisols dominated the study area (Fehrenbacher et al. 1984) with highly dark-colored Mollisols in bottomland areas near the Ohio and Mississippi rivers. Entisols were found throughout the study area on slopes prone to erosion and in sandy floodplains along riparian zones (Barnhardt 2010). Soil parent materials were mainly loess followed by alluvium and outwash (Fehrenbacher et al. 1967). Land cover of the central portion of the study area primarily consisted of closed-canopy mixed hardwood forests dominated by *Acer*, *Carya*, and *Quercus* spp. (Luman et al. 1996). Agricultural cropland with primary crop rotations of corn (*Zea mays*), soybeans (*Glycine max*), and winter wheat (*Triticum aestivum*) dominated the northern regions and areas along large rivers (Lesmeister et al. 2015). The remaining land cover of the study area comprised grasslands (primarily cattle pasture and hay fields), wetlands, open water, and urban (IDNR 1996). Human and road densities were 21.5 persons/km² and 1.5 road km/km², respectively (Lesmeister et al. 2015). The Shawnee National Forest (1,075 km²), Crab Orchard National Wildlife Refuge (178 km²), Cypress Creek National Wildlife Refuge (61 km²), along with 6 other Illinois State Parks and 15 other state-managed public areas were found within the study area. Mean temperatures of 5.4 ± 0.4 °C and mean precipitation of 26.0 ± 2.0 mm/week (NOAA 2010) were observed during the study period. The study area was classified as a humid subtropical temperate climate within the Köppen classification of climates (Ackerman 1941).

Camera trapping.

We used photographic captures of squirrel species collected during a mesocarnivore study (Lesmeister et al. 2015) and used ArcGIS 9.3

(Environmental Systems Research Institute, Redland, California) to conduct all GIS analyses. Camera trapping occurred during January to April 2008 to 2010 due to constrained access to land during fall hunting seasons and reduction in detectability of mesocarnivores during summer (O'Connell et al. 2006; Hackett et al. 2007; Crimmins et al. 2009). After identifying township and political boundaries (USGS 2004a), we divided the study area into 2.6-km² political sections and surveyed sections via stratified random sampling. Land cover data from the US Geological Survey's National Land Cover Database (USGS 2007) was used to determine percentage forest cover for each political section. The original study design by Lesmeister et al. (2015) focused on mesocarnivores, and given that species of interest such as Bobcat (*Lynx rufus*) and Gray Fox (*Urocyon cinereogentus*) were unlikely to occupy areas with little forest cover (Nielsen and Woolf 2002), political sections with <11% forest cover were removed. The remaining ~2,126 political sections were stratified based on 10% forest cover increments, and we randomly selected 360 sections to proportionally represent the forest cover of the study area.

To investigate occupancy at 2 scales (i.e., camera location and camera cluster), we surveyed political sections by deploying 3 or 4 camera traps ≥ 250 m apart (1,188 camera trap locations) to create 357 camera clusters. During 2008, we surveyed 117 political sections with 4 camera traps placed at each ($n = 468$ camera locations); while during 2009 to 2010, we surveyed 240 political sections with 3 individual cameras placed at each ($n = 720$ camera locations; Lesmeister et al. 2015) after preliminary analysis indicated no difference in detection probability or variance between 3 and 4 camera traps/camera cluster (Lesmeister DB, Southern Illinois University, Carbondale, Illinois, personal observation, 20 October 2009). Sixty

sections surveyed in 2008 were randomly selected to be surveyed for a second season in 2010. Camera traps surveyed at a location for 3 weeks with each week acted as an independent survey session, resulting in final detection matrices of 1,188 × 3 and 357 × 3 at the camera location and camera cluster scales, respectively. At each camera trap location, we used 1 digital remote camera (Cuddeback Excite, 2.0 megapixel; or Capture, 3.0 megapixel, Non Typical Inc., Park Falls, Wisconsin) with passive infrared sensors, requiring both heat and motion to be detected to trigger a photographic event, and set to be active 24 h each day. Photographic events contained a single photographic capture with a 1-min delay between photographic events. Camera traps were placed at each location ~0.5 m from the ground and aimed at a sardine and fatty acid scent disk (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, Idaho) placed 2 m from the camera. Photographic captures were visually identified for squirrel species.

Environmental variables.

We considered the effects of 18 variables on squirrel detection and occupancy at both scales (Table 1). Detection variables included: (1) precipitation; (2) temperature; (3) an interaction between precipitation and temperature; (4) previous detection; (5) survey month; (6) survey year; and (7) camera angle. We estimated angle of the camera relative to the ground as camera angle can affect detection of smaller mammal species (Rowcliffe et al. 2011). Camera angle was estimated through visual assessment of photographs and categorized as: (1) even with ground level; (2) toward ground level; or (3) away from ground level. Remotely sensed variables were calculated within a 50-ha buffer at each individual camera location, and mean

values of the camera location variables were assigned to each camera cluster site. We measured distances (m) to nearest paved road (FHWA 2000; ISGS 2004a, 2004b). We calculated remotely sensed variables representing land cover, patch size (Illinois Department of Natural Resources [IDNR]. 1996; Illinois State Geological Survey [ISGS]. 2005), and density of human structures (IDNR 1994) using FRAGSTATS 3.3 (McGarigal et al. 2002). Camera location scale habitat variables were measured following Lesmeister et al. (2008) within a 10-m buffer around each camera (e.g., total basal area, hardwood basal area; Table 1). Originating at the camera, 4 10-m transects in each cardinal direction were used to measure coarse woody debris and stem density.

Pearson’s correlation tests were used to check for correlation between variables, and variables with high correlation ($r > |0.7|$) were not included in the same model parameter (Greene and McCleery 2017; Dyck et al. 2022). Habitat variables were standardized around their means and divided by standard deviations for ease of model comparison (Hooten and Hobbs 2015).

Activity pattern.

