ASSESMENT OF OLFACTORY CONCEALMENT RELATED TO HABITAT SELECTION BY TERRESTRIAL ANIMALS

By

DILLON T FOGARTY

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Thesis Approved:

Scott R. Loss

Thesis Adviser

R. Dwayne Elmore

Samuel D. Fuhlendorf

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Abstract: Animals use habitat selection to mitigate adverse effects environmental factors may have on their fitness. For many prey species, predation by olfactory-sensing predators is an environmental factor that has devastating impacts on their fitness. To minimize risk from olfactory-sensing predators, prey should select cover that reduces their odour cues that predators use to find them. The olfactory concealment theory predicts that this can be accomplished through selection of airflow characterized by high turbulence and/or updrafts. However, few studies have investigated airflow patterns as a dimension of cover. Here, I characterized the olfactory landscape, and assessed how olfaction relates to habitat selection and nest success of grassland-nesting birds. Specifically, I measured olfactory concealment and vegetation characteristics (e.g. visual concealment, grass height, etc.) within grassland, shrubland, and forest vegetation types and at nests in grassland vegetation. At a subset of points, I tested whether visual and/or olfactory concealment influenced depredation rates of simulated prey. Additionally, I modeled the relative importance of visual concealment, as well as airflow and weather conditions associated with olfactory concealment to nest survival. I found that turbulence intensity and airflow slope varied by vegetation type, and in grasslands horizontal concealment, vegetation height and vegetation roughness were positively correlated to turbulence intensity. Additionally, in grasslands turbulence intensity was the best predictor of simulated prey depredation. Together, these findings provide the first approximation of an olfactory landscape, which could potentially be used by animals to make space use decisions and in grasslands may be able to decrease rates of predator detection. However, contrary to expectations, grassland-nesting birds did not select nest sites with significantly higher levels of turbulence intensity ($p=0.10$), but did select more overhead visual concealment. A finding that I suspect reflects a habitat selection strategy to mitigate thermal conditions. Precipitation and humidity were important predictors of nest survival and were positively related. I hypothesize that moisture-related weather conditions indirectly influences nest survival through predation by olfactory-sensing predators. Findings here support those of others that weather can have a large impact on vital rates and that in some cases, habitat selection can potentially mitigate adverse effects of weather.

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CHAPTER I

VARIATION AND DRIVERS OF AIRFLOW PATTERNS ASSOCIATED WITH OLFACORY CONCEALMENT AND ANIMAL HABITAT SELECTION

Introduction

One of the most important decisions an animal can make is how to select habitat; habitat selection greatly influences survival probability and reproductive output (Gilliam & Fraser 1987; McLoughlin, Dunford & Boutin 2005; Gibson *et al.* 2016). Due to the clear implications of habitat selection for fitness, multiple habitat selection strategies have emerged through the process of natural selection (Milinski & Heller 1978; Clark & Shutler 1999; Lima & Dill 1990; Martin 1993; Caro 2005). Characterizing animal habitat selection provides valuable information to help understand life history, predator-prey interactions and dynamics, and management of habitat.

Habitat is a multi-dimensional concept that captures all components of an organism’s surroundings relevant to survival and reproduction (Block & Brennan 1993; Hall, Krausman & Morrison 1997). Cover from predation, conspecifics, and weather is an important component of habitat. Most ecological research, including studies of animal habitat selection, have focused solely on visual aspects of cover. This focus may be partially driven by the highly developed visual system of humans and therefore the perceived primacy of sight-based cover selection. Although many studies have found visual concealment to be an important factor influencing cover selection (e.g., Martin 1992; Weidinger 2002; Latif, Heath & Rotenberry 2012; Shallow *et al.* 2015), thermal, aural and olfactory components of cover are also likely to be important for animal survival and reproduction under certain conditions (Conover 2007; Slabbekoorn & Ripmeester 2008; Conover & Borgo 2009 Carroll *et al.* 2015, 2016). Evolutionary theory dictates that prey species should select cover based on the primary detection mechanisms employed by key predators (Van Valen 1973). Because most terrestrial predator communities are dominated by species that rely on olfaction (hereafter olfactory predators) (Burghardt 1966; Nams 1997; Slotnick 2001; Hughes, Price & Banks 2010; Threlfall, Law & Banks 2013), selection of cover features that impede olfactory detection (hereafter olfactory concealment) is likely to be widespread among prey species and should result in fitness-related benefits.

