

SPATIAL DISTRIBUTION OF AERIAL PREDATORS:  
INFLUENCES ON USABLE SPACE FOR QUAIL

By

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Abstract: The likelihood of encountering a predator influences prey behavior and spatial distribution such that non-consumptive effects can outweigh the influence of direct predation. Prey species are thought to filter information on perceived predator encounter rates in physical landscapes into a landscape of fear defined by spatially explicit heterogeneity in predation risk. The presence of multiple predators using different hunting strategies further complicates navigation through a landscape of fear and potentially exposes prey to greater risk of predation. The juxtaposition of land cover types likely influences overlap in occurrence of different predators, suggesting that attributes of a landscape of fear result from complexity in the physical landscape. Woody encroachment in grasslands furnishes an example of increasing complexity with the potential to influence predator distributions. I examined the role of vegetation structure on the distribution of avian predators, and the vulnerability of a frequent prey species of those predators, Northern Bobwhite (*Colinus virginianus*). I mapped occurrences of raptors and kill locations of Northern Bobwhite to examine spatial vulnerability in relation to landscape complexity. Predator density and predation-specific mortality of Northern Bobwhite increased with vegetation complexity generated by fine-scale interspersed of grassland and woodland. Predation pressure was lower in more homogeneous landscapes where overlap of the two predators was less frequent. Predator overlap created areas of high risk for Northern Bobwhite amounting to 32% of the land area where landscape complexity was high and 7% where complexity was lower. My study emphasizes the need to evaluate the role of landscape structure on predation dynamics and reveals another threat from tree encroachment in grasslands.

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## CHAPTER I

### ESTIMATING SPATIALLY EXPLICIT RESOURCE SELECTION IN MOBILE SPECIES: AN ILLUSTRATION WITH MISSISSIPPI KITE (*Ictinia mississippiensis*)

#### **Abstract**

Conservationists need spatially explicit information on habitat use to develop effective management strategies for priority species. That information can be difficult to obtain for species that are highly mobile or occupy large home ranges. In this study, I introduce a robust approach to estimate spatially explicit resource selection for a highly mobile raptor, Mississippi Kite (*Ictinia mississippiensis*), based on data collected from line transect surveys. I compared land cover of kite detection points to randomly located points at three spatial scales. Resource selection in Mississippi Kite was driven by both fine and broad-scale vegetation characteristics. At fine scale (~13 ha), kites selected upland forest but avoided grass cover, riparian forest, and bare ground. Furthermore, kites avoided riparian forest and oil pads at broad scale (~200 ha) but selected grass and upland forest cover. Broad-scale selection also favored higher elevation and areas farther away from riparian forest. Both observed density and predicted occurrence suggested riparian avoidance. Avoidance of riparian forest is atypical for Mississippi Kite, but might be explained in this system as avoidance of areas occupied by kite predators.

**Key words:** Distribution. Mixed-grass prairie. Mississippi Kite. Offset detection. Resource selection.

## **Introduction**

Understanding habitat requirements of wildlife is a desired outcome of many ecological studies and essential to effective conservation planning (Jones 2001; Margules and Pressey 2000; Rodenhouse et al. 1997). Conservationists and wildlife managers rely on spatially explicit knowledge of habitat selection to target population recovery (Rothschild et al. 1994), establish protected areas (Pressey et al. 1993), and designate biodiversity hotspots (Myers et al. 2000). Obtaining robust spatial data needed to understand how wild animals use and select habitat can be challenging, especially for highly mobile or wide-ranging species. Traditional sampling methods for habitat studies (e.g., Bibby et al. 2000; Cody 1985) might be appropriate for species with small home ranges but can fall short when used to estimate fine scale habitat selection in wide ranging species, especially in complex landscapes (Cardador et al. 2014; Sardà-Palomera et al. 2012).

Conservationists have benefited greatly from insights gained through studies that derived point locations from telemetry and similar tracking data from marked animals (Aarts et al. 2008). Such studies are often accompanied, however, by challenges such as high capital investment, high labor cost, small sample sizes, and limitations to species that can be tracked using such technologies (Hebblewhite and Haydon 2010; Latham et al. 2015). Telemetry data can sometimes provide biased estimates of habitat selection due to inherent errors associated with spatial inaccuracy in the locations acquired and missing data in the form of failed location attempts (Frair et al. 2004; Nams 1989; White and Garrott 1986). Telemetry studies generally require that the subject be captured and handled to be fitted with a tracking device. The stress of capture and handling, and the structure of the devices themselves can occasionally result in mortality, reduction in adult body mass, behavior modification, and reduced reproductive success (Berkeley et al. 2007; Jepsen et al. 2002). These risks are exacerbated when dealing with endangered or declining species (Cooke 2008). In response to those risks, it can sometimes be difficult to obtain the permits necessary to carry out the desired studies. For example, a two-year telemetry study of giant



pandas (*Ailuropoda melanoleuca*) was based on only five individuals due to difficulties associated with obtaining permits to capture endangered species (Hull et al. 2015).

Habitat selection studies that do not include tracking of specific individuals generally tie the location of detected individuals to the location of the observer (Bibby et al. 2000; Noon 1981; Collier et al. 2013). For example, an observer will record the coordinates of a point from which an individual was detected, but that is as spatially explicit as the data can be. The individual will be associated with vegetation data from a plot or land cover within a buffer centered on the count location. This can introduce significant bias in the interpretation of habitat associations when conditions where the individual actually occurred are different from conditions at the point from which the observer detected the individual. Road-based counts in particular are susceptible to this bias because the detection location along a road is typically quite different from the occurrence location away from the road. A road-based method that allowed the capture of actual occurrence points of detected individuals, without the challenges of tracking individuals, would improve my ability to assess spatially explicit habitat selection for a large number of wide-ranging animals.

Birds of prey comprise a group of wide-ranging, highly mobile species that are generally easy to detect from road-based counts but also susceptible to road-bias in studies of habitat use (Fuller and Mosher 1987; Andersen et al. 1985; Andersen 2007; Millsap and LeFranc Jr 1988). I developed a method to obtain spatially explicit data on habitat use from road-based counts for a gregarious raptor, the Mississippi Kite (*Ictinia mississippiensis*).

The Mississippi Kite breeds in the southern United States where it occupies urban settings (Parker 1996), riparian areas, shelterbelts, oak-shrub prairies, and savannas in home ranges that average 3100 ha (Bader and Bednarz 2010). Adults are 30–37 cm in length (Dunn and Alderfer 2011) and are largely insectivorous. Mississippi Kite is a complete migrant, wintering in central South America (Juhant and Areta 2013). In North America, it occurs in two more-or-less distinct populations: the Great Plains

population consists of kites in areas of the central and southern Great Plains, including parts of Colorado, Nebraska, Kansas, Oklahoma, Texas, Arizona, and New Mexico, and the eastern population extends from the Mississippi River eastward to the Atlantic Coast (Bader 2007). Although the population has largely recovered from historical declines suffered half a century ago, it remains a species of concern in some areas (Bader and Bednarz 2009; Chiavacci et al. 2014a). In Oklahoma, Mississippi Kite has declined 2.0 % annually since 1970 (Figure S1; Sauer et al. 2011).

Spatially explicit habitat use data on Mississippi Kite are generally lacking. Bader and Bednarz (2010) conducted a two-year study of radio-collared kites in Arkansas but were limited to data from just 7 individuals. my study therefore examined spatially explicit resource selection in Mississippi Kite with a modification of a road-based sampling scheme that allowed the estimation of point locations of sighted individuals. I describe a method combining field data collection and specific GIS tools that permitted me to 1) estimate spatially explicit resource selection by Mississippi Kite at two spatial scales; 2) estimate spatial density and distribution of Mississippi Kites; and 3) predict potential suitable habitats for kites in a mixed-grass prairie ecosystem.

## **Method**

### **Study site**

Our study conducted in the Oklahoma Department of Wildlife Conservation's Packsaddle Wildlife Management Area (WMA) in western Oklahoma, USA (Figure 1). Packsaddle WMA includes ~6,475 ha of mixed-grassed prairie at elevation of 579–762 m. Annual precipitation averages 53 cm, with the majority occurring during spring and summer (DeMaso et al. 1997). Soils consist mainly of Nobscot fine sand, Nobscot-Brownfield, and Pratt-Tivoli loamy fine sand (Townsend et al. 2001; DeMaso et al. 1997). Predominant grasses in the WMA include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand

paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Forb species include western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*), erect dayflower (*Commelina erecta*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation include shinnery oak (*Quercus harvardii*), sand sagebrush (*Artemisia filifolia*), cottonwood (*Populus spp*), elm (*Ulmus spp*) and sand plum (*Prunus angustifolia*) (Townsend et al. 2001; DeMaso et al. 1997). Significantly, shinnery oak can occur as dense, low cover generally < 0.5 m in height, or it may form small, discrete patches of monotypic stands generally > 3.0 m in height.

Anthropogenic activities in this area are related mainly to oil extraction and recreational hunting. Packsaddle WMA is managed primarily for hunting and leased cattle grazing. Most of the management practices on the WMA are targeted at enhancing the population of Northern Bobwhite (*Colinus virginianus*) and other upland game species. A combination of prescribed fire and cattle grazing is applied to enhance diversity and reduce cedar encroachment.

#### Kite surveys

We surveyed Mississippi Kites in May–August 2014 and 2015. To focus on likely breeding individuals at the study site, I omitted from analysis observations collected during the first two weeks of May and in the last week of August. I used line-transect sampling to collect occurrence data. Twenty-four transects (14 upland, 10 lowland/riparian) 1–5 km in length were placed along existing roads and trails at the WMA (Augiron et al. 2015; Fuller and Mosher 1987). To reduce the chance of counting an individual more than once during a survey, I separated transects by at least 900 m. I surveyed each transect at least twice a month using a 4-wheel truck driven at 20–30 km/h (Fuller and Mosher 1987). I surveyed each transect 15 times in 2014 and 14 times in 2015. Surveys were conducted by three independent observers who scanned a distance of approximately 400 m on either side of the transect line. Surveys started ~60 minutes after sunrise to allow kites enough time to leave roosts and spread over the study area.

During surveys, I collected distances of individual sightings away from the transect line using a laser range finder. Distance estimates were primarily collected for perched birds, but when possible, I estimated distances for soaring birds from the closest structure (tree, shrub, fence pole, etc.) beneath the point of first detection. I also collected covariates that might influence detection such as observer identity, month of survey, and time of day. I categorized time of sampling (CDT) as early morning (0700–0900), late morning (0901–1100), noon (1101–1300) early afternoon (1301–1500), and late afternoon (>1500). I marked points of observation on the transect (Figure 1A) using a Garmin Montana 650 GPS unit and obtained the angle of observation from the line with a magnetic compass. Thus, I had the estimated distance and azimuth bearing from the point of observation to the point at which the bird was first detected (Figure 1B).

Using the distance and bearing recorded for each kite detection, I plotted individual detections to the point of occurrence (Figure 2) using the *Bearing Distance to Line* tool (Figure 2A) in ArcGIS 10.2 (Environmental Systems Research Institute Inc., Redlands, CA, USA). The *Bearing Distance to Line* tool creates a new feature class containing a geodetic line feature for each occurrence point constructed based on the values in the x, y coordinate fields, bearing field, and distance field. I next used the *Feature Vertices to Points* tool to create a feature class containing points at the end of each line. This new layer of offset points provided x y coordinates that represented the estimated location of each individual at the time of first detection.

#### Land cover classification

We obtained two Geo-Eye images of Packsaddle WMA (acquired 6 July 2014) through the NASA Scientific Data Purchase. The Geo-Eye images provided approximately 2 m spatial resolution in the visible (panchromatic) and relatively broad bands of blue, green, red, and near-infrared portions of the spectrum. I used the *Band Composite* tool in ArcGIS 10.2 to produce a composite spectral image of the

study site. I next performed a supervised classification on the pre-processed image using the Maximum Likelihood algorithm. My classification contained the following categories: upland forest, riparian woodland, grassland, bare ground, open water, sparse vegetation, and oil pads.

Several processes (e.g. spatial heterogeneity of resources, body size, dispersal distances, disturbances, and home range size) may govern how organisms respond to their environment at different spatial scales (Bolker 2003; Levin 1992; Wheatley and Johnson 2009). Hence, I quantified resource selection by Mississippi Kites at fine and broad spatial scales. First, I extracted land cover information centered at each estimated location (used) and a set of randomly selected available locations (Figure 2B). I selected a 200 m radius to represent a fine scale that might provide Mississippi Kite with immediate nesting and foraging resources. Next, I extracted land cover variables at 1000 m radius centered at each used and available point to represent broad scale selection consistent with estimated home range size for nesting females (Bader and Bednarz 2010). I also collected topographical and distance attributes collected across the study extent, i.e., the entire Packsaddle WMA. Distance-based variables are important for assessing habitat selection of individual points on the landscape because kites may select areas based on their proximity to resource variables without actually selecting the habitat or landscape class itself. Hence, I calculated distances from all used and available locations to the closest pixel of each open water, riparian forest, and oil pad layers. I selected riparian forest and water layers based on previous studies that associated habitat selection by Mississippi Kites with bottomland woodland (Barber et al. 1998; Kalla 1979; Evans 1981); oil pads were selected based on their possible influence on kite resource used as the dominant anthropogenic activities in the landscape. I created distance raster maps for each layer type using the *Euclidean Distance* tool.

To estimate resource availability, I generated 489 random locations (equaling the number of used locations) using the *Random Point Generator* in ArcGIS 10.2. While I cannot be entirely certain that an available location did not overlap with a used location, the randomness of the point generation at least ensured that my results are not biased. I obtained slope (degrees), aspect (degrees), and elevation (meters)

from a Digital Elevation Model (DEM) collected from the United States Geological Survey (USGS) data portal at 1/3 arc-seconds (10 m) resolution. Elevation and slope raster layers were then reclassified into 10 classes using *natural breaks* to limit the number of possible classes. To obtain topographical variables from the elevation, slope, and aspect layers, I extracted values from each layer to used and available locations using the *Extract Values to Points* tool in ArcGIS 10.2. I transformed aspect into a continuous variable by calculating the cosine of aspect (COS (Aspect)) to obtain values ranging from -1 (south) to +1 (north). To estimate resource selection functions (RSF) for Mississippi Kite, I compared vegetation and landscape characteristics at offset locations (used) and random (available) locations.

#### Statistical analyses

All Mississippi Kites sighted during surveys were recorded and georeferenced, but only detections for perched birds were used for density estimate analysis (Buckland et al. 2001). Nevertheless, other detections were retained and included in resource selection analyses. To identify areas of high selection, I developed a spatial density map based on point density analysis in ArcGIS 10.2. The *Point Density* tool calculates the density of point features around each output raster cell by defining a neighborhood around each raster cell center. Points that fall within the neighborhood are then totaled and divided by the area of the neighborhood to produce a density output. To account for multiple observations within a point, I specified a population field equal to the number of kites observed per entry. To compare densities of Mississippi Kite at upland and lowland zones of the WMA, I computed absolute densities and detection probabilities for each zone using the Multiple-Covariate Distance Sampling (MCDS) approach (Buckland et al. 2015; Marques et al. 2007). To account for the effects of multiple visits on density estimates, I computed survey efforts as the number of survey events for each transect multiple by the transect length (Buckland et al. 2015). I performed all MCDS analyses using *program Distance 6.2* (Thomas et al. 2010). For each zone, I compared a suite of *a priori* candidate models to evaluate detection probabilities in

relation to distance, the effects of the observer, time of day, and the month that surveys were done. For each model, I evaluated the half-normal, and hazard-rate key functions with cosine adjustment terms except for the no covariate models where I included the uniform key function (Buckland et al. 2015). I then ranked models using the Akaike Information Criterion corrected for small sample sizes (AICc) and collected density estimates and detection probabilities based on the best competing models within a  $\Delta AIC$  value  $< 2$ .

We estimated resource selection functions (RSFs) at fine and broad spatial scales by comparing landscape characteristics at kite occurrence (used) locations and random (available) locations using a generalized linear model (GLM) (Boyce 2006) specifying a binomial error structure and a logit link function. I coded used locations as 1 and available locations as 0. Fixed effects were defined and varied depending on the scale of the analysis (Table 1). At the broad scale, fixed effects included extracted values from topographical and distance based raster layers.

Before modeling, I performed a Pearson correlation on all variables at each scale and removed variables that were redundant ( $|r| > 0.70$ ). For example, distance to water and distance to riparian forest were strongly correlated ( $r = 0.83$ ,  $P < 0.05$ ). Therefore, only distance to riparian forest was included in the global model. Because my objective was to evaluate main effects of individual covariates and their influences on resource selection in relation to availabilities, I tested all possible combinations of additive covariates at each spatial scale using the R package MuMIn version 1.13.4 (Barton 2016). Subsequently, I ranked all models according to their AICc values (small sample size-adjusted Akaike's information criterion (Burnham and Anderson 2002)). In addition, I calculated predictions under each model. These predictions were ranked, and the best models were selected based on AICc weights across  $\Delta AICc$  of  $< 2$ . For competing models, I evaluated model-averaged estimates for variables of interest. I also calculated unconditional standard errors and 95% confidence limits (Burnham and Anderson 2002). I rescaled variables by subtracting the mean and dividing by two standard deviation to improve data interpretations.

Finally, to develop a Mississippi Kite selection model for Packsaddle WMA, I used beta coefficients from my broad scale model. Using the raster calculator tool, I multiplied each beta coefficient by the corresponding raster layer to create a binary raster layer using the equation:

$$= \beta_0 + \beta_1 x_{i1} + \dots + \beta_k x_{ik}$$

where  $X_i$  is a corresponding raster layer. The output raster was saved as “calculation 1.” Next, I computed the exponent of calculation 1 in Raster Calculator following the logistic regression formula. This new output I saved as “calculation 2.” The final predictive map representing the relative probability of used (P) was computed based on the equation:

$$P = \frac{\text{calculation2}}{(1 + \text{calculation2})}$$

## Results

We recorded 489 Mississippi Kite detections (218 in 2014 and 271 in 2015). In both years of the study, point density analysis revealed a disproportionate use of uplands compared with lowlands despite equal sampling of the two zones (Figure S2). Similarly, absolute density of Mississippi Kite was higher in the upland compared with lowland zones. During summer 2014, I recorded a mean kite density of  $2.21 \pm 0.70$  SE birds  $100 \text{ ha}^{-1}$  (95% confidence interval [CI]: 1.35–4.35) at the upland zone of the WMA, whereas mean density for the lowland zone was  $1.53 \pm 0.39$  SE  $100 \text{ ha}^{-1}$  (95% CI: 0.91–2.91). During 2015, mean density of Mississippi Kite was consistently lower at the lowland zone ( $1.47 \pm 0.65$  SE  $100 \text{ ha}^{-1}$ ; 95% CI: 1.20–3.35) of the WMA compared to its upland zone ( $2.68 \pm 0.48$  SE  $100 \text{ ha}^{-1}$ ; 95% CI: 1.04–3.01). Estimated abundances were similarly higher at the upland zones, which constituted 4680 ha of the area both years (2014:  $111.14 \pm 20.08$  SE; 2015:  $120.00 \pm 32.87$  SE) compared to the lowland zone (2014:  $39.00 \pm 9.86$  SE; 2015:  $42.00 \pm 12.26$  SE) with an area of 2750 ha. The top models from my MCDS analyses identified time of day and covariates representing observer as the most important variables



influencing kite detection at both upland and lowland zones in my study sites (Table S1). The models with hazard-rate function performed better than those with half normal or uniform key functions for each zone. At both zones, detection rates were highest for observer 1 compared with the other observers (Figure 3). The probability of kite detection was generally highest in early afternoon (1301–1500) and was lowest during the early hours of the day (0700–0900) in lowland zones, and late afternoon (>1500) in upland (Figure 3).

### Resource Selection by Mississippi Kite

We explored all possible model combinations to explain resource selection at each scale. Three top models within a  $\Delta AIC < 2$  with a cumulative weight of 0.79 were considered the most parsimonious models in explaining resource selection at the 12.56 ha scale. The models included bare ground, sparse vegetation, grassland, riparian forest, oil pads, and upland forest as the most important variables (Table 1). Kites avoided riparian vegetation, bare ground, oil pads, and grasslands at this scale and selected upland forest patches. Three of the variables at this scale (bare ground, grassland, and riparian) were significantly avoided ( $P < 0.05$ ) and one (upland forest) was significantly ( $P < 0.05$ ) selected (Table 2). At the 201.1-ha scale, two models within a  $\Delta AIC < 2$  window with a cumulative weight of 0.85 were considered most meaningful in explaining kite resource selection. Both models consisted of grassland, oil pads, sparse vegetation, upland forest, and riparian forest (Table 1). Contrary to the 12.56 ha scale, kites showed a positive significant ( $P < 0.05$ ) selection for grassland (Table 2). Selection for upland forest and sparse vegetation covers were also positive but only significant for upland vegetation (Table 2). On the other hand, kites maintained a negative relationship with oil pads and riparian vegetation. Avoidance of riparian vegetation and oil pads at the 201.1-ha scale were all significant at  $P < 0.05$  (Table 2). Distance to oil pads, distance to riparian forest, elevation, aspect, and slope were also important at driving broad scale selection or avoidance of resources by Mississippi Kite (Table 2). These variables were present at

my top two models within a  $\Delta AIC < 2$  window and having a combined Akaike weight of 0.76. The probability of kite use increased significantly ( $P < 0.05$ ) as distance to riparian forest cover increased (Figure 4A) and decreased significantly ( $P < 0.05$ ) with steeper slope (Figure 4B). My models also suggested an increased selection with increasing distance from oil pads and a significant ( $P < 0.05$ ) selection for higher elevation (Figure 4C); however, I did not detect any statistically significant effect of aspect or the interaction between slope and aspect on kite resource selection.

At the 12.56 ha scale, 57% of the total used locations were in upland forest and grassland. The least used land cover types were riparian forests and oil pads, which respectively accounted for 4% and 8% respectively. I found 17% more upland forest at used locations than at available non-use sites. Grassland vegetation was the most selected vegetation type at the 201.1-ha scale and represented 48% of used locations. At the broad scale, mean distance of used locations to riparian areas (~2198m) was ~956 m more than the mean distance of available locations to riparian areas (~1242 m). Compared with available locations, used locations were more likely to occur at higher elevations and were less likely to occur at higher values of slope.

Using beta values obtained at the broad scale, predicted distribution of Mississippi Kite highlighted two contrasting areas in terms of probability of use (Figure 5). The upland zone of the study area, received a higher predicted probability of use by Mississippi Kite, and the lowland zone, bordered by the Canadian River to the south, received a low probability of use.

## Discussion

We developed a novel method to explicitly quantify raptor resource selection using offset locations collected from field surveys. My study demonstrated that occurrence points, collected using traditional sampling techniques (e.g. line transects and point counts) over multiple survey events, can be robust in explicitly quantifying resource selection. In my case, I completed >29 repeated surveys on each designated transect over the course of two summers to provide data used in the analysis. Compared with a study design using telemetry, my method could not provide a detailed record of occurrence data for individuals over time. As a potential advantage over telemetry, my method permitted some information on habitat selection for many more individuals than it would have been practicable to capture, outfit, and track. I agree that under ideal conditions (e.g., large research budgets) using telemetry might be a preferred method for tracking wildlife species. However, for many studies, especially those on highly mobile bird species such as kites, telemetry may prove particularly challenging and costly (because of the need to perform aerial telemetry flights). Therefore, I hope that my approach will provide a quick and less expensive way to quantify fine-scale resource selection by wild species when telemetry technology is not available or cannot be applied.

Our study revealed a higher density of Mississippi Kite in the upland zone of Packsaddle WMA and suggested riparian avoidance at all spatial scales (Table 1). Previous studies, mainly within the Mississippi Alluvial Valley, demonstrated riparian preference by Mississippi Kite (Bader and Bednarz 2010; Barber et al. 1998; Evans 1981; Kalla 1979). According to these studies, kites selected large, intact stands of riparian forest. I did not find support for these selection characteristics for Mississippi Kites in my study site in western Oklahoma. Rather, birds showed strong avoidance of mature bottomland hardwood forest for smaller patches of upland woody vegetation, mainly hybrid shinnery oak (hybrid of *Q. stellate* and *Q. havardii*). Stronger selection of upland and the avoidance of riparian forests in this landscape might be a result of a suite of both biotic and environmental factors.

Several studies have demonstrated that Mississippi Kite feed predominantly on arthropods, chiefly in the orders *Homoptera*, *Orthoptera*, and *Odonata* (Bader and Bednarz 2011; Chiavacci 2010; Glinski and Ohmart 1983). In eastern Arkansas, Bader and Bednarz (2011) demonstrated that insects accounted for >80% of food items delivered to nestlings. Of the insect prey identified, at least 67% were cicadas and grasshoppers. Similarly, cicadas constituted 71% of insect prey delivered to Mississippi Kite nestlings in Arizona (Glinski and Ohmart 1983). In the Great Plains and specifically in prairie landscapes, cicadas and grasshoppers are both known to occur at higher densities in uplands compared to lowlands (Callahan Jr et al. 2000; Evans 1988; Masloski 2014). Strong selection of upland areas by the Mississippi kite at this site therefore might be related to prey abundance in upland areas.

Compared with most other raptors, Mississippi Kites return from their wintering grounds relatively late (Zalles et al. 2000), thereby devoting almost all of their time in North America to breeding. Given the relatively short time that the species devotes to breeding in North America, Mississippi Kite is likely to have a tight breeding schedule, such that re-nesting or laying a second clutch would be theoretically unattainable if a brood was lost at an advanced stage of breeding. Successful breeding is therefore critically dependent on selection of habitats that maximize breeding success. This includes selecting high quality areas away from predators. Anecdotal evidence suggest that riparian forest at Packsaddle WMA received high use by Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), and Red-tailed Hawk (*Buteo jamaicensis*). These raptors are known to be the most important nest predators of the Mississippi Kite (Chiavacci et al. 2014b; Chiavacci et al. 2014a; Miller 2005). For example, Chiavacci et al. (2014a) demonstrated that nest predation was the leading cause of nest failure in bottomland nesting Mississippi Kite and specifically identified owls as some of the top nest predators of kite's nestlings. It is therefore plausible that Mississippi Kite would minimize nest predation through selection of areas away from their main predator's preferred habitat.

My top broad-scale model suggested a negative relationship between kite occurrence and oil wells. On average, Mississippi Kite selected areas ~150 m away from oil wells than random locations. Broad-scale

avoidance of oil pads has been documented in several avian species as a strategy that improves adult survival and reproductive fitness (Hamilton et al. 2011; Hethcoat and Chalfoun 2015; Holloran 2005). Avoidance of oil wells is often attributed to habitat loss, noise pollution, and contamination from reserve pits and evaporation ponds used to store the byproducts of drilling (Jones et al. 2015). Packsaddle WMA supported at least 30 active oil wells during my study. Kite avoidance of oil wells in this landscape might be attributed to habitat loss resulting from the removal of preferred nesting vegetation around oil wells and from noise pollution from oil and gas well compressors. Impacts of chronic oil and gas compressor noise in limiting habitat use and reducing nesting and pairing success have been demonstrated in several avian species (Bayne et al. 2008; Francis et al. 2011; Habib et al. 2007). For example, Francis et al. (2011) demonstrated a significant reduction in habitat occupancy by Western Scrub-jay (*Aphelocoma californica*) and Gray Flycatcher (*Empidonax wrightii*) with increasing noise amplitude from oil and gas compressors.

Abundance of Mississippi kites at my study site was the highest compare to other studies in the central Great Plains (Allan and Sime 1943; Parker 1999; Sweet 1991). I estimated a population of  $\leq 182$  individuals in 7430 ha compare to Allan and Sime (1943) estimates of one pair per 250 ha in the Texas panhandle (<55 Km west of my study site). Unlike population estimates from previous studies that were based on highway counts, my counts were based on a more methodical surveys approach over a two years period.

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Table 1: Summary of results from resource selection models for Mississippi Kite at Packsaddle WMA, Oklahoma of 2014 and 2015. Shown are top 8 models collected at 12.56 and 201.10 ha spatial scales.

Scale (ha)		df	AICc	$\Delta AICc$	G <sub>Di</sub>
12.56	bare ground+grass+riparian forest+sparse veg.	6	1156.5	0	0.44
	bare ground+grass+oil pads+riparian forest+sparse veg.+upland forest	7	1158.2	1.71	0.19
	bare ground+grass+riparian forest+upland forest	5	1158.5	1.98	0.16
	bare ground+grass+oil pads+riparian forest+upland forest	6	1160.3	3.75	0.07
	bare ground+riparian forest+sparse veg.+upland forest	5	1160.6	4.12	0.06
	bare ground+riparian forest+upland forest	4	1161.6	5.09	0.03
	bare ground+oil pads+riparian forest+sparse veg.+upland forest	6	1162.2	5.7	0.03
	bare ground+oil pads+riparian forest+upland forest	5	1163.2	6.73	0.02
201.1	<i>Vegetation models</i>				
	bare ground+grass+riparian forest+sparse veg.+upland forest+grass*sparse veg.	7	1011	0	0.55
	bare ground+grass+oil pads+riparian forest+sparse veg.+upland forest+grass*sparse veg.	8	1012.7	1.71	0.23
	bare ground+grass+riparian forest+sparse veg.+grass*sparse veg.	6	1014.3	3.26	0.11
	bare ground+grass+oil pads+riparian forest+sparse veg.+grass*sparse veg.	7	1015.7	4.68	0.05
	bare ground+riparian forest+sparse veg.	4	1018.8	7.8	0.01
	bare ground+grass+riparian forest+sparse veg.+upland forest	6	1018.8	7.8	0.01
	bare ground+riparian forest+sparse veg.+upland forest	5	1019.1	8.08	0.01
	bare ground+grass+riparian forest+sparse veg.	5	1019.7	8.67	0.01
	<i>Topographical and spatial variables</i>				
	aspect+dist.riparian forest+dist.oil pads+elevation+slope	6	996	0	0.47
	aspect+dist.riparian forest+elevation+slope	5	997	1.02	0.28
	dist.riparian forest+dist.oil pads+elevation+slope	5	998.2	2.2	0.16
	dist.riparian forest+elevation+slope	4	999.2	3.24	0.09
	aspect+dist.oil pads+elevation+slope	5	1011.6	15.62	0
	aspect+elevation+slope	4	1012.2	16.3	0
	dist.oil pads+elevation+slope	4	1015	19.06	0
	elevation+slope	3	1015.7	19.77	0

Table 2: Model-averaged estimates for the final selected models at fine (12.56 ha), and broad scales (201.10 ha). Variables with  $p$ -values  $< 0.050$  are bolded.

Scale (ha)	Variables	Estimate	SE	Pr(> z )	Odd ratio	LCL	UCL
12.56	<b>Bare ground</b>	<b>-0.71</b>	<b>0.23</b>	<b>0.002</b>	<b>0.50</b>	<b>0.30</b>	<b>0.75</b>
	<b>Grass</b>	<b>-0.34</b>	<b>0.143</b>	<b>0.017</b>	<b>0.71</b>	<b>0.53</b>	<b>0.93</b>
	<b>Riparian forest</b>	<b>-0.86</b>	<b>0.23</b>	<b>&lt;0.001</b>	<b>0.42</b>	<b>0.26</b>	<b>0.64</b>
	Sparse veg	-0.22	0.18	0.236	0.74	0.55	0.99
	<b>Upland forest</b>	<b>0.55</b>	<b>0.17</b>	<b>0.001</b>	<b>1.67</b>	<b>1.22</b>	<b>2.31</b>
	Oil pads	-0.02	0.09	0.786	0.92	0.68	1.23
201.1	<i>Vegetation models</i>						
	<b>Grassland</b>	<b>0.48</b>	<b>0.19</b>	<b>0.01</b>	<b>1.67</b>	<b>1.13</b>	<b>2.49</b>
	<b>Oil pads</b>	<b>-0.57</b>	<b>0.2</b>	<b>0.005</b>	<b>1.13</b>	<b>0.61</b>	<b>2.07</b>
	<b>Upland Forest</b>	<b>0.51</b>	<b>0.17</b>	<b>0.002</b>	<b>1.56</b>	<b>1.13</b>	<b>2.19</b>
	<b>Riparian forest</b>	<b>-2.52</b>	<b>0.83</b>	<b>0.002</b>	<b>0.08</b>	<b>0.01</b>	<b>0.32</b>
	Sparse veg	0.03	0.12	0.824	0.90	0.59	1.37
	<i>Topographical and spatial variables</i>						
	<b>Distance to riparian forest</b>	<b>0.21</b>	<b>0.05</b>	<b>&lt;0.001</b>	<b>1.24</b>	<b>1.12</b>	<b>1.36</b>
	Distance to oil pads	0.29	0.16	0.063	1.34	0.98	1.83
	<b>Elevation</b>	<b>0.3</b>	<b>0.04</b>	<b>&lt;0.001</b>	<b>1.28</b>	<b>1.19</b>	<b>1.39</b>
	<b>Slope</b>	<b>-0.31</b>	<b>0.06</b>	<b>&lt;0.001</b>	<b>0.73</b>	<b>0.65</b>	<b>0.82</b>
	Aspect	-0.1	0.2	0.621	0.91	0.62	1.34
	Slope*aspect	-0.01	0.08	0.853	0.99	0.84	1.15

Supplementary table

Table S1: Summary details for models fitted to Mississippi Kite detection at Packsaddle Wildlife Management Area, Oklahoma, USA, 2014–2015. Detection functions were defined using parametric key including half-normal (hn), hazard-rate (hr), and uniform (unif). Also shown are density estimates (D), detection probabilities (P), and their standard errors.

site	Covariate	Key	K	Delta		D	SE	P	SE
				AIC	AIC				
Lowland	Observer	hn	2	0.000	707.571	0.014	0.014	0.461	0.049
	observer+TOD*	hn	3	0.406	707.977	0.014	0.014	0.460	0.125
	observer+month	hn	3	1.326	708.897	0.027	0.027	0.244	0.044
	observer	hr	2	3.677	711.248	0.020	0.020	0.435	0.098
	TOD	hr	2	3.679	711.251	0.015	0.015	0.436	0.098
	no coveriate	hr	2	4.046	711.617	0.018	0.018	0.360	0.087
	observer+month	hn	3	4.892	712.464	0.015	0.015	0.454	0.051
	no coveriate	hn	2	5.054	712.626	0.017	0.017	0.383	0.051
	no coveriate	unif	2	5.456	713.027	0.017	0.017	0.383	0.051
	Month	hr	2	6.205	713.777	0.019	0.019	0.355	0.041
	month+TOD	hn	3	7.885	715.456	0.015	0.015	0.429	0.134
	observer+TOD	hr	3	8.444	716.016	0.020	0.020	0.328	0.040
	TOD	hr	2	8.700	716.271	0.018	0.018	0.359	0.049
	Month	hn	2	11.541	719.113	0.013	0.013	0.505	0.043
	month+TOD	hr	3	12.989	720.560	0.020	0.020	0.338	0.041
Upland	observer+TOD	hr	8	0.000	4512.963	0.027	0.007	0.360	0.010
	no coveriate	hr	2	3.206	4516.169	0.027	0.007	0.360	0.033
	observer+month	hr	8	3.478	4516.441	0.028	0.007	0.355	0.015
	no coveriate	hn	2	5.875	4518.838	0.025	0.005	0.510	0.017
	Observer	hr	3	7.410	4520.373	0.025	0.006	0.400	0.022
	no coveriate	unif	3	7.410	4520.373	0.025	0.006	0.400	0.022
	month+TOD	hr	10	13.651	4526.614	0.029	0.007	0.336	0.012
	Month	hr	6	16.156	4529.119	0.022	0.006	0.441	0.017
	Observer	hn	3	28.768	4541.731	0.019	0.005	0.510	0.012
	observer+TOD	hn	4	30.065	4543.028	0.019	0.005	0.503	0.018
	observer+month	hn	7	35.735	4548.698	0.019	0.005	0.503	0.018
	TOD	hr	5	38.177	4551.140	0.019	0.005	0.507	0.018
	TOD	hn	5	38.177	4551.140	0.019	0.005	0.507	0.018
	Month	hn	5	39.348	4552.311	0.019	0.005	0.508	0.018
	month+TOD	hn	9	43.550	4556.513	0.019	0.005	0.505	0.018

\*TOD = time of day

## FIGURE CAPTIONS

Figure 1: Map of the Packsaddle Wildlife Management Area, Oklahoma, USA showing Mississippi Kite detection points recorded along transect lines (A), and extrapolated points after application of an offset model (B), 2014–2015.

Figure 2: A) Approximate location of each raptor detection as a function of estimated distance from observation point  $A$  and the perpendicular distance  $a$  to the bird from a point on the sampling transect  $b$ . I estimated distance to the raptor  $c$  using a laser rangefinder, and angle  $\theta$  from the transect line  $b$  using an azimuth compass. I then plotted the estimated raptor detection point  $B$  as X, Y coordinates in a GIS. B) I used the raptor detection points  $B$  as the centroids of circular land cover buffers described by radii of 200 and 1000m.

Figure 3: Detection function for Mississippi Kite plotted for three observers in uplands (A) and lowlands (B) at Packsaddle Wildlife Management Area, Oklahoma, USA, 2014–2015. Detection functions (pooled) among observers are plotted in upland (C) and lowland (D) for time of day sampling: 0700–0900 (T1), 0901–1100 (T2), 1101–1300 (T3), 1301–1500 (T4), and >1500 (T5).

Figure 4: Probability of Mississippi Kite occurrence within the significant broad scale variables at Packsaddle WMA, Oklahoma, USA, 2014–2015. Independent variables were rescaled to reduce the number of possible classes. The solid line plots the predicted relationship from the best model in table 3; dashed lines are  $\pm 1$  SE. Density of color in the gray circles indicates relative sample size.

Figure 5: Relative probability of use predicted for Mississippi Kite at Packsaddle Wildlife Management Area, Oklahoma, USA, 2014–2015.



### **Supplemental Material Figure**

Figure S1: North American Breeding Bird Survey population trend for Mississippi Kite in Oklahoma, USA 1968 –2013.

Figure S2: Point density map of Mississippi Kite occurrence at the Packsaddle Wildlife Management Area, Oklahoma USA 2014–2015.