We estimated daily activity pattern overlap (Ridout and Linkie 2009; Linkie and Ridout 2011; Cronk and Pillay 2020; Green et al. 2022) of squirrel species at the camera cluster level using kernel density estimations preformed in R version 4.0.2 (R Development Core Team 2020) through package “overlap” (Meredith and Ridout 2018). Only photographic captures ≥20 min apart were considered when the same species was detected at a camera trap location (Greene et al. 2016; Sovie et al. 2021). To account for the influence of changing sunrise and sunset times across our study period,

Table 1. Environmental variables calculated in FRAGSTATS 3.3 (McGargial et al. 2002) used to model Fox Squirrel and Eastern Gray Squirrel detection and occupancy probability in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010.

Variable acronym	Description
DIST RD ^{ab}	Distance (m) to nearest minor paved road (collectors and local roads)
STRUCT ^b	Number of human structures per hectare
PATCH AREA ^a	Patch area coefficient of variation: standard deviation/mean patch size (ha)
EDGE ^a	Total length (m) of patch edge per hectare
FOREST SHAPE ^a	Forest shape index, mean perimeter-to-area ratio of patch, increases as patch becomes less compact
AG CLUMP ^a	Agriculture clumpiness (fragmentation), range: −1 (patch maximally disaggregated) to 1 (patch maximally clumped)
FOREST PERCENT ^a	Percentage forest cover
BA ^b	Tree basal area measured in m ² /ha at camera location
HW ^b	Percentage of basal area at camera location that were hardwood trees
CWD ^b	Number of coarse woody debris ≥ 10-cm diameter counted within 1 m of 4 10-m cardinal direction transects from remote camera
STEM ^b	Number of woody stems ≥ 10-cm diameter counted within 1 m of 4 10-m cardinal direction transects from remote camera
PERCIP ^c	Sum of precipitation recorded during survey week at nearest National Weather Service station
TEMP ^c	Average temperature recorded during survey week at nearest National Weather Service station
TEMP × PERCIP ^c	Interaction of average temperature and sun precipitation recorded during survey week at nearest National Weather Service station
PREDET ^c	Detection of focal species in a previous survey session
MONTH ^c	Month survey was conducted
YEAR ^c	Year survey was conducted
ANGLE ^c	Angle of remote camera relative to the slope of the ground

^aHabitat variable included in camera cluster occupancy models.
^bHabitat variable included in camera location occupancy models.
^cSurvey-specific variable used in detection probability models.

we converted all recorded clock times to sun times through the built-in functionality of package “overlap” prior to all activity analysis (Nouvellet et al. 2012; Meredith and Ridout 2018). We compared activity patterns of eastern gray and fox squirrels to assess overlap in activity patterns between both species. To investigate if the presence of another squirrel species influenced activity patterns, we estimated the activity pattern overlap between eastern gray squirrels at camera clusters with and without detections of fox squirrels, while similarly estimating activity pattern overlap between fox squirrels at camera clusters with and without Eastern Gray Squirrel detections. We measured overlap between activity patterns using a coefficient of overlap (Δ) that determines the area under the curve formed by taking the minimum of the 2 density functions (Ridout and Linkie 2009; Linkie and Ridout 2011). The coefficient of overlap ranged from 0 (no shared activity patterns) to 1 (identical activity patterns). Temporal overlap was considered high if $\Delta \geq 0.75$, moderate if between 0.50 and 0.75, and low if $\Delta < 0.50$ (Andreoni et al. 2021). We obtained confidence intervals from 50,000 bootstrap samples to ensure stable estimates (Meredith and Ridout 2018). In all analyses, the significance threshold alpha (α) was set at 0.05.

Occupancy

We investigated occupancy dynamics of both species using single-season single-species occupancy models and single-season co-occurrence occupancy models (Rota et al. 2016) at the camera location and camera cluster scales in package “unmarked” (Fiske and Chandler 2011) in R version 4.0.2. A goodness-of-fit test (MacKenzie and Bailey 2004) conducted in package “AICcmodavg” (Mazerolle 2020) indicated the data were overdispersed; therefore, we used global model variance inflation factor $c.hat$ in calculating quasi-Akaike information criterion with correction for sample size (QAICc) and adjusting standard errors (Burnham and Anderson 2002). Every combination of detection variables without high levels of correlation was modeled while holding occupancy constant. The detection model for fox squirrels (pA) and eastern gray squirrels (pB) with the lowest QAICc at each scale was used in all subsequent occupancy models (Lesmeister et al. 2015). Single-season single-species occupancy models were run to test a priori hypotheses (Table 2) to investigate the effects of habitat variables on Fox Squirrel occupancy (ψ_A) and Eastern Gray Squirrel occupancy (ψ_B). We considered models $< \Delta 2$ QAICc to be competing (Burnham and Anderson 2004; Pittenger et al. 2018) and interpreted all variables with strong influences on occupancy (i.e., credible intervals did not overlap zero) from all competing single-season single-species models when ranked higher than the null model. All pairwise combinations of competitive single-season single-species occupancy models were considered for inclusion in the single-season co-occurrence model, and we considered the influence of variables with a strong influence on occupancy from single-season occupancy models in the co-occurrence parameter to assess the influence of habitat variables on the occupancy probability of fox squirrels conditional on eastern gray squirrels being present ($\psi_{A:B}$), as eastern gray squirrels are reported to be dominant over and displace fox squirrels (Sexton 1990; Rosenblatt 1999; Van Der Merwe et al. 2005; Peplinski and Brown 2020). Single-season co-occurrence models were compared by model weight and lowest QAICc (Akaike 1974; Ebersperger et al. 2012). We interpreted co-occurrence models that were $< \Delta 2$ QAICc of the lowest ranked model when more supported than the model holding co-occurrence constant. Additionally, we explored multi-season single-species models but failed to yield any additional insights into the occupancy dynamics of study species.

Results

Camera trapping.

We recorded 3,044 photographic captures of focal species ($n = 918$ fox squirrels, $n = 2,126$ gray squirrels) over 29,988 camera days. Fox squirrels were detected at 266 camera locations and 164 camera clusters, while eastern gray squirrels were detected at 480 camera locations and 274 camera clusters. Both species were detected at 133 and 136 camera locations and camera clusters, respectively.

Activity pattern.