Existing theory regarding olfactory concealment (Conover 2007) predicts that weather-related factors, and particularly airflow patterns, strongly influence the ability of predators to detect prey odourants. For example, wind speed and direction have been shown to influence foraging behaviour of olfactory predators (Ruzicka & Conover 2011), while moisture has been shown to influence simulated prey persistence (Ruzicka & Conover 2012; Borgo and Conover 2016a) and avian nest survival rates (Moynahan *et al.* 2007; Lehman *et al.* 2008; Webb *et al.* 2012; Dinkins *et al.* 2016). Regarding airflow characteristics, olfactory concealment theory (Conover 2007) predicts that laminar airflow (i.e., airflow with constant direction and speed) creates linear, highly concentrated odor plumes that facilitate olfactory detection and tracking. Alternatively, highly turbulent airflow (i.e. airflow with variable direction and speed) creates broad irregular odor plumes with low odorant concentrations that are difficult to detect and track. Additionally, updrafts (i.e., upward rising air) elevate odor plumes above the nose of predators and thus reduce the amount of ground area over which an odor plume is detectable, as opposed to airflow currents that are parallel to the ground or angled downward (i.e. downdrafts) (Fig. 1) (Conover 2007). Airflow is partly influenced by the structure of land surface features including vegetation, rock and debris, and topography. (Plate 1971; Raynor 1971; Garratt 1980; Gash 1986; Nord 1991). Therefore, prey species vulnerable to olfactory predators may select locations and vegetation features that are characterized by high turbulence and/or updrafts (Conover2007; Conover & Borgo 2009; Conover *et al.* 2010).

Despite the likely importance of airflow characteristics for influencing olfactory concealment, no studies have investigated drivers and variation of olfactory concealment associated airflow patterns across different spatial scales. Furthermore, a lack of empirical research linking vegetative features to airflow characteristics limits conceptual understanding of the mechanisms of olfactory concealment and may further contribute to the focus on visual characteristics of cover. At local scales, airflow patterns predictive of olfactory concealment may be related to traditionally measured vegetation characteristics of habitat (e.g., vegetation height, visual cover, plant species composition). At larger scales, airflow patterns vary consistently between major vegetation types (Raynor 1971; Wilson *et al.* 1982). This airflow variation could influence cover, and thus habitat selection at multiple spatial scales.

In this study, I conduct the first multi-scale analysis of the variation and drivers of airflow characteristics that influence olfactory concealment of animals. My specific objectives were to: (1) compare turbulence and updrafts between major vegetation types (grassland, shrubland, and forest) to characterize the olfactory landscape, (2) assess whether local-scale vegetation features often measured in animal habitat selection studies are related to these olfactory-related airflow variables, and (3) experimentally assess whether levels of turbulence and updrafts are associated with predator detection rates of simulated prey odorants, as predicted by olfactory concealment theory. This study has implications for increasing the conceptual understanding of animal habitat selection and life history evolution of predator and prey species, as well as for the management of animal habitat.

Materials and Methods

STUDY SYSTEM

The study area was located on the 4,692-ha McFarlin-Ingersoll ranch 45 km east of Tulsa, Oklahoma, USA (230 m elevation) (Fig. 2). Located within the central irregular plains ecoregion, the study area consists largely of tallgrass prairie (~62% of area), with patches of forest (~15%) and shrubland (~20%) occurring near creeks and draws, on hillsides, and in low elevation areas. The primary land use is cow-calf domestic cattle (*Bos tauras*) production, and during the 2015-2016 study period, there was an average stocking rate of 3.1 hectares per animal unit (ha/AU). Common grass species included little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and big bluestem (*Andropogon gerardi*); common grassland forbs included southern ragweed

(*Ambrosia bidentate*), western ragweed (*Ambrosia psilostachya*), common yarrow (*Achillea millefolium*), and antelope-horn milkweed (*Asclepias viridis*). Major shrub species included winged sumac (*Rhus copallinum*), coralberry (*Symphoricarpos orbiculatus*), Oklahoma blackberry (*Rubus oklahomus*), and roughleaf dogwood (*Cornus drummondii*). Dominant tree species in forested areas included blackjack oak (*Quercus marilandica*), common hackberry (*Celtis occidentalis*), sugarberry (*Celtis laevigata*), American elm (*Ulmus americana*), and hickory species (*Carya spp.*); additionally, coralberry and Carolina elephant's foot (*Elephanopus carolinianus*) were common on forest floors. Olfactory predators frequently observed in the study area included coyote (*Canis latrans*), Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), northern raccoon (*Procyon lotor*), nine-banded armadillo (*Dasypus novemcinctus*), eastern wood rat (*Neotoma floridana*), and several snake species.