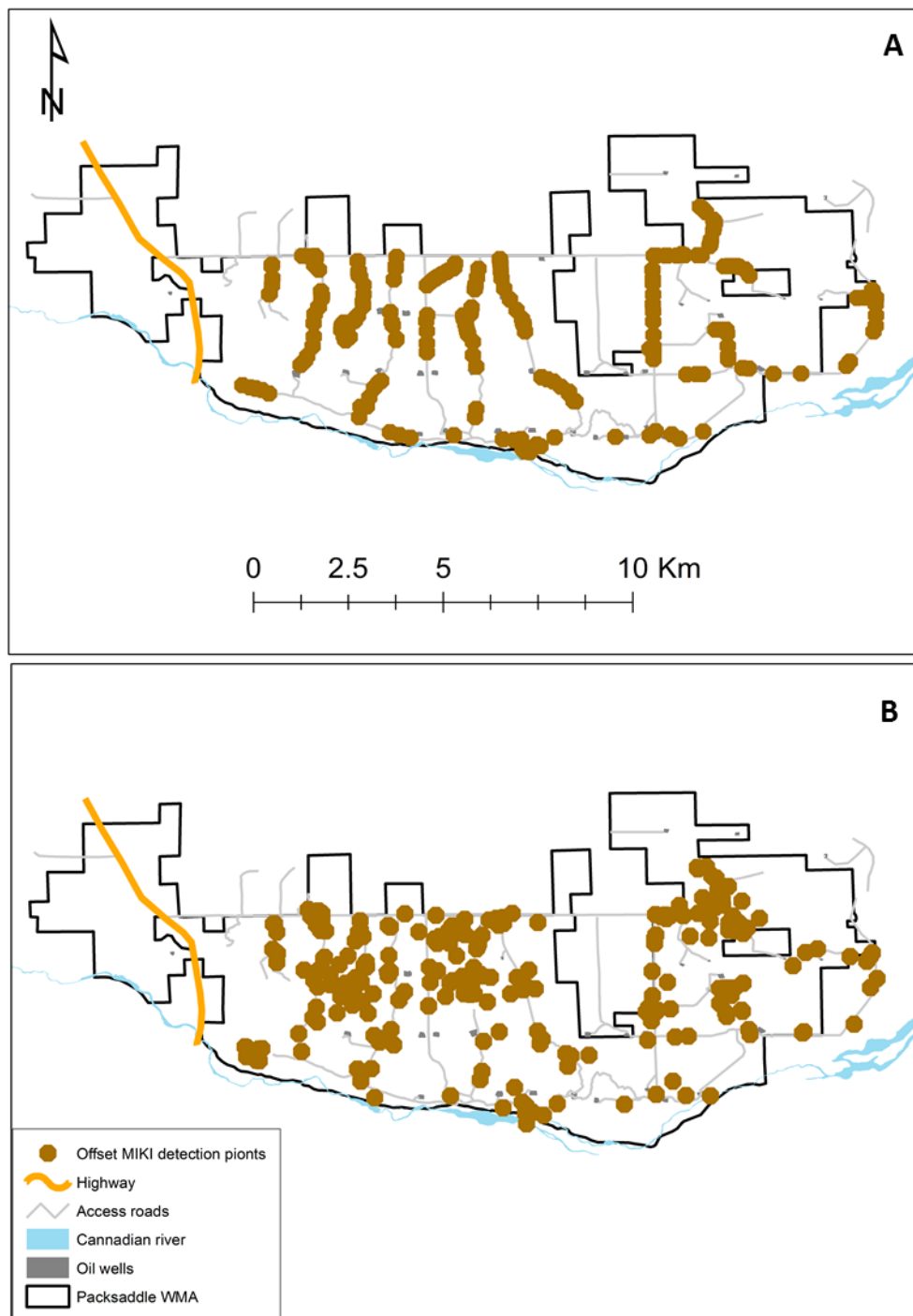


Figure 1

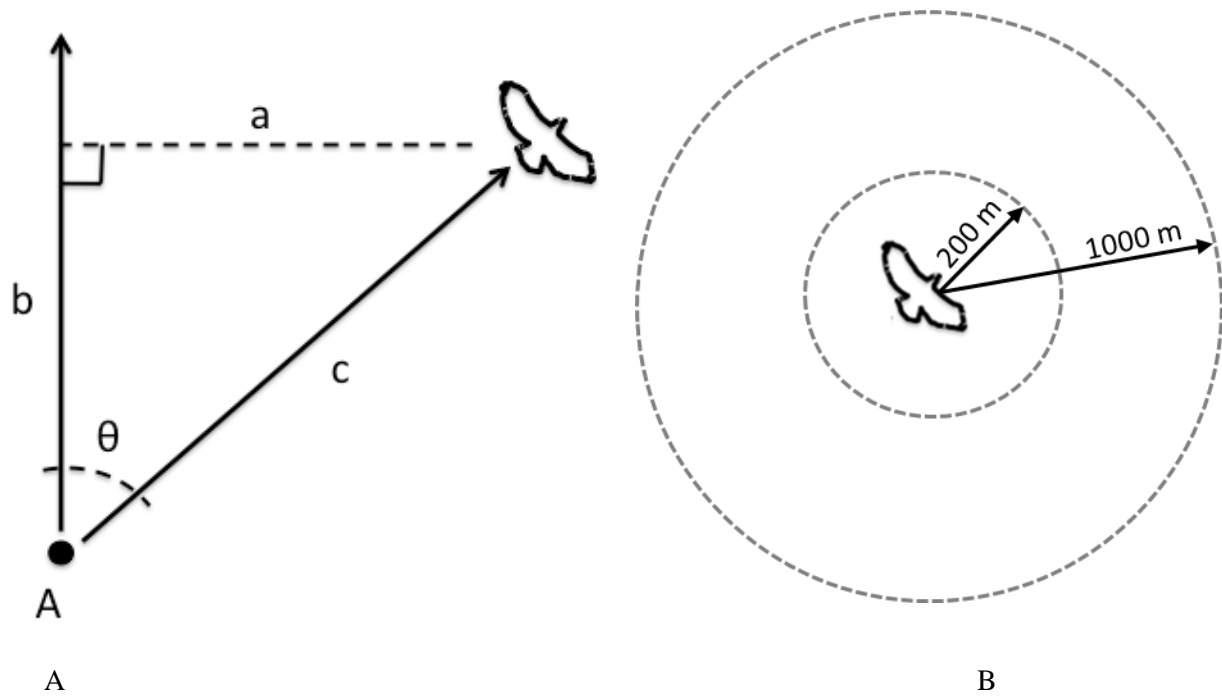


Figure 2

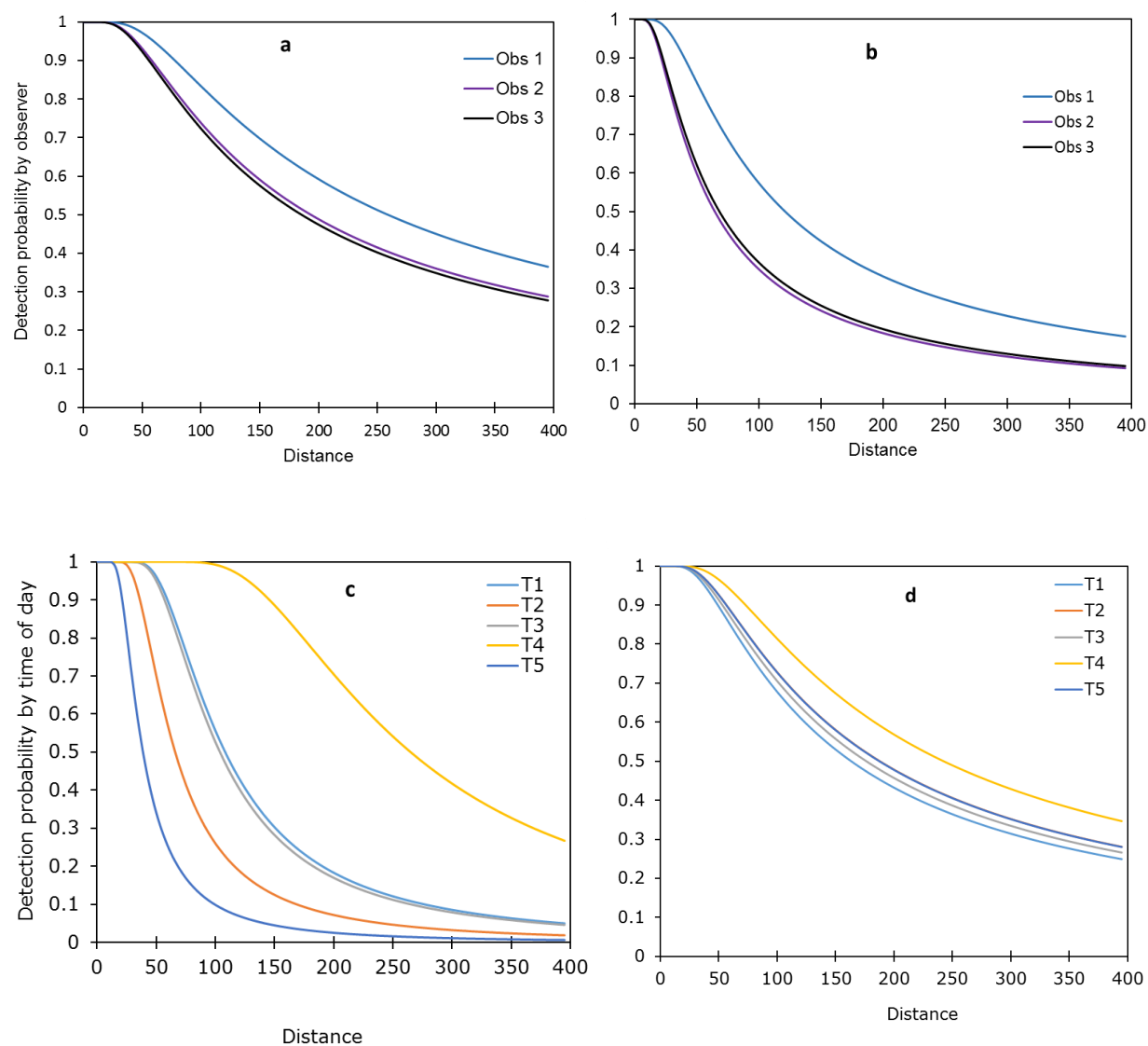


Figure 3

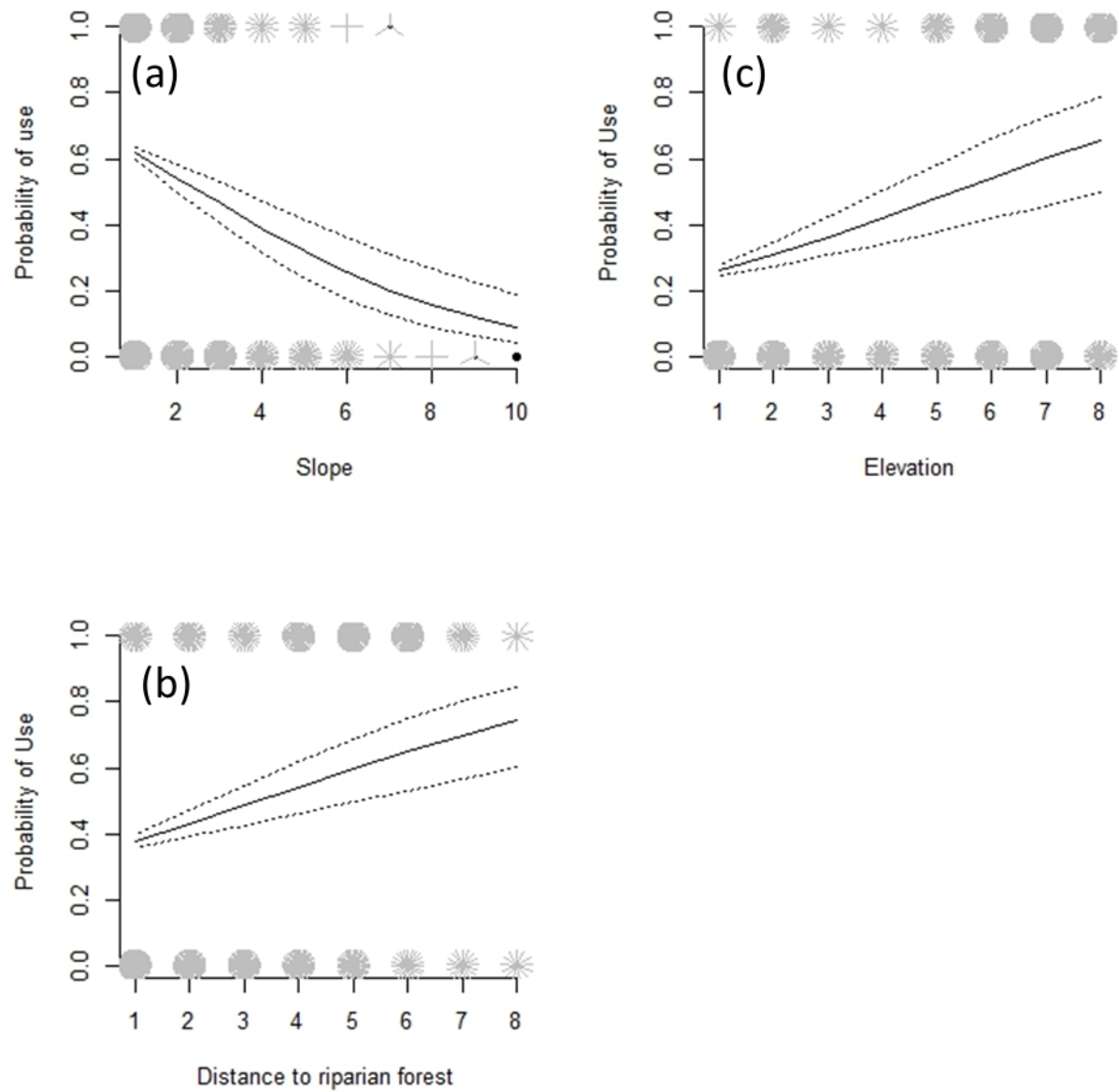


Figure 4

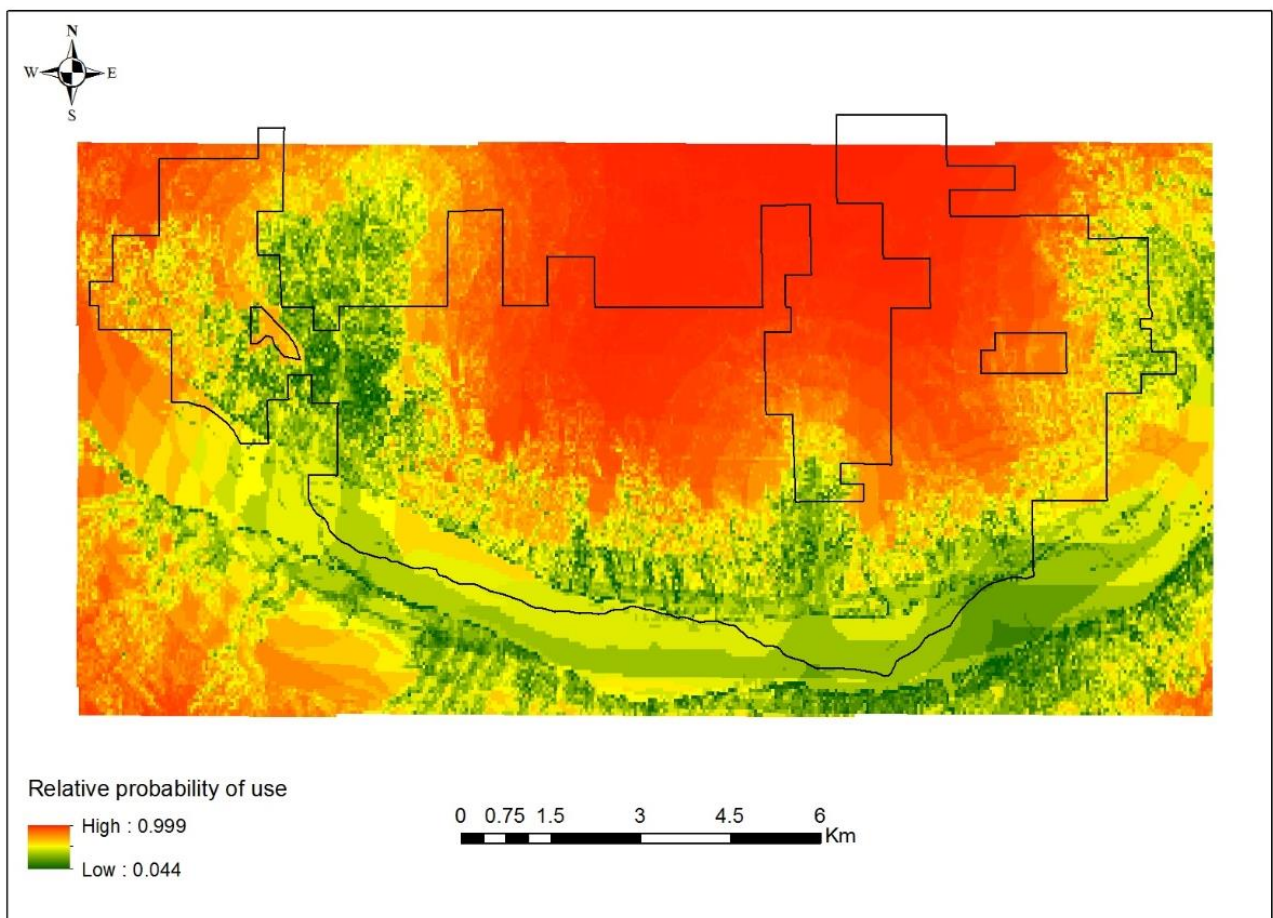


Figure 5

**Supplemental Material Figure**

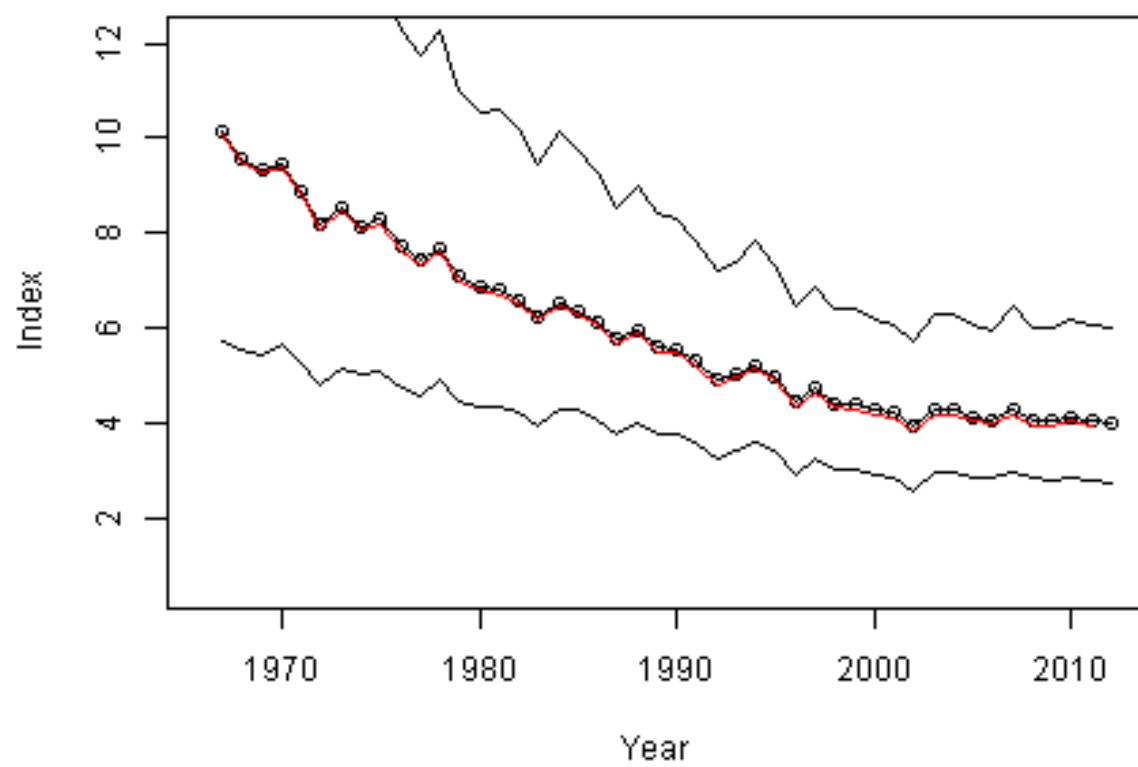


Figure S1

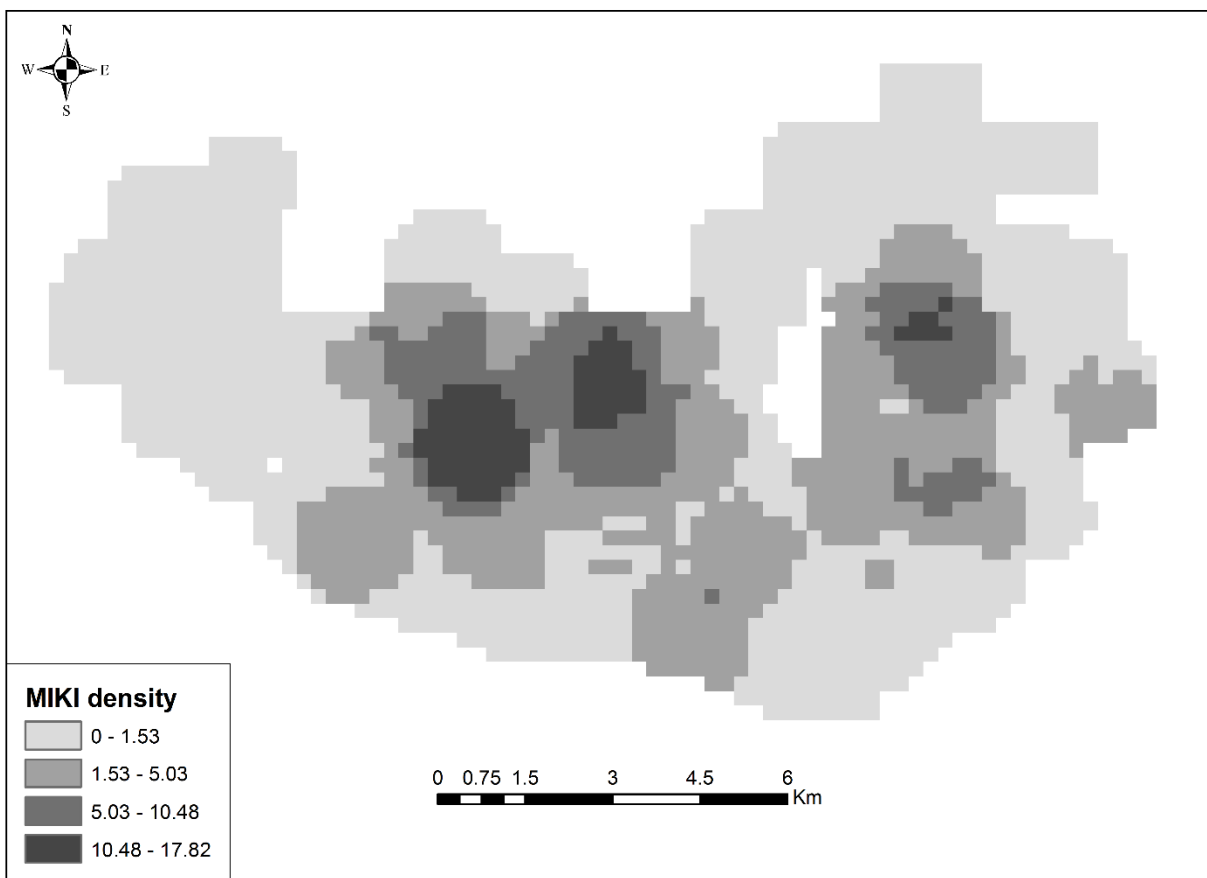


Figure S2.



## CHAPTER II

### STRUCTURAL HETEROGENEITY AFFECTS RAPTOR ASSEMBLAGES AND NICHE CHARACTERISTICS IN MIXED-GRASS PRAIRIE.

#### **Abstract**

Landscape function is largely determined by landscape structure. Evidence suggests that landscape heterogeneity often benefits generalists over sympatric specialists. The scale at which animals perceive heterogeneity varies across species and play important roles in determining species assemblages supported by different landscapes. In this study, I investigated the relative importance of landscape heterogeneity in the structuring of raptor assemblages in mixed-grass prairie. I compared niche breadth and overlap of 14 species in two landscapes that differed in heterogeneity. I used a modified line transect approach with distance sampling to map approximate first detection locations of raptors. I then compared land cover in buffered areas around detection locations to randomly selected locations at different scales. I calculated niche breadth and compared among species. Species composition was similar in both landscapes but niche characteristics differed according to heterogeneity. Raptor assemblages were better predicted by land cover composition in heterogeneous landscapes than by land cover configuration in homogenous landscapes. Six of the 14 species occupied marginal niches and narrower niche breadths in homogeneous landscapes. None of these species demonstrated marginality but occupied broader niche breadths in the heterogeneous landscapes. My study provides evidence that heterogeneity is important in providing conditions necessary to support multiple, sympatric birds of prey in mixed-grass prairie.

Species overlapped broadly under heterogeneity but less in landscapes with larger patches of distinct land cover types.

**Key words:** Heterogeneity, Niche characteristics, Niche breadth, Raptor communities, Landscape composition, Landscape configuration

## Introduction

The uneven distribution of species is often mediated by the mosaic of land cover patches in the landscapes in which they occur (Pickett & Cadenasso 1995; Stein *et al.* 2014). A structurally complex landscape is presumed to offer diverse opportunities for species to exploit resources in such a way that reduces interspecific competition, thereby promoting species diversity (Holt 1984; Wiens 1995; Tews *et al.* 2004). Empirical support for this relationship, however, is mixed: high land cover diversity (i.e., heterogeneity) has been associated with both increases and decreases in species diversity (August 1983; Ralph 1985; Van Rensburg *et al.* 2002; Hovick *et al.* 2015). For example, both compositional and configurational heterogeneity have been shown to increase the diversity of butterflies and carabid beetles in agricultural landscapes (Flick, Feagan & Fahrig 2012; Slancarova *et al.* 2014). Furthermore, landscapes that are characterized by high patch densities and small patch sizes have been shown to benefit generalist species to the detriment of habitat specialists (Devictor, Julliard & Jiguet 2008; Mahon *et al.* 2016). In these landscapes and depending on the species, structural attributes are more likely to be perceived as fragmentation rather than heterogeneity (Bertrand, Burel & Baudry 2016). In a Mesoamerican tropical rainforest ecosystem, the  $\alpha$ -diversity of generalist bird species showed positive correlation with landscapes that had lower forest cover and higher number of forest patches (Carrara *et al.* 2015). The same study also demonstrated that  $\alpha$ -diversity of specialist species that depend on large patches of distinct cover types was positively associated with large patches of old-growth forest cover and was negatively related to the percentage of secondary forest cover with higher patch density. These

studies point to the fact that anthropogenic disturbances that alter the structural metric of a landscape are likely to negatively affect specialists by placing them in competitive proximity with generalist species thus increasing their risk of extinction or extirpation. This is because interspecific competition of co-occurring species in patchy landscapes is likely to result in spatial avoidance and a reduction or loss of foraging opportunities for less competitive species though in a scale-dependent way (Turner *et al.* 1997; Fuhlendorf *et al.* 2002; Boyce *et al.* 2003).

Predators offer ample opportunities for understanding the role of mosaics on species habitat selection (Gorini *et al.* 2012). Given their important roles in determining community structure of co-occurring prey species, understanding predator distribution, community composition, abundances, and niche relationships is often important in setting landscape level conservation goals (Sánchez-Zapata & Calvo 1999; Krüger & Lindström 2001; Penteriani, Gallardo & Roche 2002; Bellocq & Gómez-Insausti 2005). The structural landscape mosaic has been shown to affect the way predators compete for resources and the attendant prey vulnerability risk (Gorini *et al.* 2012). Predator-predator competition may reduce hunting success among predators by limiting the use of habitats that provide good hunting grounds (Kauffman *et al.* 2007). On the other hand, spatial configuration of the landscape may reduce the amount of refugia available to sympatric prey species in such a way that increases the vulnerability of less competitive individuals to predation (Koivunen, Korpimäki & Hakkarainen 1998).

Vegetation cover, structure, and availability of nesting and perching substrate are often responsible for the differential distribution and composition of raptor species in many landscapes (Tapia, Kennedy & Mannan 2007). For example, Anderson (2001) demonstrated that landscape heterogeneity was the most significant predictor of direct increases in raptor diversity, density, and richness in the tropical moist forest of the Río Plitáno watershed in northeastern Honduras.

Information on the predator composition, abundance, distribution in space and time, and preferred vegetation type (i.e. organism's use of relative to its availability; (Aarts *et al.* 2008; Beyer *et al.* 2010), is

essential in making informed decisions on how best to manage for prey species, especially in landscapes where predators are believed to limit prey population substantially. This is practically relevant in the mixed-grass prairie landscapes of the Southern Great Plains where drastic decline of game bird species have been partly attributed to avian predation pressure (Cox *et al.* 2004; Hagen *et al.* 2007; Wolfe *et al.* 2007). In this study, my objectives were 1) to describe the abundance and structure of raptor communities at two mixed-grass prairies; 2) estimate the relative importance of landscape composition and landscape configuration in the structuring of raptor community assemblages in mixed-grass prairie ecosystems; and 3) describe the niche characteristics of raptor communities and the role of heterogeneity on species specialization.

## Methods

### Study areas

Our study was conducted within two Wildlife Management Areas (WMAs) located in northwestern Oklahoma. The Packsaddle WMA covers ~6,475 ha of mixed prairie with an elevation that ranges approximately 579–762 m above sea level. The average annual precipitation is ~53 cm, with the majority occurring during spring and summer (DeMaso *et al.* 1997). Soils consist mainly of Nobscot fine sand, Nobscot-Brownfield, and Pratt-Tivoli loamy fine sand (DeMaso *et al.* 1997; Townsend *et al.* 2001). Predominant grasses in the WMA include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Forb species include western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*), erect dayflower (*Commelina erecta*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation include shinnery oak (*Quercus harharvardii*), hybrid shinnery oak (*Q. stellate*), sand sagebrush (*Artemisia filifolia*), and sand plum (*Prunus angustifolia*: DeMaso *et al.* 1997;

Townsend *et al.* 2001). Anthropogenic activities in this area are related mainly to oil explorations. Beaver River WMA is ~7,163 ha in area, consisting of a mixture of upland, floodplain, and river bottom. Vegetation around the upland area is predominantly sagebrush and buffalograss (*Bouteloua dactyloides*) interspersed with sand plum thickets and gently rolling sandhills. The floodplain portion of the WMA is comprised mostly of grasses mixed with cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and American elm (*Ulmus americana*). The river bottom is mostly woody vegetation consisting of sand plum thickets and salt cedar (*Tamarix* spp: Tanner *et al.* 2015). The two WMAs are managed by the Oklahoma Department of Wildlife Conservation mainly for game hunting. Most of the management practices on the WMAs are targeted at enhancing the population of the Northern Bobwhite (*Colinus virginianus*) and other game species. A combination of prescribed grazing by cattle and prescribed burns (mostly at Packsaddle) are conducted to increase landscape heterogeneity and to minimize tree encroachment.

#### Raptor survey

To quantify raptor occurrences, I followed standard distance sampling protocols based on line transect surveys (Bibby *et al.* 2000; Buckland *et al.* 2001). I established 14 line transects at Packsaddle and 16 at Beaver River WMA. All but two transects at Packsaddle were placed along existing trails or roads (Fuller & Mosher 1987; Augiron *et al.* 2015) and measured between 2–5 km in length totaling 49.42 Km at Packsaddle and 58.98 km at Beaver River. I surveyed each transect at least twice each month between Jan. 2013–Dec. 2015. To reduce the chance of counting an individual more than once, I placed transect lines along trails separated by a distance  $\geq 900$  m (Greenwood & Robinson 2006). An observer, sometimes accompanied by a driver, scanned a distance of approximately 400 m on either side of the transect line for raptors from a truck that was driven at a speed of 20–30 km per h (Andersen 2007). I georeferenced each raptor detection at the point of observation using a Garmin Montana 650TM GPS unit and estimated their distances from the transect line using a Nikon 8398 ACULON laser range finder. I

also obtained the angle of observation from the observer using an azimuth compass. To develop a spatially explicit model of raptor – habitat association, I plotted each georeferenced point to the point of actual occurrence in time using the “Bearing Distance to Line” tool in ArcGIS 10.2 (Atuo and O’Connell in review). This tool created a new feature class containing a geodetic line feature for each predator occurrence point constructed based on the values in the x, and y coordinate fields, angle of observation, and detection distance. Next, I used the “Feature Vertices to Points” tool to create a feature class containing a georeferenced points at the end of each geodetic line feature. These new points containing x,y coordinates represented the actual location of the individual bird at the time it was sighted. Thus, I developed a new layer of offset points that represented the actual locations of individual sightings collected during surveys.

## Vegetation Classification

We collected vegetation variables from a 10 m resolution imagery acquired through the National Agriculture Imagery Program (NAIP). The imagery which was acquired in 2015 is pre-processed and classified by the Oklahoma Department of Wildlife Conservation and can be obtained at [http://www.wildlifedepartment.com/facts\\_maps/ecoregions.htm](http://www.wildlifedepartment.com/facts_maps/ecoregions.htm). First, I clipped the land cover map to my study extent in order to reduce the number of land cover classes and processing time. The original vegetation map included a layer of 31 land cover classes for Packsaddle and 24 classes for Beaver River. Hence, I reclassified each layer by combining similar vegetation classes to create a new layer containing 9 dominant vegetation cover types (landscape composition variables) for Packsaddle and 8 classes for Beaver River (Table 1). To estimate landscape level raptor-habitat association, I stratified each study site into squared polygons of 1000 m x 1000 m. Within each polygon, I extracted landscape composition (vegetation) variables within an 800 m radius buffer centered at a centrally placed point location in the polygon. Next, I overlaid my offset raptor locations over the stratified maps and summarized raptor abundances within each polygon.

## Configurational variables

To obtain landscape configuration variables at each site, I used the raster-split tool in ArcMap to split my land cover rasters layers into 50 raster segments (cells) of 1000 x 1000 m for Packsaddle and 45 cells of 1000 x 1000 m for Beaver River. Using these smaller segments, I selected several landscape level metrics to quantify the structure of the landscape mosaic available in each cell. I also quantified class level metrics focusing on the area and configuration of three main land cover types that represent the dominant vegetation cover in each landscape (Packsaddle: sandhill shinnery, upland woodland, and riparian woodland; Beaver River: mixed-grass prairie, upland shrub, and riparian woodland). For landscape level metrics, I quantified indices of (1) Shannon Diversity (SHDI), measures the diversity of the landscape mosaic based on information on the number of patches and extent of each patch type; (2) edge length (EL), measures the total edge segments of all patch types without contrast weighting; (3) the perimeter-area fractal dimension (PAFRAC), provides a global measure of landscape complexity; (4) patch density (PD), measures the total density of individual patches in the landscape; (5) landscape shape index (LSI) provide a standardized measure of total edge or edge density that adjusts for the size of the landscape. At the class level, I calculated (1) Percentage of like adjacencies (PLADJ) which measures the degree of aggregation of focal patch types; (2) Total edge (TE) which is an absolute measure of total edge length of a particular patch type; and (3) number of patches (NP) which measure the number of distinct patches in each cell. In addition to the landscape configuration matrices listed above, I also calculated elevation and slope from the Digital Elevation Model (DEM) in ArcGIS 10.2.2. DEM data were collected from the United States Geological Survey (USGS) data portal at 1/3 arc-seconds (10 m) resolution. For each landscape cell, I extracted elevation and slope values based on a centrally place point in the cell.

## Data analysis

We assessed raptor species richness and sample coverage (a measure of sample completeness expressed as the proportion of total number of individuals in a community that belong to the species represented in the sample) using the extrapolation and rarefaction methods (Chao *et al.* 2014). Using the iNEXT package v2.0.5 (Hsieh, Ma & Chao 2016) in R, I completed 100 bootstrap runs for each sample and extrapolated the number of species to twice the number of individuals in each sample. Given that coverage-based rarefaction is known to provide minimal biases of community species richness by keeping the ratio of species richness instead of compressing it (Chao & Jost 2012), I plotted both individual-based species accumulation curves and sample coverage curves for each site (Figure 1).

We used multivariate analyses to demonstrate the relationship between multiple raptor species and the environmental gradients. I quantified the impact of landscape heterogeneity on raptor communities by performing direct gradient analyses and variation partitioning in Canoco 5.03 (ter Braak & Smilauer 2012). For all analyses, I log transformed ( $\log(x+1)$ ) my abundance data and down weighted rare species to dampen effects of extreme samples (ter Braak & Smilauer 2012; Šmilauer & Lepš 2014). Prior to performing analyses, I log transformed a selection of the landscape composition variables to maximize the linearity of their relation and ensure that the ecological importance of all the land cover types was considered (Šmilauer & Lepš 2014; Neumann *et al.* 2016).

To understand effects of landscape composition and landscape configuration on raptor assemblages, I performed separate partial canonical correspondence analyses (pCCA) for each variable sets. For each analysis, I selected variables that best summarized the effects of landscape composition or landscape configuration on raptor assemblages using partial interactive forward selection (pIFS). This allowed the removal of collinear and redundant variables from the pCCA model (ter Braak & Smilauer 2012; Šmilauer & Lepš 2014). For each pIFS, I included significant variables that were collected over a global Monte-Carlo permutations test with 999 iterations. In each model, I determined the significance of explanatory variables using a p-value  $< 0.05$  (ter Braak & Smilauer 2012). I applied the false discovery rate method to adjust the significance values for potential inflated family-wise type 1 errors, thus reducing



the likelihoods of false significance (ter Braak & Šmilauer 2012; Šmilauer & Lepš 2014). To further determine the unique and shared contributions of the landscape composition and configuration variables in explaining raptor species composition, I performed a variance partitioning of the important variables identified by the pIFS models for each site. The variance partitioning procedure quantifies whether and to what degree the variability in raptor assemblages at each study site is explained by landscape composition variables only, landscape configuration variables only, or whether the overlap of the two variable sets together has an additive explanatory effect (Legendre 2008; Šmilauer & Lepš 2014).

To estimate the ecological niche filled by each raptor species within each community, I performed an Outlying Mean Index (OMI) analysis (Dolédéc, Chessel & Gimaret-Carpentier 2000) using the same set of landscape composition and landscape configuration variables as in the pCCA models. The OMI or species marginality analysis is a multivariate analysis technique (based on Principle Component Analysis) that measures the distance between the mean habitat conditions used by a species (species centroid) and the mean habitat conditions that exist in the study landscape. An OMI analysis places each species along a habitat gradient (niche hyperspace) based on its habitat requirements. A measure of how far a species occurs away from the origin of the niche hyperspace is termed its marginality. Hence, the marginality of a species under investigation depends on its deviation from the origin of the niche hyperspace. Species with higher marginality scores select unique environmental conditions different from the mean available conditions in the landscape. The OMI analysis also calculates a species' tolerance (i.e. species niche breadth). Species with higher tolerance values can occupy varying habitat conditions (generalist species) while those with low tolerance values are limited in their habitat use (specialists). The OMI technique also addresses some of the limitations of CCA and Redundancy Analysis (RDA), which are best suited for data with unimodal distribution (with respect to CCA) or linear distribution (with respect to RDA) (Dolédéc, Chessel & Gimaret-Carpentier 2000). Unlike the CCA which tend to over-emphasize rare species in an ordination output, the OMI technique makes no assumptions about species responses to environmental variables thus assigning equal weights to all sample units irrespective of their species

abundance scores (Dolédéc, Chessel & Gimaret-Carpentier 2000). I performed the OMI analysis using the ade4 package (Chessel, Dufour & Dray 2016) in program R, and determined significance of the OMI based on a Monte Carlo simulation of 999 random permutation values of species marginalities. Finally, I used a two-sampled student t-test to obtain the difference in landscape heterogeneity by comparing patch densities collected within each 1000 m x 1000 m cells between my study systems.

## Results

We recorded 3230 raptor detections belonging to 19 species at the Beaver River WMA and 2348 detections of 15 species at the Packsaddle WMA (Table 2). The Red-tailed Hawk (*Buteo jamaicensis*) and Northern Harrier (*Circus cyaneus*) were the most abundant species, respectively constituting 36 % and 31 % of detected species at Beaver River, and 35 % and 13 % at Packsaddle (Table 2). Species with less than 10 detections were excluded from my ordination analysis. At both study sites, raptor abundances were significantly higher during winter than they were in summer. Species diversity was  $6.13 \pm 0.19$  during winter and  $4.49 \pm 0.12$  during summer at Beaver River. Diversity at Packsaddle WMA was  $5.07 \pm 0.15$  in winter and  $5.03 \pm 0.14$  in summer. Overall species richness was slightly greater at Beaver River WMA than Packsaddle WMA (Figure 1). Confidence intervals of rarefaction-extrapolation curves for the two study sites overlapped (Figure 1) indicating that the two sites have shared similarities in species richness both in the number of species detected and when extrapolated to twice the number of detected individuals. For both sites, the rarefaction-extrapolation curves approach asymptote (Figure 1a) and the sample coverages were at ~100 % (Figure 1b) indicating that raptor assemblages were adequately sampled and that most of the species in these landscapes were detected. The sample, however, did not represent a complete census of raptor species in the area due the occasional appearance of new wintering species during my survey period.

Landscape composition and raptor communities

Partial canonical correspondence analysis (pCCA) for compositional environmental variables explained 32.3% of the total variation in raptor assemblages at Beaver River WMA ( $F = 2.9$ ,  $p = 0.003$ ) but only 3.5% ( $F = 4.0$ ,  $p = 0.36$ ) at Packsaddle WMA. The partial interactive forward selection analysis identified 3 explanatory variables (prairie, upland woodland, and riparian woodland) at Beaver River and four variables (sandhill shinnery, upland woodland, riparian woodland, and prairie) at Packsaddle as variables that best summarized the effects of landscape composition on raptor assemblages (Figure 3). At both sites, the influence of vegetation variables on raptor assemblages was related to the hunting behavior of individual species. For example, raptors species that typically hunt from perches, such as Red-tailed Hawk (*Buteo jamaicensis*), Cooper's Hawk (*Accipiter cooperii*) and Sharp-shinned Hawk (*Accipiter striatus*), were associated with compositional variables that provided perches for hunting (figure 2). Conversely, Northern Harrier and other species that do not typically hunt from perches were more likely to be associated with open prairie vegetation (Figure 2). The Swainson's Hawk (*Buteo swainsoni*) and Ferruginous Hawk (*Buteo regalis*) showed association with prairie vegetation at Packsaddle WMA (Figure 2a) but were mostly generalists in their habitat selection at Beaver River WMA (Figure 2b).

#### Landscape configuration and raptor communities

Forward selection of configurational variables suggested that the edge length of riparian woodland, elevation, and the edge length of upland shrub cover were the most significant ( $P < 0.05$ ) variables influencing raptor distribution at the Beaver River WMA. The three variables together explained 17.1% of the total variation in raptor assemblages at this landscape. A global permutation test with 999 Monte-Carlo permutations indicated that this association was significant (pCCA,  $F = 5.0$ ,  $p = 0.01$ ; Figure 3a). The edge length of riparian woodland was the most important variable accounting for 6.6% of the total variation and 32.6% of the explained variation in raptor assemblages. The two other variables; elevation and edge length of upland shrub respectively accounted for 5.8% and 4.7% of the total variation, and 28.2% and 22.9% of the explained variation in raptor assemblages. At the Packsaddle WMA, the

interactive forward selection identified total edge length of upland shrub land, Shannon Diversity Index, total edge length of riparian woodland, and elevation as variables that best summarized the effects of landscape configuration on raptor assemblages. Landscape configuration variables explained 13.1% of the total variation in raptor assemblages. My global permutation test over 999 Monte-Carlo permutations for raptor association with landscape configuration variables at Packsaddle was significant (pCCA,  $F = 5.2$ ,  $p = 0.031$ ). Elevation ( $P = 0.03$ ) was the most important variable accounting for 6.2% of the total variation and 37% of the explained variation in raptor assemblages. Shannon Diversity Index ( $P = 0.74$ ), Total edge length of Riparian woodland ( $P = 0.69$ ), and total edge length upland shrub land ( $P = 0.75$ ) respectively accounted for 2.1%, 2.3% and 2.0% of the total variation and, 37%, 12.5%, and 13.4% of the explained variation in raptor assemblages. The two main accipiter at the Packsaddle WMA (Cooper's Hawk and Sharp-shinned Hawk) were associated with higher elevation (Figure 3a). Ferruginous Hawk, Mississippi Kite, Swainson's Hawk and Prairie Falcon (*Falco mexicanus*) were more associated with upland woodland edge (Figure 3a). The Red-tailed Hawk, Northern Harrier and American Kestrel (*Falco sparverius*) showed no strong association with any of the configuration variables (Figure 3a). The Turkey Vulture (*Cathartes aura*) and the Great Horned Owl (*Bubo virginianus*) were more associated with landscape heterogeneity and riparian woodland edge (figure 3b). At the Beaver River WMA, most of the "perch and hunt" raptors were associated with edge of riparian woodland and upland shrub vegetation (Figure 3b).