Activity patterns between eastern gray and fox squirrels were different with a moderate and significant overlap coefficient ($\Delta = 0.63$, CI = 0.60 to 0.67, $P < 0.0001$). Fox Squirrel activity peaked at mid-day, while Eastern Gray Squirrel activity peaked at dawn and dusk. Comparisons of activity patterns for fox squirrels ($\Delta = 0.91$, CI = 0.84 to 0.96, $P = 0.70$) and eastern gray squirrels ($\Delta = 0.93$, CI = 0.90 to 0.96, $P = 0.58$) between camera clusters with and without the other species were not significant and had high overlap coefficients, indicating similar activity patterns (Fig. 2).

Occupancy

The global models indicated that $c.hat$ for Fox Squirrel single-species models were 1.3 and 1.5 at the camera location and camera cluster scales, respectively, while $c.hat$ for eastern gray squirrels were > 4 for both the camera location and camera cluster scales. Detection and occupancy varied between species and scales for the single-species single-season occupancy models (Table 3). Fox Squirrel detection and occupancy probabilities were higher at the cluster scale ($P = 0.53 \pm 0.17$ [SE], $\psi = 0.50 \pm 0.17$) than the location scale ($P = 0.41 \pm 0.14$ [SE], $\psi = 0.26 \pm 0.09$). Similarly, Eastern Gray Squirrel detection and occupancy probabilities were higher at the cluster scale ($P = 0.56 \pm 0.15$ [SE], $\psi = 0.84 \pm 0.23$) than the location scale ($P = 0.47 \pm 0.11$ [SE], $\psi = 0.47 \pm 0.07$).

The detection model with lowest QAICc for fox squirrels (pA) at the camera location scale included month and year, and the detection model with lowest QAICc for fox squirrels at the camera cluster scale included precipitation, temperature, and detection of a Fox Squirrel in the previous survey period. The detection model with lowest QAICc for eastern gray squirrels (pB) at the camera location scale included camera angle, month, year, and detection of gray squirrels in the previous survey period, and the detection model with lowest QAICc for eastern gray squirrels at the camera cluster scale included camera angle, precipitation, detection of a gray squirrel in the previous survey period, and the interaction between precipitation and temperature.

Two competing single-species models explained Fox Squirrel occupancy best at the camera location scale, and 4 competing single-species explained Fox Squirrel occupancy at the camera cluster scale. Two competing single-species models explained Eastern Gray Squirrel occupancy best at the camera location scale, and 13 competing single-species models explained Eastern Gray Squirrel occupancy at the camera cluster scale (Table 4). The best location-scale single-species model to explain Fox Squirrel occupancy indicated that Fox Squirrel occupancy increased at sites with more hardwood basal area ($\psi_A \beta_{HW} = 0.51$, SE = 0.14) and further from paved roads ($\psi_A \beta_{Distance\ to\ road} = 0.29$, SE = 0.09; Fig. 3), while the best cluster-scale single-species model to explain Fox Squirrel occupancy indicated Fox Squirrel occupancy decreased as percentage forest cover increased ($\psi_A \beta_{percentage\ forest\ cover} = -1.32$, SE = 0.37; Fig. 3). The best location-scale single-species model to explain Eastern Gray Squirrel occupancy indicated that Eastern Gray Squirrel occupancy increased at sites with more hardwood basal area ($\psi_B \beta_{HW} =$

Table 2. Occupancy models to investigate a priori hypotheses about habitat variables influencing occupancy of fox squirrels and eastern gray squirrels in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010. Variables are defined in Table 1.

Model	Scale	Hypothesis
DIST RD	Cluster	Anthropogenic Influence
STRUCT	Cluster	Anthropogenic Influence
FOREST SHAPE	Cluster	Forest Structure
FOREST PERCENT	Cluster	Forest Structure
EDGE	Cluster	Landcover Complexity
PATCH AREA	Cluster	Landcover Complexity
AG CLUMP	Cluster	Landcover Complexity
DIST RD + STRUCT	Cluster	Anthropogenic Influence
FOREST SHAPE + FOREST PERCENT	Cluster	Forest Structure
PATCH AREA + EDGE	Cluster	Landcover Complexity
EDGE + AG CLUMP	Cluster	Landcover Complexity
PATCH AREA + EDGE + AG CLUMP	Cluster	Landcover Complexity
PATCH AREA + EDGE + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + EDGE + FOREST PERCENT	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + FOREST PERCENT	Cluster	Landcover Complexity and Forest Structure
EDGE + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
EDGE + FOREST PERCENT	Cluster	Landcover Complexity and Forest Structure
AG CLUMP + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
AG CLUMP + FOREST PERCENT	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + EDGE + AG CLUMP + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + EDGE + AG CLUMP + FOREST PERCENT	Cluster	Landcover Complexity and Forest Structure
PATCH AREA + EDGE + FOREST PERCENT + FOREST SHAPE	Cluster	Landcover Complexity and Forest Structure
DIST RD + STRUCT + PATCH AREA + EDGE + AG CLUMP + FOREST SHAPE + FOREST PERCENT	Cluster	Global
HW	Location	Forest Structure
BA	Location	Forest Structure
STEM	Location	Ground Cover
CWD	Location	Ground Cover
DIST RD	Location	Anthropogenic Influence
BA + HW	Location	Forest Structure
CWD + STEM	Location	Ground Cover
BA + HW + CWD + STEM	Location	Forest Structure and Ground Cover
DIST RD + BA + HW	Location	Anthropogenic Influence and Forest Structure
DIST RD + CWD + STEM	Location	Anthropogenic Influence and Ground Cover
DIST RD + BA + HW + CWD + STEM	Location	Global

0.32, SE = 0.15) with lowest predicted occupancy at sites where no hardwood trees were present (Fig. 4). Single-species cluster-scale models for Eastern Gray Squirrel occupancy had little support and all confidence intervals for the beta coefficients of habitat covariates overlapped zero (Appendix I).

There was 1 co-occurrence model at the location scale that was more supported by lower QAICc and higher model weight than the model with the co-occurrence model held constant (Table 5). This model indicated that fox squirrels were more likely to occupy sites further away from the road when eastern gray squirrels were present ($\Psi_{A:B} \beta_{\text{Distance to road}} = 0.22$, SE = 0.13; Fig. 5). However, as the

confidence interval for the beta coefficient overlapped zero, distance to nearest road only had a weak effect only Fox Squirrel conditional occupancy. There were no co-occurrence models at the camera cluster scale that were more supported than the model with the co-occurrence parameter held constant.