LANDCOVER CLASSIFICATION AND SAMPLING DESIGN

Land cover within the study area was reclassified with ArcGIS (Redlands, California, USA) from the Oklahoma ecological systems classification (Diamond et al. 2014) (Appendix S1) into grassland, shrubland, forest and non-use cover categories (see Appendix S1 for list of non-use cover categories). Within each land cover type (excluding non-use cover), I used geospatial modeling environment software (Beyer 2012) to create 50 randomly located clusters, each consisting of 3 sampling points separated by ≥50 m, and with all clusters separated by ≥ 100 m (total of 450 points). Upon ground-truthing, any points that were not representative of the assigned cover type were reclassified to the appropriate cover type, thus a single cluster could contain points from more than one cover type. Points that were not representative of grassland, shrubland, or forest were eliminated. Of the 450 points generated the logistical constraints of the study allowed me to sample 278 points (110 grassland, 83 shrubland, and 85 forest). From this set of points, I eliminated points on slopes >10% to control for the effects of terrain on airflow and thus better isolate the effect of vegetation features rather than landform on airflow.

FIELD METHODS

Measurement of olfactory concealment variables

Field sampling took place between 1000 and 1700 hours from 1 April – 31 July 2015 and 2016 on days when ambient wind speeds were between 7–24 km per hour. A sonic anemometer (CSAT3, Campbell Scientific, Utah, USA) was used to quantify air velocity in three dimensions at each point, with readings taken every second for 30 minutes at a height of 25 cm above ground. To prevent the structure of the anemometer base from affecting airflow readings, the anemometer was faced directly into the direction of the wind. Output data were recorded as velocity in each dimension in a u,v,w coordinate system; where the u-axis was aligned parallel to the ground in the direction the anemometer was pointed, the w-axis was aligned vertically, and the v-axis was aligned parallel to the ground and perpendicular to the u-axis. Based on these readings, mean velocity in a two-dimensional plane (U) was calculated as the square root of $u^2 + v^2$. Turbulence (T) was then calculated as the standard deviation of U. Because T and U are positively correlated, I also calculated turbulence intensity (TU) as T/U. This variable reflects turbulence per unit area rather than turbulence per unit time and is therefore useful for understanding how animal odour plumes dissipate spatially (Conover 2007). I also calculated mean velocity on the w-axis (W)—with positive values indicating an updraft and negative values indicating a downdraft—and W was used to calculate airflow slope (WU) as W/U. This variable provides and index for the horizontal distance over which an animal odour plume is detectable to terrestrial predators and is thus more ecologically meaningful than updraft/downdraft.

Measurement of vegetation variables

Several vegetation variables were also measured within a 1 m^2 plot centered at each sample point (hereafter, plot-scale variables). Within this plot, the height of the tallest understory plant of any type, as well as the tallest grass blade/stem were recorded, as were percent cover of grass, forb, shrub, and non-vegetated ground. To measure overhead visual concealment at each plot center, angle of obstruction (AOB) was used (Kopp *et al.* 1988). For AOB, a pole and digital level were used to record the angle in the vertical plane (0–90°, starting at 90° straight above the point) at which a direct line of sight from 1.5 m to ground level is first obstructed (90° indicates complete obstruction). The AOB measurement was repeated in eight cardinal directions, with the average of the readings providing an index of visibility from above, a measurement especially relevant to detection by avian predators. To measure horizontal visual concealment, a 2.5 cm-width cover pole divided into four 10 cm-tall segments (starting at ground level) was observed from a height of 1 m and a distance of 4 m, with the observer estimating percent obstruction (0-20, 21-40, 41-60, 61-80, 81-100%) of each segment (similar to Griffith & Youtie 1988). This measurement was repeated in four cardinal directions, and the average of all readings was used as an index of horizontal concealment within 40 cm of ground level.