#### Variation partitioning

The total amount of the variation explained by landscape composition and landscape configuration variables shows that at each study site, the separate effects of landscape composition and configuration were significant at  $P < 0.05$  (Monte Carlo tests with 999 permutations). The total variation captured by both configuration and composition variables was 31.6 % at Beaver River WMA (Figure 4a) and 33.5 % at Packsaddle WMA (Figure 4b). Landscape composition explained a greater proportion (20.2 %,  $P =$

0.001) of the variation at Beaver River whereas the reverse was the case at Packsaddle where a greater proportion of the variation (25.1 %,  $P < 0.001$ ) was explained by configurational variables. Landscape configuration and composition respectively explained 9.5 % ( $P = 0.005$ ) and 5.7 % ( $P = <0.001$ ) of the variation at Beaver River and Packsaddle WMAs. The joint effect at both study sites (1.9 % at Beaver River and 2.7 % at Packsaddle) indicated some degree of explanatory overlap between landscape composition and landscape configuration variables at these two study systems.

#### Raptor communities and niche characteristics

The OMI analysis shows that 6 of the 14 raptors (43 %) included in my analysis for the Beaver River WMA, demonstrated significant deviation (i.e. marginal niches) from the mean compositional landscape conditions available on the landscape. Five (36 %) of the 14 species also demonstrated marginal niches from the mean landscape configurational conditions available at Beaver River (Table 3). Contrary to Beaver River WMA, none of the species examined at the Packsaddle WMA demonstrated any marginality with the mean landscape composition or landscape configuration conditions available on the landscape (Table 3). Fifty-five percent of the raptors species that I examined at Beaver River WMA and all of the ones I examined at Packsaddle WMA had low OMI index values and high residual tolerance index values both indicating low to no niche specialization for these species (Table 3).

#### Landscape heterogeneity

Patch density was significantly higher ( $P < 0.001$ ) at Packsaddle WMA than Beaver River WMA indicating a higher degree of landscape heterogeneity at Packsaddle WMA. Mean patch density within sampled cells was  $19.44 \pm 0.89$  SE for Packsaddle WMA and  $9.87 \pm 0.49$  SE for Beaver River WMA.

#### **Discussion**

We found that raptor assemblages were similar in terms of community composition but differed greatly in their niche characteristics between study sites. In the landscape with higher landscape heterogeneity, raptor species assemblage were better explained by landscape configuration than they by landscape composition, with elevation, edge length of upland shrub, and the edge length of riparian woodland being the most important explanatory variables. Further, most of the species in the more heterogeneous landscape demonstrated generalist behavior in their association with the major vegetation types. Conversely, in the more homogenous landscape, landscape composition became more important to raptor assemblages

The dominant upland vegetation at Packsaddle WMA is Shinnery Oak mixed with grass (DeMaso *et al.* 1997). Although the height of shinnery stems is typically <0.5 meters, those individuals that have hybridized with post oaks (*Quercus stellata*) regularly form mottes with stems of 3–4 m in height (Hall 2015). The presence of these hybrid mottes thus provides hunting perches for raptors that typically hunt from perches (these species will naturally select traditional woody habitats like riparian woodlands). The abundant upland grassland patches also provide excellent habitats for traditional grassland specialists like the Northern Harrier that do not typically hunt from perches. The abundance of woody vegetation in upland grassland areas thus offers ample opportunities for increased raptor composition, abundance, and likelihood of interspecific competition.

Based on an OMI analysis, none of the raptor species included in my analysis for the Packsaddle WMA showed a significant ( $P < 0.05$ ) deviation from the mean environmental conditions available in the landscape (Table 3). At the Beaver River WMA, which contained larger vegetation, species overlap was low. For example, half of the raptor species included in my analysis for Beaver River demonstrated significant ( $P < 0.05$ ) deviation from the mean compositional heterogeneity of the landscape. Five of the species also responded by showing significant deviations from to the mean landscape configuration variables available in the landscape (Table 3).

These results emphasize the effect of spatial heterogeneity on the dynamics of species interaction and structure of raptor communities. At the Beaver River WMA with low patch density, raptors appeared to associate with vegetation types that best supported their hunting strategies. For example, the Red-tailed Hawk that typically hunts from perches was more associated with riparian woodland that provided perching substrate. This cover type also provided trees large enough to support their relatively large nests. On the other hand, Northern Harrier does not typically require perches for hunting nor trees to nest, and was strongly associated with upland grass cover. At the Packsaddle WMA, these same species showed no specific or strong associations with any of the vegetation cover types available in the landscape.

While competition is the most frequently documented interaction among sympatric species that rely on similar resources, my results supported studies that have demonstrated that species interactions are more frequently mediated by the structural mosaic of the landscape (Danielson 1991; Cornulier & Bretagnolle 2006; Gorini *et al.* 2012). Increases in configurational heterogeneity where large continuous expanses of unique vegetation patches are broken into smaller ones (Hargis, Bissonette & David 1998; Fahrig *et al.* 2011), reduces the average patch size for specialist species. Hence, even the most specialized species can be forced into selecting multiple cover types that puts them in close competitive proximity with traditional generalist species (Hanski 1995). While landscape level heterogeneity enhances the competitive abilities of generalist species, specialist can be placed at competitive disadvantage depending on patch requirements and average patch size (Tattersall *et al.* 2002; Fahrig *et al.* 2011; Bertrand, Burel & Baudry 2016). Poor competitors with limited dispersal abilities are either displaced to low quality habitat or outcompeted by generalist species (Amarasekare 2008; Hanski 2008; Lin, Hsieh & Miki 2013). For example, (Palmer 2003) demonstrated that spatial heterogeneity associated with *Odontotermes* mounds strongly influences the dynamics of competition and community structure in acacia ants. Competitively dominant ants are disproportionately successful in displacing more subordinate species in high heterogeneous patches, while competitively subordinate species were more successful in less heterogeneous patches. Similarly, (Kurki *et al.* 1998) showed that increase landscape complexity resulting

from habitat fragmentation alters the competitive behavior of two potential generalist mammalian predators: Red fox (*Vulpes vulpes*) and the Pine Marten (*Martes martes*) in forested landscapes. Habitat fragmentation which increases patch densities and reduces patch sizes tend to favor the more generalist Red Fox to the disadvantage of Pine Marten.

Avian predators offer ample opportunities for understanding the role of landscape mosaic on intraspecific and interspecific species interactions. Also, given the important roles that raptors play in determining community structures of co-occurring prey species, knowledge of interspecific interactions among predatory raptor species are often relevant for conservation planning. For example, the co-occurrence and competition between multiple predator species are likely to put a prey population under intense pressure prior to density dependent prey switching. Prey species under these systems will need to evolve anti-predation strategies to avoid attack from multiple generalist predators with different hunting strategies. Spatial heterogeneity have been shown to greatly enhance the rate at which predator reduce prey population by increasing prey vulnerability and predator hunting success (Gorini *et al.* 2012).

Overall, my study provides insights into the role of landscape heterogeneity in structuring interspecific habitat partitioning by raptor communities my study supports the growing hypothesis that landscape heterogeneity plays a major role in shaping the co-occurrence of sympatric species. Raptor communities responded differently to changes in landscape heterogeneity by increasing space use overlap in more heterogeneous landscapes while partitioning space use in a less heterogeneous landscape. Information of this nature can be relevant in structuring conservation and land management decisions at the landscape scale. It may seem obvious that the greater the diversity of cover types in a landscape, the more species that landscape is able to accommodate. Nonetheless, it is equally important to take into account the relationship between patch diversity and patch size. For any given area in the landscape, an increase in the number of cover types will certainly result in a decrease in the amount of each (Fahrig *et al.* 2011). This can negatively affect habitat-specialists that often rely on large patches of distinct cover types for population persistence depending on the scale. At the landscape scale, maintaining large patches of



distinct cover types may benefit specialist species while reducing competition among generalist species. My study underscores the significance of landscape heterogeneity as an underlying condition for species distribution and community coexistence in mixed-grassed prairie ecosystems. Specifically, I focused on understanding the influence of landscape composition, and landscape configuration on the distribution of ecologically sensitive species (raptors) at a management-relevant scale in mixed-grass prairie ecosystems. My analyses were based on a broad scale relevant for landscape level management or/and conservation actions. Nonetheless, I suggest that further studies that will look at the effects of different spatial scales will be important in disentangling the effects of scale on composition and configuration at these landscapes.

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Table 1: Description of the landscape composition and landscape configuration variables calculated for each 1000 m X 1000 m cells

Variable category	Variables
Class level variable	Configurational variables
	Length (m) of riparian woody cover
	Length (m) of upland woody cover
	Length (m) of riparian shrub cover
	Length (m) of riparian shrub cover
	Number of isolated upland woodland patches
	Number of isolated riparian woodland patches
	Number of isolated riparian shrub land patches
	Number of isolated upland shrub land patches
Landscape level	Landscape shape index
	Percentage of like adjacencies
	Slope
	Elevation
Composition variable	
Woodland	Area (m <sup>2</sup> ) of riparian woody cover
	Area (m <sup>2</sup> ) of upland woody cover
Shrubland	Area (m <sup>2</sup> ) of riparian woody shrub cover
	Area (m <sup>2</sup> ) of upland woody shrub cover / shinnery motte
Grassland	Area (m <sup>2</sup> ) of grass/prairie cover
Pasture land	Area (m <sup>2</sup> ) of agricultural land
Open water	Area (m <sup>2</sup> ) open water including dams, rivers, lakes
Barren/ bare areas	Area (m <sup>2</sup> ) of completely bare land,
Sandhill shinnery	Area (m <sup>2</sup> ) of Sandhill shinnery cover



Table 2: Relative abundance (RA) of raptor species occurring at the Packsaddle and Beaver River Wildlife Management Areas. Species that are marked with an asterisk (\*) had < 10 detections and were not included in any of the ordination analyses.

Species	Code	Scientific Names	Beaver		Packsaddle		Breeding
			Occurrence	RA	Occurrence	RA	
Turkey Vulture	TUVU	<i>Cathartes aura</i>	X	10.19	X	14.25	X
Northern Harrier	NOHA	<i>Circus cyaneus</i>	X	29.95		11.86	
Mississippi Kite	MIKI	<i>Ictinia mississippiensis</i>	X	1.39	X	22.21	X
Sharp-shinned Hawk	SSHA	<i>Accipiter striatus</i>	X	1.03	X	0.53	
Cooper's Hawk	COHA	<i>Accipiter cooperii</i>	X	1.72	X	1.46	
Broad-winged Hawk*	BWHA	<i>Buteo platypterus</i>	X	0.19		0.00	
Swainson's Hawk	SWHA	<i>Buteo swainsoni</i>	X	3.30	X	2.39	X
Red-tailed Hawk	RTHA	<i>Buteo jamaicensis</i>	X	33.31	X	31.59	X
Ferruginous Hawk	FEHA	<i>Buteo regalis</i>	X	0.78	X	0.18	
Rough-legged Hawk*	RLHA	<i>Buteo lagopus</i>	X	0.08		0.00	
Golden Eagle	GOEA	<i>Aquila chrysaetos</i>	X	0.14		0.00	
Bald Eagle	BAEA	<i>Haliaeetus leucocephalus</i>	X	0.08		0.00	
Osprey*	OSPR	<i>Pandion haliaetus</i>		0.00	X	0.09	
Merlin*	MERL	<i>Falco columbarius</i>	X	0.06	X	0.04	
American Kestrel	AMKE	<i>Falco sparverius</i>	X	15.82	X	13.94	X
Prairie Falcon	PRFA	<i>Falco mexicanus</i>	X	0.47	X	0.18	
Peregrine Falcon*	PEFA	<i>Falco peregrinus</i>	X	0.08	X	0.04	
Short-eared Owl*	SEOW	<i>Asio flammeus</i>		0.00	X	0.04	X
Barred Owl*	BAOW	<i>Strix varia</i>		0.00	X	0.09	X
Great Horned Owl	GHOW	<i>Bubo virginianus</i>	X	0.78	X	1.11	X
Burrowing Owl	BUOW	<i>Athene cunicularia</i>	X	0.61		0.00	X
Eastern Screech Owl*	ESOW	<i>Megascops asio</i>	X	0.03		0.00	X

Table 3: Results of the Outlying Mean Index (OMI) analysis showing the relationships between raptor species, landscape composition, and landscape configuration variables at Beaver River and Packsaddle Wildlife Management Areas, Oklahoma, USA, 2013–2015. Inertia = variance or weighted sum of squared distances to the origin of the environmental axes; OMI = outlying mean index (marginality); Tol = tolerance index, which represents niche breadth of the two predators across the measured environmental variables; RTol = residual tolerance. Italicized terms represent the percentages of variability corresponding to a specific statistic. P = frequency based on number of random permutations (out of 10,000) that yielded a higher value than the observed outlying mean index ( $P \leq 0.05$  indicates a significant influence of the environmental variables for a species). Significant variables are bolded.

Site	Species	Landscape composition								Landscape configuration							
		inertia	OMI	Tol	Rtol	omi	tol	rtol	P-value	inertia	OMI	Tol	Rtol	omi	tol	rtol	P-value
Beaver	AMKE	7.32	0.10	1.25	5.97	1.40	17.10	81.50	0.25	5.23	0.07	0.70	4.47	1.20	13.40	85.40	0.39
	BAEA	5.05	0.60	0.31	4.14	11.80	6.10	82.10	0.73	4.14	0.58	0.58	2.98	14.10	14.00	71.90	0.62
	BUOW	2.10	1.71	0.12	0.27	81.30	5.90	12.80	0.63	2.18	1.92	0.00	0.26	87.90	0.20	11.90	0.44
	<b>COHA</b>	<b>6.57</b>	<b>0.89</b>	<b>0.99</b>	<b>4.70</b>	<b>13.50</b>	<b>15.10</b>	<b>71.40</b>	<b>&lt;0.001</b>	4.96	0.53	0.85	3.58	10.60	17.20	72.20	0.07
	FEHA	4.97	0.77	0.31	3.90	15.40	6.20	78.40	0.07	<b>5.82</b>	<b>0.84</b>	<b>0.41</b>	<b>4.57</b>	<b>14.40</b>	<b>7.00</b>	<b>78.60</b>	<b>0.01</b>
	<b>GHOW</b>	<b>7.71</b>	<b>1.36</b>	<b>0.67</b>	<b>5.67</b>	<b>17.70</b>	<b>8.70</b>	<b>73.60</b>	<b>0.02</b>	5.63	0.58	1.38	3.66	10.40	24.50	65.10	0.18
	GOEA	4.47	0.63	0.88	2.96	14.10	19.70	66.20	0.79	5.34	0.85	1.29	3.20	15.90	24.20	59.90	0.53
	<b>MIKI</b>	<b>8.93</b>	<b>1.27</b>	<b>1.52</b>	<b>6.15</b>	<b>14.20</b>	<b>17.00</b>	<b>68.80</b>	<b>&lt;0.001</b>	<b>6.32</b>	<b>0.70</b>	<b>1.24</b>	<b>4.38</b>	<b>11.10</b>	<b>19.60</b>	<b>69.20</b>	<b>0.02</b>
	<b>NOHA</b>	<b>7.45</b>	<b>0.15</b>	<b>1.82</b>	<b>5.48</b>	<b>2.00</b>	<b>24.40</b>	<b>73.60</b>	<b>0.05</b>	5.48	0.03	0.81	4.63	0.60	14.90	84.50	0.52
	PRFA	8.22	0.63	1.58	6.02	7.60	19.20	73.20	0.27	6.38	0.27	1.57	4.54	4.20	24.60	71.30	0.59
	<b>RTHA</b>	<b>7.85</b>	<b>0.16</b>	<b>1.76</b>	<b>5.94</b>	<b>2.10</b>	<b>22.40</b>	<b>75.60</b>	<b>&lt;0.001</b>	5.82	0.08	1.46	4.28	1.40	25.00	73.50	0.07
	SSHA	9.65	1.20	1.16	7.29	12.40	12.00	75.60	0.06	<b>5.44</b>	<b>0.91</b>	<b>0.64</b>	<b>3.88</b>	<b>16.80</b>	<b>11.80</b>	<b>71.40</b>	<b>0.05</b>
	<b>SWHA</b>	<b>7.09</b>	<b>0.18</b>	<b>1.49</b>	<b>5.42</b>	<b>2.60</b>	<b>21.00</b>	<b>76.40</b>	<b>0.04</b>	<b>5.46</b>	<b>0.09</b>	<b>0.78</b>	<b>4.59</b>	<b>1.70</b>	<b>14.30</b>	<b>84.00</b>	<b>0.20</b>
	<b>TUVU</b>	<b>6.82</b>	<b>0.57</b>	<b>1.55</b>	<b>4.70</b>	<b>8.40</b>	<b>22.80</b>	<b>68.90</b>	<b>&lt;0.001</b>	<b>5.43</b>	<b>0.32</b>	<b>1.12</b>	<b>3.99</b>	<b>5.80</b>	<b>20.70</b>	<b>73.50</b>	<b>0.01</b>
Packsaddle	AMKE	6.63	0.40	1.16	5.07	6.10	17.50	76.40	0.36	8.38	0.29	3.62	4.46	3.50	43.20	53.30	0.70

COHA	5.85	0.62	1.05	4.18	10.60	18.00	71.40	0.25	7.90	0.63	1.63	5.63	8.00	20.70	71.30	0.45
FEHA	3.69	0.94	0.30	2.45	25.50	8.10	66.40	0.55	8.43	1.84	0.37	6.22	21.80	4.40	73.80	0.30
GHOW	7.96	1.07	0.47	6.42	13.40	5.90	80.70	0.46	6.80	0.64	0.85	5.31	9.40	12.50	78.10	0.84
MIKI	5.21	0.38	0.87	3.96	7.40	16.80	75.90	0.44	8.45	0.55	1.94	5.96	6.50	22.90	70.60	0.36
NOHA	5.84	0.31	1.35	4.18	5.30	23.20	71.60	0.51	7.86	0.51	2.05	5.31	6.50	26.00	67.50	0.34
PRFA	8.29	0.68	0.88	6.72	8.30	10.70	81.10	0.85	10.88	1.81	5.74	3.33	16.70	52.80	30.60	0.49
RTHA	6.15	0.28	1.17	4.70	4.60	19.00	76.40	0.15	7.77	0.07	1.03	6.68	0.80	13.30	85.90	0.93
SSHA	6.90	0.43	0.94	5.53	6.20	13.70	80.20	0.47	7.43	0.23	1.16	6.04	3.10	15.60	81.30	0.88
SWHA	5.80	0.20	1.64	3.96	3.40	28.30	68.30	0.59	8.42	0.32	2.55	5.55	3.80	30.30	65.90	0.45
TUVU	6.36	0.18	0.91	5.27	2.90	14.40	82.80	0.59	8.65	0.44	1.78	6.44	5.00	20.50	74.40	0.21

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## Figures legend

Figure 1: (right) Individual-based integrated extrapolation-rarefaction curves and (left) species richness as a function of sample coverage for Beaver River, and Packsaddle WMAs, Oklahoma, USA, 2013–2015. Solid lines indicate interpolations and dashed lines indicate extrapolated data. Shaded areas represent 95 % confidence intervals

Figure 2: The first two axes of partial canonical correspondence analysis (pCCA) biplots illustrating significant landscape composition variables (as identified by partial interactive forward selection) that explains raptor assemblages at Packsaddle (left) and Beaver River (right) WMAs, Oklahoma, USA, 2013–2015. Refer to table 1 for an explanation of species codes and table 2 for a description of landscape composition variables.

Figure 3: The first two axes of partial canonical correspondence analysis (pCCA) biplots illustrating significant landscape configuration variables (as identified by partial interactive forward selection) that explains raptor assemblages at Packsaddle (left) and Beaver River (right) WMAs, Oklahoma, USA, 2013–2015. Refer to table 1 for an explanation of species codes and table 2 for a description of landscape composition variables.

Figure 4: Results of variation partitioning for the total raptor community composition in terms of fractions of variation explained by landscape composition and configuration variables at Beaver River (a) and Packsaddle (b) WMAs, Oklahoma, USA, 2013–2015. *A* and *B* represent unique effects of landscape composition and configuration variables; while the overlapping area (*C*) indicates their joint effects.

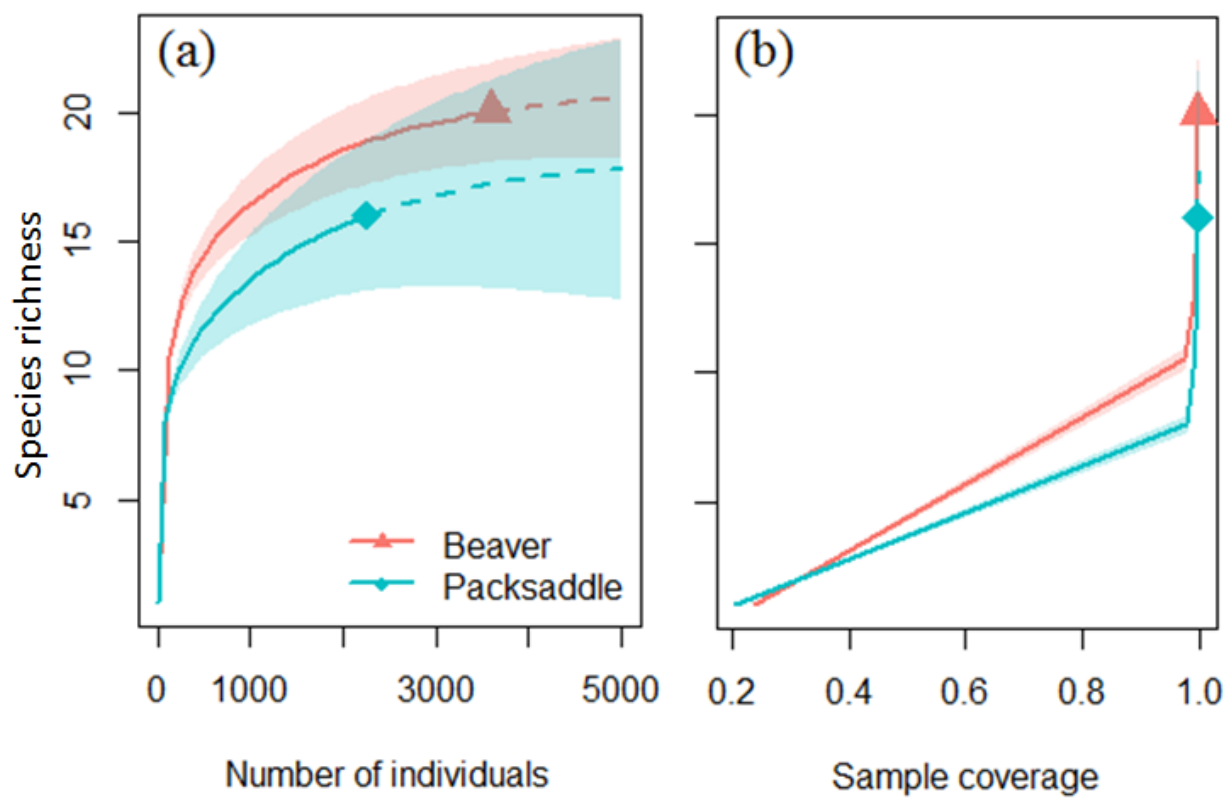


Figure 1

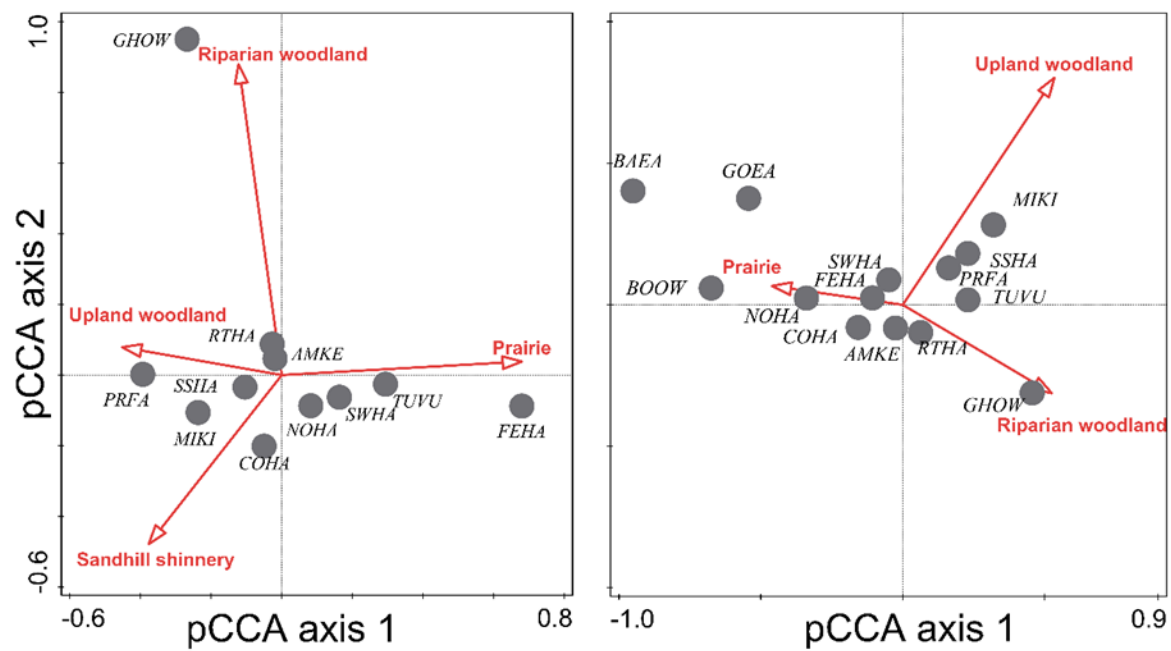


Figure 2

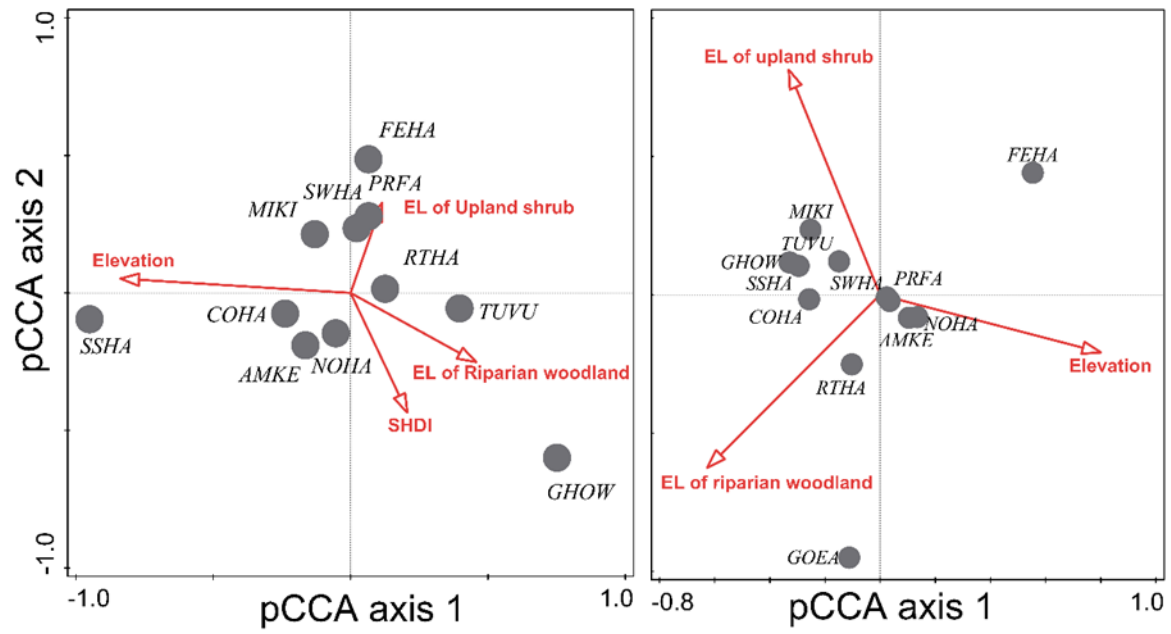
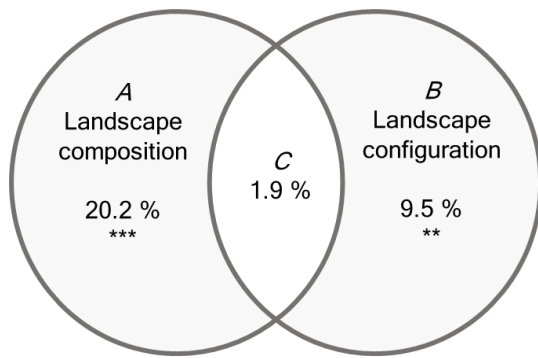
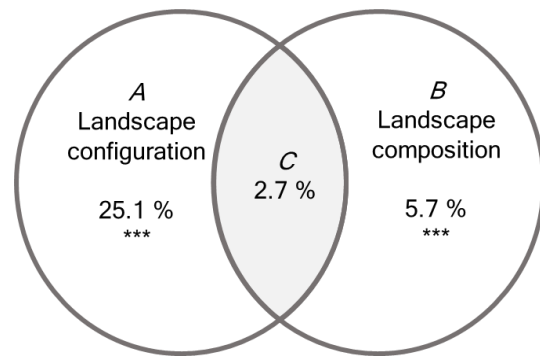


Figure 3



(a) Beaver River



(b) Packsaddle

Figure 4



## CHAPTER III

### THE FUNCTIONAL ROLE OF COMPOSITIONAL HETEROGENEITY FOR SYMPATRIC PREDATORS IN MIXED-GRASS PRAIRIE

#### **Abstract**

Sympatric predators are predicted to partition resources, especially under conditions of food limitation. Spatial heterogeneity influences landscape function and might play an important role in partitioning resource use by potentially competing predators. The southern Great Plains supports high densities of wintering, sympatric raptors that rely on a similar prey base. I assessed potential mechanisms for coexistence by determining the scales at which two of these predators, Red-tailed Hawk and Northern Harrier, partition space use within two mixed-grass prairie landscapes. I found that both predators demonstrated significant, fine scale discrimination in habitat use in homogeneous landscapes, but were more often sympatric in heterogeneous landscapes. Broad scale spatial segregation was also more pronounced in homogeneous landscapes but not in heterogeneous landscapes. At both study sites, fine scale selection by Northern Harrier was more likely associated with upland grassland, whereas Red-tailed Hawk was more closely associated with tree cover. Overall, ecological niche breadth of the two predators was mediated by spatial heterogeneity. Red-tailed Hawk used a wide variety of cover types in heterogeneous landscapes but specialized on riparian forest areas in homogeneous landscapes. Northern Harrier specialized on upland grasslands in homogeneous landscapes but selected different cover types in heterogeneous landscapes. My study supports the growing body of evidence that local interactions

among sympatric competitors may vary in strength across gradients of habitat complexity and heterogeneity. Moreover, my study demonstrates that spatial heterogeneity can modify predator foraging behavior such that a generalist predator may tend toward specialist foraging behavior if heterogeneity is reduced.

**Key words:** Competition, Heterogeneity, Landscape, Niche breadth, Northern Harrier, Predator, Red-tailed Hawk, Resource segregation,

## **Introduction**

Understanding effects of spatial heterogeneity on interference, coexistence, niche separation, and differential habitat selection among species is a key concept in community ecology (Kalcounis-Rüppell and Millar 2002; MacArthur 1972; Preisser et al. 2005; Ryall and Fahrig 2006). Studies of ecological segregation or diet overlap between sympatric species often seek to explain how species or populations might differ in their use of limited resources (González-Solís et al. 1997; Soto and Palomares 2015; Traba et al. 2013). For example, MacArthur (1958) found that five closely related species of *Setophaga* (nee *Dendroica*) warblers coexisted in boreal forest by foraging in different portions of trees. Although these warblers overlapped broadly at home range scales, each specialized behaviorally to partition resources at the scale of individual trees. Habitat selection and niche separation are complex processes that are influenced by temporal and spatial gradients (Fretwell and Calver 1969).

Generalist predators feed on multiple alternate prey species according to availability at a given point in space and time (Begon et al. 2006; Hanski et al. 1991; Ryall and Fahrig 2006). In systems with competing generalist predators, resource partitioning is expected because interspecific competition is likely to occur for preferred and similar limited resources. As a result, I expect to see co-adaptations between competing individuals towards habitat selection strategies that enhance maximum resource exploitation. These strategies may be shaped by evolutionary origin, proximal factors (e.g., proximity to

resources), presence of heterospecific individuals, or anthropogenic influences (Morris 2003). In landscapes, land cover varies from simple to complex at different spatial scales, variation that influences selection and competition. Abilities of predators to sight, pursue, capture, and consume prey species are often influenced by structural complexity of the landscape (Gorini et al. 2012). Spatial heterogeneity can lead to an increase or a decrease in hunting success depending on the specific behavioral characteristics of the predator (Oliver et al. 2009). In the presence of a sympatric competitor, the quest for increased hunting success may result in habitat segregation or overlap in favor of habitats that support individual behavioral (hunting) characteristics.

Habitat selection and niche segregation/overlap are hierarchical processes in which patterns that are detected are frequently dependent on several spatial and temporal scales (Denno et al. 2005; Kotliar and Wiens 1990; Morris 2003). At broad scales, multiple species overlap in habitat selection while segregation is likely to occur at finer scales such as the microhabitat level (Morris 1987; Soto and Palomares 2015; Traba et al. 2013). Habitat selection can also vary temporally with consequences for competing species. For example, seasonally low resource availability during winter increases interspecific and intraspecific competition in temperate environments (Ardia and Bildstein 1997; Diggs et al. 2011; Holmes et al. 1986; Pulliam and Mills 1977). During these constrained periods, competition is high and I expect to see broad overlap in habitat selection among species with similar resource requirements.

The southern Great Plains of the United States supports multiple species of diurnal raptors, with annual residents, breeding migrants, and wintering migrants represented. During winter when energetic demands are high for species, population densities of Red-tailed Hawk (*Buteo jamaicensis*) and Northern Harrier (*Circus cyaneus*) reach their annual peaks in this region and can lead to competition. Both species are opportunistic predators of small mammals, birds, reptiles, and amphibians (Collopy and Bildstein 1987; Fletcher et al. 2003; Preston 1990; Preston and Beane 2000; Redpath and Thirgood 1999; Turner et al. 2014). The two raptors differ in foraging behaviors and habitat, but during winter, both feed extensively on abundant cotton rats (*Sigmodon hispidus*), ground-dwelling birds, and reptiles in the Great Plains

(Behney et al. 2011; Lish 2015; Turner et al. 2014). In this study, I compared resource partitioning between Red-tailed Hawks and Northern Harriers overwintering in the Great Plains. First, I examined winter densities and spatial distribution to identify spatial overlap and/or segregation during periods of known scarcity. Secondly, I examine habitat selection over environmental variables that were summarized at local and broad scales in order to determine the scale for co-existence. Thirdly, I investigated the role of compositional heterogeneity on resource segregation in these sympatric predators.

## Method

### Study sites

Our study was conducted within two wildlife management areas (WMAs) managed by the Oklahoma Department of Wildlife Conservation in western Oklahoma, USA. Packsaddle WMA (Figure 1a) covers ~6,475 ha of mixed prairie with an elevation 579–762 m asl. Average annual precipitation is 67 cm, with the majority occurring during spring and summer (DeMaso et al. 1997). Soils consist mainly of Nobscot fine sand, Nobscot-Brownfield, and Pratt-Tivoli loamy fine sand (DeMaso et al. 1997; Townsend et al. 2001). Predominant grasses in the WMA include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Forb species include western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*), erect dayflower (*Commelina erecta*), and prairie sunflower (*Helianthus petiolaris*). Woody vegetation includes shinnery oak (*Quercus harharvardii*), sand sagebrush (*Artemisia filifolia*), post oaks (*Quercus stellata*), sand plum (*Prunus angustifolia*), and hybrid shinnery motte (DeMaso et al. 1997; Townsend et al. 2001; Hall 2015). Although the height of shinnery stems is typically <0.5 meters, those individuals that have hybridized with post oaks regularly form mottes with stems of 3–4 m in height (Hall 2015). Beaver River WMA (Figure 1b) is ~7,163 ha in area, consisting of

a mixture of upland, floodplain, and river bottom. Vegetation in uplands is predominantly sagebrush and buffalograss interspersed with sand plum thickets and gently rolling sandhills. The floodplain part of the WMA comprised mostly of grasses mixed with cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and American elm (*Ulmus americana*). The river bottom (generally dry riverbed) is woody vegetation consisting of sand plum thickets and salt cedar (*Tamarix* spp). The mean annual precipitation is ~48 cm.

Both WMAs are managed for game hunting with an emphasis on Northern Bobwhite (*Colinus virginianus*). Both include units leased for cattle grazing; Packsaddle is also managed with prescribed fire. Oil and gas extraction is also widespread at Packsaddle WMA.

#### Predator surveys

We conducted surveys for Red-tailed Hawk and Northern Harrier during November-May, 2013–2015. I surveyed 30 line transects (14 at Packsaddle 16 at Beaver River) ranging 2–9 km in length. The length for all transects was 49.42 Km for Packsaddle and 58.98 km for Beaver River. All but two transects at Packsaddle WMA were placed along existing trails (Augiron et al. 2015; Fuller and Mosher 1987). To reduce the chance of counting an individual more than once per survey, transect lines were separated by a distance of at least 900 m (Greenwood and Robinson 2006). I surveyed each transect at least twice a month (260 total surveys) using a 4-wheel drive truck driven at a speed of 20–30 km h<sup>-1</sup> (Andersen 2007). During each survey, an observer, scanned for raptors a distance of approximately 450 m on either side of the transect line. I georeferenced (Garmin Montana 650TM GPS) each detection at the point of observation and estimated distance from the transect line using a laser rangefinder and angle of observation from the observer using an azimuth compass.

To develop a spatially explicit model of predator distribution, I plotted each detection point to the point of occurrence in time using the “Bearing Distance to Line” tool in ArcGIS 10.2. This tool created a new

feature class containing a geodetic line feature for each predator occurrence point constructed based on the values in the x and y coordinate fields, angle of observation, and detection distance. Next, I used the “Feature Vertices to Points” tool to create a feature class containing a georeferenced points at the end of each geodetic line feature. These new points containing x, y coordinates represented the approximate location of individual birds at the time of detection. Thus, Instead of merely recording the observation point from transects, I could plot offset points to more accurately reflect snapshots of spatially explicit occurrence.

### Vegetation classification

We obtained Geo-Eye images for Beaver River and Packsaddle WMA through the Oklahoma Department of Wildlife Conservation. Two Geo-Eye areal images were acquired in July of 2014 with approximately 2 m spatial resolution in the visible (panchromatic) spectrum with relatively broad bands of blue, green, red, and near-infrared portions of the spectrum. The acquired bands were stacked to produce a composite image using the “Band Composite” tool. The land cover maps for 2014 were considered adequate for my vegetation classification, as there were no significant landscape changes in the year before or after 2014.

To obtain vegetation and landscape attributes for each study site, I performed a supervised classification on the pre-processed image using the Maximum Likelihood algorithm. Identified land cover classes at Packsaddle included upland forest, riparian forest, grassland, bare ground, water, sparse vegetation cover, and oil installation. At Beaver River, identified land cover classes were upland shrub, riparian forest, grassland, sparse vegetation cover, and bare ground.

To model habitat selection, I extracted land cover information centered at each used (offset point) location of Red-tailed Hawk and the Northern Harrier at two spatial scales. First, I created 300 m radius buffers centered at each occurrence point to represent a microhabitat scale (28.27 ha) that might provide immediate foraging resources. I then extracted the proportion of pixels representing each vegetation cover type. At the

landscape level, I collected environmental variables that were summarized into three groups (vegetation, topographical, distance related covariates). To collect vegetation variables, I created buffers of 1000 m radius (201.06 ha) to represent broad scale vegetation use for both species based on 50–95% home range sizes estimated for the two species (Arroyo et al. 2014; Stout et al. 2006). I then, extracted the proportion each vegetation cover type. Next, I calculated Euclidean distances from used and available (randomly selected) locations to the closest layer paved roads, access roads, rivers, and oil pads. Distance-based variables are important for assessing habitat selection and are especially effective for assessing selection of individual points on the landscape since species may select areas based on their proximity to resources without actually selecting the habitat or landscape class itself. I obtained topographical variables (i.e. aspect, slope, and elevation) from the Digital Elevation Model (DEM). DEM data were collected from the United States Geological Survey (USGS) data portal at 1/3 arc- seconds (10 m) resolution. I linearized aspect into two continuous variables; northness (the cosine of aspect) and eastness (the sine of aspect) (Domínguez and Dirzo 1995). To compare resource use to availability, I generated random locations equaling the number of use locations for each species and created buffers similar to those created for used locations. I extracted vegetation variables for both use and random (available) locations using the zonal statistics tool. I then estimated habitat selection by comparing environmental characteristics at used locations to the ones collected at available locations.

We quantified the landscape spatial heterogeneity at each study site within three concentric buffer areas of 50 m, 100 m, and 200 m radii centered around 100 random points per WMA that were generated from the random point generator in ArcGIS 10.2. Multiple scale buffers were necessary due to expected scale-specific responses of my study organisms. To avoid overlapping of these buffers, I specified a minimum distance of 400 m between points. Within each buffer, I extracted the number of pixels that represented each vegetation class. Next, I used the Shannon diversity index to compute compositional heterogeneity based on the number of vegetation classes within each buffer and obtained a diversity index for each site

by calculating the mean diversity of all buffers (Fahrig et al. 2011; Gustafson 1998). I then compared heterogeneity between both studied sites using a paired sampled t-test.

## Data analyses

We performed my analyses in three major steps. First, I performed distance analyses to estimate species abundance and detection probabilities. Second, I analyzed habitat selection of each species in ecological space. Third, I performed a discriminant analysis of the habitat used to test for spatial segregation or overlap in the ecological niche of the two species.