Discussion

Habitat characteristics and spatial partitioning appeared to be more influential than temporal partitioning for eastern gray and fox squirrels in southern Illinois, United States. Activity patterns of both

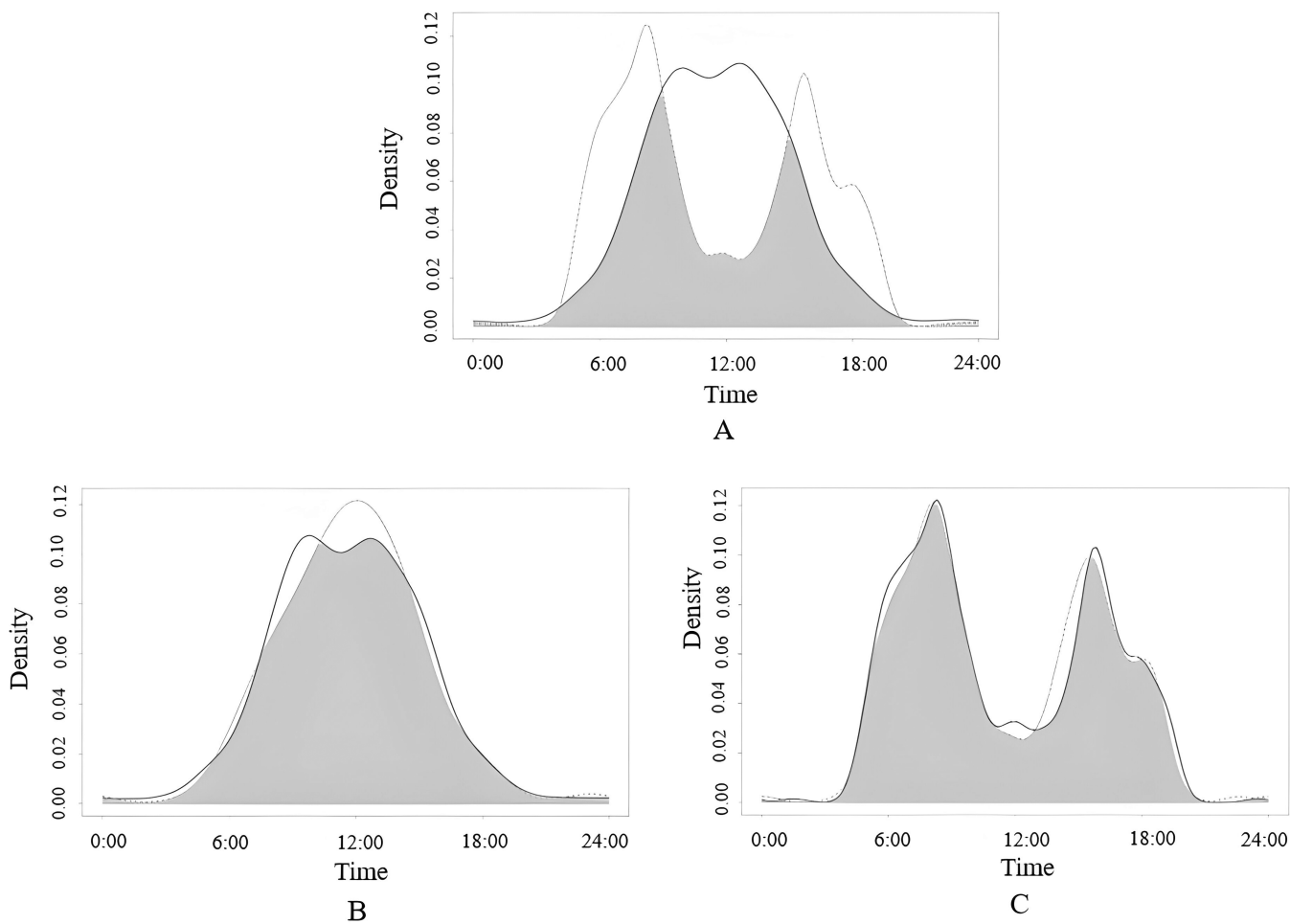


Fig. 2. Kernel analysis estimating overlap between daily activity patterns of (A) fox squirrels (solid line) and eastern gray squirrels (dashed line), (B) fox squirrels at sites with eastern gray squirrel detections (solid line) and fox squirrels at sites without eastern gray squirrel detections (dashed line), and (C) eastern gray squirrels at sites with Fox Squirrel detections (solid lines) and eastern gray squirrels at sites without Fox Squirrel detections (dashed lines). Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, during January to April 2008 to 2010.

Table 3. Model-averaged estimated detection (P) and occupancy (ψ) probabilities with standard error of fox squirrels and eastern gray squirrels from competing single-season single-species occupancy models. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010.

Species	Camera location		Camera cluster	
	P	ψ	P	ψ
Fox Squirrel	0.41 ± 0.14	0.26 ± 0.09	0.53 ± 0.17	0.50 ± 0.17
Eastern Gray Squirrel	0.47 ± 0.11	0.47 ± 0.07	0.56 ± 0.15	0.84 ± 0.23

species were distinct but appeared to be unaffected by the presence of the other species. We found strong evidence for the effects of forest characteristics and anthropogenic influences on occupancy of both species. Likely because the study area was forest-dominated, we detected eastern gray squirrels (i.e., mature forest associated) more often than fox squirrels (Edwards et al. 1998). As others noted, we also found that environmental characteristics affecting squirrels differed by species and scale (Greene and McCleery 2017; Sovie et al. 2020; Hefty and Koprowski 2021). Fox Squirrel occupancy was influenced by forest structure and anthropogenic influences at the small scale while affected by only forest structure at the larger scale. Conversely, Eastern Gray Squirrel occupancy was primarily affected by forest structure at the small scale. Co-occurrence of squirrel species was affected by anthropogenic influences at the small scale.

Activity patterns.