Additional vegetation variables were sampled along a 16 m transect oriented parallel to the wind direction during the time of sampling (hereafter, transect-scale variables). From the sample point, transects extended 12 m in the upwind direction and 4 m in the downwind direction. These distances were based on expected characteristics of airflow around a surface feature (e.g. shelterbelt) 2 m in height. Specifically, airflow is known to be altered by a surface feature to a distance of approximately 2 times the height of the surface feature in the upwind direction and 6 times the height of the feature in the downwind direction (dimensions are within the ranges reported by Plate (1971) and similar to those used by Borgo & Conover (2016a)). Transects were thus designed to capture all surface features ≤2 m in height that influenced airflow patterns at the sample point. Vegetation height was recorded along transects at 1 m intervals, and transect-scale average vegetation height and standard deviation of vegetation height (an index of surface roughness, hereafter vegetation roughness) were also calculated. Estimates of percent cover of grass, forb, shrub, and non-vegetated ground were made at 2 m intervals and used to calculate transect-scale average percent cover (see Table 1 for a complete list of predictor variables).

Olfactory concealment and predator detection

At a subset of points sampled in 2016, and immediately after measuring vegetation variables, 2 quail eggs were placed on the ground and scented with 1200 mg of fish oil (600 mg per egg). The next day (between 23 and 25 hours after egg placement), the point was revisited to determine if the eggs remained intact or had been depredated. Eggs were considered depredated if at least one egg was gone or no longer intact and successful when both eggs were intact (similar to artificial nest studies; e.g. Bayne & Hobson 1997;

Roos & Pärt 2004). Predator detection surveys were conducted at all points sampled in 2016 when farm-raised quail eggs were available and when field personnel were able to revisit the eggs the following day ($n = 92$).

STATISTICAL ANALYSES

All analyses were conducted in R Version 3.2.2 (R Core Team 2015). A preliminary analysis using t-tests (assessed at $\alpha = 0.05$) indicated that points within clusters were more similar to each other than the entire sample of points for each cover type. I therefore used mixed-effects models with cluster as a random factor to account for non-independence of points within clusters. To test for an influence of vegetation cover type on turbulence intensity and airflow slope, I used linear mixed models (LMM; lmer function in lme4 package) with cover type as the fixed effect. To assess significance of the cover type variable (at $\alpha = 0.05$), I used a likelihood ratio test to compare these models to a null model that only contained an intercept term and the cluster random effect. To compare group means of airflow variables, I used Tukey's Honest Significant Difference (HSD) *post hoc* tests (significance assessed at $\alpha = 0.05$ using glht function in package multcomp).

We also used LMM's to characterize the relationship between olfactory concealment variables and vegetation variables within each cover type. For each cover type, I first plotted all predictor variables (i.e. vegetation variables described above and in Table 1) against response variables (i.e. turbulence intensity and airflow slope), and I only further considered predictor variables if they appeared to be related with the response variable upon visual examination of plots (Appendix Fig. S1-6). For this variable set, I used Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002) to assess support for all univariate models relative to the null model, with model assessments based on ΔAIC_c values (ΔAIC_c values 0 – 2 indicating strong relative support) and AIC_c weights. Because AIC_c is solely a measure of relative model support and does not necessarily indicate model fit or variable effect size, I also calculated Pearson's correlation coefficients (r) to provide an index of relationship strength for each predictor variable ($r \geq 0.5$ indicates highly correlated, r between 0.3 and 0.5 indicates moderately correlated, and $r < 0.3$ indicates weak or no correlation; r categories are the same used by Raudsepp-Hearne, Peterson & Bennett 2010). Both ΔAIC_c rankings and Pearson's correlation coefficients were used to make inferences, thus allowing us to focus my conclusions on predictor variables most likely to predict airflow response variables within each cover type.

For the egg survival experiment, I used generalized linear mixed models (GLMM; glmer in package lme4) with a binomial error structure and logit link function to model the relationship between egg survival and both visual and olfactory concealment variables within each cover type individually. For both visual and olfactory variable sets, I created models to test for singular and additive effects; additive models were specifically created to test for possible synergistic effects of concealment on egg survival. To assess relative strength of support for models, I compared a null model to all visual ($n = 3$) and olfactory ($n = 3$) models and assessed model support based on ΔAIC_c and model weights.