At each study site, I estimated a distance detection function for each species by computing detection probabilities for each species using the Multiple-Covariate Distance Sampling (MCDS) approach (Buckland et al. 2015; Marques et al. 2007). The detection function model estimates detection probabilities with increasing distances from transect lines. For each study site, I compared a suite of *a priori* candidate models including half-normal, hazard-rate, and uniform function keys with cosine adjustment terms. I included different covariates (time of the day, month of survey, observer ID, and their interactions) to increase the explanatory power of my models. I treated all covariates as factors including time of day categorized into 5 time intervals: morning (0700–0900), late morning (0901–1100), mid-day (1101–1300), afternoon (1301–1500), and late afternoon (>1500). I ranked models using the Akaike Information Criterion (AIC) and collected detection probabilities based on the best competing models within a  $\Delta AIC$  value <2. For each species, I estimated detection corrected density based on the best model for the detection function. I truncated distances for both species to 450 m at the two sites based on transect width. To account for effects of multiple visits on density estimates, I computed survey efforts as the number of survey visits for each transect multiple by the transect length. I performed all distance analyses using program *Distance* 6.2 (Thomas et al. 2010).



We characterized habitat selection for each predator by comparing environmental variables collected at occurrence points to those collected from random points. I used the Generalized Mixed Linear Model (GLMM) approach with binomial error structures to estimate habitat selection at both study scales. At each level, I included year as a random effect to account for variation in raptor abundance across the two sampling seasons. Fixed effects were defined and varied depending on the study site and scale of analysis. At the broad scale, fixed effects included vegetation extracted from land cover maps, topographical variables extracted from the DEM for each site, and distance related covariates measured as Euclidean distances to identified landscape features. I performed a Pearson Correlation on all variables at each scale and removed variables that were redundant ( $|r| > 0.7$ ).

To reduce model complexity, I employed a two-step approach to build habitat selection models. First, I identified the environmental variables associated with habitat selection by Red-tailed Hawk and Northern Harrier in my study region based on previous studies (McConnell et al. 2008; Preston 1990) and developed models based on these known variables. Second, using these parsimonious models as bases, I developed a set of *a priori* candidate models by examining the additive and interactive roles of additional covariates. I then ranked and averaged all candidate models according to their Akaike's information criterion values adjusted for small sample size (AICc; Burnham and Anderson 2002) using the MuMIn package (Barton 2015). I considered competing models within a  $\Delta AICc < 2$  as important in explaining habitat selection. Prior to statistical analysis, I standardized all environmental variables to a mean of 0 and a standard deviation of 1 to improve variable interpretation.

To estimate the ecological space filled by the Red-tailed Hawk and the Northern Harrier, I performed an Outlying Mean Index analysis (OMI) (Dolédec et al. 2000) using the R package ADE4 (Dray and Dufour 2007). The OMI, or species marginality analysis, is a multivariate analysis technique (based on Principle Component Analysis) that measures the distance between the mean habitat conditions used by a species (species centroid) and the mean habitat conditions that exist in the study landscape. An OMI analysis places species along a habitat gradient (niche hyperspace) based on their mean abundances. The hyperspace

represents the theoretical niche of a species that can tolerate all habitat conditions available in the study area (i.e. a species that is distributed uniformly across the landscape). Marginality is a measure of how far a species occurs away from the origin of the niche hyperspace. Hence, the marginality of a species depends on its deviation from the origin of the niche hyperspace. Species with higher marginality scores represent a deviation from the mean conditions available in the landscape. The OMI analysis also calculates a species' tolerance (i.e. species niche breadth). A species' tolerance determines the geographical space that it can occupy and the amount of resources available to it (Hurlbert 1978). Species with higher tolerance values (generalists) can occupy varying habitat conditions while those with low tolerance values (specialists) are limited in their habitat use. I estimated niche space parameters (marginality and tolerance) for Red-tailed Hawk and the Northern Harrier at the microhabitat scale only because GLMM analyses demonstrated significant overlap at higher scales. I determined significance of the OMI based on a Monte Carlo simulation of 10,000 random permutation values of species marginalities.

## **Results**

We completed a total survey effort (total transect length x number of visits) of 4576.83 km at Beaver River and accumulated 963 detections of the Red-tailed Hawk and 681 detections of the Northern Harrier. At Packsaddle, I surveyed a total of 4028.38 km and recorded 558 detections of Red-tailed Hawk and 241 detections of Northern Harrier. The best detection models for Red-tailed Hawk detection included observer and time of day at Packsaddle (Table S1), and the variables observer and month at Beaver River WMA (Table S2). At Packsaddle WMA, the best model for Northern Harrier detection included month of survey and observer (Table S2). Northern Harrier detection at Beaver River was best explained by month of survey (Table S2). At both sites, the Hazard-rate key function provided the strongest support for Red-tailed Hawk, and Northern Harrier detection (Table S1 and S2). Generally, mean detection probabilities were higher at Beaver River than Packsaddle WMA (Figure S1) and higher for Red-tailed Hawk than for

Northern Harrier (Figure S1). Estimated density of Red-tailed Hawk was slightly higher at Beaver River  $1.77 \pm 0.01$  (95 % CI: 1.64–1.90) /100 ha than at Packsaddle  $1.37 \pm 0.01$  (95 % CI: 1.20–1.47) /100 ha. Northern Harrier density was  $2.470 \pm 0.002$  (95 % CI: 2.240–2.720) /100 ha at Beaver River and  $2.22 \pm 0.02$  (95 % CI: 1.87–2.64) /100 ha at Packsaddle WMA.

### Landscape heterogeneity

We found a significantly higher heterogeneity ( $P < 0.001$ ) at Packsaddle for all tested scales. For example, mean Shannon's Diversity Index for Packsaddle was [50 m radius =  $1.05 \pm 0.03$  SE (standard error), 100 m radius =  $1.17 \pm 0.03$  SE, and 200 m radius =  $1.22 \pm 0.02$  SE] compared to Beaver River with mean indices of (200m radius =  $0.91 \pm 0.03$  SE, 100m radius =  $0.98 \pm 0.03$  SE, and 200m radius =  $1.01 \pm 0.03$  SE).

## Habitat selection

### Microhabitat selection

At the fine scale, I evaluated 32 a priori models for Red-tailed Hawk selection at Beaver River and 47 at Packsaddle. At Beaver River, I evaluated 29 models for Red-tailed Hawk selection and 27 models for Northern Harrier selection. Models consisted of additive and interactive combinations of vegetation covariates and a random effect of year. Habitat selection by Red-tailed Hawk and Northern Harrier varied depending on the scale of study and on the studied landscape.

#### *Microhabitat selection at Beaver River*

At Beaver River, the most approximating model for Northern Harrier habitat selection included grass cover, bare ground, upland shrub cover, and sparse vegetation. The second model, which was the only

other model within  $\Delta AICc < 2$ , was considered as a nested version of the approximating model with two additional uninformative covariates (Table 1; Arnold 2010). Both top models ( $\Delta AICc < 2$ ) indicated that harriers selected for grassland and upland shrub cover while avoiding bare ground, sparse vegetation, and riparian woodland (Table 1). For Red-tailed Hawk selection, I interpreted the model containing grass cover, and riparian forest cover as its only fixed effects to be the single best approximating model since all models within  $AICc < 2$  contained these two variables (Table 1). All other models within  $\Delta AICc < 2$  were thus considered as nested versions of the approximating model with additional uninformative covariates (Arnold 2010). All top models within ( $\Delta AICc < 2$ ) shows that Red-tailed Hawk selected for Riparian forest, upland shrub cover, and bare ground while avoiding grass cover. Unconditional parameter estimates based on model averaging indicated that all four variables in the approximation model were statistically ( $P < 0.05$ ) significant in informing Northern Harrier selection while selection for riparian forest cover, and avoidance of grass cover were the only significant ( $P < 0.05$ ) variables for Red-tailed Hawk selection at Beaver River (Figure 2).

#### *Microhabitat selection at Packsaddle*

We interpreted two competitive models as best-approximating models for Red-tailed Hawk selection at Packsaddle WMA. They included the models with riparian forest as its only fixed-effect, and the model with riparian forest and oil pads (Table 2). All other models within the  $\Delta AICc < 2$  penalty were interpreted as nested versions of the riparian forest only model with uninformative covariates (Table 2). Generally, Red-tailed Hawk selection was in favor of riparian forest, upland forest, and sparse vegetation while oil pads, bare ground, and grass cover were avoided (Table 2). Similar to Red-tailed Hawk selection, I considered two competing models (i.e. the model with upland forest cover as its only fixed effect, and the model containing grass cover, upland forest, and an interaction between grass cover and upland forest) as best approximating models. I interpreted other models with  $\Delta AICc < 2$  as nested

versions of the upland forest only model with uninformative variables (Table 2). Northern Harriers selected grass cover, upland forest, and an interaction between upland forest and grass cover. On the other hand, bare ground, riparian forest, and areas with sparse vegetation cover were avoided (Figure 3). Unconditional parameter estimates based on model averaging suggested that riparian forest was the most significant ( $P < 0.05$ ) variable for Red-tailed Hawk selection while grass cover and upland forest were the most significant ( $P < 0.05$ ) variables for Northern Harrier selection at Packsaddle WMA (Figure 3).

#### Broad scale selection

##### *Broad scale vegetation selection at Beaver River*

We evaluated 31 models for Northern Harrier selection and 53 models for Red-tailed Hawk selection at Beaver River WMA. In each case, I identified the best approximating models and interpreted other models within  $\Delta AICc < 2$  as nested versions of the best approximating models model with uninformative variables (Arnold 2010). Importance variables for Northern Harrier selection included positive association with grass cover, upland shrub cover, and areas with sparse vegetation cover (Table 1). Riparian forest was the only variable within  $\Delta AICc < 2$  that was avoided. The best approximating model for Red-tailed Hawk selection suggested selection for riparian forest, riparian shrub, and upland shrub cover (Figure 2) while avoiding bare areas, grass cover, and areas with sparse vegetation cover. Based on an unconditional parameter estimates grass cover was the most significant ( $P < 0.05$ ) variable for harrier selection while riparian forest, riparian shrub, and upland shrub cover were the most significant variables for Red-tailed Hawk selection at Beaver River WMA (Figure 2).

##### *Broad scale vegetation selection at Packsaddle*

At Packsaddle WMA, the best approximating model and the only model within  $\Delta AICc < 2$  for Red-tailed Hawk selection had three variables: grass cover, riparian forest, and upland forest. All three were positively associated with Red-tailed Hawk selection. Of the 59 models that were evaluated for Northern Harrier selection, I interpreted two competing models with  $\Delta AICc < 2$  as the best approximating models (Table 2). They included one model with grass cover as its only fixed effect, and the other with grass cover and upland forest as fixed effects (Table 2). The two models together with their nested versions suggested that harrier selected for grass cover, bare ground, upland forest, and areas with sparse vegetation cover. They however avoided riparian forest. Conditional averaging did not identify any significant difference for any of the variables evaluated for the Red-tailed Hawk (Figure 3) suggesting that the species did not discriminate in its habitat choice at broad scale. Meanwhile similar estimates for Northern Harrier suggested that selection for grass cover, upland forest, and an avoidance of riparian forest were only marginal significant in informing broad scale selection by harriers (Figure 3).

#### *Selection in relation to distance from major landscape features*

Global models with four distance related covariates were in each case interpreted as best approximating models for Northern Harrier and Red-tailed Hawk selection at Beaver River (Table 1). All four measured covariates for Northern Harrier, and three covariates for Red-tailed Hawk selection at Beaver River differed significantly ( $P < 0.05$ ) from random (Figure 2). Both species significantly selected areas that were away from paved roads and oil pads (Figure 2). However, the likelihood of harrier selection decreased significantly with increasing distances to riparian forest while Red-tailed Hawk selected areas that were in proximity to riparian forest (Figure 2). At Packsaddle, the best approximating model for Red-tailed Hawk selection contained the variables distance to paved roads as its only fixed effects. Other nested models within  $\Delta AICc < 2$  included distance to river, and distance to oil pads as important variables for Red-tailed Hawk selection (Table 2). The likelihood of Red-tailed Hawk selection was in favor of

increasing distances away from paved roads, and oil pads. The likelihood of selection however increases with decreasing proximity to river (Figure 3). The best approximating model for Northern Harrier included all modeled distance related covariates at Packsaddle (Table 2). However, unconditional model averaging suggest that distances to paved roads and river were the most important variables informing harrier selection at Packsaddle WMA. Overall, the likelihood of harrier selection increase further from paved roads and riparian forest (Figure 3).

#### *Selection in relation to topographical variables*

We evaluated 27 models for each species at each site to understand the effects of topographical variables on selection. At Packsaddle WMA, I considered the model with slope and the quadratic term for elevation as the best approximating model for Northern Harrier habitat selection (Table 2). Selection increased as elevation increase and decrease with increasing degree of slope (Figure 2). The model with slope as its only fixed effect was considered as the best approximating model for Red-tailed Hawk (Table 2). It was also the only model within  $\Delta AICc < 2$  with an Akaike's weight of 0.54. The model suggests that Red-tailed Hawk habitat selection decreased as the degree of slope increased (Figure 3). Conditional model averaging suggested that slope, and quadratic elevation variables were the most significant ( $P < 0.05$ ) for Northern Harrier selection. Whereas, slope was the most significant variable for Red-tailed hawk selection (Figure 3).

At Beaver River WMA, the slope only model was the only model with  $\Delta AICc < 2$  of the 27 models evaluated for Northern Harrier selection (Table 1). Hence, I interpreted it as the best approximating model for Northern Harrier selection at Beaver River. The model suggested a decreasing likelihood of harrier selection with increasing degree of slope (Figure 2). Two competing models were considered as the best approximating models for Red-tailed Hawk selection. They included the model with two fixed effects (slope and quadratic elevation), and the model with quadratic elevation as the only fixed effect (Table 1).

The likelihood of Red-tailed Hawk selection increased with increasing degree of slope and decreased with elevation (Figure 2). Based on conditional model averaging, slope and elevation (both in its linear and quadratic forms) were the most significant ( $P < 0.05$ ) variables for Red-tailed Hawk selection whereas decreasing degree of slope was the most significant variable for Northern Harrier selection at Beaver River WMA (Figure 2).

### Niche overlap

The amount of marginality accounted for by OMI analysis at Beaver River was 95% for the first axis (x-axis) and 5% for the second axis (y-axis). Similarly, marginality was 75% on the first axis and 25% on the second axis at Packsaddle. The niche position and niche breadth values of the two species demonstrate variation in niche measures at the two study sites. The overall OMI analysis representing the mean sensitivity of the two predators to environmental variables was significant ( $P < 0.005$ ) at Beaver River but not at Packsaddle. At Beaver River, the Monte-Carlo Randomization Test showed that both marginality and tolerance values were significantly different from 0 (i.e. the reference point of the total niche space) for Red-tailed Hawk ( $P < 0.001$ ) and Northern Harrier ( $P = 0.023$ ). Ordination diagrams show that the two species occupied different axes and were separated from each other in terms of the environmental space (Figure 4). At Packsaddle, marginality and tolerance values for both species did not differ from 0 ( $P > 0.05$ ) based on the Monte-Carlo Randomization Test. Compare with the Northern Harrier, I recorded a higher marginality and lower tolerance values for Red-tailed Hawk at Beaver River (Table S2). Converse to selection patterns at Beaver River, I recorded a lower marginality value and a higher tolerance value for the Red-tailed Hawk compared to the Northern Harrier at Packsaddle, Red-tailed Hawk had a higher tolerance value than the Northern Harrier at Packsaddle. (Table S2). My ordination diagrams for Packsaddle suggested a positive association of Red-tailed Hawk with both sides of the second axis (Figure 4). At Beaver River WMA, the first OMI axis was driven by elevation and the proportion of



grassland at the positive end of the gradient and by sparse vegetation cover at the opposite end. On the other hand, the second axis was positively influenced by forest cover, riparian shrub, and cosine of aspect. Shrub and the sin of aspect were at the negative end of the gradient were. Consequently, the presence of the Red-tailed Hawk was best discriminated by the presence forest cover, riparian shrub and shrub cover whereas harriers were more positively associated with higher elevation and by the proportion of grassland (Figure 5a). The first OMI-axis at Packsaddle was positively influenced elevation and negatively by grass while the second axis was driven by the cosine of aspect, slope and riparian forest at the positive end of the gradient and by the proportion of bare ground and oil pads at the negative end. Accordingly, Red-tailed Hawk was positively associated with riparian and upland woody cover while Northern Harrier demonstrated positive affinity for grassland (Figure 5b).

## **Discussion**

Heterogeneous landscapes offer many opportunities for understanding species habitat selection and interactions with other species. Species interactions in heterogeneous and dynamic landscapes often deviate from those that may occur in homogeneous and static systems such as those used in controlled experiments and model simulations (Gorini et al. 2012). In more heterogeneous landscapes with a variety of vegetation types, the distribution and availability of resources is often distributed such that opportunities for coexistence or segregation are largely dependent on the scale of study. Even among generalist consumers with different degrees of specialization, patterns of habitat selection may result in ecological separations or overlaps with implications for community functionalities (Soto and Palomares 2015; Tattersall et al. 2002). Using two generalist and sympatric avian predators, the Red-tailed Hawk and the Northern Harrier, I assessed habitat selection in two landscapes with varying degrees of heterogeneity where both species coexist during the non-breeding phase of their life histories.

Based on my GLMM approach, local scale habitat selection assessment revealed spatial segregation along a gradient of environmental variability (Figure 1), likely due to different levels of species specialization. Red-tailed Hawk and Northern Harrier showed substantial levels of habitat specializations at finer scales. At both study sites, Northern Harrier showed higher affinities for shrublands, and open grassland whereas Red-tailed Hawk was more associated with woody vegetation cover (woodlands and shrublands). Although Red-tailed Hawk and Northern Harrier are considered generalist predators (Kane 2012; Orians and Kuhlman 1956; Redpath and Thirgood 1999; Turner et al. 2014), their typical hunting strategies differ. Red-tailed Hawk is a “sit-and-wait” hunter and typically hunts from perches (Lish 2015; Preston and Beane 2000). Hunting perches in my study provided by woodland and shrub cover are likely to positively influence foraging habitat selection by Red-tailed Hawk. Fine scale association of non-breeding Red-tailed Hawks with woody vegetation cover has been documented by previous studies (Bobowski et al. 2014; Garner and Bednarz 2000; Ingold 2010). Anthropogenic structures including electric poles, electric lines, non-functional windmills, and fence poles are also known to offer perch platforms for Red-tailed Hawk (Bobowski et al. 2014). In both of my study sites, these structures were present mostly in uplands and were less used by Red-tailed Hawk. The association of Red-tailed Hawk with areas that provided natural perches is consistent with other studies in the southern Great Plains that have demonstrated preferential selection of natural woodland as opposed to anthropogenic perches (Bobowski et al. 2014).

Unlike Red-tailed Hawk, Northern Harrier does not require perches for hunting (Behney et al. 2012). Harriers forage low over the vegetation surface frequently changing direction and pace, seemingly in response to fine-grained variation in vegetation and prey availability (Simmons 2000). These hunting adaptations allow Northern Harrier to reduce competition with the sit-and-wait raptors such as the Red-tailed Hawk by exploiting areas with less woody vegetation. At both study sites, fine scale selection by the Northern Harrier was associated with upland areas which is predominantly grassland and sagebrush at Beaver River and a mosaic of grass, shinnery oak, and hybrid shinnary oak at Packsaddle. In the Great

Plains, Northern Harriers are known to maximize their foraging efficiency selecting areas with large patches of grass cover (Johnson and Igl 2001; Littlefield et al. 2005; Paprocki et al. 2015). Harriers feed on a wide variety of small mammal and birds (MacWhirter and Bildstein 1996; Thirgood et al. 2000). Harrier selection of upland grassland in my study systems might be an adaptation to improve prey capturing and foraging efficiencies while avoiding competition with other predators. At both study sites, harriers selected bare areas and areas with sparse vegetation cover less than was proportionally available. Though several studies have reported an inverse relationship between avian predator foraging habitat selection and density of vegetation cover (Baker and Brooks 1981; Bildstein 1987; Wakeley 1978), Preston (1990) reported that both Northern Harrier and Red-tailed Hawk overwintering in central Arkansas avoided bare areas as well as areas with sparse vegetation cover. Preston (1990), suggested that such areas might be less attractive because they may contain significantly fewer prey species than other patch types. At both of my study sites, harriers showed avoidance of these bare ground areas. Mean Euclidean distances between used locations and land cover types were greater than those between topographic variables at the landscape scale. Based on my parameter estimates for habitat selection at the two study sites, Red-tailed Hawk showed significant avoidance of oil pads by selecting areas with increasing distances from them, while harriers avoided riparian woodlands by selecting areas further from rivers.

At the broad scale, the two species co-occurred, and showed great spatial overlap at Packsaddle WMA. This was evident from the lack of clear significant association with any of the vegetation covariates that were evaluated in my study. Both species selected a wide variety of vegetation types with no strong affinity to any specific type (Figure 3). Nonetheless, Northern Harrier showed marginal significant selection for grass cover, upland forest, and avoidance of riparian forest an indication that the species was less specialized than the Red-tailed Hawk. Structural composition at Beaver River (less heterogeneous) permitted both species to maintain a higher degree of habitat specialization at Beaver River compared to Packsaddle. The two species avoided each other by selecting environmental covariates that supported

their hunting behavior. The Red-tailed Hawk maintained its selection for riparian woody cover while the Northern Harrier selected for a wider variety of vegetation types (Figure 2).

Vegetation studies in the Great Plains have shown that woody cover tends to increase with increasing slope and grass cover increases with increasing elevation (Archer 1995; Hall 2015; Liu et al. 2013). Consistent with these studies, Red-tailed Hawks selected areas of lower elevation while the Northern Harrier selected higher elevations. These selection patterns were particularly obvious at Beaver River where the vegetation structure clearly followed the patterns of zonation with tree cover restricted to bottomland, and lower elevation. At Packsaddle where the structural complexity of the landscape allows for a substantial amount of tree cover at upland (higher elevation) and lowland areas, topography was a poor predictor of Red-tailed Hawk selection. Nonetheless, Northern Harrier maintained selection for higher elevation consistent with its hunting strategy. None of the aspect variables was important for Red-tailed Hawks or Northern Harriers selection.

The output of my OMI analysis indicates extensive use of the landscapes by the Northern Harrier and the Red-tailed Hawk. Patterns of habitat selection indicated some degree of overlap between the two predators depending on the heterogeneity of the landscape. For example, the Northern Harrier was a better generalist at Beaver River where compositional heterogeneity was relatively low while the Red-tailed Hawk maintained a narrower and more marginal niche. Nevertheless, at Packsaddle where heterogeneity was relatively high, the two species demonstrated high spatial overlap though the Red-tailed Hawk had a broader niche breathe (Table S3). Consequently, the two predators showed significant segregation in the amount of space occupied by each species at Beaver River, with the Red-tailed Hawk occupying the most distinct habitat selection of the two species. In heterogeneous landscapes competing species are less likely to show distinct spatial segregation in their habitat selection (Holt 1984; Laiolo 2013) since an increase in landscape heterogeneity is likely to reduce species distribution and occupancy of patches of the different cover types (Fahrig et al. 2011). In my case, I recorded significant separation in the distribution of Red-tailed Hawk, and Northern Harrier at Beaver River WMA, which had

comparatively low compositional heterogeneity compared to Packsaddle. On the contrary, the two predators showed great overlap in their distribution at the Packsaddle WMA. Spatial heterogeneity at Packsaddle resulted most from the presence of Hybrid shinnery motte, which mimics clusters of forest vegetation in upland zones. This habitat mosaic provided perches for the sit-and-wait hunting strategy of the Red-tailed Hawk hence increasing its spatial tolerance.

Distribution and habitat selection of predators are often explained by hunting successes associated with certain cover types, and the presence of competitors (Gorini et al. 2012). However, spatial heterogeneity can modify predators hunting abilities, strategies, and efficiencies across the landscape with attendant impact on hunting successes. While presence of an intra-guild competitor may result in spatial avoidance and resource segregation in less heterogeneous landscapes like Beaver River, it is likely to increase the strength of apparent competition in a more heterogeneous landscape (Latham et al. 2013). At Packsaddle, spatial heterogeneity likely offers increased hunting opportunities by increasing possible space use for both the Red-tailed Hawk and the Northern Harrier. Nevertheless it put both predators in competitive proximity possibly creating a system of trade-offs between increased hunting areas and possible reduced energy intake.

Our study supports the growing body of evidence that local interactions among sympatric competitors may vary in strength across gradients of habitat complexity and heterogeneity. Most importantly, my study demonstrates that spatial heterogeneity can modify predator foraging behavior such that a generalist predator may tend toward specialist foraging behavior if heterogeneity is reduced. I demonstrated that differences in fine-scale habitat selection might be responsible for the realized niche segregation and overlap between the Red-tailed Hawk and the Northern Harrier along heterogeneity gradients. My study provides new insights into how spatial heterogeneity shapes community structures and interactions between generalist predator species.

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Table1: Summary of results from GLMM resource selection models for Red-tailed Hawk (RTHA) and Northern Harrier (NOHA) at Beaver River Wildlife Management Area, Oklahoma, USA, 2013–2015. Shown are the top 3 models or all nested models (> 3 nested models) with associated degrees of freedom (df), AICc,  $\Delta$ AICc and Akaike model weights (G<sub>i</sub>) collected at fine and broad scales.

Scale (ha)	Species	model	df	AICc	$\Delta$ AICc	G <sub>i</sub>
<b>Fine (28. 27)</b>	NOHA	bare ground+grass+upland shrub+sparse veg.	5	884.60	0.00	0.59
		bare ground+grass+riparian shrub+upland shrub+sparse veg.	6	886.70	2.11	0.21
		bare ground+grass+upland shrub+sparse veg.+riparian forest	6	887.60	2.99	0.13
	RTHA	bare ground+grass+riparian shrub+upland shrub+riparian forest	7	1429.60	0.00	0.13
		grass+riparian shrub+upland shrub+riparian forest	6	1429.80	0.16	0.12
		riparian shrub+upland shrub+riparian forest	5	1430.10	0.50	0.10
		grass+riparian shrub+upland shrub	6	1430.20	0.57	0.10
		bare ground+grass+riparian shrub+upland shrub	5	1430.50	0.89	0.08
		bare ground+grass+upland shrub+riparian forest	6	1430.60	0.96	0.08
		grass+upland shrub	4	1431.00	1.35	0.07
		grass+upland shrub+riparian forest	5	1431.30	1.72	0.06
		<b><i>Vegetation variables</i></b>				
<b>Broad (201.06)</b>	NOHA	sparse veg+upland shrub+riparian forest	5	923.50	0.00	0.11
		sparse veg+grass+riparian forest	5	924.00	0.50	0.09
		riparian forest	3	924.10	0.59	0.08
		sparse veg+riparian forest	4	924.20	0.62	0.08
		upland shrub+riparian forest	4	924.60	1.03	0.07
		sparse veg+upland shrub+riparian forest+grass	6	924.60	1.07	0.06
		grass+upland forest	4	924.90	1.41	0.05
	RTHA	bare ground+riparian shrub+upland shrub+riparian forest	8	1376.60	0.00	0.29
		bare ground+riparian shrub+upland shrub	7	1377.70	1.07	0.17
		bare ground+grass+riparian shrub+upland shrub+riparian forest	9	1378.10	1.47	0.14
		riparian shrub+upland shrub+riparian forest	7	1378.50	1.88	0.11
		<b><i>Distance variables</i></b>				
	NOHA	dist.paved roads+dist.access roads+dist. oil pads+ dist. River	5	473.60	0.00	1.00
		dist.paved roads+dist.access roads+dist. oil pads	4	498.10	24.53	0.00
		dist.access roads+dist. oil pads+ dist. River	4	498.90	25.27	0.00
	RTHA	dist.paved roads+dist.access roads+dist. oil pads+ dist. River	5	419.90	0.00	0.644
		dist.paved roads+dist. oil pads+ dist. River	4	421.10	1.18	0.356
		dist.access roads+dist. oil pads+ dist. River	4	480.60	60.71	0.00
		<b><i>Topographical variables</i></b>				
	NOHA	slope	2	929.90	0.00	0.751
		elevation	2	935.70	5.74	0.043
		cosine aspect	2	935.70	5.75	0.042
	RTHA	elevation <sup>2</sup>	2	1511.00	0.00	0.479
		elevation <sup>2</sup> +slope	3	1512.30	1.33	0.246
		elevation+elevation <sup>2</sup>	3	1513.70	2.71	0.124

Table 2: Summary of results from GLMM resource selection models for the Red-tailed Hawk (RTHA) and the Northern Harrier (NOHA) at Packsaddle Wildlife Management Area, Oklahoma, USA, 2013–2015. Shown are the top 3 models or all nested models (> 3 nested models) with associated degrees of freedom (df), AICc,  $\Delta$ AICc and Akaike model weights (GDS) collected at fine and broad scales.

Scale (ha)	Species	Model	df	AICc	$\Delta$ AICc	G <sub>Di</sub>
<b>Fine (28.27)</b>	NOHA	grass+upland forest+grass*upland forest	4	518.60	0.00	0.13
		bare ground+grass+upland forest+grass*upland forest	5	519.90	1.36	0.07
		grass+riparian forest+upland forest+grass*upland forest	5	520.10	1.50	0.06
		Grass+upland forest+sparse veg+grass*upland forest	5	520.20	1.68	0.06
		upland forest	2	520.40	1.82	0.05
	RTHA	oil pad+riparian forest	4	696.00	0.00	0.11
		bare ground+oil pad+riparian forest	5	696.50	0.49	0.09
		riparian forest	3	696.50	0.52	0.09
		sparse veg+riparian forest	4	697.60	1.57	0.05
		upland forest+riparian forest	4	697.70	1.70	0.05
		grass+oil pad+riparian forest	5	697.80	1.77	0.05
		oil pad+upland forest+riparian forest	5	697.90	1.85	0.05
		oil pad+sparse veg+riparian forest	5	697.90	1.87	0.04
		grass+riparian forest	4	697.90	1.90	0.04
	<b><i>Vegetation</i></b>					
<b>Broad (201.06)</b>	NOHA	grass+upland forest	3	262.10	0.00	0.09
		grass	2	263.10	1.01	0.06
		bare ground+grass+upland forest	4	263.80	1.64	0.04
		riparian forest	2	263.80	1.66	0.04
		grass+sparse veg+upland forest	4	263.90	1.78	0.04
	RTHA	grass+riparian forest+upland forest	4	722.70	0.00	0.87
		bare ground+oil pad+riparian forest+sparse veg	5	728.70	5.99	0.04
		bare ground+grass+riparian forest+sparse veg+upland forest	6	729.50	6.78	0.03
	<b><i>Distance variables</i></b>					
	NOHA	dist.access road+dist.paved road+dist.oil pads+dist.river	5	73.40	0.00	0.46
		dist.access road+dist.paved road+dist.river	4	74.00	0.63	0.34
		dist.access road+dist.river	3	76.40	3.05	0.10
	RTHA	dist.paved road	2	564.70	0.00	0.30
		dist.paved road+dist.river	3	564.80	0.09	0.29
		dist.paved road+dist.oil pads	3	565.70	0.97	0.19
		dist.paved road+dist.oil pads+dist.river	4	566.00	1.30	0.16
	<b><i>Topographical variables</i></b>					
	NOHA	elevation <sup>2</sup> +slope	3	258.30	0.00	0.39
		slope	2	259.00	0.78	0.27
		elevation <sup>2</sup> +slope	2	260.00	1.76	0.16
	RTHA	slope	2	711.10	0.00	0.55
		cosine aspect	2	714.40	3.35	0.10
		sine aspect	2	715.00	3.94	0.08

Table S1: Summary details for models fitted to Northern Harrier (NOHA) and Red-tailed Hawk (RTHA) at Packsaddle Wildlife Movement Area, Oklahoma, USA, 2013–2015. Detection functions were defined using parametric key including half-normal (hn), hazard-rate (hr), and uniform (unif). Also shown are effective detection width (ESW), P-values for  $\chi^2$  (Chi-p), and Kolmogorov–Smirnov (KS) goodness-of-fit tests.

Species	Name	Key function	par	$\Delta$ AIC	AIC	ESW	Chi-p	K-S
NOHA	observer x TOD	HR	10	0.00	4350.34	189.72	7E-04	0.02
	observer	HR	6	4.05	4354.40	201.85	9E-03	0.31
	observer	HN	5	12.95	4363.29	201.54	2E-02	0.24
	observer x month	HR	13	14.28	4364.62	198.83	3E-04	0.26
	observer x month	HN	12	17.27	4367.61	196.38	5E-04	0.12
	month x TOD	HN	12	51.13	4401.47	201.24	5E-04	0.05
	month	HN	8	52.79	4403.13	204.73	4E-03	0.22
	month x TOD	HR	13	55.22	4405.57	207.86	1E-03	0.14
	month	HR	9	55.48	4405.82	215.26	1E-02	0.41
	TOD	NR	6	67.36	4417.71	210.84	2E-02	0.10
	no covariate	HR	2	70.28	4420.62	219.98	2E-01	0.29
	TOD	HN	5	72.81	4423.15	216.44	1E-02	0.10
	observer x TOD	HR	1	75.60	4425.95	219.80	3E-02	0.10
	no covariate	HN	1	75.60	4425.95	219.80	3E-02	0.10
	no covariate	Unif	2	76.26	4426.60	210.91	4E-02	0.18
RTHA	observer	HR	6	0.00	11058.07	240.28	1.0E-04	0.20
	TOD x observer	HR	10	2.56	11060.63	232.94	4.9E-06	0.07
	month x observer	HR	17	11.09	11069.16	237.26	0.0E+00	0.31
	time x observer	HN	9	20.36	11078.43	233.45	8.9E-06	0.13
	observer	HN	5	24.54	11082.61	235.36	7.6E-05	0.07
	month	HR	13	24.74	11082.81	241.21	9.5E-07	0.29
	month x observer	HN	16	32.48	11090.55	232.71	6.0E-08	0.17
	month	HN	12	43.64	11101.71	235.48	1.1E-06	0.22
	TOD x month	HR	16	46.58	11104.65	235.42	6.0E-08	0.29
	TOD x month	HN	16	46.58	11104.65	235.42	6.0E-08	0.29
	TOD	HR	6	50.51	11108.58	253.85	2.5E-04	0.48
	TOD	HN	5	50.78	11108.85	239.26	5.9E-05	0.18
	no covariate	HR	2	53.54	11111.61	255.75	1.5E-03	0.40
	no covariate	Unif	1	58.10	11116.17	248.26	4.1E-04	0.21
	no covariate	HN	1	60.23	11118.30	241.92	2.9E-04	0.12

\*TOD = Time of day

Table S2: Summary details for models fitted to Northern Harrier (NOHA) and Red-tailed Hawk (RTHA) detection at Beaver River Wildlife Management Area, Oklahoma, USA, 2013–2015. Detection functions were defined using parametric key including half-normal (hn), hazard-rate (hr), and uniform (unif). Also shown are effective detection width (ESW), P-values for  $\chi^2$  (Chi-p), and Kolmogorov–Smirnov (KS) goodness-of-fit tests.

Site	Species	Name	Key function	par	$\Delta$ AIC	AIC	ESW	Chi-p	K-S
Beaver	NOHA	month	HN	10	0.00	20.00	193.05	0.00	0.03
		month	HR	11	2.00	22.00	203.87	0.00	0.03
		TOD x month	HN	14	8.00	28.00	191.43	0.00	0.03
		observer x month	HN	14	8.00	28.00	187.00	0.00	0.03
		observer	HR	6	13991.09	14011.09	187.55	0.00	0.03
		observer x TOD	HR	10	13992.55	14012.55	187.89	0.00	0.03
		observer x month	HR	15	14001.51	14021.51	188.78	0.00	0.03
		observer	HN	5	14041.04	14061.04	203.19	0.05	0.03
		observer x TOD	HN	9	14041.53	14061.53	202.18	0.01	0.03
		TOD x month	HR	15	14082.56	14102.56	205.33	0.00	0.03
		TOD	HR	6	14114.70	14134.70	208.12	0.00	0.03
		TOD	HN	5	14119.31	14139.31	212.02	0.03	0.03
		unif	Unif	4	14126.60	14146.60	208.34	0.17	0.03
		HN	HN	2	14127.49	14147.49	201.01	0.14	0.03
		HR	HR	2	14134.90	14154.90	220.80	0.02	0.03
	RTHA	observer x month	HR	18	0.00	16821.96	279.35	0.00	0.07
		month	HR	13	9.87	16831.83	280.34	0.00	0.10
		month X TOD	HR	17	11.42	16833.38	277.54	0.00	0.06
		observer x month	HN	17	15.14	16837.10	248.54	0.00	0.00
		month	HN	12	25.10	16847.06	251.04	0.00	0.00
		month x TOD	HN	16	27.41	16849.37	250.29	0.00	0.00
		observer + TOD	HR	11	44.57	16866.53	282.03	0.00	0.14
		observer	HN	6	47.74	16869.70	254.45	0.00	0.00
		TOD	HR	6	47.74	16869.70	254.45	0.00	0.00
		Observer + TOD	HN	10	52.18	16874.14	253.91	0.00	0.00
		HN	HN	2	86.89	16908.85	285.87	0.00	0.04
		HR	HN	2	87.13	16909.09	290.57	0.00	0.08
		TOD	HR	6	87.23	16909.19	293.10	0.00	0.09
		TOD	HN	5	87.67	16909.63	258.99	0.00	0.00
		Unif	Unif	3	89.20	16911.16	284.12	0.00	0.03

\*TOD = Time of day



Table S3: Outlying Mean Index (OMI) analysis between Red-tailed Hawk (RTHA) and Northern Harrier (NOHA) to a suite of environmental variables at Beaver River and Packsaddle Wildlife Management Areas, Oklahoma, USA, 2013–2015. Inertia = variance or weighted sum of squared distances to the origin of the environmental axes; OMI = outlying mean index (marginality); Tol = tolerance index, which represents niche breadth of the two predators across the measured environmental variables; RTol = residual tolerance. Italicized terms represent the percentages of variability corresponding to a specific statistic. P = frequency based on number of random permutations (out of 10,000) that yielded a higher value than the observed outlying mean index ( $P \leq 0.05$  indicates a significant influence of the environmental variables for a species).

Site	Species	<i>inertia</i>	<i>OMI</i>	<i>Tol</i>	<i>Rtol</i>	<i>omi</i>	<i>tol</i>	<i>rtol</i>	P-value
Beaver River	RTHA	11.71	0.32	2.47	8.92	2.70	21.10	76.20	<0.001
	NOHA	10.28	0.10	1.27	8.91	1.00	12.40	86.60	0.020
Packsaddle	RTHA	8.54	0.02	1.35	7.17	0.20	15.90	83.90	0.360
	NOHA	6.89	0.18	0.79	5.93	2.50	11.40	86.10	0.170

## Figure legend

Figure 1: Occurrence points of Red-tailed Hawk (green) and Northern Harrier (purple) at Packsaddle (a) and Beaver River (b) WMAs in Oklahoma, USA, 2013–2015.

Figure 2: Beta coefficients of ( $\beta$  + 95% CI) for habitat selection by Northern Harrier and Red-tailed Hawk at Beaver River Wildlife Management Area in Oklahoma, USA, 2013–2015. Coefficients were collected from a resource selection function of each species at >28 ha (a) and > 201 ha (b). Additional coefficients for topographical and distance related covariates are presented (c). The level of significance is denoted by asterisk where  $P < 0.05 = *$ ;  $P < 0.01 = **$ ; and  $P < 0.001 = ***$ .

Figure 3: Beta coefficients of ( $\beta$  + 95% CI) for habitat selection by Northern Harrier and Red-tailed Hawk at Packsaddle Wildlife Management Area in Oklahoma, USA, 2013–2015. Coefficients were collected from a resource selection function of each species at >28 ha (a) and > 201 ha (b). Additional coefficients for topographical and distance related covariates are presented (c). The level of significance is denoted by asterisk where  $P < 0.05 = *$ ;  $P < 0.01 = **$ ; and  $P < 0.001 = ***$ .

Figure 4: Outlying Mean Index (OMI) analysis of Red-tailed Hawk (RTHA) and Northern Harrier (NOHA) at Beaver River (a) and Packsaddle (b) WMAs in Oklahoma, USA, 2013–2015. The points represent weighted positions of each species in ecological niche space. The figure represents the ecological position of the two species in the n-dimensional hypervolume representing fine-scale environmental variability. The ellipses show the 95% confidence interval around the mean.

Figure 5: Canonical weights of environmental variables at Beaver River (a) and Packsaddle (b) WMAs in Oklahoma, USA, 2013–2015. The figure represents the contribution of environmental variables to the definition of the niche parameters of species in the OMI analysis. The length of the arrow describes the relative importance of each variable in the analysis, and the direction of the arrow indicates among-variable correlations.

Figure S1: Hazard rate detection function plots showing the detection probabilities of four individual observers for Red-tailed Hawk (a), Northern Harrier (b) at Packsaddle WMA, and Red-tailed Hawk (c), Northern Harrier (d) at Beaver River WMA in Oklahoma, USA, 2013–2015.