Our prediction regarding activity patterns of squirrel species was partially supported. Similar to previous research (Weigel et al. 1989; Sovie et al. 2019), we observed a unimodal activity pattern for fox squirrels that peaked around midday, and a bimodal activity pattern for eastern gray squirrels that peaked around dawn and dusk. While competition has been hypothesized as a possible reason for activity differences between these species (Larson and Sander 2022), alternatives have also been suggested. Because eastern gray squirrels are smaller than fox squirrels (Brown and Yeager 1945; Whitaker and Mumford 2009; Thorington et al. 2012), eastern gray squirrels may be active during crepuscular hours to avoid diurnal avian predators that are more likely to target smaller prey, while fox squirrels with larger bodies are not as vulnerable to these increased predation

Table 4. Quasi-Akaike information criterion (QAICc), delta QAICc (Δ QAICc), model weights, and number of parameters (K) for candidate and null single-season single-species occupancy models of fox squirrels and eastern gray squirrels. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010. Habitat variables are defined in Table 1.

Species	Scale	Model	QAICc	Δ QAICc	Model weight	K
Fox Squirrel	Camera location	DIST RD + BA + HW	1,741.23	0	0.61	8
		DIST RD + BA + HW + CWD + STEM	1,742.22	0.99	0.37	10
		Null	1,768.23	26.99	<0.01	5
	Camera cluster	FOREST PERCENT	267.35	0	0.31	7
		EDGE + FOREST PERCENT	268.46	1.11	0.18	8
		AREA + FOREST PRECENT	268.91	1.56	0.14	8
		AG CLUMP + FOREST PERCENT	269.03	1.67	0.13	8
		Null	286.94	19.58	<0.01	6
Gray Squirrel	Camera location	HW	876.30	0	0.34	8
		BA + HW	878.23	1.93	0.13	9
		Null	879.09	2.79	0.08	7
	Camera Cluster	Null	355.52	0	0.13	7
		AG CLUMP	356.47	0.95	0.08	8
		EDGE	356.60	1.07	0.08	8
		PERCENT FOREST	356.64	1.12	0.08	8
		STRUCT	357.19	1.67	0.06	8
		FOREST SHAPE	357.22	1.70	0.06	8
		DIST RD	357.24	1.72	0.06	8
		AG CLUMP + FOREST PERCENT	357.43	1.91	0.05	9
		EDGE + AG CLUMP	357.50	1.98	0.05	9

risks (Steele and Koprowski 2001; Sovie et al. 2019). Alternatively, differences in activity patterns may be a ghost of competition past that drove the evolution of both species toward partitioning instead of merely being a learned behavior (Rosenzweig 1979; Connell 1980; Ben-Shlomo et al. 1995). Conflicting study results (Edwards and Guynn 1995; Edwards et al. 1998; Derge and Yahner 2000; Sovie et al. 2020) may be attributed to differences in geographical and temporal scales or study design (Greene and McCleery 2017). For instance, Derge and Yahner (2000) used line transects to investigate diurnal activity patterns, whereas Sovie et al. (2019) utilized camera traps and reported findings similar to ours.

While we found no support for temporal partitioning, other studies suggested that temporal partitioning among squirrels may be seasonally driven and affected by resource availability (Sovie et al. 2019; Larson and Sander 2022). Given that our study occurred during winter months, we were unable to assess interactions between the species year-round or in other seasons when resource availability varied. Larson and Sander (2022) proposed that temporal partitioning may occur during autumn when increased food resources attract both species. Given that winter is a period of reduced food availability for squirrels (Gurnell 1996), both species utilize a scatter-hoarding strategy by making single deposits into wide-ranging food caches (Robin and Jacobs 2022) and will often recache seeds or nuts to remember cache placement, avoid

competition, and potentially optimize dispersion of resources as caches are depleted (Bartlow et al. 2018; Robin and Jacobs 2022). During autumn, temporal partitioning by squirrels may be more beneficial to avoid competition as squirrels seek to obtain and protect food resources by employing evasive behaviors. However, during winter, such strategies would be less beneficial, as scatter-hoarding squirrels rely on caches near nest trees (Stapanian and Smith 1978; Smith and Reichman 1984) and recaching (Bartlow et al. 2018).

Occupancy

Previous studies reported that fox squirrels have lower and patchier occupancy than eastern gray squirrels within the southern reaches of their distributional ranges (Amspacher et al. 2019; Pynne et al. 2020). However, in Midwestern landscapes with intensive row-crop agriculture, fox squirrels have higher occupancy than eastern gray squirrels (Moore and Swihart 2005; Rizkalla et al. 2009). Both squirrel species in southern Illinois exhibited detection and occupancy rates similar to squirrel populations further south (Amspacher et al. 2019; Sovie et al. 2020) with Fox Squirrel occupancy lower at both the camera location and camera cluster scales. This may be partially due to our study area being composed primarily of mixed-hardwood associations (Luman et al. 1996). Both species use acorns, beechnuts, hickory nuts, and walnuts for food (Steele and Koprowski 2001; Whitaker and Mumford 2009; Thornton et