Results

After removing points on slopes >10%, 231 total points within 89 clusters remained, including 108 points (40 clusters) in grasslands, 70 points (31 clusters) in shrublands, and 53 points (27 clusters) in forests. Data from these 231 points were used to address my first two objectives. For my egg predation experiment, I used data from the 92 points sampled in 2016, including 33 points (12 clusters) in grassland, 32 points (11 clusters) in shrubland, and 27 points (10 clusters) in forest cover.

COMPARISON OF OLFACTORY CONCEALMENT VARIABLES AMONG VEGETATION COVER TYPES

Likelihood ratio tests indicated a significant effect of vegetation type on both turbulence intensity ($\chi^2 = 11.44$, df = 2, $p < 0.01$) and airflow slope ($\chi^2 = 79.20$, df = 2, $p < 0.001$). Tukey's (HSD) tests indicated that turbulence intensity was significantly higher in shrubland and grassland than in forest (Fig. 3a). Airflow slope was significantly greater in shrubland than in grassland but similar to airflow slope in forest; there was no difference in airflow slope between forest and grassland (Fig. 3b). In other words, air currents in shrubland and grassland were characterized by greater change in velocity and direction per unit area (i.e., high turbulence intensity) than in forest, and air currents in shrubland had a greater tendency to move upward over a short horizontal distance (i.e., high updraft slope) than in grasslands (see also Appendix S2 for β±SE and CIs).

RELATIONSHIPS AMONG VEGETATION VARIABLES AND OLFACTORY CONCEALMENT VARIABLES

For all three vegetation types, visual assessment of airflow slope plotted against vegetation variables indicated no strong relationships and thus precluded further analysis

(Appendix Fig S4-6). For the analysis of turbulence intensity in grasslands, seven variables from the initial candidate variable set were analyzed (Tables 2, 3), and of these variables, turbulence intensity was strongly correlated ($r \geq 0.5$) with four and moderately correlated (r between 0.3 and 0.5) with one. Turbulence intensity was strongly positively correlated with plot-scale horizontal concealment (β±SE = 0.002 ± 0.001; $r = 0.62$), grass height (β±SE = 0.002 ± 0.000; $r = 0.60$), and vegetation height (β±SE = 0.002 ± 0.000; $r = 0.59$), and transect-scale vegetation height (β±SE = 0.002 ± 0.000; $r = 0.55$). Turbulence intensity was moderately positively correlated with transect-scale vegetation roughness (β±SE = 0.005 ± 0.001; $r = 0.47$). From the set of univariate models assessed with AICc, the plot-scale horizontal concealment model ($\Delta AIC_c = 0.00$, ωi = 0.92) was the only model receiving strong support ($\Delta AIC_c < 2$), providing further evidence that horizontal concealment was the best predictor of turbulence intensity in grasslands. For the analysis of turbulence intensity in shrublands, five variables from the initial candidate variable set were analyzed (Tables 2, 3), and all had weak or no correlation ($r \leq 0.3$) with turbulence intensity, despite three variables receiving apparent strong support in AICc rankings (plot-scale and transect-scale non-vegetated cover and plot-scale horizontal concealment). For the analysis of turbulence intensity in forests, four variables from the initial candidate variable set were analyzed (Tables 2, 3), and of these, turbulence intensity was moderately positively correlated with two: plot-scale grass height (β±SE = 0.002 ± 0.000; $r = 0.42$) and plot-scale forb cover (β±SE = 0.002 ± 0.001; $r = 0.38$). From the set of univariate models assessed with AICc, plot-scale grass height ($\Delta AIC_c = 0.00$, ωi = 0.90) was the only model receiving strong support, further suggesting that grass height was the best predictor of turbulence intensity in forests.

NATURAL EXPERIMENT OF OLFACTORY CONCEALMENT AND PREDATOR DETECTION

For the experimental test of predator scent detection in grasslands, four models received strong support ($\Delta AIC_c < 2$), including two olfactory models (a turbulence intensity model and an additive model with both turbulence intensity and airflow slope), the null model, and one univariate visual model (plot-scale horizontal concealment) (Table 4). Based on the top model—the only model ranking above the null model—turbulence intensity was positively related to egg success ($\beta \pm SE = 10.826 \pm 6.700$). For the scent detection experiment in shrubland, two models received strong support ($\Delta AIC_c < 2$), including the null model and a univariate visual model (plot-scale overhead concealment). The top model was the null model, indicating that the cover variables measured were poor predictors of egg success. For the scent detection experiment in forest, four models received strong support ($\Delta AIC_c < 2$), including two univariate visual models (plot-scale horizontal concealment and overhead concealment), the null model and a bivariate visual model (horizontal concealment + overhead concealment). Based on the top two models—the only models ranking above the null model—egg success was positively related to horizontal concealment ($\beta = 0.042 \pm 0.022$) and overhead concealment ($\beta = 0.070 \pm 0.043$).