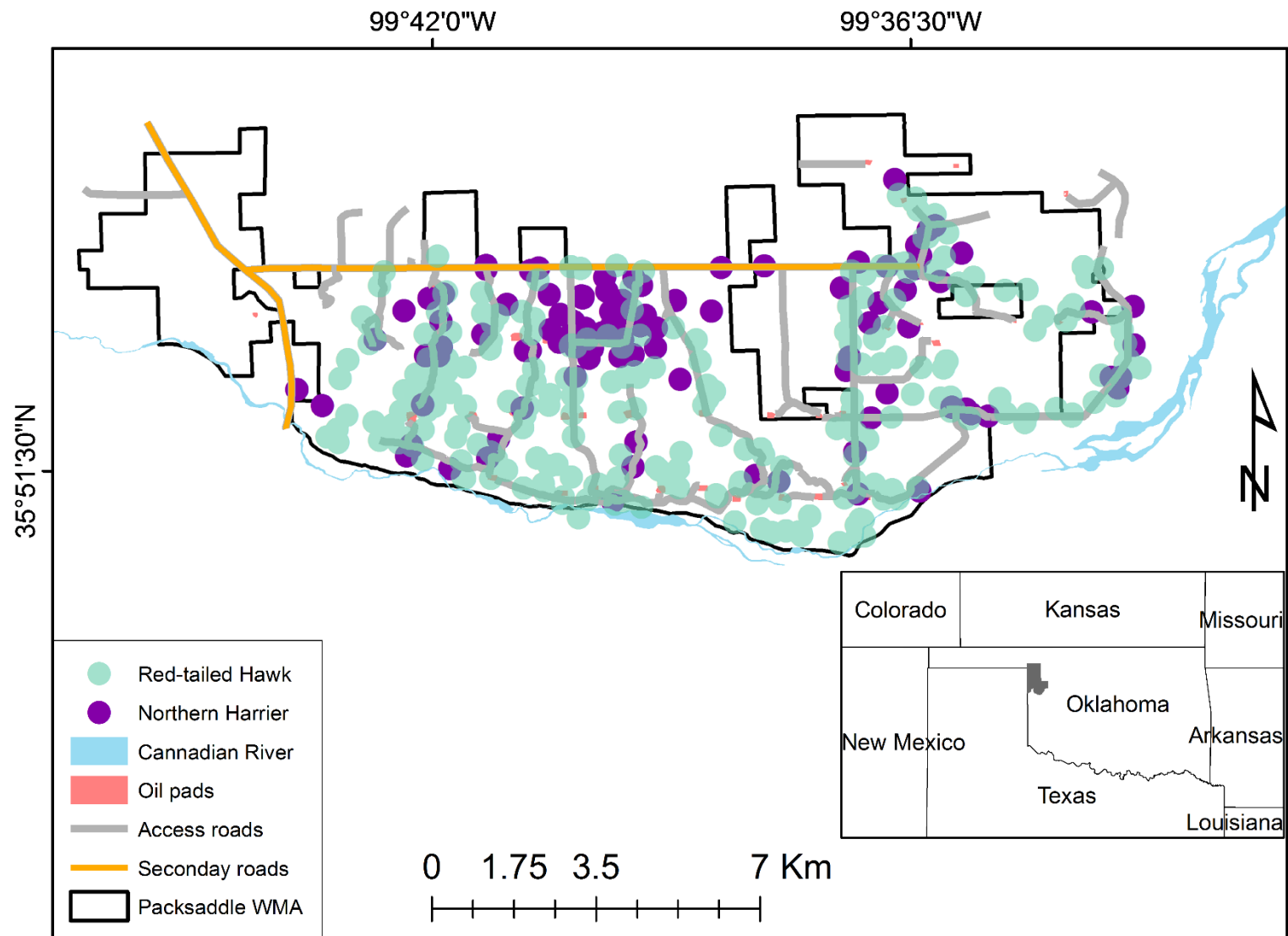


Figure 1a

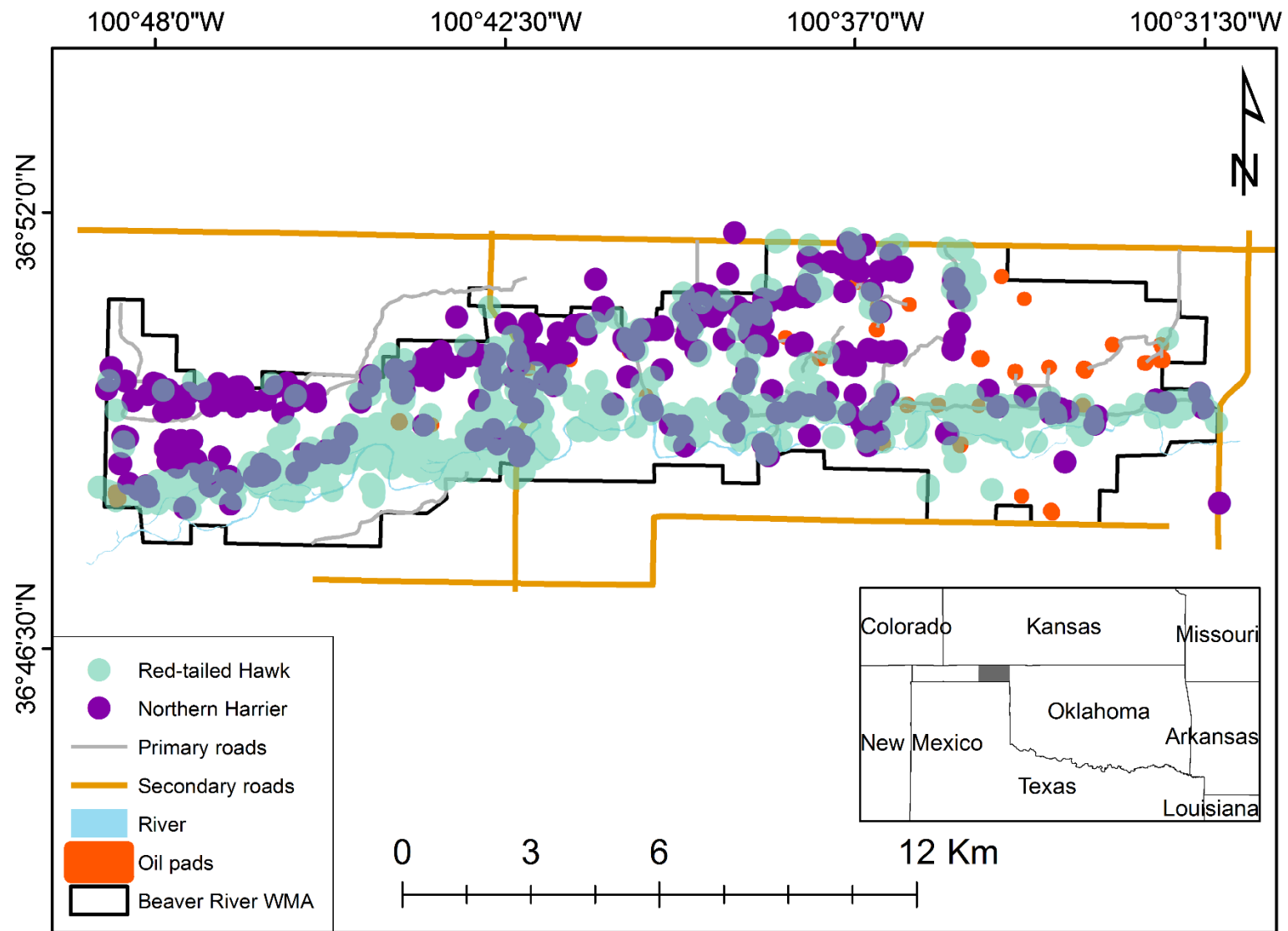


Figure 1b

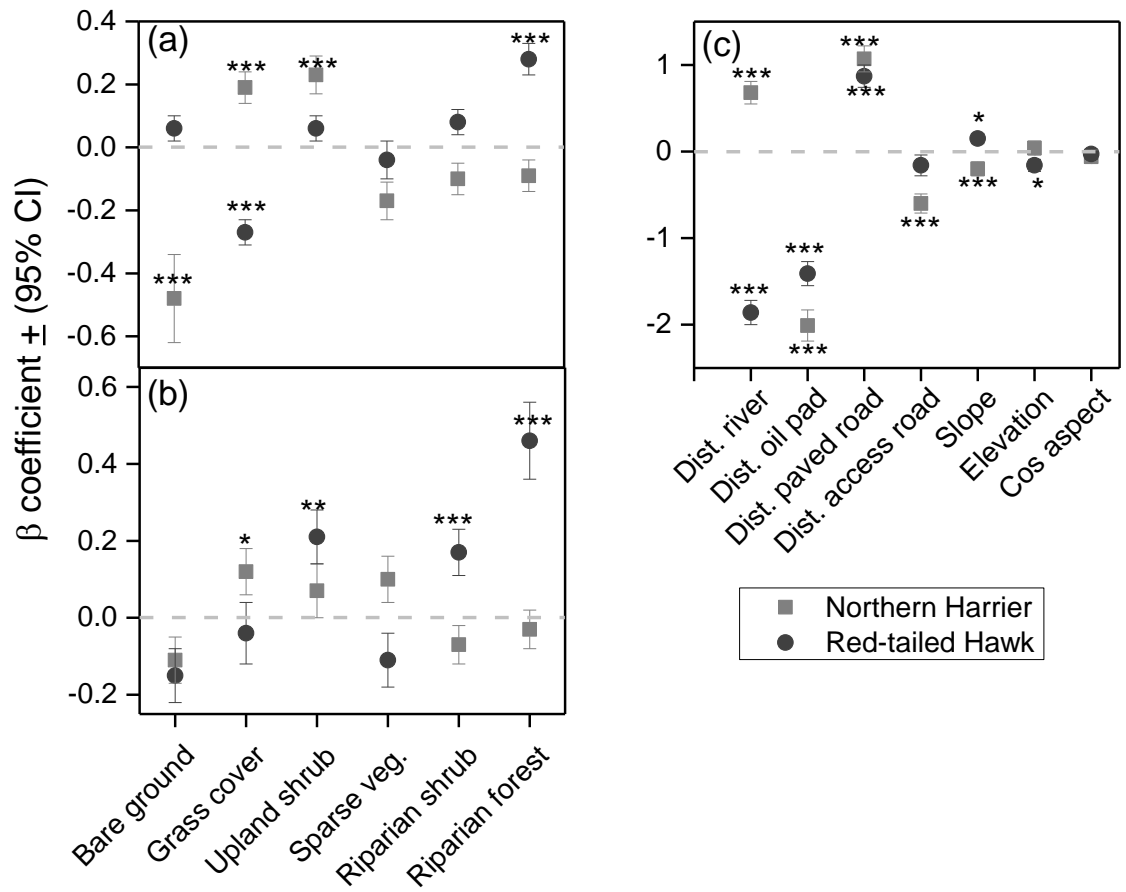


Figure 2

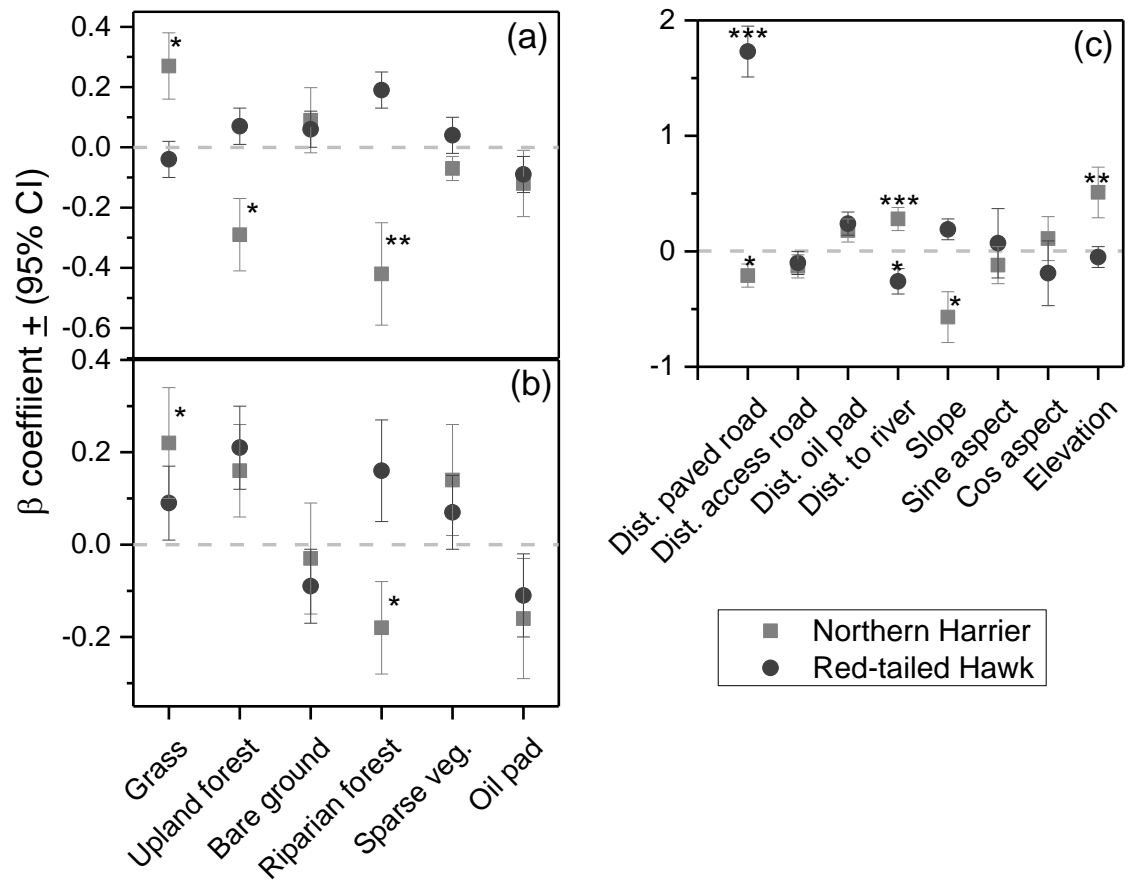
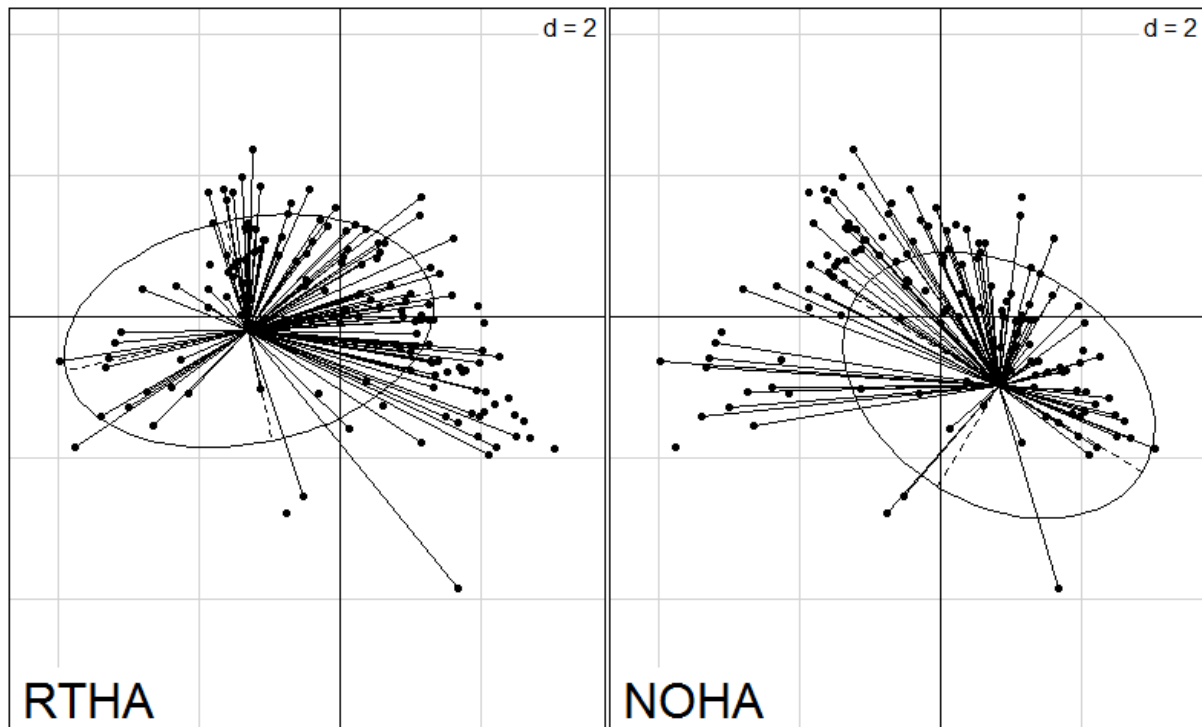


Figure 3

(a) Beaver River WMA



b) Packsaddle WMA

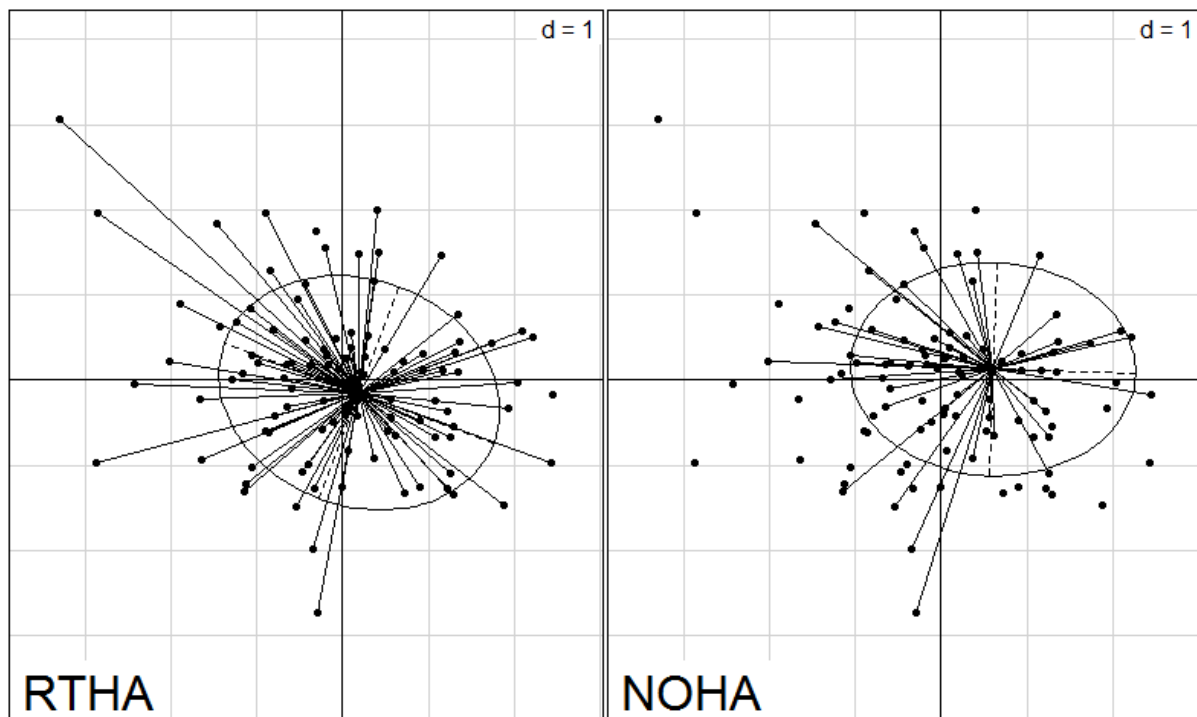
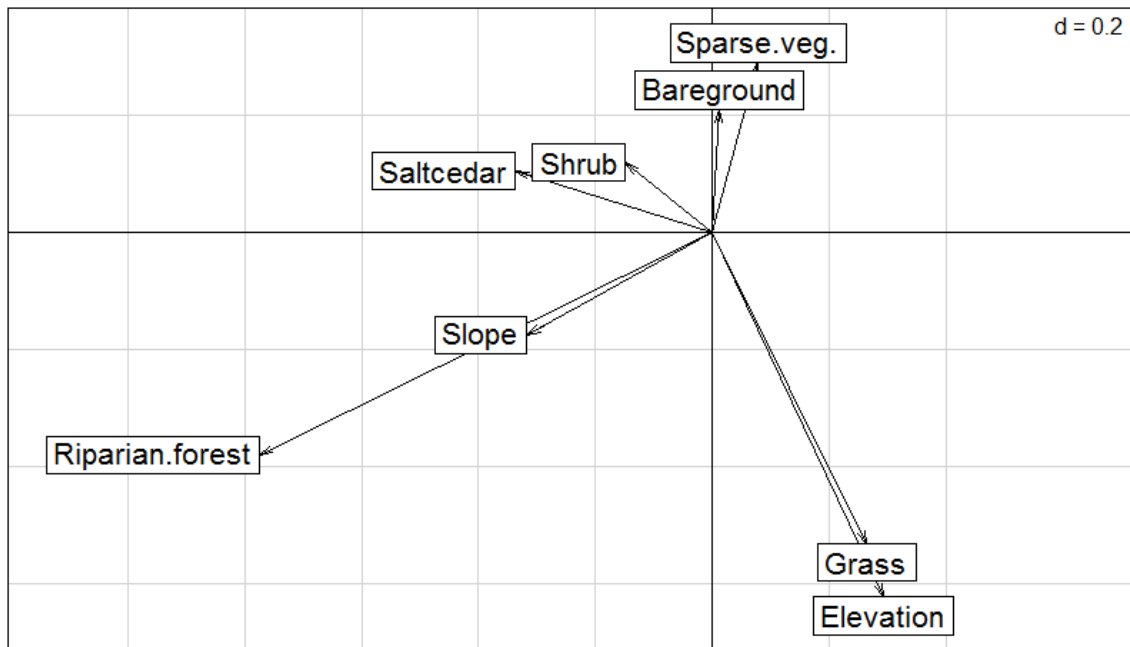


Figure 4



a) Beaver River WMA



a) Packsaddle WMA

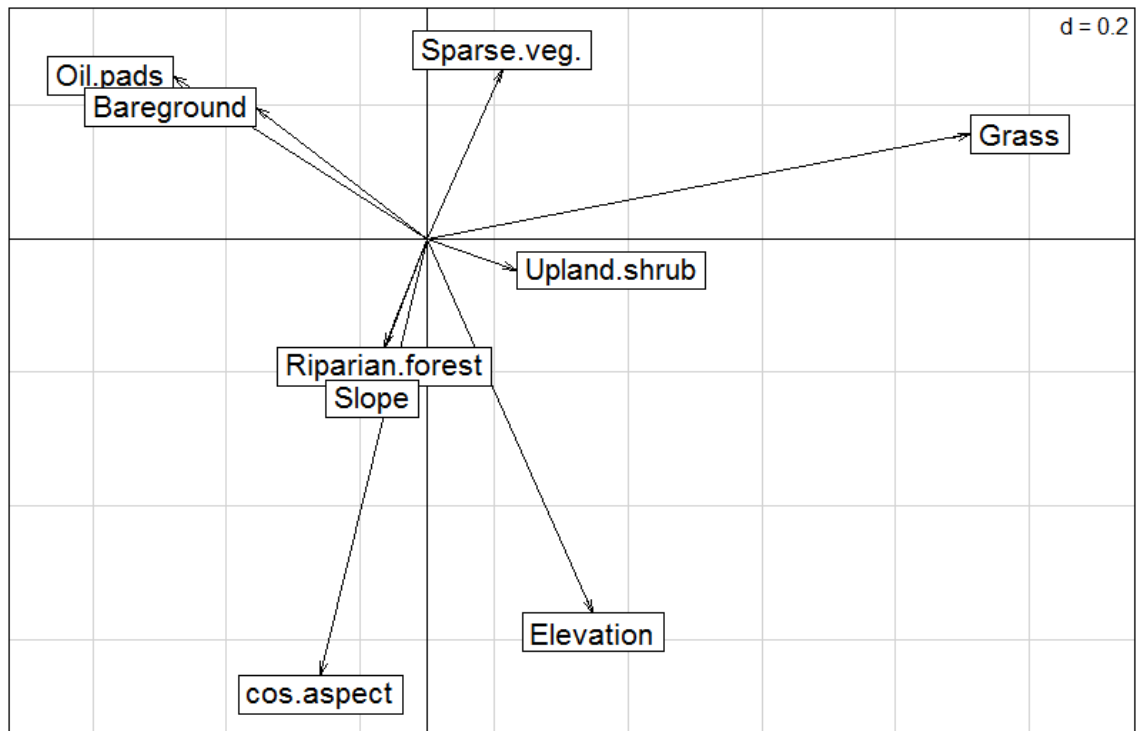


Figure 5

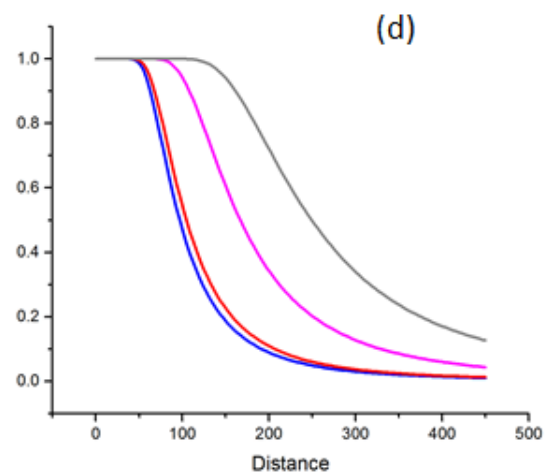
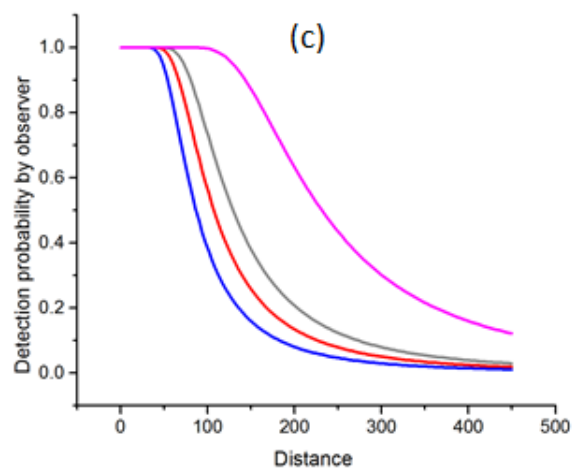
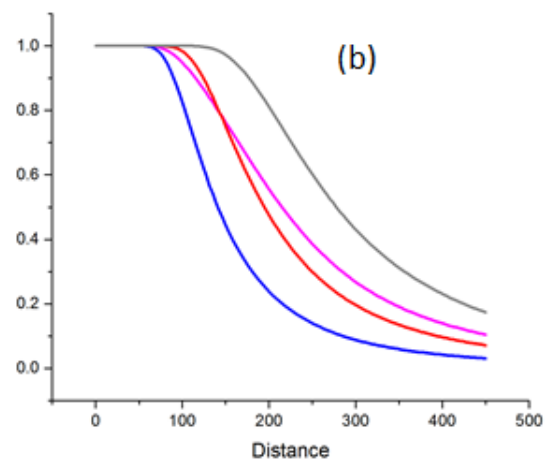
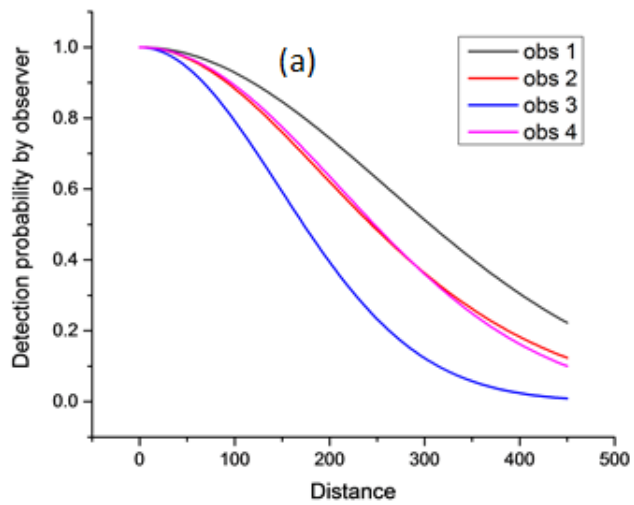


Figure S1

## CHAPTER IV

### LANDSCAPE CHARACTERISTICS AND PREDATOR PROXIMITY INFLUENCE NEST SITE SELECTION IN MISSISSIPPI KITE

#### **Abstract**

Selecting nesting cover that minimizes predation risk and improves breeding success is one of the most important decisions in the life history of a bird. This is because natural selection exerts strong selective pressure on species during the breeding period such that eggs, nestlings, and attending adults are more vulnerable to predation. In this study, I assess the importance of local habitat characteristics, food abundance, and predation risk on nest site selection and nest survival in a gregarious raptor species, the Mississippi Kite. At the nest site scale, Mississippi Kites selected areas with closed canopy, taller trees, higher number of trees, and short grass. At a broader scale, Mississippi Kite selected for upland woody vegetation (trees and shrubs) for nesting and this selection was not related to food abundance. However, Mississippi Kite reproductive success was negatively influenced by proximity to predators, which tended to be found in riparian woodland, which Mississippi Kite avoided. Notwithstanding, Mississippi Kite nest survival was the highest reported at 80%. Although previous studies often associated Mississippi Kite nest site selection with bottomland and riparian forest, their choice of these sites may largely be dictated by available vegetation structure. Therefore, landscape changes that restricts woody vegetation to

riparian habitats may reduce nesting options and compel species to select available areas irrespective of predation risk. My study emphasizes the importance of predation risk in understanding species habitat association because its isolation may results in misleading interpretations.

**Key words:** Nest site selection, nest survival, Mississippi Kite, intraguild predation, predator avoidance

## **Introduction**

Ecological food chains are complex but often drive space use and foraging decisions of organisms (Pimm 1982, Cattin et al. 2004, Begon et al. 2006). The need to “eat without being eaten” is one of the most important factors that determine an organism’s persistence and reproductive fitness (Davies et al. 2012). Prey species must select habitat that offers a balance between foraging opportunities and predation risk. Generally, prey species will respond to predator attacks by becoming more vigilant, joining a larger group, or moving to safer locations (Cresswell 2011, Quinn and Cresswell 2012). For nesting birds, such responses may include active nest defense (Picman et al. 1988), concealing nests from predators (Holway 1991, Mainwaring et al. 2015), quick re-nesting after a predation event (Schmidt and Whelan 2010), nesting in low risk areas further from known predator preferred nest sites (Gamauf et al. 2013), or nesting close to a “protector predator” that might deter potential nest predators (Mönkkönen et al. 2007). Indeed, the decision on where to place a nest is of utmost importance because natural selection exerts strong selective pressure on species during the breeding period such that eggs, nestlings, and attending adults are highly vulnerable to predation (Mainwaring et al. 2015). Furthermore, given that nest productivity (success or failure) is a strong determinant of fitness, an assessment of predation risk by nesting individuals is an important component of nest site selection in most birds (Mönkkönen et al. 2009). For many birds, nest predation is the primary cause of nest failure (Ricklefs 1969, Martin 1993, DeGregorio et al. 2016), and selecting nest sites away from predators is a major strategy to limit predation risk and

improve breeding success (Møller 1989, Fontaine and Martin 2006, Dinkins et al. 2012, Gamauf et al. 2013).

Studies focusing on avian nesting habitat selection and survival in relation to predators are common in the literature, often suggesting that avian species will either nest close to (Thomson et al. 2006a, Mönkkönen et al. 2007) or further from (Dinkins et al. 2012, Vedder et al. 2014) predators as an anti-predator strategy. Nonetheless, little attention has been given to the reality that predators themselves are often prey for other predatory species (intraguild predation; Polis et al. 1989, Holt and Polis 1997, Arim and Marquet 2004). Several studies have shown that several raptors species and their nestlings are killed by larger raptors as prey (Hakkarainen and Korpimäki 1996, Sergio et al. 2003a, Sergio and Hiraldo 2008). For example, Eurasian Eagle Owl (*Bubo bubo*) is known to prey on adult and nestling Black Kite (*Milvus migrans*) (Sergio et al. 2003a). In many cases, habitat needs of prey and predator mirror each other in a number of ways. The prey species is often compelled to select less risky areas in order to avoid dominant predators even if the habitat is of low quality (Cresswell 2008).

The Mississippi Kite (*Ictinia mississippiensis*) is gregarious raptor that breeds in the south-central and southeastern United States where it is known to occupy a wide range of vegetation types (Parker 1996). The Mississippi Kite feeds largely on insects of the Homopteran (e.g. cicada), Orthopteran (e.g. grasshoppers), and Odonatan (e.g. dragonfly) orders (Bader and Bednarz 2009). Occasional feeding on other vertebrates (birds, small mammals and reptiles) has also being reported (Bader and Bednarz 2011). Traditionally, it is known to breed in riparian areas, shelterbelts, oak-shrub prairies, and savannas (Parker 1974, 1999, Bader and Bednarz 2009, Chiavacci 2010). Adult males and females look alike and measure about 30–37 cm in length with a wingspan of about 75–83 cm (Dunn and Alderfer 2011). The Mississippi Kite is a complete migrant (every individual migrates south) and winters in Central and South America (Bildstein 2006). Compared to most raptors, Mississippi Kites return from their wintering grounds relatively late (Bolen and Flores 1993) essentially devoting almost all of their time in North America to breeding. Arrival in their breeding grounds varies between the last week of April and the first week of

May, depending on location (Bolen and Flores 1993, Zalles et al. 2000), and departure is in early autumn (Bildstein 2006). Given the relatively short time that Mississippi Kites spend on their breeding grounds, it is likely to have a tight breeding schedule such that re-nesting or laying a second clutch would be theoretically unlikely if a brood was lost at an advance stage of breeding. Successful breeding is therefore critically dependent on selection of nesting sites that maximize breeding success. This includes selecting nest cover away from predators. The Red-tailed Hawk (*Buteo jamaicensis*) and the Great Horned Owl (*Bubo virginianus*) are reportedly the most common avian predators of Mississippi Kite's nests (Parker 1974, Miller 2005, Bader and Bednarz 2009, Chiavacci et al. 2014). By the time Mississippi Kite arrive on the breeding grounds, these two predators have already established breeding territories and are often in advance stages of their nesting periods (Houston et al. 1998, Preston and Beane 2000). Given that a major anti-predatory strategy in many species is to select nest sites further from known predators (Rauter et al. 2002, Monclús et al. 2009, Gamauf et al. 2013), I expect to see similar strategies for nest site selection by Mississippi Kite in the presence of intraguild predators.

Our study investigated nest site choice and nest survival by the Mississippi Kite in relation to other raptors (Red-tailed Hawk and Great Horned Owl) in a heterogeneous mixed-grass prairie landscape. Specifically, I investigated nest site selection by the Mississippi Kite at two spatial scales (nest site and broad scales) in order to understand the proximate (microhabitat) and landscape level factors that are related Mississippi Kites nesting habitat selection. I also evaluated spatial relationships between Mississippi Kite and predator nest sites to understand the extent to which predation risk influences nest site choice and nest survival. Finally, I quantified additional influence of food abundance on kite nest site selection by assessing abundance of insect prey within major vegetation types in my study system.

## Methods

### Study site

We conducted my study at Packsaddle Wildlife Management Area (WMA) located in western Oklahoma (Figure 1). Packsaddle WMA covers ~6,475 ha of mixed-grassed prairie at 579–762 m asl. The average annual precipitation is ~53 cm, with the majority falling as rain in spring and summer (DeMaso et al. 1997). Soils consist mainly of Nobscot fine sand, Nobscot-Brownfield, and Pratt-Tivoli loamy fine sand (DeMaso et al. 1997, Townsend et al. 2001). Woody vegetation consists of bottomland cottonwood (*Populus deltoides*), willow (*Salix spp.*), hackberry (*Celtis spp.*), and elm (*Ulmus spp.*) along the Canadian River, with shinnery oak (*Quercus harvardii*) and hybrid shinnery mottes in the uplands (Hall 2015). Shinnery oak occurs in many places as monotypic stands with stems is typically <0.5 m and growing in association with bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), sand paspalum (*Paspalum stramineum*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and sand dropseed (*Sporobolus cryptandrus*). Scattered throughout the uplands are discrete patches of taller shinnery oaks that have hybridized with post oaks (*Quercus stellata*) to form mottes with stems of 3–4 m in height (Hall 2015).

Packsaddle WMA is managed for public hunting by the Oklahoma Department of Wildlife Conservation (ODWC) with an emphasis on upland game birds. Most of the management practices on the WMA are targeted at enhancing the population of Northern Bobwhite (*Colinus virginianus*) through a combination of prescribed grazing by cattle (*Bos taurus*) and prescribed burns. In addition, Packsaddle WMA has been developed for oil and natural gas extraction, and both human activity and associated infrastructure is widespread.

## Nest searches

We conducted systematic searches for raptor nests in February–August 2013–2015. I used display flights, courtship flights, cast pellets, and fecal stains on the ground and/or leaves as cues to locating nests (Fuller and Mosher 1987). Because raptors do not nest in random locations (Fuller and Mosher 1987), I concentrated my search efforts around likely nest sites habitat (e.g. trees and shrubs large enough to support a raptor nest). When possible, I observed breeding birds carrying nesting materials using a spotting scope (20–45X) until a nest location was identified.

When a nest was found, I noted its status (i.e. whether it was active or not) and recorded its coordinates using a Garmin Montana 650<sup>TM</sup> GPS unit to enhance monitoring. I inspected for breeding evidence (e.g., presence of eggs or chicks) by remote observation and by observing nest contents reflected in a mirror attached to an extendable pole ~15 m in length (Figure S1; Pagel and Thorstrom 2007, Steenhof and Newton 2007). I considered a nest as active when it contained one or more eggs or nestling(s), or if it was obviously under construction with attending adults present. In each case, I identified the nesting species based on nest architecture, egg characteristics (Baicich and Harrison 1997), and attending birds, if present. I defined nest age as the time in days from when the first egg was laid. A majority of Mississippi Kite nests were discovered at early stages of nest construction, or incubation phase, therefore I could estimate precisely when the first egg was laid. For nests that were found later, I estimated nest age based on clutch completion, onset of incubation, and the size and appearance of nestlings.

We revisited inactive nests (without eggs, nestlings, or fresh linings) at least once a week to determine their status and categorized them as not used or abandoned after 6 weeks if no egg was found. I also visited active nests at 3–5 day intervals before, during, and after incubation to assess nest survival and fledgling production. I considered a nest successful if it fledged at least one chick; otherwise, it was considered failed. Breeding success was defined as the number of fledged chicks per nest. I examined the causes of nest failure by searching an area <50 m radius around failed nests for predation evidence (e.g.



eggshells, bloodstains, broken feathers, and carcasses), anthropogenic activities, nest remains (e.g., from storm damage). I described the reasons for nest failure as unknown in cases where I could not find any evidence of predation, human activities, or weather related events.

#### Nest site characteristics

Reproductive output of birds is influenced by factors operating at multiple scales (Penteriani and Faivre 1997, Sergio et al. 2003b, Bloom et al. 2013, Hovick and Miller 2013). I characterized the nesting cover of Mississippi Kite by measuring vegetation and landscape attributes surrounding each nest at two spatial scales. I considered a nest site scale as an area  $\leq 12.56$  ha around the nesting tree representing the core foraging area of nesting individuals. I also considered a broad scale of  $\leq 314.16$  ha (1000 m radius) around the nest tree to correspond approximately to the home range of Mississippi Kites (250 ha) in the Central Great Plains (Allan and Sime 1943).

To characterize vegetation and landscape attributes at the nesting habitat scale, I identified the nest tree and measured diameter at breast height (DBH). I obtained nest height and heights of nesting trees using a vertex hypsometer (Haglof Inc., Madison, MS, USA). I estimated the percentage of canopy cover around the nest into four categories as none (0% cover), low (1–30%), moderate (31–60%) and high (61–100%) using a spherical convex densiometer (Forest Densiometers, Bartlesville, Oklahoma). I determined the percentage of nest concealment from terrestrial predators by estimating the amount of leaves, branches or twigs around the nest from the four cardinal directions at 15 m from the base of the nest tree and categorized nest concealment as poor (0–25%), fair (26–50%), good (51–75%) and excellent (76–100%; Buij et al. 2013). I counted the number of trees (DBH  $\geq 30$  cm or  $\geq 3$  m high) categorized by species from a subsample of 50 m-radius circular plot centered on the nest tree. To quantify ground cover, I estimated grass height, and percentage of ground cover (to the nearest 5%), in four 10-m<sup>2</sup> sub-plots taken in the four cardinal directions at 20 m from the nest tree and collapse them to obtain mean scores of each variable per

nest site. I carried out all measurements at the end of the breeding season to avoid disturbance to nesting birds.

From each nest location, I used the *random point generating* tool in ArcGIS 10.2 (Environmental Systems Research Institute Inc., Redlands, CA, USA) to identify comparison locations. At each random plot, I sampled the nearest tree from the center of the plot with diameter  $\geq 30$  cm or height  $\geq 3$  m respectively corresponding to the minimum DBH and height used by a Mississippi Kite in my study area. For broad scale characterization of nest locations, I established 1000 m buffers around nest and random locations in a GIS and compared land cover within the buffered areas. I used a 10 m resolution National Agriculture Imagery Program (NAIP) land cover image collected from the data portal of the Oklahoma Department of Wildlife Conservation and reclassified the land cover raster into 10 land cover classes (Table 1). Using the *zonal statistics* tool, I extracted the number of pixels representing the amount of each land cover type within buffered areas. I also calculated 10m resolution data on elevation, slope, and terrain roughness (degree of terrain ruggedness calculated as the standard deviation of elevation) from a Digital Elevation Model (DEM) layer (USGS data portal at 1/3 arc-seconds). To evaluate nest site selection by Mississippi Kites in relation to conspecifics and known predators, I obtained distance related variables by estimating Euclidian distances from nest sites and random plots to the nearest neighbor, nearest Red-tailed Hawk or Great Horned Owl nest.

### Insect sampling

Grasshoppers (orthoptera), cicadas (hemiptera), and dragonflies (odontata) constitute at least 90% of Mississippi Kite diets (Bader and Bednarz 2011). To estimate prey availability, I sampled these insects at 57 randomly selected locations in uplands (n = 29) and lowlands (n = 28). Sampled locations were generated using a random number generator. At each location, I established a 10 m x 10 m plot centered

on the random point and estimated the abundance of grasshopper, cicadas, and dragonflies by counting the number of flushed individuals during a diagonal walk through the plot (Gardiner et al. 2005).

We resampled each plot after one week using the sweep netting technique in order to obtain arthropod biomass. At each plot, I completed 20 sweeps working diagonally across the plot. I transferred arthropods from the sweep nets into zip bags containing acetone and stored in the refrigerator. I conducted all insect sampling activities in July corresponding to the peak breeding period of Mississippi Kite in the Great Plains. I identified all arthropods in each sample to order levels and obtained biomass of cicadas and grasshopper by measuring their dry weight using a Sartorius ENTRIS analytical balance. Sweep nets were not effective in capturing dragonflies; hence, I did not include their biomass in my analysis.