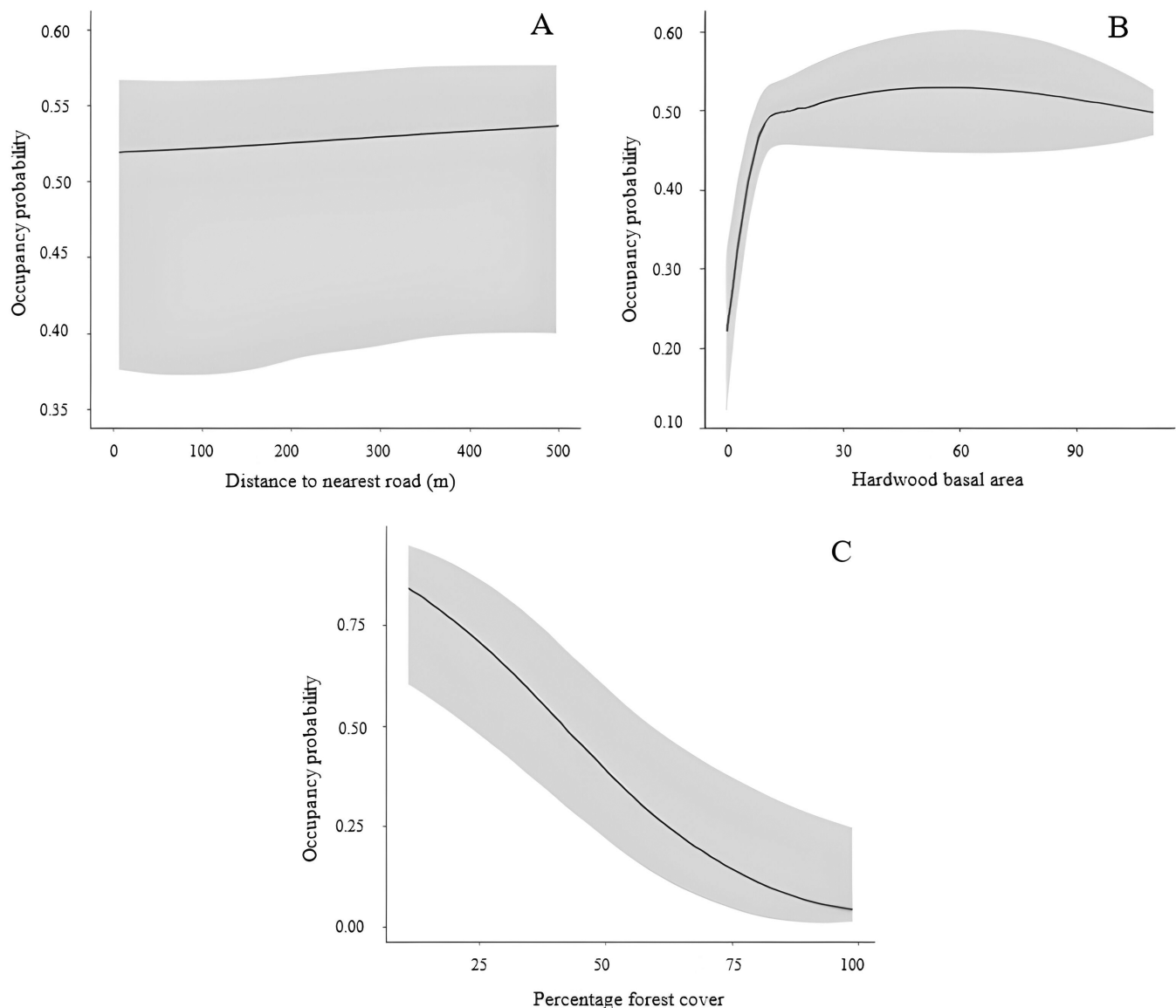


Fig. 3. Relationship between Fox Squirrel occupancy and (A) camera location scale distance to nearest road (m), (B) camera location scale hardwood basal area, and (C) camera cluster scale percentage forest cover with 95% confidence intervals (gray area) based on model-averaged results from competitive single-species occupancy models. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, during January to April 2008 to 2010.

al. 2012), and while resources were prevalent throughout the study area (Luman et al. 1996), many suitable sites fell within mature or heavily forested areas, such as the Shawnee National Forest, that eastern gray squirrels prefer. Furthermore, studies have reported eastern gray squirrels displacing and outcompeting fox squirrels (Sexton 1990; Rosenblatt 1999; Van Der Merwe et al. 2005; Peplinski and Brown 2020). Additionally, Brown (1984) suggested that eastern gray squirrels in Illinois may reduce food availability to levels insufficient to support breeding female fox squirrels, which would further lower Fox Squirrel occupancy.

Contrary to our predictions, distance to nearest road influenced Fox Squirrel occupancy and had a weak effect on the co-occurrence of study species. Previous studies indicated that fox squirrels have lower occupancy closer to roads, potentially due to higher mortality risks from traffic (Burton and Doblar 2004) and predator presence (Tigas et al. 2002; Kolowski and Nielsen 2008). However, we only noted the influence of roads on Fox Squirrel occupancy at the camera location scale. Given that fox squirrels can inhabit developed

areas successfully (Whitaker and Mumford 2009; Thorington et al. 2012), these effects likely do not affect broader distributions or inhibit occupancy of developed areas across larger geographic areas. Additionally, we observed that sites further from roads were more likely to have eastern gray and fox squirrels co-occur. Given fox squirrels avoidance of roads (McCleery et al. 2007; Fey et al. 2016) and that eastern gray squirrels are associated with mature forest structures (Edwards et al. 1998), sites further away from roads likely attract both species by providing food resources and shelter while also reducing mortality risks associated with roads. This pattern was only observed at the camera location scale and had weak support, and as both species are capable of thriving in heavily urbanized and altered landscapes (McCleery et al. 2007; Parker and Nilon 2008; Larson and Sander 2022), the influence of roads across larger areas may have been obscured or less influential than other environmental characteristics.

As observed by others, we found that Fox Squirrel occupancy was influenced by forest structure and spatial scale. Given that fox