#### Burn date and nest placement

We obtained data on periodic prescribe fire regimes between 2004 and 2015 from the management of the Packsaddle WMA. Packsaddle WMA is subdivided into 6 management units. As part of the management practice to improve native flora and fauna, prescribed burning is applied to part, or all of  $\leq 3$  units each year with a fire return interval of 3–10 years. Prescribed burns were generally conducted in February or March, but a few plots were burned in summer, fall, or winter. I considered a nest to be in a burned plot if all or part of an area within 50 m of the nesting tree was burned in the current or previous year. I calculated time since last burn (in years) for nest locations and random plots.

#### Data Analysis

We conducted separate analyses for nest site selection and nest survival in relation to environmental variables in my study system. First, I analyzed Mississippi Kite nest site selection by comparing data obtained from nest sites to those collected at random locations. I categorized nest locations as “used” and

coded them as 1 while random locations were categorized as “available” and coded as 0. At each scale, I developed Resource Selection Functions (Manly et al. 2007) by contrasting measurements of each variable between used and available locations using Generalized Linear Mixed Models (GLMM) approach, specifying a binomial distribution (Zuur et al. 2009). I included year as a random effect to account for temporal variation in nest number over the duration of my study. To avoid multicollinearity, I performed a Pearson correlation on all variables at each scale and only included one of the correlated variables ( $|r| \geq 0.7$ ) in my models. Model building was based on *a priori* hypothesis. At each scale, I developed a set of *a priori* candidate models by examining the additive roles of variables on nest site selection. I did not include variable interactions in candidate models because preliminary analyses revealed that their inclusion did not improve model fit. At the broad scale, I categorized variables into 3 groups based on factors that shared common features (i.e. topography, vegetation, and proximity variables). I ranked and averaged all candidate models belonging to each group according to their AICc values (small sample size-adjusted Akaike’s information criterion; Burnham and Anderson 2002) using the R package MuMIn package version 1.15.6 (Barton 2016). I considered competing models within a  $\Delta AICc < 2$  as important in explaining Mississippi Kite nest site selection. Prior to statistical analysis, I standardized all environmental variables to a mean of 0 and a standard deviation of 1 to improve data interpretations. I also compared focal nesting tree characteristics between Mississippi Kite, Red-tailed Hawk, and Great Horned Owl using a the one-way ANOVA. Prior to performing the ANOVA analysis, I checked data for normality and  $\log(x + 1)$  transformed the data where necessary to meet the assumptions of normality. I evaluated the differences in insect abundance and biomass between upland and lowland zones of the WMA using a 2-sample Welch’s *t-test*.

We modeled daily nest survival rate of Mississippi Kite using the R package RMARK version 2.1.14 (Laake and Rexstad 2007, Laake et al. 2015), which implements the nest survival model in program MARK (Colorado State University, Ft. Collins, Colorado). I created encounter histories for all nests monitored following the suggestions of Cooch and White (2008). Because I were interested in the influence that

predators and conspecifics may have on nest survival, I included Euclidian distances of successful and failed nests to Red-tailed Hawk, Great Horned Owl, and conspecifics as covariates. In each case, I included only the nests that were lost due to possible avian predation. Because predation risk was likely to vary over the duration of the nesting season, I included age of nest and linear or quadratic effect of survey period as covariates in my model. I evaluated model supports based on AIC<sub>c</sub> (Anderson 2002). To compare model performance and evaluate support for explanatory variables, I calculated differences in AIC<sub>c</sub> values ( $\Delta$ ) and Akaike weights ( $G_i$ ). Next, I performed model averaging to obtain parameter estimates ( $\beta$ ) and 95 % confidence intervals (Anderson 2002) for each covariate. I used model-averaged parameters to predict daily survival rates over a 70 exposure days starting from the clutch initiation date (Bolen and Flores 1993, Parker 1999).

## Results

We located and monitored 102 Mississippi Kite 33 Red-tailed Hawk, and 23 Great Horned Owl nests nest attempts (Figure 1). Yearly nest attempts for the Mississippi Kite include 37 in 2013, 42 in 2014, and 23 in 2015. For the Red-tailed Hawk, I identified and monitored 6, 14, and 13 nest attempts in 2013, 2014, and 2015, respectively. In addition, I identified 5 nest attempts for the Great Horned Owl in 2013, 11 in 2014, and 7 in 2015.

### Nest site characteristics

Four variables of nesting tree (nest height, nest tree height, nest concealment, and DBH), differed significantly across nest sites of Mississippi Kites, Great Horned Owls, and Red-tailed Hawks (Table 2). Red-tailed Hawk nested in significantly larger and taller trees followed by the Great Horned Owl, and Mississippi Kite in that order (Table 2). Nest concealment was highest in Mississippi Kite, ranging from

moderate to highly concealed (Figure S2). Great Horned Owl nests were the least concealed (Figure S3), with a majority of the nests (>60%) poorly concealed. Nest concealment in Red-tailed Hawk (Figure S4) was between those of Mississippi kites and Great Horned Owl with nest concealment ranging between 40–90% (i.e. fairly conceal to highly conceal). I did not find any differences in the height of grass, number of trees within a 20 m radius of the nesting trees, or in the percentage of ground cover across nest sites of the three species (Table 2). The species of nesting trees differed among the 3 raptor species. A majority of all Mississippi Kite nests (>65%) were in hybrid shinnery oak (Figure 2). Other tree species included hackberry (*Celtis occidentalis*), black locust (*Robinia pseudoacacia*), soapberry (*Sapindus spp.*), post oak, and eastern cottonwood (Figure 2). The dominant nesting tree species for Red-tailed Hawks was the eastern cottonwood (>72%, Figure 2). American elm (*Ulmus americana*), hybrid shinnery oak, and eastern red cedar (*Juniperus virginiana*) constituted the remaining <30% of Red-tailed Hawks nesting trees (Figure 2). Great Horned Owl nested in previous nests of Red-tailed Hawks, Swainson's Hawks (*Buteo swainsoni*), and Mississippi Kites. Great Horned Owl nesting trees included eastern cottonwood (64%) and hybrid shinnery oak (36%; Figure 2).

#### Micro habitat nest site selection in Mississippi Kite

At the fine scale, I evaluated 26 *a priori* models for Mississippi kite nesting habitat selection consisting of additive combinations of 7 covariates (tree height, tree canopy, number of trees, number of shrub, percent concealment, grass height, and percent ground cover) and a random effect of year. All top models within  $\Delta AICc < 2$  contained the variables canopy height and number of trees (Table XXXX). Hence, I interpreted the model containing the variables (i.e. canopy height and number of trees) as its only fixed effects to be the single best approximating model. All other models within  $\Delta AICc < 2$  were considered as nested versions of the approximating model with additional uninformative covariates (Table 3). All top models within the  $\Delta AICc < 2$  suggested that four variables (canopy height, grass height, number of trees,

and tree height) where most important in informing kite's nest site locations. Furthermore, a parameter estimation of the global model identified two variables (canopy height and number of trees) as most significant ( $p < 0.05$ ). The probability of kite nesting selection increased with both canopy height and number of trees (Figure 3). Also, the probability of selection suggested a positive relationship with tree height ( $p = 0.061$ ) and negative non-significance relationship with grass height ( $p = 0.08$ ; Figure 3).

#### Broad scale nest site selection by Mississippi Kite

Broad scale analyses of nest site selection were based on vegetation, distance matrices to major landscape features, and topographical variables. In each case, I identified the models containing the most informative variable(s) as its only fixed effect(s) within  $\Delta AICc < 2$  as the best approximating models, and interpreted all other models within the  $\Delta AICc < 2$  penalty as nested versions of that model with additional uninformative covariates (Arnold 2010). For distance related models, the best-approximating model contained the variables distance to conspecifics, distance to roads, distance to Red-tailed Hawk nests, and distance to Great Horned Owl nests (Table 4). Parameter estimates obtained through model averaging suggests that the probability of kite's nest site selection increased with increasing distance away from nesting Red-tailed Hawks and Great Horned Owls (Figure 4), but decreased as distances to conspecifics and roads increased (Figure 4). The mean kite nesting distance was  $2511.84 \pm 91.65$  m away from Red-tailed Hawk nests,  $1746.75 \pm 89.93$  from Great Horned Owls,  $233.07 \pm 39.16$  m from roads, and  $156.86 \pm 14.67$  m from conspecifics. The best approximating model for vegetation related variables included riparian woodland, upland shrub cover, and upland woodland (Table 3). Grass cover was present as an uninformative variable in the second model within  $\Delta AICc < 2$ . Model averaging demonstrated that the probability of nest site selection by Mississippi Kites increased significantly ( $p < 0.05$ ) with upland shrub and upland woody vegetation, but decreased with increasing grass and riparian woody cover (Figure 5). For topographical variables, the model with elevation as its only fixed effect was the single best-

approximating model, while the second model within  $\Delta AICc < 2$  was interpreted as its nested versions containing slope as an uninformative covariate (Table 4). Consequently, elevation was the strongest predictor of nest site selection with the probability of selection significantly in favor of higher elevation (Figure 6). Nest site selection was also significantly affected by slope with the probability of selection decreasing at higher degrees of slope (Figure 6).

### Nest survival

Daily nest survival was based on a 70-day nesting period with 35 days of incubation and 35 days of brood rearing assuming incubation begins with the laying of the first egg (Parker 1999). I obtained a daily nest survival rate based on 80 Mississippi Kite nests that were active during the summers of 2013 – 2015. In all, 67 nests (80%) survived to fledging (at least one chick), while 16 (20%) failed at different stages of the nesting period. Seven (9%) of the nests failed during incubation mainly due to wind storm (3%), predation (5%), and nest abandonment (1%). Post incubation survival was also high with only 9 (11%) nest loss mainly to predation. I considered 3 models within  $\Delta AICc < 2$  as competing (Table 4). All competing models describing nest survival rates included the variables nest age, distance to Red-tailed Hawk nest, distance to Great Horned Owl nest, and distance to conspecifics. In fact, all competing models containing these variables had a cumulative Akaike weight of 0.91. Mississippi Kite nest survival probability was generally high at Packsaddle WMA ( $0.91 \pm 0.01$ ). Daily nest survival increased with increasing distance to nesting Red-tailed Hawks (Figure 7a) ranging from 0.963 [95 % confidence interval (CI): 0.877 – 0.989] for nests that were  $< 100$  m to 0.990 (95 % CI: 0.971 – 0.996) for nests that were  $> 4500$  m away from nesting Red-tailed Hawks. Similarly, the probability of daily survival increased with increasing distance to nesting Great Horned Owl (Figure 7b) ranging from 0.948 (CI: 0.894 – 0.975) for distances  $< 100$  m to 0.999 (CI: 0.998 – 0.999) for distance  $> 2000$  m. On the contrary,



daily nest survival decreased with increasing distance to nesting conspecifics (Figure 7c) ranging from 0.974 (95 % CI: 0.949 – 0.989) for nest < 100 and 0.935 (95 % CI: 0.824 – 0.978) for distance > 4500 m.

### Insect abundance

General insect abundance (i.e. grasshoppers, cicadas, and dragonfly) did not differ significantly between upland than lowland areas ( $t_{(55)} = 1.069$ ,  $P = 0.29$ ), although mean abundance was higher in upland ( $14.38 \pm 2.29$ ) than lowland ( $10.82 \pm 2.41$ ). Similarly, insect biomass did not differ between the two areas ( $t_{(55)} = 0.93$ ,  $P = 0.35$ ). Grasshoppers were the most abundant insects accounting for (77%) of all sampled insects, followed by cicadas (13%), and dragonflies (9%). Mean abundance of grasshoppers, dragonflies, and cicadas in upland were  $10.24 \pm 2.11$  SE,  $1.17 \pm 0.51$  SE, and  $1.72 \pm 0.65$  SE respectively compared to  $1.07 \pm 0.25$  SE,  $2.11 \pm 0.55$  SE, and  $6.86 \pm 2.38$  SE at the lowland zone. The Welch's *t*-test revealed a significantly higher grasshopper abundance in upland than lowland areas ( $t_{(55)} = 4.31$ ,  $P < 0.001$ ). Furthermore, dragonfly abundance was significantly higher in lowland areas ( $t_{(55)} = 2.11$ ,  $P = 0.040$ ). I did not find any differences in cicadas abundance between the upland and lowland zones ( $t_{(55)} = 1.27$ ,  $P = 0.22$ ).

### Discussion

One of the most important decisions of any breeding bird is where to place its nest (Latif et al. 2012) because reproductive fitness is largely dependent on nest survival. Predation is therefore likely to impose strong direct selection on where a bird may choose to place its nest. My study presents current information on nest site selection by an avian predator in response to intraguild predator distribution. Previous studies of nesting habitat selection by the Mississippi Kites, mostly in the Mississippi River Valley (Parker 1974, Bader and Bednarz 2010, Chiavacci 2010, Bader and Bednarz 2011), have shown

that they preferentially select riparian and bottomland forests for nesting. On the contrary, kites in my study system selected smaller upland woody vegetation, mainly hybrid shinnery oak (Figure 2). In fact, kites in this landscape demonstrated strong avoidance for riparian forest having larger and taller trees. Nesting trees were in the range of 20–95 cm in DBH and between 3–18 m in height. Both the average tree height (8.33 m) and average tree DBH (52.40 cm) for nesting trees at my study site were in sharp contrast to previous studies where kites selected nesting trees with average heights  $\geq 32$  m and average DBH  $\geq 75$  cm (Bader and Bednarz 2010, Chiavacci 2010).

Nest site selection increased with number of trees and with increased canopy cover. These vegetation characteristics are important in shielding nests from the sky thereby reducing the ease of detection by avian predators (Rodriguez et al. 2006, Bader and Bednarz 2010, Buij et al. 2013). Placing nests in areas with surrounding trees likely reduces nest losses to windstorms, which is a major contributor to pre-hatching nest losses. Although kites selected nesting trees substantially shorter than in previous studies (Bader and Bednarz 2010, Chiavacci 2010), they selected trees that were much taller compared to non-used trees. This is consistent with the observation of Barber et al. (1998) who noted that the Mississippi Kite preferred emergent trees that provides easy access to nests. At broad scale, the most important vegetation attributes predicting nest placement by Mississippi Kite were increased amount of upland shrub and upland forest cover. Hybrid shinnery mottes are the dominant shrub cover at Packsaddle and are mainly at the upland zone of the WMA. Although the height of shinnery stems is typically  $\leq 0.5$  meters, those individuals that have hybridized with post oaks regularly form mottes with stems of  $\geq 3$  m in height (Hall 2015). The presence of these hybrid mottes together with a few upland trees thus provides nesting cover for breeding Mississippi Kites in this landscape.

Mississippi Kite nest survival in my study was the highest of any known study. For example, Barber et al. (1998) recorded only 22% nest survival for Mississippi kites nesting in the floodplain forests along the Mississippi River in southeastern Missouri. Similarly,  $\leq 29\%$  of all nest attempts by the Mississippi kite in the Mississippi River Valley were successful (Bader and Bednarz 2009, Chiavacci 2010, Chiavacci et al.

2014). In all previous studies, nest predation from snakes and avian predators were the primary cause of nest failure. In fact, Chiavacci et al. (2014) identified the Red-tailed Hawk and Great Horned Owl as top avian predators of Mississippi Kite nests. In my study site, the Red-tailed Hawk and Great Horned Owl nested predominantly in riparian vegetation away from Mississippi Kites nests. Riparian nesting habitat selection by the Red-tailed Hawk and the Great Horned Owl in the Great Plains is well supported by previous studies (Tubbs 1980, Preston and Beane 2000, Actkinson et al. 2007, McConnell et al. 2008). Among the three raptors studied by McConnell et al. (2008) in northwestern Oklahoma, Red-tailed Hawks nested exclusively in riparian woodland. Similarly, 92% of all Great Horned Owl detections obtained during a playback survey in central Oklahoma were within riparian woodland (Winton 1997). Nesting tree species also differ between Mississippi Kites and the Red-tailed Hawk. While Red-tailed Hawks nested almost exclusively ( $\geq 70\%$ ) on large cottonwood trees usually along riparian woodland,  $\geq 65\%$  of all Mississippi Kite nests were on hybrid shinnery oak which I classified as upland shrubs. The disproportional selection of cottonwood trees by nesting Red-tailed Hawks in this landscape is consistent with McConnell et al. (2008) and likely due to their ability to support the relative large Red-tailed Hawk nest. In addition to providing safe nesting site away from predators, hybrid shinnery mottes were presumably preferred by Mississippi Kites because they occurred in mottes thus providing dense canopy relevant for nest concealment. Great Horned Owl did not build their own nests but nested on previous nests of other raptors species, especially Red-tailed Hawks. This was possible because nest site selection by the Great Horned Owl occurs in advance of spring arrival of Red-tailed Hawks and Mississippi Kites.

Mississippi Kite feeds predominantly on arthropods mainly of the orders *homoptera*, *orthoptera*, and *odonata* (Glinski and Ohmart 1983, Bader and Bednarz 2011, Chiavacci et al. 2014). Greater than 80% of food items delivered to nestlings in eastern Arkansas were insects (Bader and Bednarz 2011). I did not find a significant difference in the overall distribution of insect prey between upland and riparian zones in my study. While grasshoppers were most abundant in upland, dragonfly abundance was higher in the riparian zone, and cicadas did not differ between the two habitat zones. The lack of difference in prey

items between the two zones suggest that kite selection of uplands may not be related to prey abundance. Terrain ruggedness did not influence kites nest site selection, rather they selected higher elevation to avoid top predators that nested in lower elevations mainly in riparian woodland.

Although Mississippi Kite nesting preference was not independent of habitat preference, I found evidence that the presence of predators influenced nesting pattern of kites in my study site. Nests were significantly further from Red-tailed Hawk and Great Horned Owl nests than I would expect to see if nest sites were selected at random. Likewise, Mississippi Kites that nested close to Red-tailed Hawks had a higher chance of losing their nestlings. Evidence exists that raptors and other bird species that breed in proximity to top avian predators may suffer significant nest losses to predation. For example, Eurasian Honey Buzzards (*Pernis apivorus*), that nested in proximity to the Northern Goshawk (*Accipiter gentilis*) in eastern Austria recorded higher chick mortality than those that nested further away (Gamauf et al. 2013). Also, several smaller species of owl are known to select breeding sites away from larger relatives in attempt to avoid predation (Hakkarainen and Korpimäki 1996, Sergio and Bogliani 2000, Sergio et al. 2003a).

Our results show that nesting close to conspecifics improved daily kite's nest survival. Mississippi Kite nests were either in groups (loose colonies) of 2–5 or solitary. Bader and Bednarz (2009) suggested that such group nesting behavior by Mississippi Kites in the Great Plains may be important in deterring diurnal nest predators. Group nesting is likely to improve predator detection and increase the number of individuals available for mobbing potential predators away from nests. Group nesting Mississippi Kites could therefore benefit from communal predator detection and defense, thus increasing the probability of nest success. Also, studies that investigated nesting success in communally nesting raptor found increased defense behavior with group size (Arroyo et al. 2001, Coulson et al. 2008). My findings were however in contrast to Glinski and Ohmart (1983) that found no differences in breeding success between solitary and group nesting Mississippi Kites in Southwestern United States. However,  $\geq 80\%$  of all nest failures in

their study occurred before the eggs were hatched, while only one of the two post-incubation mortality was attributed to predation (the other was due to starvation).

While my study recorded substantial spatial segregation in nest site selection between Mississippi Kite and its top avian predators, previous studies recorded high spatial overlap between Mississippi kites, Red-tailed Hawk, and Great Horned Owl with high predation events. In the Mississippi River Valley floodplains where nest failure are reportedly high and fledging success is low, Mississippi kites are known to select bottomland woodland, riparian forest, and large cottonwood trees which are known preferred nesting habitats for the Red-tailed Hawk, Great Horned Owl, and other top avian predators (Bednarz and Dinsmore 1982, McConnell et al. 2008, Chiavacci 2010). It is therefore evident that the substantial spatial segregation in nesting habitats between Mississippi Kite and its intraguild predators in my study site might account for their high nesting success in the Great Plains. Following their late arrival in their breeding grounds at a time when potential predators have already established breeding territories, Mississippi kites are able to identify risky sites and select breeding sites further from predators. Landscape changes that limit or restrict woody vegetation to riparian areas reduces nesting options and may compel kites to select available areas irrespective of predation risk. Breeding in such areas thus increases the likelihood of nest mortality or indirect trait-mediated fitness consequences in the form of reduced clutch size, loss of foraging opportunities, and weight loss. For example, Pied Flycatchers (*Ficedula hypoleuca*) that nested close to Eurasian Sparrowhawks (*Accipiter nisus*) pay a fitness cost in terms of reduced clutch sizes (Thomson et al. 2006b), possibly because resources for reproduction were invested in anti-predation behavior. In the Great Plains, the presence of medium-sized trees in uplands apparently provides alternative nesting cover for Mississippi Kite and improves their reproductive success.

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## Tables

Table 1: Descriptions of covariates used in modeling nest site selection and daily nest survival rate (DSR) of Mississippi Kite in Oklahoma, USA, 2013–2015.

	Variables	Definition
Nest site level variables	Nest height	Vertical height of a nest from the ground
	Tree height	Height of a tree where a nest is placed
	Diameter at breast height (cm)	Diameter of the nesting tree at 1.37m above ground
	Canopy cover	the percentage of the horizontal forest area occupied by vertical projection of tree crowns
	Tree species	Species of the nesting tree
	Nest concealment (%)	Proportion of vegetation obstruction of view from above nest
	Number of trees	Woody plants $\geq 4\text{m}$ within 50 m of a nesting tree
	Number of shrub	Woody plants $\leq 4\text{m}$ within 50 m of a nesting tree
	Grass height (m)	Mean taken at 4 sub-plots 20–50m from nesting tree
	Ground cover (%)	Percentage of ground that is covered by litter or grass collected from 4 sub-plots within 50 m but 20 m from the nesting tree
	Nesting bird	Raptor species nesting
	Nest contents	Contents of a nest (i.e. eggs, chicks, or empty)
	Number of eggs	Number of eggs in the nest
	Number of chicks	Number of chicks in the nest
	Nest age	Age of nest at the date of discovery
	Nest fate	Successful "0" or failed "1"
	Cause of failure	Reasons for nest failure
Broad scale variables	Mixed-grass	Composition of mixed-grass in a 1000m buffer centered around a nesting tree
	Riparian wood	Composition of riparian woody cover in a 1000m buffer centered around a nesting tree
	Riparian shrub	Composition of riparian shrub cover in a 1000m buffer centered around a nesting tree
	Upland wood	Composition of upland woody cover in a 1000m buffer centered around a nesting tree
	Oil pads	Composition of oil pads cover in a 1000m buffer centered around a nesting tree
	Upland shrub	Composition of upland shrub cover in a 1000m buffer centered around a nesting tree
	Open water	Composition of open water cover in a 1000m buffer centered around a nesting tree
	Pasture	Composition of pasture cover in a 1000m buffer centered around a nesting tree

	Sandhill shinnery	Proportion of sandhill shinnery vegetation cover in a 1000 m buffer centered around a nesting tree
	Time since fire	Time since last fire
Distance variables	Distance to RTHA	Euclidian distance from a nest site to closest Red-tailed Hawk nest location
	Distance to GHOW	Euclidian distance from a nest site to closest Great Horned Owl nest location
	Distance to MIKI	Euclidian distance from a nest site to closest Mississippi Kite nest location
	Distance to water	Euclidian distance from a nest site to closest water body nest location
	Distance to roads	Euclidian distance from a nest site to closest access road
	Distance to oil pad	Euclidian distance from a nest site to closest oil pad
Topographical variables	Elevation	Topographical height of a nest location
	Slope	Steepness of a nest location
	Roughness	Standard deviation of elevation
	Elevation <sup>2</sup>	Square of elevation
	Slope <sup>2</sup>	Square of slope

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Table 2: Comparison of the nest site characteristics of Mississippi Kite, Red-tailed Hawk, and Great Horned Owl at Packsaddle WMA, Oklahoma, USA, 2013–2015. Significance of 2-sample Welch's *t*-test comparing the characteristics across the three. DBH = Diameter at breast height.

Variables	Mississippi Kite		Red-tailed Hawk		Great Horned Owl		F	sig
	Mean	SE	Mean	SE	Mean	SE		
Nest height (m)	6.47	0.28	11.30	0.66	9.36	0.91	32.53	<0.001
Tree height (m)	8.33	0.28	13.39	0.71	11.57	0.80	34.55	<0.001
Nest concealment (%)	31.91	2.48	47.42	4.92	30.00	6.77	4.81	0.013
Numb. of trees	3.75	0.57	6.06	1.41	3.93	1.58	1.66	0.190
Grass height (m)	0.31	0.03	0.32	0.06	0.35	0.15	0.08	0.920
Ground cover (%)	44.22	3.32	53.79	5.83	48.93	9.81	1.03	0.360
DBH (cm)	52.40	1.57	238.33	14.22	162.14	28.10	174.46	0.000



Table 3: Top 10 additive models for nest site selection of Mississippi Kites at the nest site level in Oklahoma, USA, 2013–2015. All models included an intercept term and random effect of year. The top model included canopy height (m) and the number of trees (woody stems within 50m of the nest tree). Models list the number of parameters (K), Akaike weights ( $\text{G}\hat{\text{D}}_i$ ), and log-likelihood (LL). The asterisk (\*) indicates the best-approximating model.

Model structure	K	df	AIC	$\Delta\text{AIC}$	$\text{G}\hat{\text{D}}_i$	LL
canopy cover + no. of trees*	4	4	87.50	0.00	0.38	-34.00
canopy cover + no. of trees + tree height	5	5	88.00	0.49	0.30	-31.81
ground cover + no. of trees	4	5	89.30	1.82	0.15	-32.47
canopy cover + grass height + no. of trees + tree height	6	6	90.00	2.47	0.11	-30.36
canopy cover + no. of shrub + no. of trees + tree height	6	6	92.70	5.24	0.03	-31.75
canopy cover + grass height + o. of shrub + no. of trees + tree height	7	7	94.30	6.85	0.01	-30.11
canopy cover	3	3	96.70	9.19	0.00	-41.04
canopy cover + tree height	4	4	96.80	9.30	0.00	-38.65
canopy cover + grass height	4	4	97.00	9.50	0.00	-38.75
canopy cover + grass height + ground cover + no. of shrub + no. of trees + tree height	8	8	97.50	10.00	0.00	-29.25

Table 4: Top 10 additive models for nest site selection of Mississippi Kites at the broad scale in Oklahoma, USA, 2013–2015. All models included an intercept term and random effect of year. The top model included canopy height (m) and the number of trees (woody stems within 50m of the nest tree). Models list the number of parameters (K), Akaike weights ( $\Delta_i$ ), and log-likelihood (LL). The asterisk (\*) indicates the best-approximating model.

Models	K	df	AICc	$\Delta$ AIC	$\Delta_i$	LL
<b><i>Distance variables</i></b>						
dist.consp.+dist.road+dist.RTHA	5	5	149.10	0.00	0.20	-69.40
dist.consp.+dis.oilpads+dist.road+dist.RTHA	6	6	149.30	0.19	0.18	-68.43
dist.consp.+dist.road+dist.RTHA+ dist.GHOW	6	6	151.00	1.87	0.08	-69.27
dist.consp.+dist.river+dist.road+dist.RTHA	6	6	151.10	1.91	0.08	-69.29
dist.consp.+dist.oilpads+dist.road+dist.RTHA+ dist.GHOW	7	7	151.20	2.10	0.07	-68.31
dist.consp.+ time.fire +dist.road+dist.RTHA	6	6	151.30	2.13	0.07	-69.40
dist.consp.+dist.GHOW+dist.oilpads+dist.road+dist.RTHA	7	7	151.30	2.19	0.07	-68.35
dist.consp.+dist.river+dist.oilpads+dist.road+dist.RTHA	7	7	151.50	2.31	0.06	-68.41
dist.consp.+dist.river+dist.road+dist.RTHA+time.fire	7	7	152.90	3.76	0.03	-69.14
dist.road+dist.RTHA	4	7	153.10	4.00	0.03	-69.25
<b><i>Vegetation variables</i></b>						
riparian.shrub+upland.shrub+upland.wood	5	5	179.00	0.00	0.54	-76.96
prairie+riparian.shrub+upland.shrub+upland.wood	6	6	179.60	0.59	0.40	-74.74
riparian.shrub+upland.shrub	4	4	184.60	5.55	0.03	-82.24
prairie+ riparian.shrub +upland.shrub	6	5	185.50	6.49	0.02	-80.20
riparian.shrub+Sandhill.shinnery+upland.shrub+upland.wood+water	7	7	188.70	9.63	0.00	-76.75
Pasture+prairie+Riparian.shrub+Sandhill.shinnery+upland.shrub+upland.wood	8	8	189.40	10.41	0.00	-74.63
riparian.shrub+upland.shrub+water	5	5	189.50	10.45	0.00	-82.18
pasture+prairie+Riparian.shrub+Sandhill.shinnery+upland.shrub+upland.wood+water	9	9	194.40	15.32	0.00	-74.57
pasture+riparian.shrub+sandhill.shinnery+upland.shrub	6	6	194.40	15.41	0.00	-82.15
upland.shrub	3	3	194.80	15.81	0.00	-89.89
pasture+prairie+Riparian.shrub+Sandhill.shinnery+upland.shrub	7	7	195.20	16.21	0.00	-80.04
upland.shrub+upland.wood	4	4	197.80	18.72	0.00	-88.83

***Topographical variables***

elevation	3	2	225.80	0.00	0.56	-107.66
elevation+slope	4	3	226.90	1.12	0.32	-105.61
elevation+elevation <sup>2</sup>	4	3	230.10	4.31	0.07	-107.20
elevation+roughness	4	3	231.00	5.22	0.04	-107.66
elevation+slope+elevation <sup>2</sup> +slope <sup>2</sup>	6	5	234.70	8.88	0.01	-104.27
slope+roughness+roughness <sup>2</sup>	5	4	236.10	10.34	0.00	-107.61
elevation <sup>2</sup>	3	2	238.30	12.57	0.00	-113.95
elevation <sup>2</sup> +slope <sup>2</sup> +roughness <sup>2</sup>	5	4	243.80	18.01	0.00	-111.44
elevation+slope+roughness+Elevation <sup>2</sup> +slope <sup>2</sup> +roughness <sup>2</sup>	8	7	245.00	19.24	0.00	-104.22
slope	3	2	253.10	27.28	0.00	-121.30

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Table 5: Ranking of candidate model sets describing daily nest survival of Mississippi Kite at Packsaddle WMA, Oklahoma, 2013–2015. The top 15 models are presented. Included for each model are number of parameters (K), Akaike’s Information Criterion values corrected for small sample sizes (AICc),  $\Delta AICc$ , Akaike weight ( $G\hat{O}_i$ ), and model deviance.

model n	K	AICc	$\Delta AICc$	$G\hat{O}_i$	Deviance
S(~nest age + dist.RTHA + dist.consp)	4	118.86	0.00	0.54	110.85
S(~nest age + dist.RTHA+dist.GHOW)	4	119.60	0.73	0.37	113.59
S(~nest age + chicks)	3	122.55	3.68	0.09	116.54
S(~dist.RTHA + dist.GHOW)	3	137.93	19.07	0.00	131.92
S(~dist.RTHA)	2	139.19	20.32	0.00	135.18
S(~nest age + dist.GHOW)	3	140.01	21.15	0.00	134.00
S(~dist.RTHA + dist.roads)	3	140.33	21.46	0.00	134.32
S(~dist.RTHA + dist.oilpad)	3	140.39	21.53	0.00	134.38
S(~dist.RTHA + concealment)	3	140.52	21.65	0.00	134.51
S(~dist.RTHA + dist.GHOW + dist.consp + dist.roads)	5	141.16	22.30	0.00	131.14
S(~chicks)	2	144.89	26.02	0.00	140.88
S(~nest age + dist.consp)	3	146.56	27.69	0.00	140.54
S(~dist.GHOW + dist.oilpad)	3	150.54	31.67	0.00	144.53
S(~dist.GHOW)	2	150.87	32.00	0.00	146.86
S(~Dist.GHOW + concealment)	3	152.83	33.97	0.00	146.82
S(~date)	2	158.96	40.09	0.00	154.95
S(~dist.consp)	2	159.49	40.63	0.00	155.49
S(~nest age + dist.roads)	3	164.12	45.26	0.00	158.11

## Figure legends

Figure 1: Distribution of nest sites for Mississippi Kite, Red-tailed Hawk, and Great Horned Owl at Packsaddle WMA, 2013–2015.

Figure 2: Proportion of tree species selected for nesting by Mississippi Kite, Red-tailed Hawk, and Great Horned Owl at Packsaddle WMA, 2013–2015.

Figure 3: Predicted probability of significant ( $p < 0.001$ ) covariates for Mississippi Kite nesting habitat selection. All covariates were standardized to a mean of 0 and a standard deviation of 1 to improve data interpretations. Shaded areas represent 95% confidence intervals.

Figure 4: Predicted probability of significant ( $p < 0.001$ ) distance related covariates for Mississippi Kite nesting habitat selection at Packsaddle WMA. All covariates were standardized to a mean of 0 and a standard deviation of 1 to improve data interpretations. Shaded areas represent 95% confidence intervals.

Figure 5: Predicted probability of significant ( $p < 0.001$ ) vegetation covariates for broad scale Mississippi Kite nesting habitat selection at Packsaddle WMA. All covariates were standardized to a mean of 0 and a standard deviation of 1 to improve data interpretations. Shaded areas represent 95% confidence intervals.

Figure 6: Predicted probability of significant ( $p < 0.001$ ) topographical covariates for Mississippi nesting habitat selection at Packsaddle WMA. All covariates were standardized to a mean of 0 and a standard deviation of 1 to improve data interpretations. Shaded areas represent 95% confidence intervals.

Figure 7: Daily nest survival rates (95% CI) of Mississippi Kite nests in relation to distance to: (a) conspecifics, (b) Red-tailed Hawk nests, and (c) Great Horned Owl nests. Solid lines represent predicted probabilities and dashed lines 95% confidence intervals.

Figure S1: Nest monitoring by observing contents reflected in a mirror attached to an extendable pole ~15 m in length.

Figure S2: Nest of Mississippi Kite with a two weeks old nestling at Packsaddle Wildlife Management Area, Oklahoma, USA, 2015. Photo by Case Wyatt.

Figure S3: Nest of Great Horned Owl with three weeks old nestlings at Packsaddle Wildlife Management Area, Oklahoma, USA, 2015. Photo by Fidelis Atuo.

Figure S5: Nest of Red-tailed Hawk with ~ 6 weeks old fledglings at Packsaddle Wildlife Management Area, Oklahoma, USA, 2015. Photo by Case Wyatt.

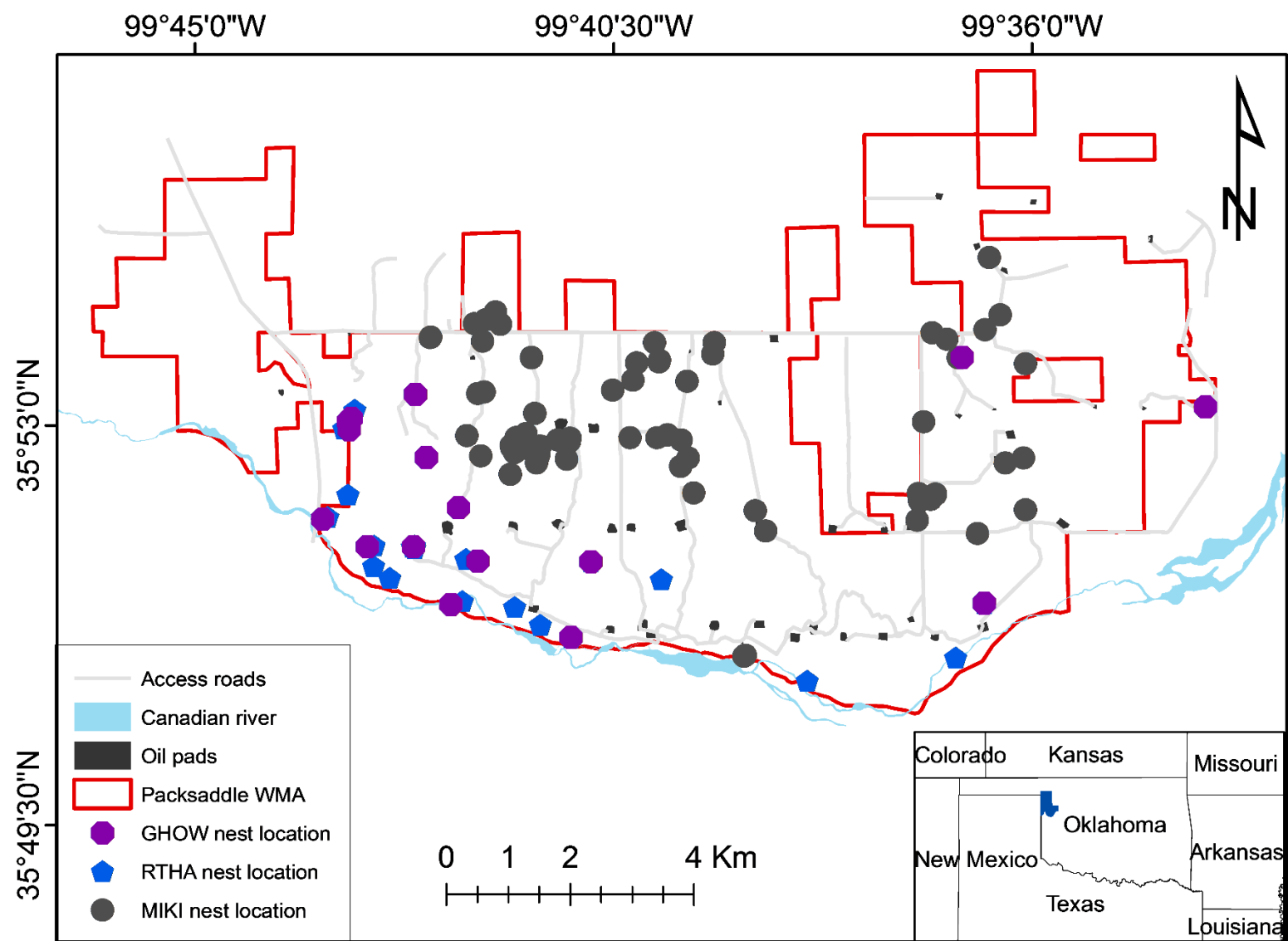


Figure 1

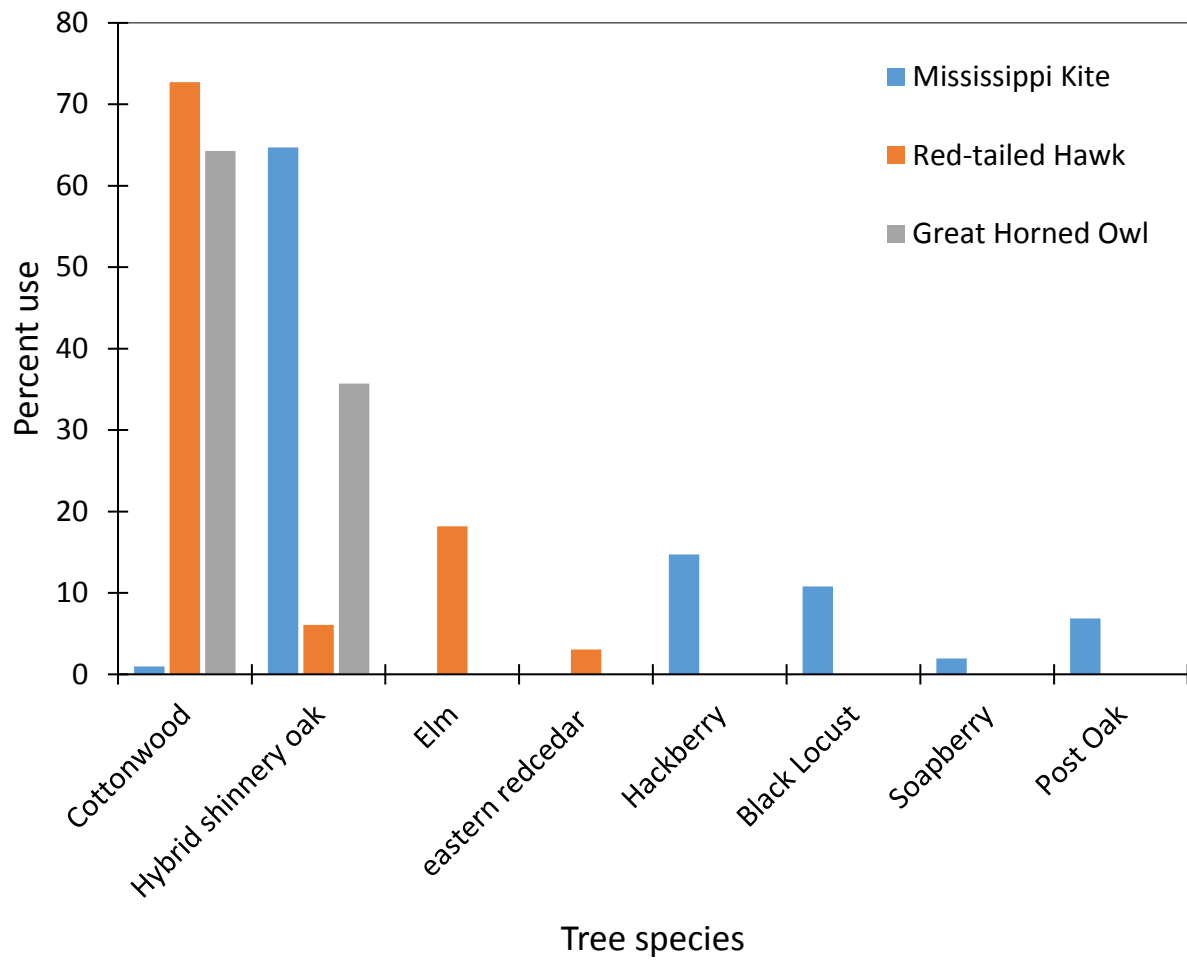


Figure 2:



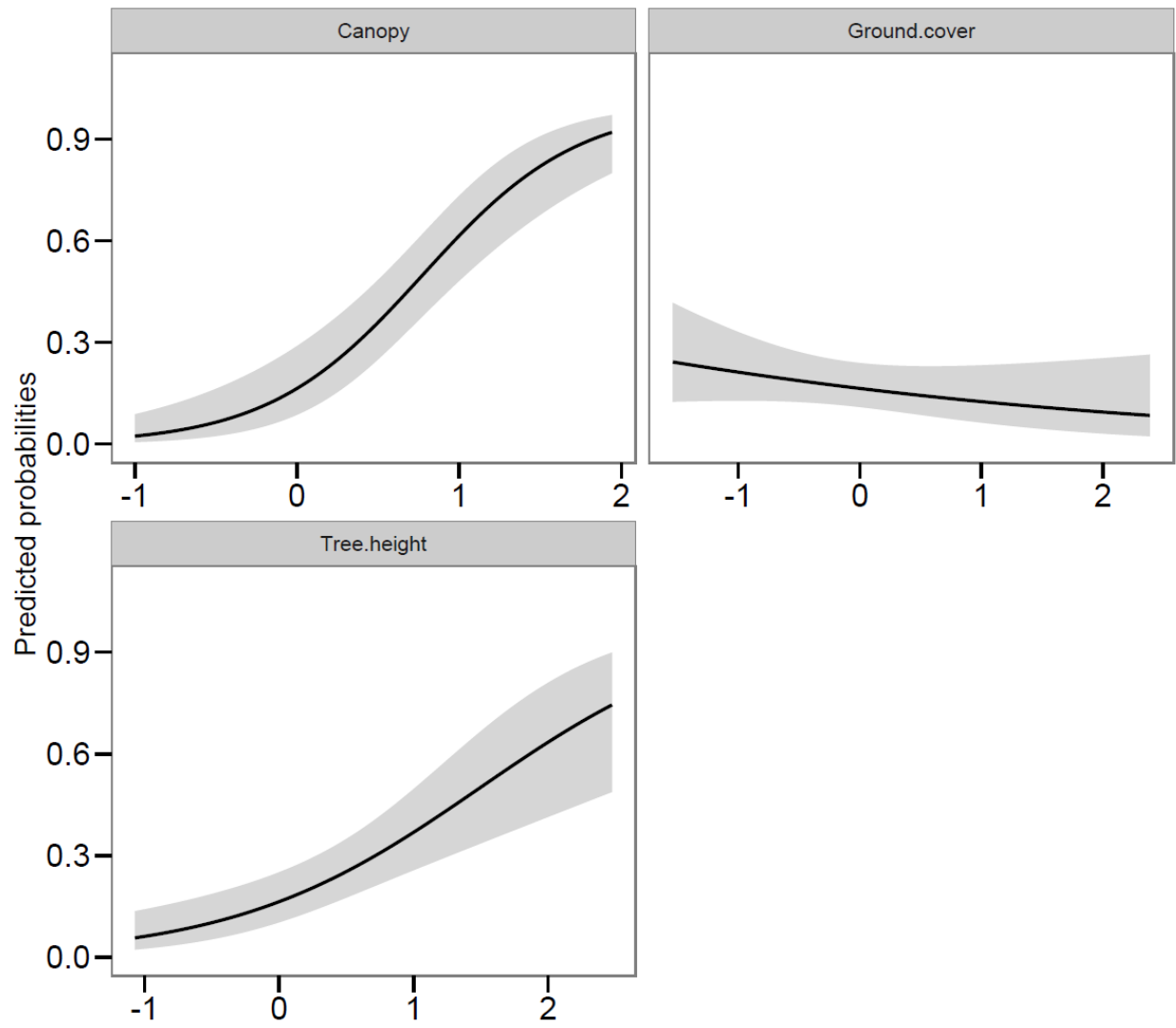


Figure 3

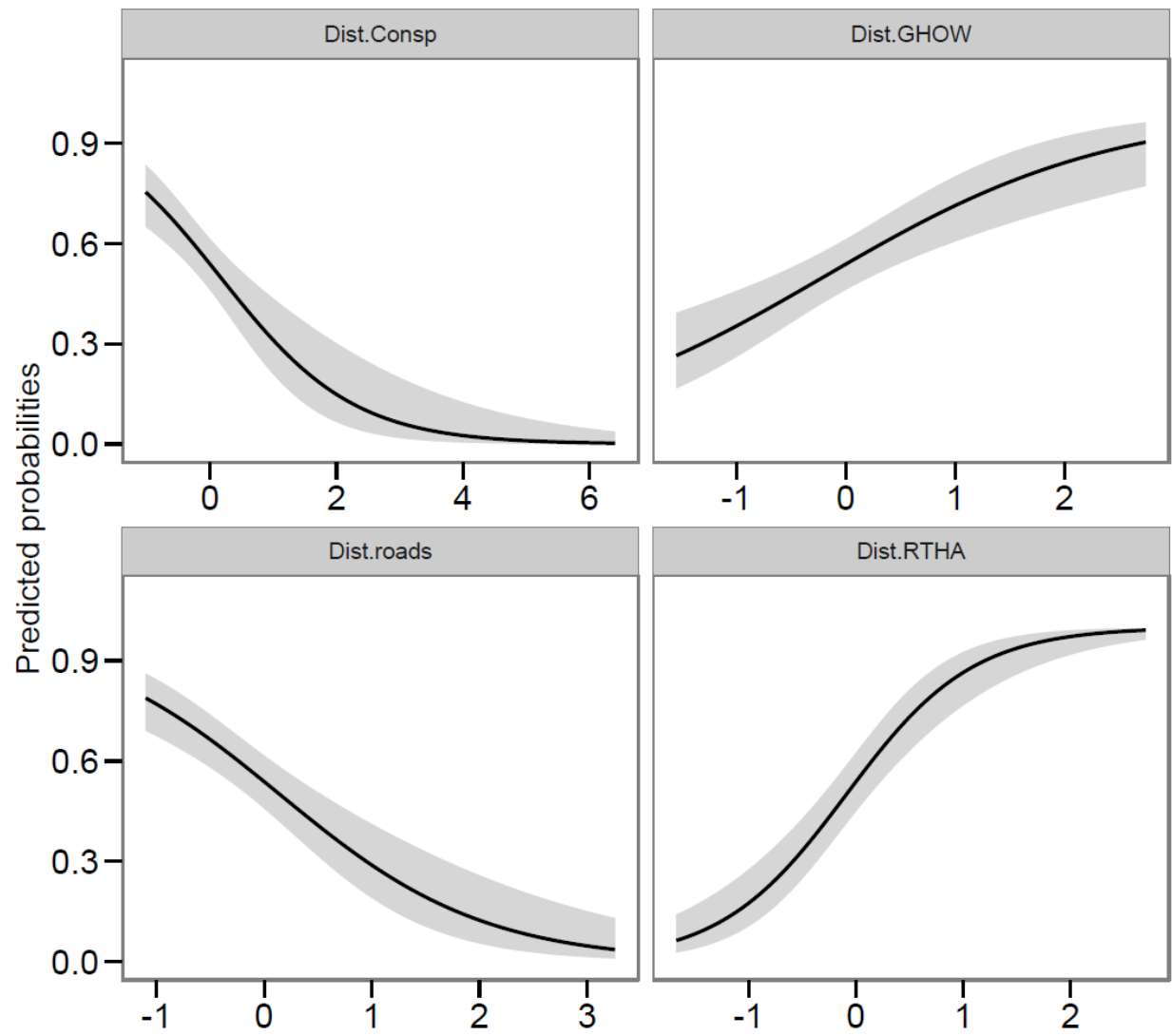


Figure 4

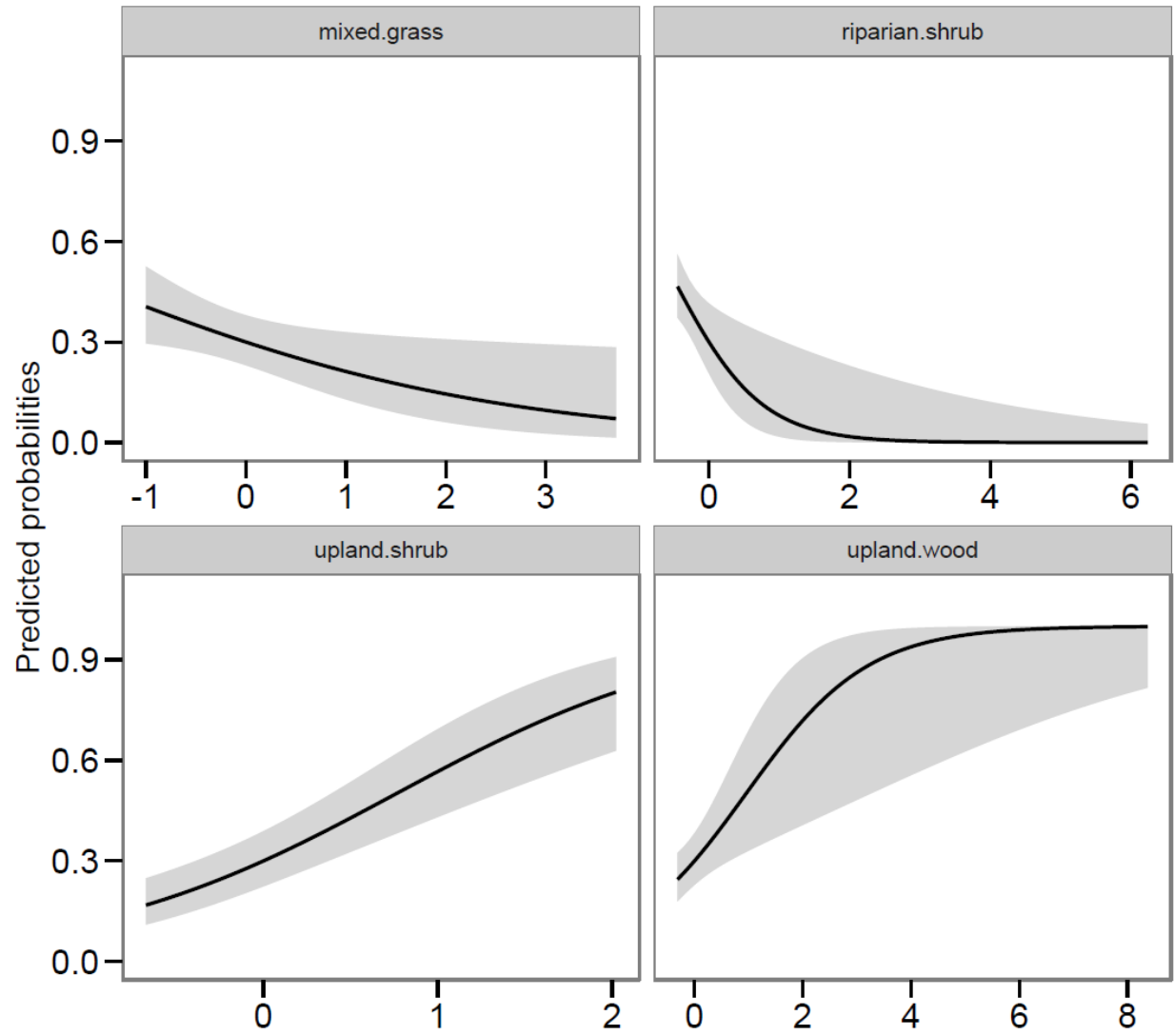


Figure 5

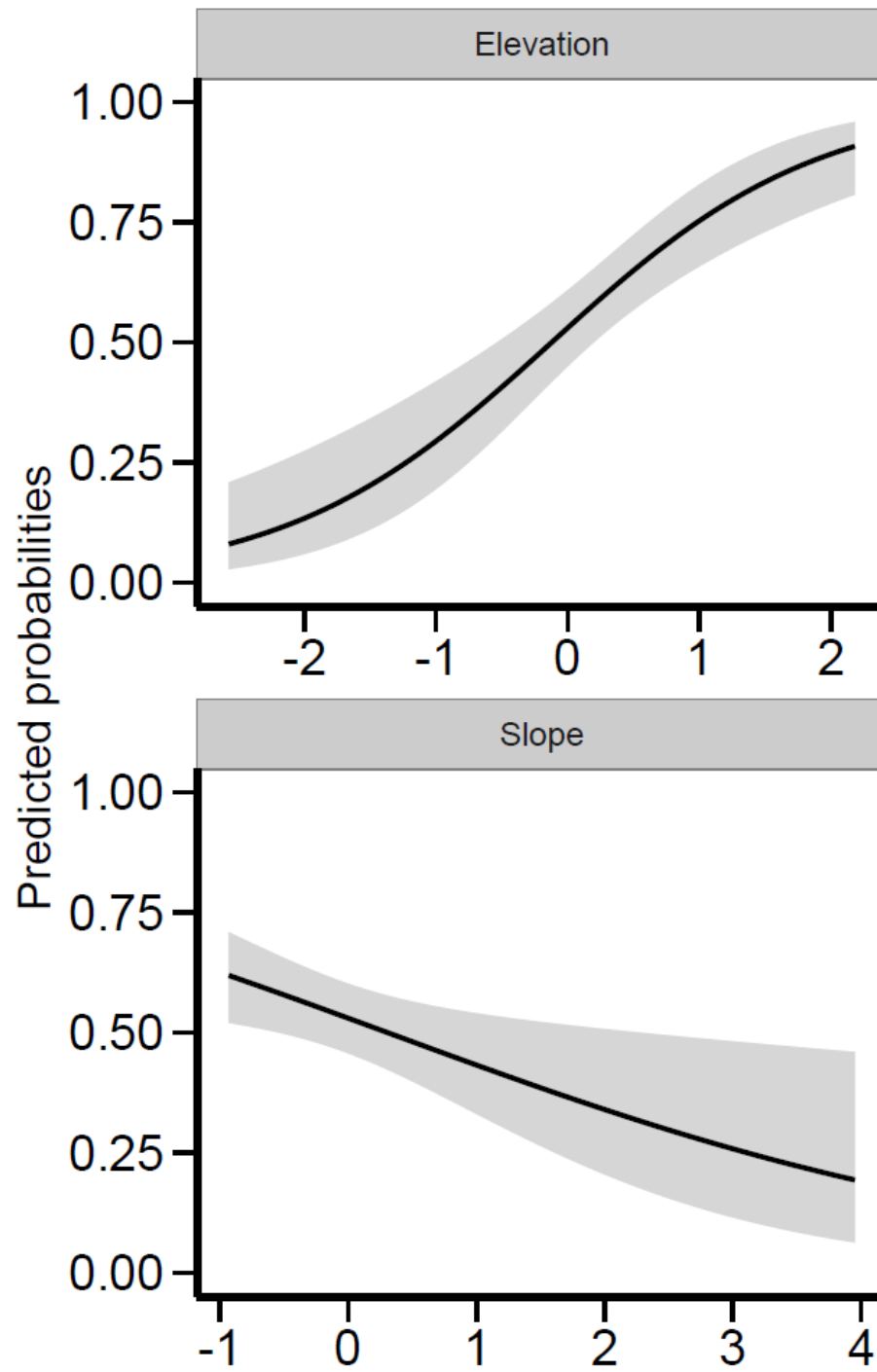


Figure 6

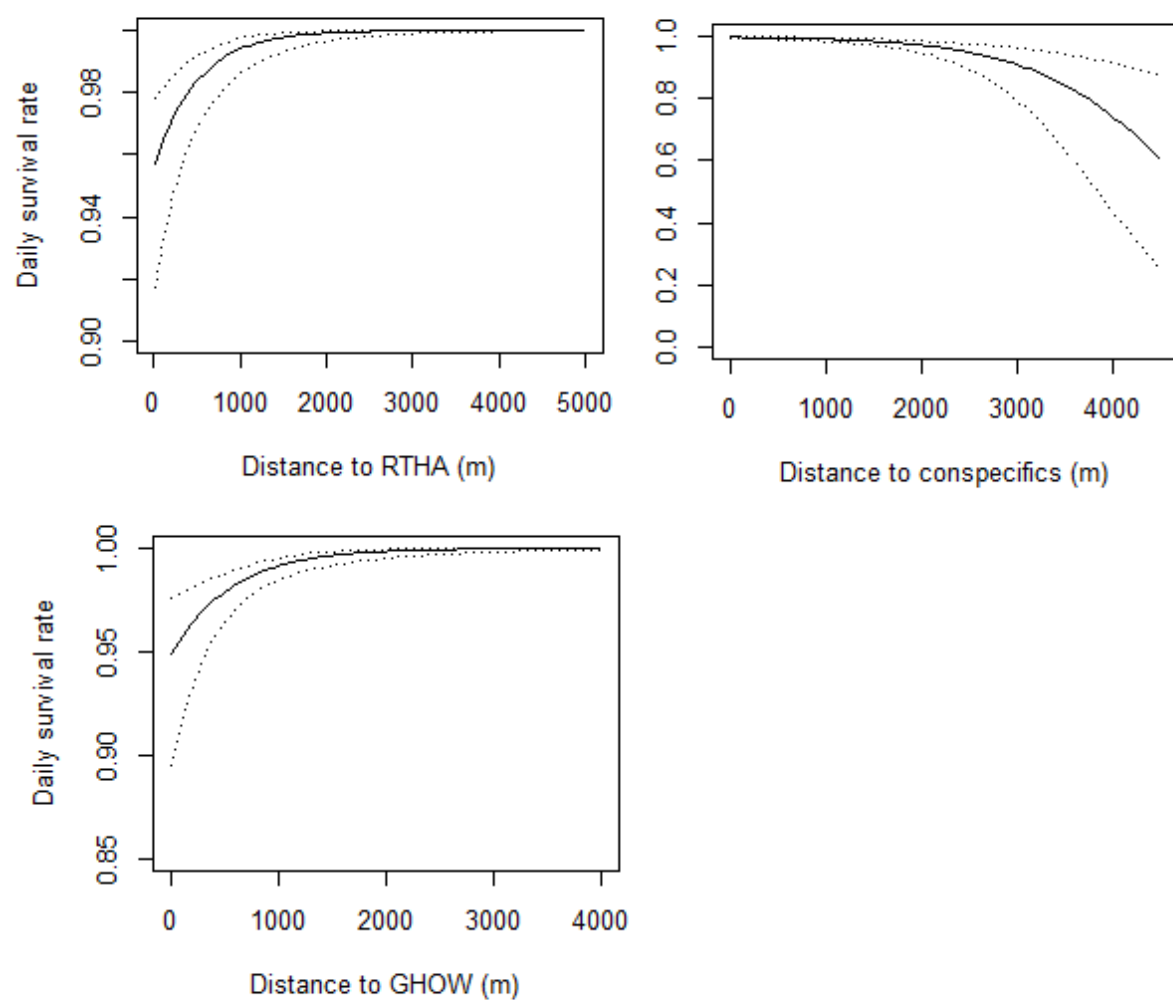


Figure 7



Figure S1



Figure S2





Figure S3



Figure S5

## CHAPTER V

### THE LANDSCAPE OF FEAR AS AN EMERGENT PROPERTY OF HETEROGENEITY: CONTRASTING PATTERNS OF PREDATION RISK FOR A GROUND FORAGING BIRD IN GRASSLAND ECOSYSTEMS

#### **Abstract**

The likelihood of encountering a predator influences prey behavior and spatial distribution such that non-consumptive effects can outweigh the influence of direct predation. Prey species are thought to filter information on perceived predator encounter rates in physical landscapes into a landscape of fear defined by spatially explicit heterogeneity in predation risk. The presence of multiple predators using different hunting strategies further complicates navigation through a landscape of fear and potentially exposes prey to greater risk of predation. The juxtaposition of land cover types likely influences overlap in occurrence of different predators, suggesting that attributes of a landscape of fear result from complexity in the physical landscape. Woody encroachment in grasslands furnishes an example of increasing complexity with the potential to influence predator distributions. I examined the role of vegetation structure on the distribution of two avian predators, Red-tailed Hawk (*Buteo jamaicensis*) and Northern Harrier (*Circus cyaneus*), and the vulnerability of a frequent prey species of those predators, Northern Bobwhite (*Colinus virginianus*). I mapped occurrences of the raptors and kill locations of Northern Bobwhite to examine spatial vulnerability in relation to landscape complexity. Predator density and predation-specific mortality of Northern Bobwhite increased with vegetation complexity that favored fine-scale interspersed of



grassland and woodland. Predation pressure was lower in more homogeneous landscapes where overlap of the two predators was less frequent. Predator overlap created areas of high risk for Northern Bobwhite amounting to 32% of the land area where landscape complexity was high and 7% where complexity was lower. My study emphasizes the need to evaluate the role of landscape structure on predation dynamics and reveals another threat from tree encroachment in grasslands.

**Key words:** Predation risk, Habitat complexity, Landscape of fear, Northern Bobwhite, Avian predators, Vegetation structure

## **Introduction**

An animal's use of space within its home range is in large measure determined by competing pressures to acquire food, mates, or other needs while avoiding predation. In addition to the various vegetation patches that comprise the physical landscape of a home range, many animals perceive and respond to a landscape of fear defined by spatially heterogeneous risk of predation (Laundré et al. 2014). In the seminal study illustrating the concept, Laundré et al. (2001) described increases in prey vigilance and corresponding decreases in foraging time among some elk (*Cervus elephas*) exposed to new threats of predation from reintroduced wolves (*Canis lupus*) following a 50-year absence in Yellowstone National Park, USA. In addition to expanding to different species of predators and prey, subsequent work has addressed both temporal and spatial variability in the landscape of fear (Tolon et al. 2009) and experimental approaches to better quantify lost foraging time due to the perceived threat of predation (Matassa and Trussell 2011). These studies suggest both that the landscape of fear has merit as an organizing theory in ecology and that the non-consumptive effects of predators can have greater influence on the spatial use and behavior of their prey than direct loss to predation (Matassa and Trussell 2011, Laundré et al. 2014). Landscapes of fear are dynamic according to changes in predator populations and, presumably, changes in land cover that affect the spatial distribution of predators.

Temperate grasslands and shrublands are dynamic ecosystems that in recent decades have experienced widespread increases in woody vegetation in many ecoregions. In addition to expansion of industrial agriculture, changes in climate, CO<sub>2</sub> concentration, livestock grazing, and fire frequency have been specifically implicated as drivers (Coppedge et al. 2008, Fuhlendorf et al. 2008, Twidwell et al. 2013). In the Central Great Plains of the United States, woody encroachment in grasslands and shrublands is likely to introduce structural complexity that benefits avian predators and increases the vulnerability of their prey (Preston 1990). For predators that typically hunt from perches, the presence or increase of tree cover in grasslands expands their effective hunting radius thus increasing the “vulnerability landscape” for their prey species. Complex vegetation structure has been shown to increase the abundance and diversity of generalist predators with attendant consequences for prey (Oliver et al. 2009, Gorini et al. 2012, LaManna et al. 2015). For example, Andersson et al. (2009) found that predator hunting efficiency increased with perch availability and perch height in open landscapes. Compared with hovering, predators hunting from perches minimize their energy cost, and are able to increase their prey detection and capture efficiency (Kramer and McLaughlin 2001, Leyhe and Ritchison 2004, Tomee et al. 2011).

Changes in land cover of grasslands have contributed to long-term population declines in grassland birds (Peterjohn and Sauer 1999, Brennan and Kuvlesky, Jr. 2005). Population declines have been attributed to several factors including land use change due to habitat fragmentation, pesticide use, and predation (Askins 1993, Vickery et al. 1995, Vickery et al. 1999, Askins 2001, McClure et al. 2013, Mineau and Whiteside 2013, Kalyn Bogard and Davis 2014). Upland game birds have particularly been affected by these changes with population trends of several species plummeting to historical lows (Schroeder et al. 2004, Aldridge et al. 2008, Link et al. 2008, Hagen et al. 2009, Hernández et al. 2013). The Northern Bobwhite (*Colinus virginianus*), for example, has experienced the most severe long-term population decline of any North American bird species (Sauer et al. 2011) and is listed as “Near Threatened” under the IUCN/BirdLife threat criteria (International 2016). Since 2000, the United States’ population is estimated to be declining at 3.7% annually (Sauer et al. 2011). Predators can play a large role in such

declines. For example, in the Longholm Moor of southern Scotland, Thirgood et al. (2000) demonstrated that raptor predation alone accounted for 70% of winter and 90% of summer predation mortality in Red Grouse (*Lagopus scotica*). Two main predators, Peregrine Falcon (*Falco peregrinus*) and Hen Harrier (*Circus cyaneus*, conspecific with Northern Harrier), were responsible for all predation incidences in this species.

The role of spatial heterogeneity in mediating predator-prey interactions has been established in some experimental studies (Pacala et al. 1990, Bergström et al. 2006, Chalfoun and Martin 2009, Fortin et al. 2015, Banks and Gagic 2016), but replication in landscapes has received less attention. Where studied in the field, the importance of spatial heterogeneity in enhancing predators' ability to kill prey (Lecomte et al. 2008, Zub et al. 2008, Oliver et al. 2009) or preys' ability to evade predators (Warfe and Barmuta 2004, Kauffman et al. 2007) has been confirmed. The degree to which heterogeneity influences both predators and prey suggests that the perceived landscape of fear could be an emergent property of the physical landscape that variably increases and decreases the likelihood of overlap between two or more species of predators.

The mixed-grass prairie of western Oklahoma provides unique opportunities for investigating the role of landscape complexity in altering predation risk for declining prey species. The region is dominated by mixed-shrubs but tree encroachment in recent decades has dramatically altered landscape structure (Hall 2015). The region supports multiple species of migratory diurnal raptors either as overwintering residents or stop-over migrants. Many of these predators rely on similar sources of food; hence, increased diversity and abundance during these periods could constitute additive threats to vulnerable declining prey species such as Northern Bobwhite.

In the Central Great Plains, Northern Harrier and Red-tailed Hawk (*Buteo jamaicensis*) are the most frequent avian predators of Northern Bobwhite (Rollins and Carroll 2001, Turner et al. 2014). In this study, I aimed to: 1) examine the role of structural complexities on the fine-scale distribution of two avian

predators; 2) evaluate predation risk for quail across a gradient of vegetation complexity; and 3) map the overlap between predator habitat selection and Northern Bobwhite vulnerability to quantify a landscape of fear in physical landscapes that vary in heterogeneity.

## Methods

### Study sites

We conducted my study at Packsaddle and Beaver River wildlife management areas (WMAs) in northwestern Oklahoma. Packsaddle WMA covers ~6,475 ha of mixed-grassed prairie with an elevation that ranges approximately 579–762 m above sea level. The average annual precipitation is ~53 cm, with the majority occurring during spring and summer (DeMaso et al. 1997). The dominant vegetation is sand shinnery oak (*Quercus harharvardii*) mixed with other herbaceous plants. Detailed vegetation and landscape characteristics of the area are described in DeMaso et al. (1997), Townsend et al. (2001), and Hall (2015). Beaver River WMA is ~7,163 ha in area, consisting of a mixture of upland, floodplain, and river bottom with a mean annual precipitation is ~7.6 cm. Vegetation around the upland area is predominantly sagebrush (*Artemisia filifolia*) and buffalograss (*Bouteloua dactyloides*) interspersed with sand plum (*Prunus angustifolia*) thickets and gently rolling sandhills. The floodplain portion of the WMA is comprised mostly of grasses mixed with cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and American elm (*Ulmus americana*). The river bottom is made of mostly woody vegetation consisting of sand plum thickets and salt cedar (*Tamarix* spp) (Tanner et al. 2015). The Oklahoma Department of Wildlife Conservation manages the two WMAs mainly for hunting. Most of the management practices on the WMAs are intended to increase the population of the Northern Bobwhite and other game species. A combination of prescribed grazing by cattle and prescribed burns are conducted (mostly at Packsaddle) to promote the growth of native forbs. There is also significant oil exploration and extraction at Packsaddle WMA.

## Raptor surveys

We collected raptor abundance data from 14 line transects at Packsaddle WMA and 16 at Beaver River WMA. Transects measured 2–5 km in length and were placed along existing roads based on protocols described in Fuller and Mosher (1987), Bibby et al. (2000), and Augiron et al. (2015). I surveyed transects at least twice a month from January 2013–December 2015. I placed transect lines non-randomly along trails separated by a distance  $\geq 900$  m to reduce the chance of counting an individual more than once (Buckland et al. 2001, Greenwood and Robinson 2006). Surveys were carried out by one primary observer occasionally supported by a second person who acted primarily as a driver. The observer scanned a distance of approximately 400 m on either side of the transect line for raptors from a truck that was driven at a speed of 20–30 km/h (Andersen 2007). For each detection, I estimated the distance of the bird from the transect line using a Nikon 8398 ACULON laser range finder. I georeferenced each detection at the point of observation using a Garmin Montana 650TM GPS unit. I also obtained the angle of observation from the observer using an azimuth compass. To develop a spatially explicit model of raptor-habitat association, I plotted each georeferenced point to the estimated point of occurrence in time using an offset technique described by Atuo and O’Connell (in review).

## Northern Bobwhite mortality sites

We obtained data on quail mortality locations from collaborative and concurrent quail telemetry studies at Packsaddle and Beaver River WMAs. All mortality sites were discovered through telemetry tracking of tagged birds. Detailed descriptions on quail trapping and tracking techniques are provided in Carroll et al. (2015) for Packsaddle WMA, and Tanner et al. (2015) for Beaver River WMA. Based on expert knowledge, Northern Bobwhite found dead were categorized into 4 mortality causes: (i) raptor predation, (ii) mammal predation, (iii) unknown predation, and (vi) non-predation related mortality. I included only

raptor specific predation events in my analysis. I accumulated 179 raptor related quail mortality events at Beaver River and 210 at Packsaddle.

#### Habitat delineation

We quantified land cover used by Northern Harrier and Red-tailed Hawk, and that surrounding mortality sites for Northern Bobwhite, with 10-m resolution imagery acquired through the National Agriculture Imagery Program (NAIP). The imagery was acquired in 2015 and had been pre-processed and classified for the state of Oklahoma by the Oklahoma Department of Wildlife Conservation (ODWC) ([http://www.wildlifedepartment.com/facts\\_maps/ecoregions.htm](http://www.wildlifedepartment.com/facts_maps/ecoregions.htm)). The original land cover map contained 31 land cover classes for Packsaddle WMA and 24 classes for Beaver River WMA. I reclassified the land cover layer into 9 dominant cover types at Packsaddle WMA (mixed-grass, riparian woodland, riparian shrub, upland woodland, oil pads, upland shrub, open water, barren, and sandhill shinnery oak) and 8 at Beaver River WMA (mixed-grass, riparian woodland, riparian shrub, upland woodland, upland shrub, open water, pasture, and barren). In addition to vegetation attributes, I also calculated topographical attributes to include elevation, slope, and terrain roughness (degree of terrain ruggedness calculated as the standard deviation of elevation) from the Digital Elevation Model (DEM) layer. I obtained DEM data from the United States Geological Survey (USGS) data portal at 1/3 arc-seconds (10 m) resolution.

Based on the number of occurrence points (use locations) for Northern Harrier and Red-tailed Hawk, I specified an equal number of random points to represent available locations using the random number generator in ArcGIS 10.2.2 (Environmental Systems Research Institute Inc., Redlands, CA, USA). I then developed concentric buffers of 1000 m radius centered on used and available points of each raptor to represent their approximate territories (Janes 1984, Stout et al. 2006, Arroyo et al. 2014) and extracted the proportion of individual land cover types within each buffer. Similarly, I imposed buffers of 500 m radius centered on quail kill and random non-kill locations and extracted vegetation variables. Although kill

locations were identified with specific coordinates from transmitters, I established the broad buffer around those coordinates to accommodate possible differences between actual kill location and the location where a transmitter was found. Predators are known to move their prey *post mortem* (Kemper et al. 2013) such that the foraging site may be several meters away from where the prey's vulnerable location. A concurrent study on Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) in western Oklahoma found that the average distance between last living location (last transmitter signal) and first mortality location was  $546 \pm 165$  m ( $n = 21$ ) based on a one-hour period (Ashly Unger, *personal communication*). In that same study, live prairie-chickens move ~128 m in one hour, suggesting that the dead birds were moved *post-mortem*.

#### Data analysis

We estimated average Northern Bobwhite seasonal vulnerability between the breeding and non-breeding season by comparing densities of killed birds per hectare using a paired sample t-test. I also compared average mortality between the two sites based on the number of mortality events per hectare.

Given that quail vulnerability to raptor predation may differ across seasons, I examined temporal patterns in predator densities for the breeding and non-breeding seasons of the Northern Bobwhite. I estimated detection corrected densities of Red-tailed Hawk and Northern Harrier using program Distance 6.2 (Thomas et al. 2010). I estimated distance detection functions using the Multiple-Covariate Distance Sampling (MCDS) approach (Marques et al. 2007, Buckland et al. 2015). The detection function model estimates detection probabilities with increasing distances from transect lines. For each study site, I compared a suite of *a priori* candidate models including half-normal, hazard-rate, and uniform function keys with cosine adjustment terms. I included different covariates (time of the day, month of survey, observer ID, and their interactions) to increase the explanatory power of my models. I then ranked models

using Akaike's Information Criterion (AIC) and collected density estimates and detection probabilities based on the best competing models. Best models were those within a  $\Delta AIC$  window of  $<2$ .

We used resource selection functions (RSFs) (Manly et al. 2002) to assess Red-tailed Hawk and Northern Harrier habitat selection, and Northern Bobwhite vulnerability. I used the Generalized Linear Mixed Model (GLMM) approach to compare environmental variables collected at raptor occurrence points to those collected from random points. I followed the same approach to compare environmental variables collected at Northern Bobwhite kill sites to those collected from randomly selected non-kill locations. In both cases, I specified binomial error structures and included year as a random effect to account for variation in predator abundances, or Northern Bobwhite mortality across three sampling years. For each model, I defined fixed effects to include vegetation, topographical, and distance (measured as Euclidean distance between used or available points and identified landscape structures) variables. I performed a Pearson correlation on all variables to check for multicollinearity. In the absence of significant correlations ( $|r| > 0.7$ ), I included all measured variables in my models.

To reduce complexity for all RSF models, I used a two-step approach to build habitat selection models. First, I evaluated all possible model combinations derived from the main effects of raptor habitat use, main effects of Northern Bobwhite vulnerability, and the interaction effects in both cases. In the second step, I selected the most important models from the all-possible candidate model sets based on its AICc values (Burnham and Anderson 2002). Using these models as bases, I evaluated the possibility of improving model fit by examining the additive and interactive roles of additional covariates (Zuur et al. 2009). When the additional covariate improved, the starting model (i.e. has a lower log-likelihood), it was retained, otherwise it was removed and the iterative process continued. I then ranked all candidate models according to their AIC values adjusted for small sample size (Burnham and Anderson 2002) using the MuMIn package (Barton 2015) in R program. I considered competing models within a  $\Delta AICc < 2$  as important in explaining habitat selection in raptors or landscape vulnerability in Northern Bobwhite. I evaluated model-averaged estimates for variables of interest in competing models, and calculated



unconditional standard errors and 95% confidence limits (Burnham and Anderson 2002). Prior to statistical analysis, I standardized all environmental variables to a mean of 0 and a standard deviation of 1 to improve data interpretations. I used parameter estimates from my RSFs models to generate maps of relative probability of use for Northern Harrier and Red-tailed Hawk, and relative predation risk for Northern Bobwhite. I created distance raster files from distance covariates (i.e. distance to roads, distance to oil pads, and distance to river) and included individual layers of slope, elevations, and ruggedness to my model.

To compare the resulting output map of Northern Bobwhite predictive predation risk to those of Red-tailed Hawk and Northern Harrier habitat use, I converted the continuous predictive values of each map to categorical outputs based on pre-set cutoff thresholds. For each species, I specified a threshold of relative probability of use or vulnerability based on the methods described in York et al. (2011). I then multiplied the three categorical raster layers in “raster calculator” to obtain a categorical map with 8 classes, each representing the degree of Northern Bobwhite predation risk (1 = low use by Red-tailed Hawk, low use by Northern Harrier, and low risk to Northern Bobwhite; 2 = low use by Red-tailed Hawk, low use by Northern Harrier, but high risk to Northern Bobwhite; 3 = high use by Northern Harrier, but low risk to Northern Bobwhite; 4 = high use by Northern Harrier and high risk to Northern Bobwhite; 5 = high use by Red-tailed Hawk but low risk to Northern Bobwhite; 6 = high use by Red-tailed Hawk, but high risk to Northern Bobwhite; 7 = high use by Red-tailed Hawk and Northern Harrier, but low risk to Northern Bobwhite; 8 = selected by Red-tailed Hawk and Northern Harrier, and high risk to Northern Bobwhite). Then, I calculated the proportion of each predation risk category relative to my study area based on the number of pixels in each category.

Next, I compared levels of vegetation complexity (number of vegetation classes) across three predation risk classes; i.e. areas where Northern Bobwhite was vulnerable to 1) Northern Harrier only, 2) Red-tailed Hawk only, and 3) both Red-tailed Hawk and Northern Harrier (double predator overlap). To do this, I generated 60 random points for each predation risk class at each WMA. Next, I developed buffers of 100

m radius centered on each random point and extracted the number of pixel representing each vegetation cover type. I selected 100 m radius buffers in order to minimize the number of vegetation classes. I then compared vegetation complexity across the three predation risk classes using a one-way analysis of variance (ANOVA) approach. I used Tukey HSD test to assess within-group variation. Except for density analysis, I performed all statistical analyses in program R version 3.3.1 (R Core Team 2016)

## Results

Quail vulnerability differed between the two sites, with a mean mortality density of  $0.18 \pm 0.02 \text{ ha}^{-1}$  at Packsaddle, and  $0.09 \pm 0.01 \text{ ha}^{-1}$  at Beaver River. At both sites, quail vulnerability was higher ( $P < 0.05$ ) during the non-breeding season compared with the breeding season (Figure 1), suggesting a possible higher predation specific mortality for adult birds. Densities of Red-tailed Hawk and Northern Harrier were higher during the non-breeding season than during the breeding season (Figure 2). Compared with Northern Harrier, non-breeding densities of Red-tailed Hawk were slightly higher at each study site, but significantly ( $P < 0.05$ ) higher during the breeding season (Figure 2).

We developed predictive maps depicting the relative landscape vulnerability of the Northern Bobwhite to avian predation risk at Packsaddle and Beaver River WMAs. The models for predictive mapping of quail vulnerability included vegetation composition, elevation, slope, distance to water, and distance to anthropogenic structures (e.g. oil pads). At Beaver River WMA, Northern Bobwhite appeared to be most vulnerable to raptor predation at higher elevations farther away from riparian woodland (Figure 3). Similarly, a vulnerability map for Packsaddle showed that Northern Bobwhites were more likely to be vulnerable to raptor predation at higher elevations, in mixed vegetation (mixture of shinnery oak shrub and grass cover), and in areas near oil pads (Figure 3). Predicted quail vulnerability was relatively low at low elevation close to riparian woodland. Overall, my results indicated a broader area of vulnerability at Packsaddle compared to Beaver River (Figures 3 and 4).

We identified two competing models ( $\Delta AIC_c < 2$ ) to explain quail vulnerability at Packsaddle (Table S1). Both models included mixed-grass, riparian shrub, upland woodland, and upland shrub. The two models were well supported, receiving a cumulative Akaike weight of 0.61. I identified three competing models to explain Northern Bobwhite vulnerability at Beaver River (Table S1). These models together accounted for 65% of the cumulative weight of evidence ( $AIC_w = 0.65$ ) and included mixed-grass, pasture, riparian shrub, riparian woodland, and upland woodland. Based on resource selection coefficients, the relative probability of Northern Bobwhite mortality at Packsaddle WMA was positively predicted by increasing upland woody shrub, but decreased with increasing patches of mixed-grass riparian shrub and riparian woodland (Table 1). Similarly, at Beaver River, the likelihood of predation specific Northern Bobwhite mortality decreased significantly with grass and riparian woodland (Table 2).

The best supported models for predator resource selection at Packsaddle showed Red-tailed Hawk selection positively associated with riparian woodland, upland shrub, upland woodland, and riparian shrub, but negatively associated with grass cover (Table 1). These variables were included in the top complete models ( $\Delta AIC_c < 2$ ) with a cumulative  $AIC_c$  weight of 0.73 (Table S2). Conversely, Northern Harrier selection increased with grass cover and upland shrub, but decreased with riparian woodland and riparian shrub cover (Table 1). The top complete models identified grass cover and upland shrub as the most important variables for Northern Harrier selection in this landscape (Table 1). At Beaver River, the most supported models for Red-tailed Hawk selection included the variables riparian woodland, grass cover, and bare ground (Table S3). The likelihood of Red-tailed Hawk selection increased with riparian woodland cover, but decreased with grass cover, and bare ground (Table 3). Northern Harrier selection was positively associated with grass cover, pasture, and upland shrub cover, but decreased with riparian woodland (Table 2). These variables were present in the top competing model ( $\Delta AIC_c < 2$ ) and received a cumulative AIC weight of 0.7 (Table S3).

Selection-vulnerability overlap

We evaluated the degree of overlap between habitat selection of Red-tailed Hawk and Northern Harrier, and Northern Bobwhite vulnerability to identify areas of highest risk for Northern Bobwhite. I quantified habitat overlap into eight categories based on raster calculations (Figure S1). I considered areas where Northern Bobwhite vulnerability overlapped with Red-tailed Hawk and Northern Harrier selection (double predator overlap) as most risky areas for Northern Bobwhite. This high predation-risk space represented ~32% of the total area of Packsaddle WMA, and ~7% of Beaver River WMA based on pre-set selection-vulnerability thresholds. Likewise, areas where Northern Bobwhite was least vulnerable to raptor predation constituted ~13% and ~3% for Packsaddle and Beaver River WMAs respectively. At Packsaddle WMA, quail vulnerability overlapped more with Red-tailed Hawk (~27%) than with Northern Harrier selection (~14%). This was different at Beaver River where the degree of overlap was higher with Northern Harrier (~24%) than with Red-tailed Hawk (~6%).