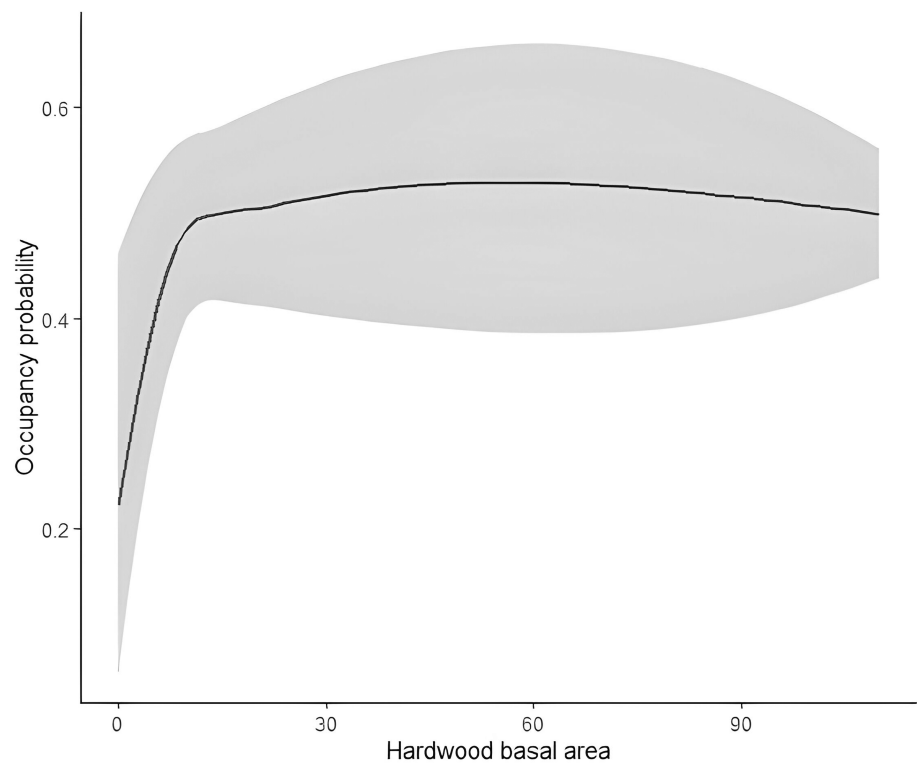


Fig. 4. Relationship between Eastern Gray Squirrel occupancy probability and camera location scale hardwood basal area with 95% confidence intervals (gray area) based on model-averaged results from competitive single-species occupancy models. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, during January to April 2008 to 2010.

Table 5. Quasi-Akaike information criterion (QAICc), delta QAICc (Δ QAICc), model weights, and number of parameters (K) for single-season co-occurrence occupancy models of fox squirrels and eastern gray squirrels. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010.

Scale	Model parameters			QAICc	Δ QAICc	Model weight	K
	Eastern Gray Squirrel occupancy model	Fox Squirrel occupancy model	Co-occurrence model				
Camera location							
	HW	DIST RD+ BA + HW	DIST RD	4,396.54	0	0.20	17
	HW	DIST RD+ BA + HW	Constant	4,396.79	0.24	0.18	16
	HW	DIST RD+ BA + HW	CWD	4,397.68	1.13	0.11	17
	BA + HW	DIST RD + BA + HW	STEM	4,397.93	1.39	0.10	18
	HW	DIST RD + BA + HW	DIST RD + CWD + STEM	4,398.00	1.46	0.10	19
	HW	DIST RD + BA + HW	BA + HW + CWD + STEM	4,398.13	1.59	0.09	18
Camera cluster							
	AG CLUMP	FOREST PERCENT	Constant	623.15	0	0.16	15
	AG CLUMP	FOREST PERCENT	DIST RD	623.67	0.52	0.13	16
	AG CLUMP	FOREST PERCENT	EDGE	624.50	1.35	0.08	16
	AG CLUMP	FOREST PERCENT	STRUCT	624.82	1.67	0.07	16
	AG CLUMP	FOREST PERCENT	AG CLUMP	624.86	1.71	0.07	16
	AG CLUMP	FOREST PERCENT	AREA	624.91	1.76	0.07	16
	AG CLUMP	FOREST PERCENT	FOREST PERCENT	624.96	1.81	0.07	16

squirrels are associated with open or edge forest structures (Derge and Yanher 2000) and savannas (Thorington et al. 2012), we expected to find higher occupancy probabilities at sites with these characteristics. However, our results indicated that fox squirrels had higher occupancy with more hardwood basal area at the camera location scale and higher occupancy with lower percentage forest cover at

the camera cluster scale. Other studies reported that fox squirrels prefer open or fragmented forests (Weigl et al. 1989; Greene and McCleery 2017; Amspacher et al. 2019) and the importance of spatial scale on Fox Squirrel occupancy (Sovie et al. 2020), and our results support these findings. Fox squirrels use hardwood trees for food resources and nesting (Thorington et al. 2012) and would be

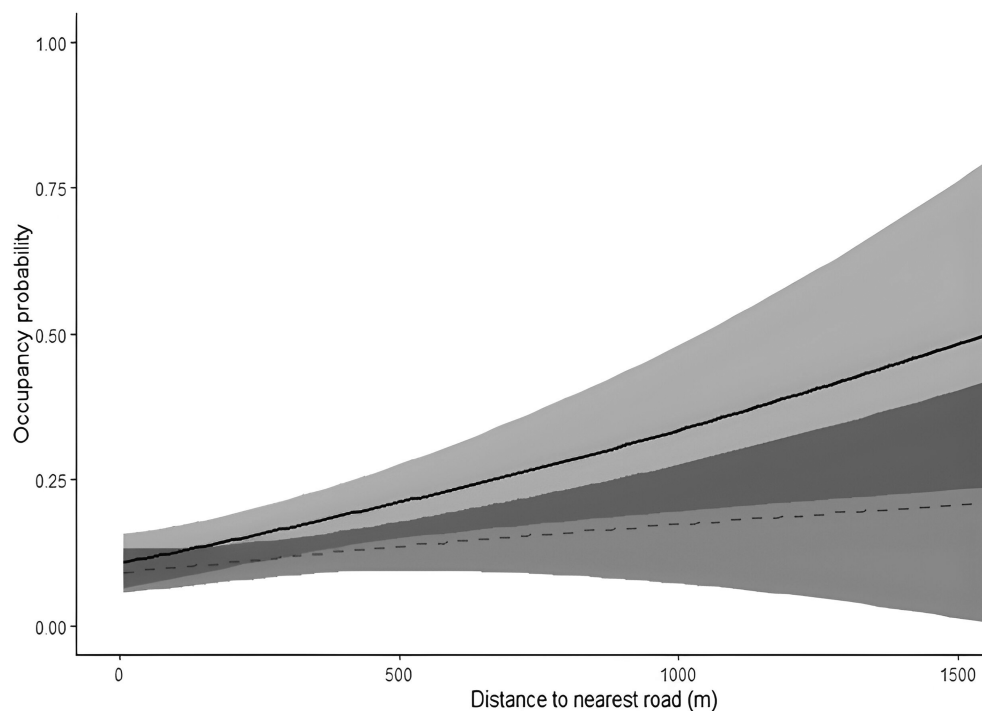


Fig. 5. Relationships between Fox Squirrel occupancy and distance to nearest road (m), given Eastern Gray Squirrel absent (dashed line) or present (solid line), with 95% confidence intervals (gray area). Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, during January to April 2008 to 2010.

attracted to such sites with more hardwood basal area. However, given that Fox Squirrel occupancy decreased with more percentage forest cover at the larger scale, this species is likely selecting for stands with hardwood trees that are not part of a dense, contiguous forest structure spanning large geographic areas. Rather our findings reveal that fox squirrels prefer heterogeneous landscapes even in Central Hardwood forests, similar to findings from other ecoregions (McCleery 2009; Lewis et al. 2021).