An examination of vegetation complexities across three contrasting areas of quail predation risk (i.e. vulnerable to Northern Harrier only, vulnerable to Red-tailed Hawk only, and vulnerable to both Red-tailed Hawk and Northern Harrier) revealed significant differences at both Packsaddle WMA ( $F_{20, 223} = 8.07$ ,  $P < 0.001$ ), and Beaver River WMA ( $F_{13, 60} = 16.81$ ,  $P < 0.001$ ). Generally, I found greater vegetation complexities in areas of high vulnerability compared to least vulnerable areas (Figure 5). At Packsaddle WMA, these differences were significantly greater ( $P < 0.05$ ) for areas of double predator overlap than areas where quail vulnerability overlapped with individual predators (Figure 5). Similarly, vegetation complexity in areas of double overlap at Beaver River WMA was significantly higher compared to overlap with Northern Harrier but not Red-tailed Hawk (*post-hoc* test:  $P < 0.001$ ; Figure 5).

## Discussion

Our study assessed the potential predation risk of Northern Bobwhite in relation to top avian predators in mixed-grass ecosystems with different heterogeneity gradients. Northern Bobwhite predation attributed to avian predators at Packsaddle and Beaver WMA peaked in the winter (nonbreeding season). High quail mortality in the winter was consistent with the cumulative densities of Red-tailed Hawk and Northern Harrier at that time of the year and was higher compared to the breeding season. Several species of raptors winter in the central Great Plains (Berry et al. 1998, Behney et al. 2012). For example, Northern Harrier does not breed in any of my study sites but arrives as early as July and leaves late in spring. This migration pattern of the Northern Harrier in the central Great Plains was previously reported by Littlefield et al. (2005). The arrival of these wintering visitors and the presence of overwintering residents create a robust and diverse suite of predatory birds that interact to increase predation pressure on vulnerable prey species. It is therefore plausible that the high vulnerability of Northern Bobwhite to predation at this time of the year is due to multiple attacks from predators with different hunting strategies. This creates a contrasting landscape of fear such that avoidance of one predator might increase predation risk to another; a phenomenon often referred to as “risk enhancement” (Sih et al. 1998). This has been well demonstrated in mammalian predator-prey interactions (Gorini et al. 2012). For example, a study examining predation risk to European Roe Deer (*Capreolus capreolus*) from humans and Eurasian Lynx (*Lynx lynx*) showed that the interaction of two predators created areas of contrasting risk that double predation risk for roe deer in the same landscape (Lone et al. 2014). Similarly, when faced with attack from two mammalian predators, elk’s avoidance of wolves by selecting denser vegetation cover exacerbated their risk of direct predation by cougars (Atwood et al. 2009).

Low winter survival of Northern Bobwhite in the central Great Plains has been reported by previous studies and is largely attributed to predation and weather extremes (Cox et al. 2004, Holt et al. 2012). Higher mortality of quail during winter translates to fewer individuals for reproduction during the subsequent spring and summer. Conservation efforts often focus on nest, chick, and juvenile survival

(Trine 1998, Taylor et al. 2012, Schreiber et al. 2016), but a growing body of empirical evidence suggests that adult survival is sometimes critical to population viability (Crouse et al. 1987, Weimerskirch et al. 1997, Sanz-Aguilar et al. 2015, Scheele et al. 2016).

Resource selection analysis indicated clear differences in broad scale habitat use between Red-tailed Hawk and Northern Harrier at the relatively homogeneous Beaver River WMA but greater overlap in the comparatively heterogeneous Packsaddle WMA. Red-tailed Hawk employs a sit and watch strategy (Preston 1990, Lish 2015) that allows it to launch attacks at its prey from a perch while Northern Harrier forages by hovering low over grasslands, frequently changing its direction and pace in response to fine-grained variation in habitat and prey availability (MacWhirter and Bildstein 1996). This attribute allows the Northern Harrier to sight, pursue, and capture its prey (often ground dwelling birds, and rodents) with relative ease. The two species together constitute the most important avian predators of Northern Bobwhite in the central and southern Great Plains (Turner et al. 2014). At Beaver River, harriers showed significant preference for uplands, selecting large patches of grassland vegetation while Red-tailed Hawks were primarily restricted to riparian woodlands. Both species however show great overlap at Packsaddle thus enlarging the landscape of predation risk for vulnerable prey species. I also found that spatial variation in Northern Bobwhite predation risk was a function of vegetation complexities inherent in a study system. At both study sites, quail were most vulnerable to predation at areas of high vegetation complexities. This was most evident in the relatively high mortality rates of Northern Bobwhite that I recorded at Packsaddle WMA. Compared to Packsaddle, bobwhite kill locations at Beaver River mostly concentrated in upland grassland, pastures, and upland shrub cover types.

Vegetation structure at Beaver River WMA provides large patches that allow avian predators to specialize. For example, upland vegetation in this landscape is predominantly mixed shrub (Tanner et al. 2015) and mostly devoid of trees. This limits the hunting efficiency of “perch and hunt” predators such as Red-tailed Hawk. Hence, prey species inhabiting these broad grassland patches are subjected to predation from the grassland specialist Northern Harrier but they are generally immune to predation from Red-tailed

Hawk. At Packsaddle WMA, the vegetation is mixed-shrub with mottes of hybrid shinnery oak distributed across the landscape (Hall 2015, Carroll et al. 2016). Shinnery oak (*Quercus havardii*) is typically <0.6 m tall, but those that have hybridized with post oak (*Quercus stellata*) often form mottes up to 6–8 m in height (Pettit 1986, Hall 2015). The distribution of these mottes in upland grasslands provides a network of elevated perches that creates conditions suitable for perch and hunt predators that normally avoid grassland (Newton 2010, Behney et al. 2012). The presence of hunting perches in open grassland at Packsaddle WMA increases the diversity of raptors in uplands and expands the area of high predation risk across the landscape (Denno et al. 2005). Unlike Beaver River, Northern Bobwhite at Packsaddle thus has to deal with predation risk from multiple avian predators, and this risk is spatially correlated with a higher net mortality rate. In this case, the benefits from shifting space use are small because avoidance of a predator in one cover type may result in exposure to another in a different cover type. A large body of evidence shows that when predation risk is homogeneous, it is easier for prey species to develop anti-predation strategies that reduce net risk (Sih et al. 1998, Sih 2005, Thaker et al. 2011, Cresswell and Quinn 2013). Patterns of bobwhite mortality (Figure 3), together with low vulnerability risk at Beaver River support this hypothesis. Furthermore, bobwhite vulnerability was widely spread across the Packsaddle landscape with significant kills occurring where woody vegetation mixed with grass cover. This is an indication that landscape level complexities resulting from reduction in patch sizes of unique vegetation types may create pockets of edge effects capable of reducing the amount of safe habitats for prey species (Denno et al. 2005). One anti-predatory response of Northern Bobwhite to a modeled avian predator was to fly into dense vegetation of ~38 cm tall (Perkins et al. 2014). Therefore, alterations in the landscape matrix that changes the nature in which background refugia are nested, creates an unstable dynamic in the ability of bobwhite to avoid their top predators. This creates a disparity between bird abundance and the proportion that avian predators can potentially kill. I saw a decrease in mortality as grassland patches increased in size. This is consistent with other studies on avian mortality resulting from raptor predation. Beyond a threshold distance of 30 m from predator cover, Redshank (*Tringa tetanus*)

predation by Eurasian Sparrowhawks (*Accipiter nisus*) decreased significantly and approached uniformity (Cresswell et al. 2010).

Despite their role in altering the predation risk gradient in grassland ecosystems, mottes of hybrid shinnery oak act as important thermal refugia for ground dwelling birds during periods of high weather extremes. Carroll et al. (2016) noted that these tall shrubs reduced ground temperatures by 10°C more than other vegetation cover types during peak diurnal heating. Under extreme conditions, patches that might be avoided in a landscape of fear could be attractive in a “landscape of survival.” The predation-starvation risk hypothesis predicts that birds will avoid risky habitats until starvation risk exceeds predation risk (Cresswell and Whitfield 2008, Cresswell et al. 2010). Yasué et al. (2003) demonstrated that increased energy requirements from extreme cold were sufficient to increase use of conditionally-beneficial patches normally avoided due to predation risk. Northern Bobwhite may trade off predation risk by seeking refuge in risky habitats during periods of extreme conditions. Such trade-offs are seasonal, however, as predation risk from raptors is lower when shinnery oak mottes are sought for thermal refuge from high temperatures in summer.

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Table 1. Model-averaged coefficients estimating the predicted habitat selection for Red-tailed Hawk and Northern Harrier. Also included are model-averaged coefficients estimating the predicted habitat vulnerability for Northern Bobwhite (NOBO), at Packsaddle Wildlife Management Area in western Oklahoma, United States, 2013–2015.

	Red-tailed Hawk			Northern Harrier			NOBO mortality		
	B	SE	Pr(> z )	B	SE	Pr(> z )	B	SE	Pr(> z )
(Intercept)	-0.01	0.06	0.81	-0.42	0.07	< 2e-16	-0.65	0.07	< 2e-16
Upland shrub	0.06	0.06	0.29	0.09	0.07	0.18	0.40	0.17	0.02
Pasture	-0.30	0.13	0.025	-0.01	0.07	0.86	-0.15	0.17	0.39
Riparian forest	0.03	0.06	0.55	0.18	0.07	0.01	-0.17	0.16	0.31
Upland wood	0.02	0.06	0.66	0.00	0.08	0.98	0.00	0.15	0.98
Riparian shrub	0.01	0.06	0.86	-0.05	0.08	0.52	-0.54	0.19	0.01
Grass cover	-0.08	0.06	0.17	-0.10	0.08	0.24	-0.49	0.19	0.01
Bare ground	0.01	0.06	0.89	0.11	0.07	0.11	0.11	0.17	0.54

Table 2. Model-averaged coefficients estimating the predicted habitat selection for Red-tailed Hawk, and Northern Harrier plus predicted habitat vulnerability for Northern Bobwhite (NOBO), at Beaver River Wildlife Management Area in western Oklahoma, United States, 2013–2015.

Variables	Red-tailed Hawk			Northern Harrier			NOBO mortality		
	$\beta$	SE	Pr(> z )	$\beta$	SE	Pr(> z )	$\beta$	SE	Pr(> z )
(Intercept)	-0.37	0.05	***	0.06	0.06	0.33	-0.03	0.07	0.70
Grass cover	-0.20	0.05	***	0.20	0.06	***	-0.28	0.15	0.07
Pasture	-0.57	0.11	***	0.60	0.13	***	-0.71	0.16	***
Bare ground	-0.25	0.13	0.05	-0.05	0.06	0.42	-0.16	0.15	0.28
Riparian wood	0.08	0.04	0.09	-0.08	0.06	0.19	-0.15	0.16	0.34
Upland shrub	-0.05	0.04	0.28	0.09	0.06	0.13	-0.29	0.16	0.07
Riparian shrub	0.02	0.04	0.67	-0.08	0.06	0.17	-0.55	0.17	***

Table S1: Model selection results of Northern Bobwhite vulnerability at Beaver River and Packsaddle Wildlife Management Areas in Oklahoma, USA, 2013 – 2015. For each study site, top 10 models are presented. Included for each model are number of parameters (K), Akaike's Information Criterion values corrected for small sample sizes (AICc), delta AICc ( $\Delta AICc$ ), and Akaike weight ( $\omega_i$ ).

Site	Models	df	AICc	$\Delta AICc$	$\omega_i$
Packsaddle	Grass+riparian shrub+upland wood	4	390.86	0.00	0.38
	Grass+riparian shrub+riparian wood+upland shrub	5	391.83	0.97	0.23
	Grass+riparian shrub+upland wood	5	392.91	2.06	0.13
	Grass+riparian shrub+riparian wood+upland wood	6	393.90	3.04	0.08
	Grass+riparian shrub	3	394.64	3.78	0.06
	grass+upland shrub	3	395.65	4.79	0.03
	Grass+riparian shrub+riparian shrub	4	396.40	5.54	0.02
	grass+upland shrub	3	396.64	5.78	0.02
	Grass+riparian shrub+upland wood	4	396.66	5.80	0.02
	Upland shrub	2	396.73	5.87	0.02
Beaver	Grass+pasture+riparian shrub+upland wood	5	462.40	0.00	0.30
	Grass+pasture+riparian shrub+riparian wood+upland wood	6	463.37	0.97	0.18
	Grass+pasture+riparian shrub	4	464.10	1.70	0.13
	Pasture+riparian wood+riparian shrub	4	464.48	2.08	0.11
	Pasture+riparian shrub	3	464.63	2.23	0.10
	Grass+pasture+riparian shrub+riparian wood	5	465.37	2.96	0.07
	pasture+riparian shrub+riparian wood +upland shrub	5	465.57	3.17	0.06
	pasture+riparian shrub+ riparian wood	4	465.92	3.52	0.05
	Pasture+riparian wood	3	472.79	10.39	0.00
	Grass+pasture+riparian wood	4	472.91	10.51	0.00

Table S2: Model selection results for Red-tailed Hawk (RTHA) and Northern Harrier (NOHA) habitat selection Packsaddle Wildlife Management Areas in Oklahoma, USA, 2013 – 2015. For each species, the top 10 models are presented. Included for each model are number of parameters (K), Akaike's Information Criterion values corrected for small sample sizes (AICc), delta AICc ( $\Delta AICc$ ), and Akaike weight ( $\omega_i$ ).

Models	K	AICc	$\Delta AICc$	$\omega_i$
<i>RTHA</i>				
upland shrub+riperian shrub	3	724.11	0	0.31
upland shrub+riparian wood	3	724.83	0.72	0.22
upland shrub+upland wood	3	725	0.89	0.20
upland shrub+grass	3	725.17	1.06	0.18
grass	2	728.49	4.37	0.03
grass+upland shrub+upland wood	4	728.67	4.55	0.03
riparian wood	2	730.31	6.19	0.01
pasture	2	730.6	6.48	0.01
pasture+riparian wood	3	734.52	10.41	0
riparian wood+grass	3	736.49	12.38	0
<i>NOHA</i>				
grass	2	476.57	0	0.65
grass+upland shrub	3	478.41	1.84	0.16
grass+upland wood	3	480.49	3.92	0.09
grass+bare ground	3	480.66	4.09	0.08
grass+riparian shrub+riparian wood	4	486.36	9.8	0
grass+bare ground+upland shrub	4	486.4	9.83	0
grass+bare ground+riparian shrub	4	486.43	9.86	0
grass+bare ground+riparian wood	4	487.42	10.85	0
grass+bare ground+riparian shrub+pasture	4	487.92	11.35	0
grass+pasture+riparian wood+upland wood	5	492.87	16.3	0
bare+riparian wood+riparian shrub	4	494.39	17.82	0
grass+bare ground+upland shrub+riparian shrub+pasture	6	496	19.43	0

Table S3: Model selection results for Red-tailed Hawk (RTHA) and Northern Harrier (NOHA) habitat selection Beaver River Wildlife Management Areas in Oklahoma, USA, 2013 – 2015. For each species, the top 7 models are presented. Included for each model are number of parameters (K), Akaike's Information Criterion values corrected for small sample sizes (AICc), delta AICc ( $\Delta AICc$ ), and Akaike weight ( $\omega_i$ ).

RTHA	df	AIC	$\Delta AICc$	$\omega_i$
riparian forest+grass+bare ground	4	1083.04	0	0.45
riparian forest+grass	3	1083.26	0.23	0.40
riparian forest+grass+pasture+bare ground	5	1086.75	3.71	0.07
riparian forest+grass+upland shrub	4	1088.67	5.63	0.03
riparian forest+grass+upland shrub+bare ground	5	1088.73	5.69	0.03
riparian forest+grass+riparian shrub	4	1089.84	6.8	0.01
riparian forest+grass+upland shrub+pasture+bare ground	6	1092.68	9.64	0
NOHA				
pasture+grass+upland shrub+riparian forest	5	655.89	0	0.70
pasture+grass	3	659.84	3.95	0.10
pasture+grass+riparian forest	4	660.15	4.26	0.08
pasture+grass+bare ground	4	661.3	5.41	0.05
pasture	2	662.11	6.22	0.03
pasture+grass+riparian shrub+upland shrub	5	663.93	8.03	0.01
pasture+grass+upland shrub+riparian wood	5	664.16	8.27	0.01

## Figure legends

Figure 1: Mean densities of Northern Bobwhite kills at Beaver River and Packsaddle Wildlife Management Areas during the breeding and non-breeding seasons.

Figure 2: Mean densities of Northern Harrier and Red-tailed Hawk during the breeding and non-breeding seasons of the Northern Bobwhite at Packsaddle (a) and Beaver River (b) Wildlife Management Areas in western Oklahoma, USA, 2013–2015.

Figure 3: The predicted relative probability of Northern Bobwhite vulnerability (a), Northern Harrier (b), and Red-tailed Hawk (c) habitat selection predicted by resource selection function at Beaver River Wildlife Management Area in western Oklahoma, USA, 2013–2015.

Figure 4: The predicted relative probability of Northern Bobwhite vulnerability (a), Northern Harrier (b), and Red-tailed Hawk (c) habitat selection predicted by resource selection function at Packsaddle Wildlife Management Area in western Oklahoma, USA, 2013–2015.

Figure 5: Mean levels of vegetation classes collected from 100 m radius plots of predicted Northern Bobwhite vulnerability to Northern Harrier (NOHA), Red-tailed Hawk (RTHA), and Red-tailed Hawk plus Northern Harrier (Both) at Packsaddle and Beaver River WMAs, Oklahoma, USA, 2013–2015.

Figure S1: Predicted overlap map between Red-tailed Hawk (RTHA) and Northern Harrier selection (NOHA), and Northern Bobwhite (NOBO) vulnerability at Packsaddle WMA, Oklahoma, USA, 2013–2015.

Figure S2: Predicted overlap map between Red-tailed Hawk (RTHA) and Northern Harrier selection (NOHA), and Northern Bobwhite (NOBO) vulnerability at Beaver River WMA, Oklahoma, USA, 2013–2015.



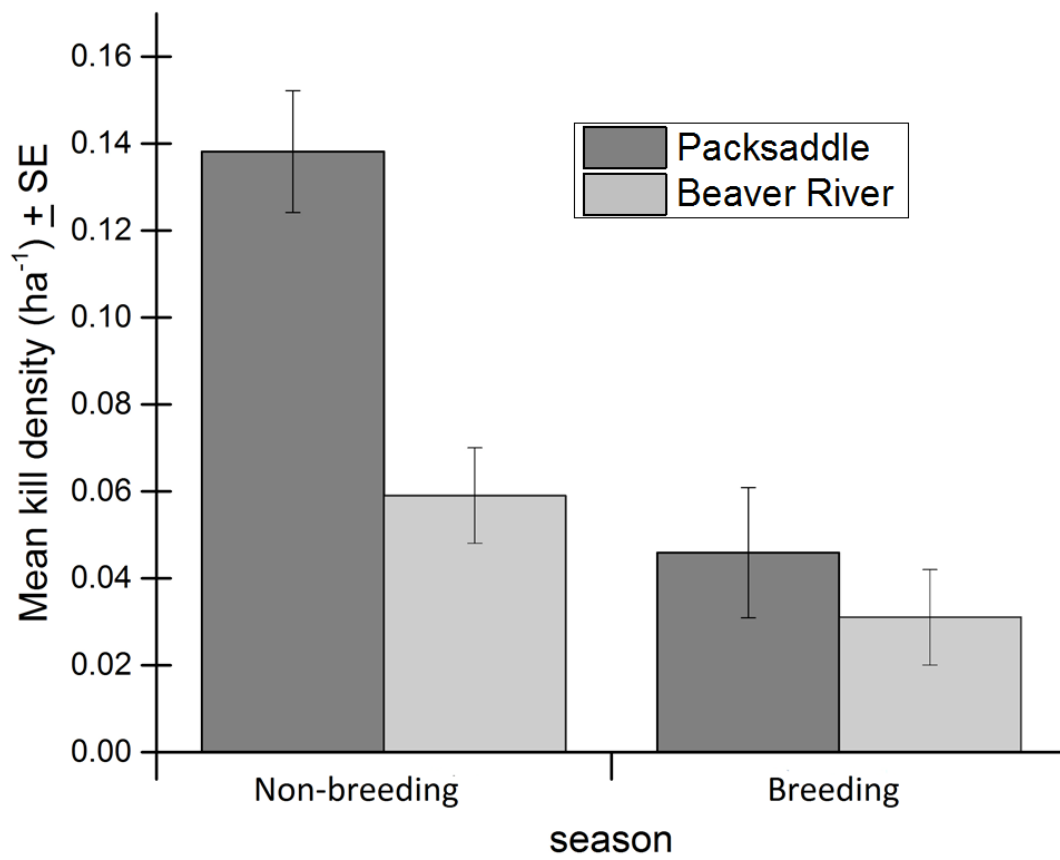


Figure 1

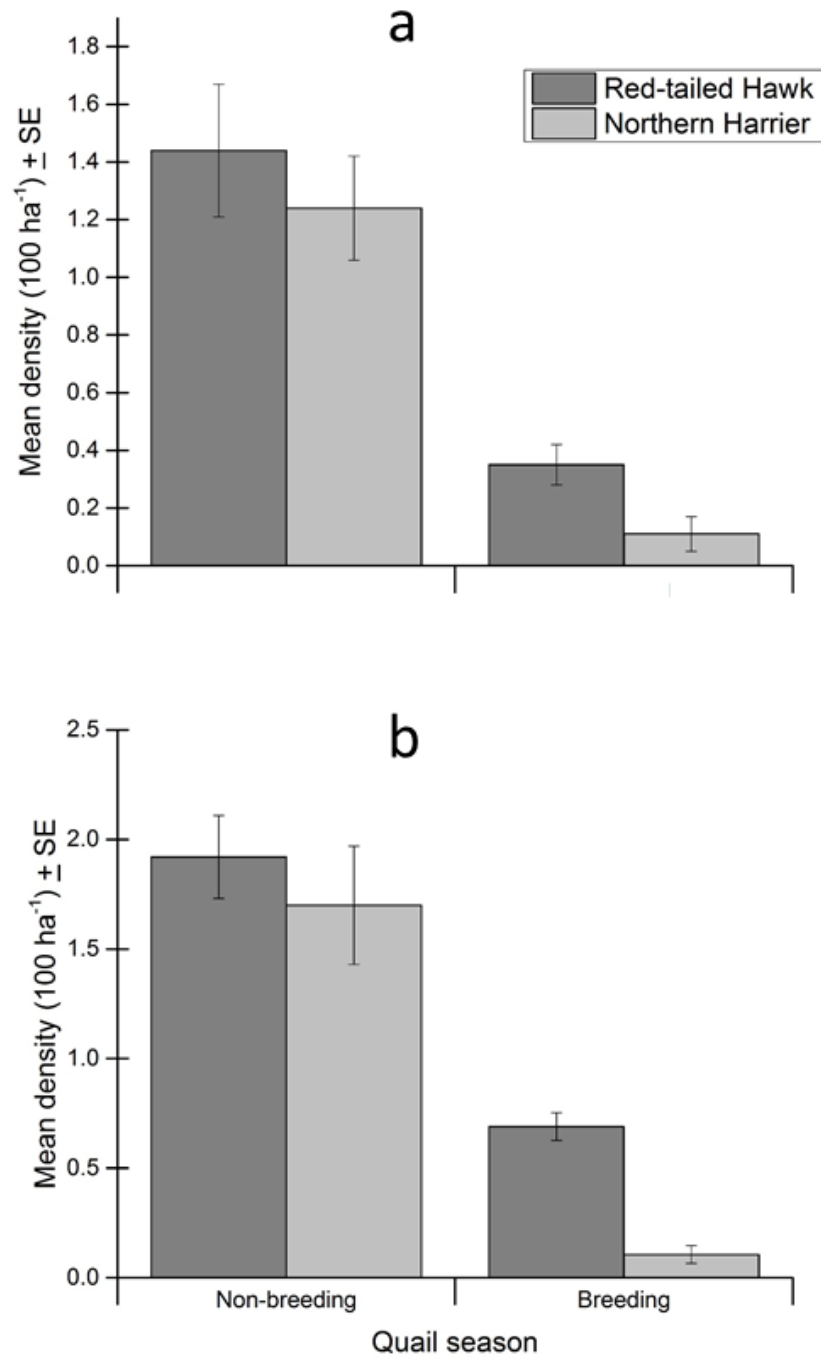


Figure 2

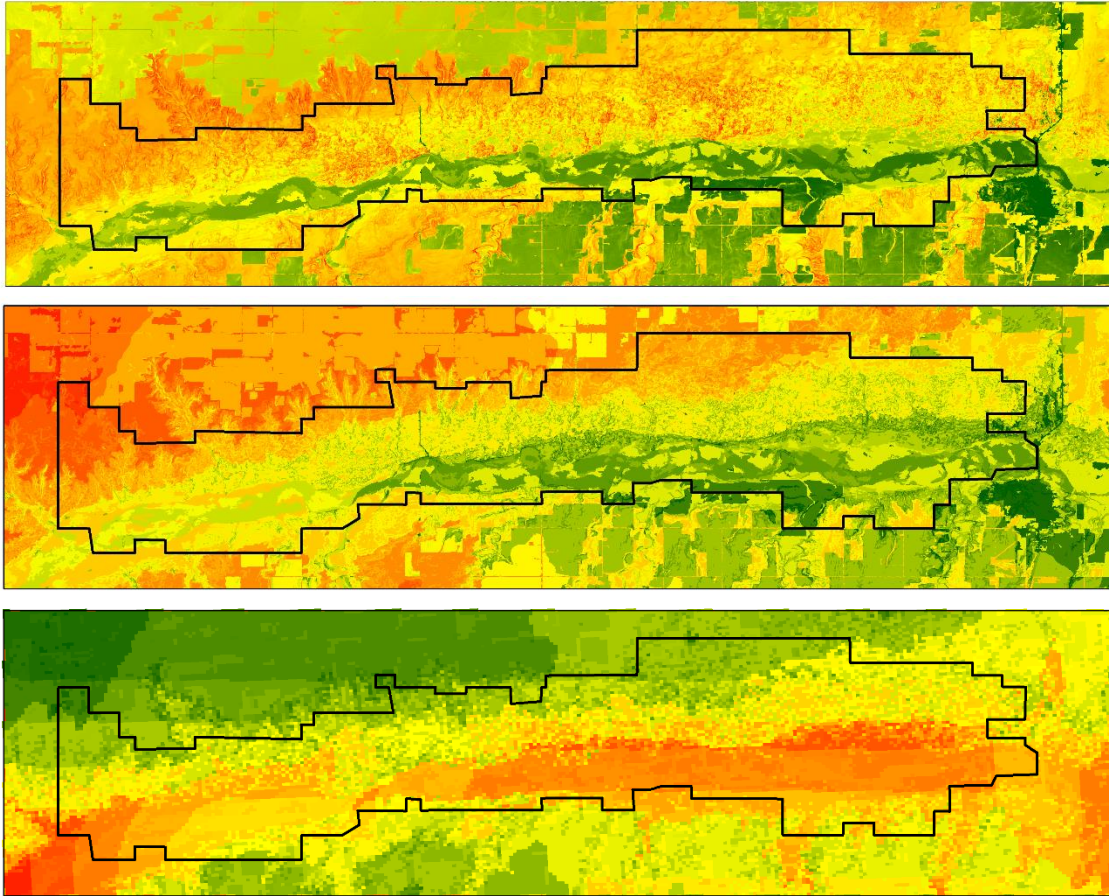


Figure 3

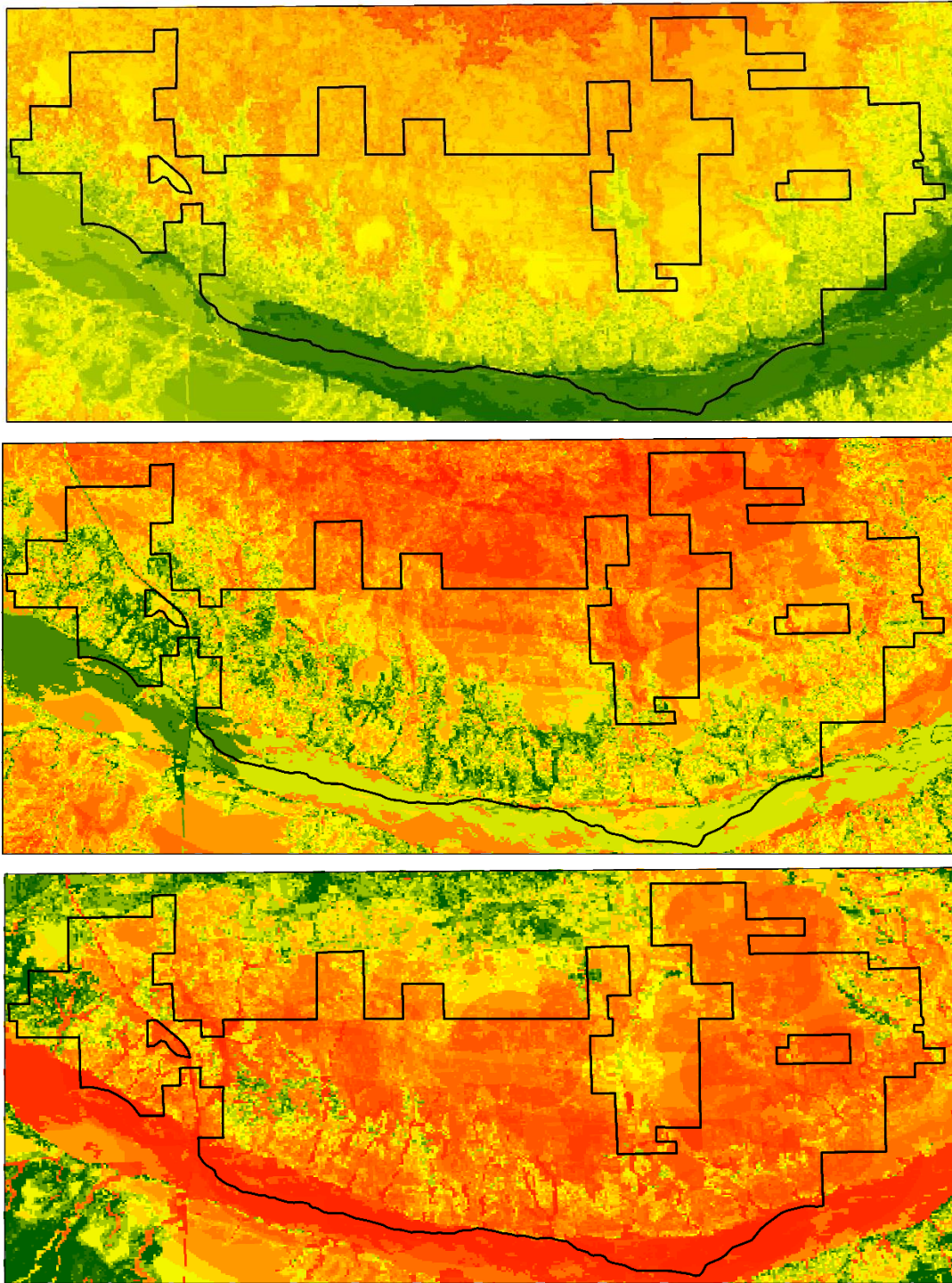


Figure 4

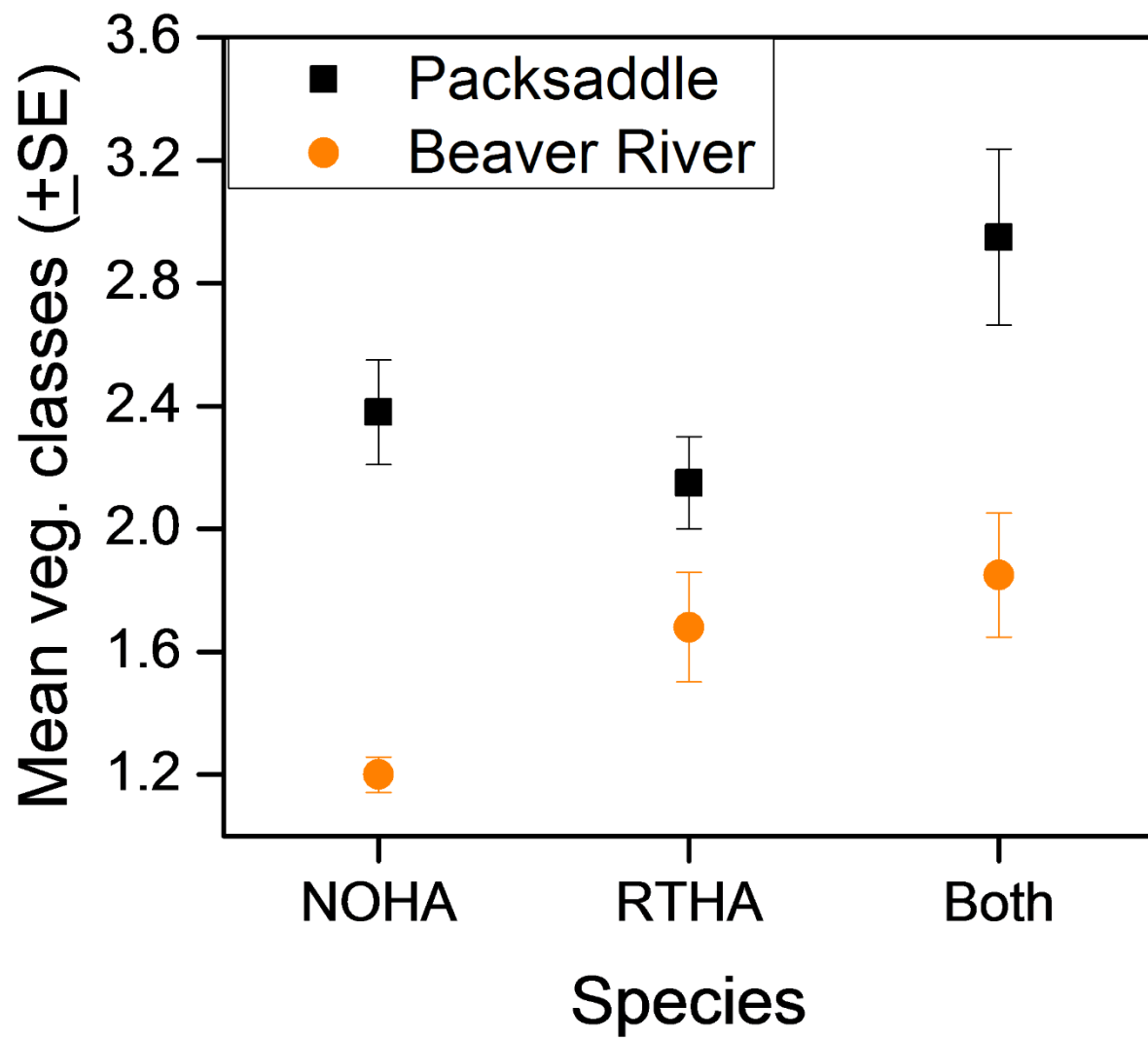


Figure 5

# Supplementary materials: Figures

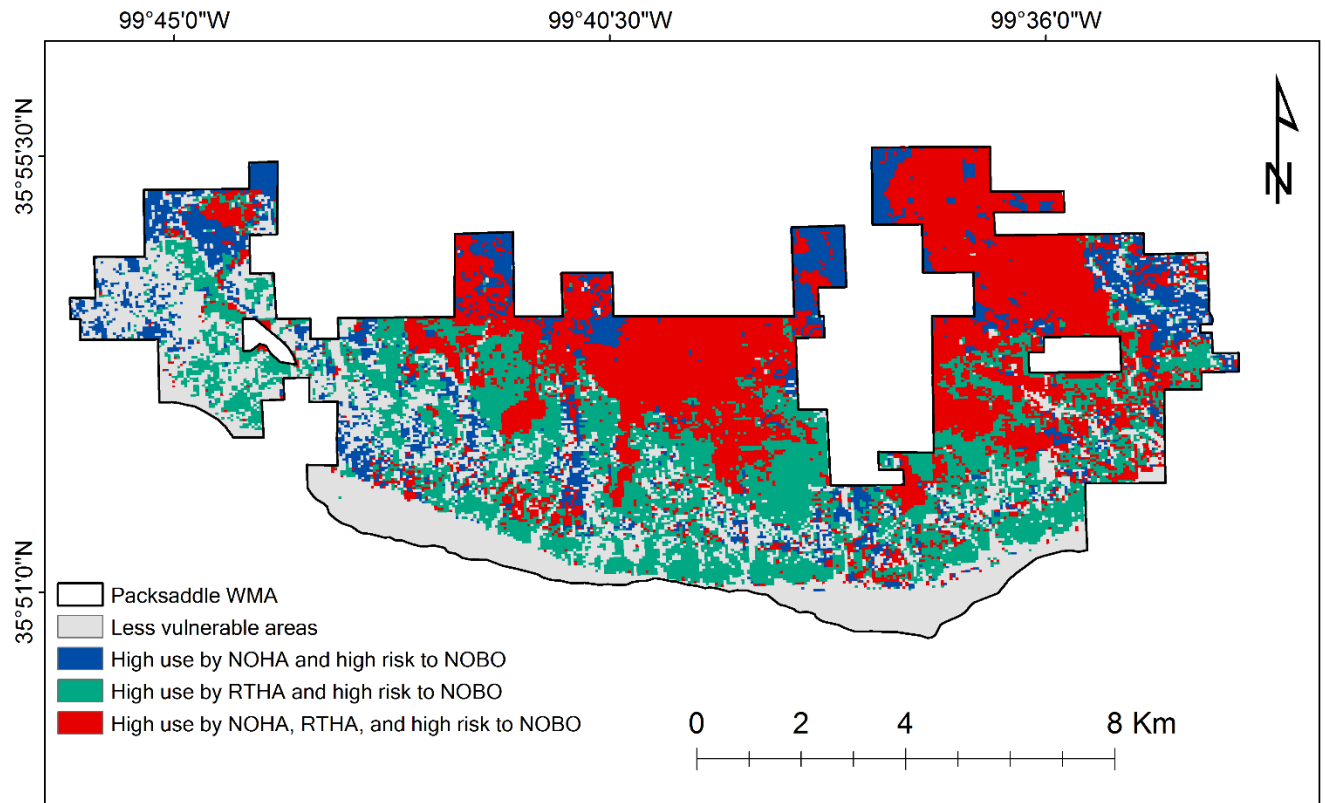


Figure S1

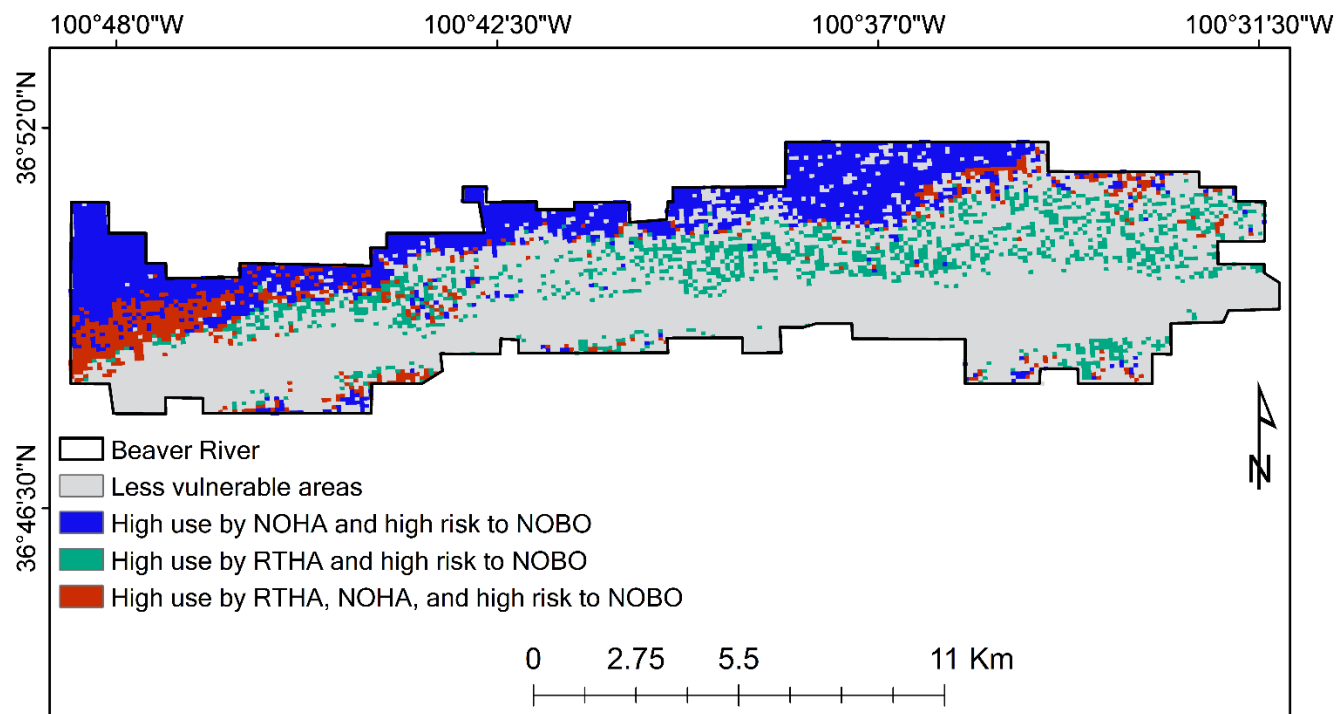


Figure S2

## VITA

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