Our predictions for Eastern Gray Squirrel occupancy were partially supported as Eastern Gray Squirrel occupancy was higher at sites with increased hardwood basal area at the camera location scale, but we found no support for the influence of ground cover. Eastern gray squirrels use hardwood species, such as Sugar Maple (*Acer saccharum*), Black Oak (*Quercus velutina*), White Oak (*Q. alba*), and Northern Red Oak (*Q. rubra*) for food and shelter (Nixon et al. 1978; Weigl et al. 1989; Williams 2011). Gray squirrels primarily use such trees for cavities to rear winter litters (Allen 1982) and increased basal area implies more available cavities. This finding was consistent with previous research indicating eastern gray squirrels inhabit extensive hardwood forests (Flyger and Gates 1982; Edwards et al. 1998) and suggests that at smaller scales eastern gray squirrels seek areas with more hardwood trees. However, we found that occupancy probabilities had a nonlinear relationship to increased basal area with occupancy probabilities, plateauing after a sharp increase. Given that eastern gray squirrels are generalists capable of exploiting many systems (Williams 2011; Amspacher et al. 2019), this may reflect their capability of inhabiting areas with fewer hardwood trees. Furthermore, North American scatter-hoarding tree squirrels have been noted to cache seeds in areas ideal for seedling establishment (Steele and Yi 2020) and with higher risk of predation to avoid pilfering, frequently resulting in caches away from canopy cover (Steele et al. 2011) or with less ground cover (Steele et al. 2015). Given that our study occurred during the winter months when eastern gray squirrels would be relying on such caches, our results may

be influenced by the time spent by eastern gray squirrels in such areas. This result may also have obscured the influence of ground cover on Eastern Gray Squirrel occupancy. Although eastern gray squirrels utilize thick groundcover and understories (Edwards et al. 1998) for cover from predators (Leaver et al. 2017), we found no support for the influence of such habitat characteristics on Eastern Gray Squirrel occupancy. Bland (2016) noted that eastern gray squirrels selected for cache sites with less woody debris cover that favor seedling establishment. Thus, the winter use of cache sites in areas with less groundcover may have masked the influence of these habitat characteristics on eastern gray squirrels.

Contrasting methods and results among studies necessitate additional research to further understand the ecology of squirrels. Multiscale studies investigating these species were primarily from the southern United States (Meehan 2007; Fletcher et al. 2016; Boone et al. 2017; Greene and McCleery 2017; Pynne et al. 2020; Sovie et al. 2020, 2021; Hefty and Koprowski 2021) with few recent studies elsewhere (Moore and Swihart 2005; Salyers 2006), necessitating similar, multiscale studies in other areas of distributional ranges of these species (Greene and McCleery 2017; Sovie et al. 2019). Furthermore, novel data collection approaches outside of camera traps, such as bio-loggers and accelerometers (Wassmer and Refinetti 2016, 2019; Studd et al. 2018; Wassmer et al. 2020), should be employed to assess activity patterns. Year-round studies to assess how seasonality may influence squirrel activity patterns outside of urban environments (McCleery et al. 2007; Larson and Sander 2022) would also be beneficial (Wassmer and Refinetti 2016, 2019).

In conclusion, habitat characteristics and spatial scale appear to be more influential than peak activity times in partitioning fox and eastern gray squirrels in Central Hardwood forests.

Fox Squirrel occupancy reflected a preference for forest structures with concentrations of hardwood stands in a fragmented or open forest, while eastern gray squirrels had higher occupancy at sites with denser forest structures. Furthermore, study species were more

likely to occur together at sites further away from roads. The role of spatial scale was apparent as both species exhibited differing patterns of occupancy relative to scale. While we noted different activity patterns between both species, we found little evidence for temporal partitioning, suggesting that current activity patterns are either driven by other ecological forces or a ghost of competition past.

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Author contributions

JJR helped conceptualize the study, conducted formal analysis and model creation, and writing the original draft; DBL conceptualized the study, collected and curated data, and helped edit and revise the manuscript; CKN conceptualized the study, secured funding and resources for the study, provided supervision and project management, and assisted with writing the original draft.

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Conflict of interest

None declared.

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Appendix I

Beta coefficients (β) and 95% confidence intervals (CIs) for variables in the competing single-season single-species occupancy models of fox squirrels and eastern gray squirrels. Data were collected from camera trap surveys in the 16 southernmost counties of Illinois, United States, January to April 2008 to 2010.

Species	Scale	Variable	β	CI
Fox squirrel	Camera location	DIST RD ^a	0.29	0.12, 0.46
		BA	0.04	−0.16, 0.24
		HW ^a	0.51	0.24, 0.79
		CWD	0.19	−0.47, 0.85
		STEM	0.13	−0.25, 0.25
	Camera cluster	FOREST PERCENT ^a	−1.32	−2.05, −0.59
		EDGE	0.29	−0.29, 0.87
		AREA	−0.21	−0.78, 0.36
		AG CLUMP	0.24	−0.55, 1.03
Eastern gray squirrel	Camera location	HW ^a	0.32	0.02, 0.62
		BA	0.05	−0.25, 0.35
	Camera cluster	AG CLUMP	−0.59	−1.99, 0.81
		EDGE	0.36	−0.36, 1.05
		FOREST PERCENT	−0.34	−0.99, 0.32
		STRUCT	−0.20	−0.75, 0.35
		FOREST SHAPE	0.26	−0.67, 1.18
		DIST RD	0.25	−0.61, 0.74

^aVariables that do not have confidence intervals overlapping 0, indicating a strong effect on occupancy.