Discussion

This study was the first to quantify and document correlates of airflow variables associated with olfactory concealment across multiple spatial scales. I found that turbulence intensity and airflow slope vary with vegetation features, both across major vegetation cover types and in relation to small-scale vegetation characteristics (e.g., vegetation height, percent cover, and visual concealment). I also provide experimental evidence indicating that turbulence intensity influences olfactory concealment and predator detection of prey items within grasslands. My findings provide new insights into animal cover selection by suggesting that prey species could potentially select for and benefit from vegetation features that reduce odorant detectability, a trait that can in turn influence predator detection and prey survival and abundance (Hudson, Dobson & Newborn 1992; Carthey, Bytheway & Banks 2011; Price & Banks 2016). Additionally, because I found strong correlations between olfactory variables and visual features of vegetation, I suggest that apparent habitat selection for visual concealment may in some cases actually reflect selection for olfactory concealment.

COMPARISON OF OLFACTORY CONCEALMENT VARIABLES AMONG VEGETATION COVER TYPES

Shrublands and grasslands were characterized by significantly greater turbulence intensity than forests, and updraft slope was greater in shrublands than grasslands and intermediate in forests. Previous research into airflow dynamics in the boundary layer provides relevant context for these findings. In all cover types, airflow above the vegetation canopy is streamline (i.e. parallel to the ground in a relatively consistent direction) (Raynor 1971; David *et al.* 1982). However, within vegetation canopies (hereafter, the mixing zone), mixing occurs between streamline and slower moving air currents, thus generating high levels of turbulence (Raupach *et al.* 1996). In grasslands and shrublands, this mixing zone occurs close to ground-level (Wilson *et al.* 1982). In the interior of forests, the mixing zone is in the upper canopy, and both the turbulence to velocity ratio and turbulence intensity increase lower in the canopy (Baldacchi & Meyers 1988; Shaw, Den Hartog & Neumann 1988; Amiro 1990) until a point several meters above ground-level is reached, where streamline airflow no longer penetrates, turbulence intensity begins to decrease, and air movement is instead generated by infrequent injections of air from the upper canopy (Raynor 1971; Baldacchi & Meyers 1988; Amiro 1990). The tendency for high-turbulence conditions to occur much higher above the ground in forests than in grasslands and shrublands likely explains why I observed the lowest turbulence intensity readings in forests and airflow slope values near zero.

As opposed to forest interiors, forest edges downwind of grasslands are characterized by highly turbulent airflow (Stacey 1994; Irvine *et al.* 1997) due to the collision of streamline airflow with the abrupt forest edge, which creates an updraft zone extending horizontally into the forest to a distance roughly 10-15 times the height of the forest edge (Stacey 1994; Irvine *et al.* 1997, Lee 2000). In contrast, grasslands downwind of forest edges are characterized by a downdraft zone that extends roughly eight times the height of the forest edge into the grassland (Lee 2000). Shrublands, which are often structurally similar to forest edges should experience updrafts in a zone 10-15 times the height of the tallest vegetation, which can comprise a majority of the shrubland for small patches of this cover type. Thus, for landscapes similar to my study area, in which grasslands, shrublands, and woodlands are interspersed in a mosaic, shrublands and grasslands would be expected to disproportionally experience updrafts and downdrafts, respectively, thus explaining the airflow slope patterns I observed.

RELATIONSHIPS AMONG VEGETATION VARIABLES AND OLFACTORY CONCEALMENT VARIABLES

I documented strong relationships between turbulence intensity and vegetation features in grasslands, but not in shrublands or forests. I hypothesize that this pattern occurred because the near-ground vegetation features I measured in grasslands were directly interacting with streamline airflow. While in shrublands and forests, the interaction with streamline airflow occurred with vegetation further from the airflow sampling point that may not have been measured. I did observe moderate relationships between airflow variables and vegetation features in forests. In forests with open understories (e.g. savannahs and open woodlands), a vertical profile of streamwise-velocity can be bimodal with one peak in the subcanopy near ground level and another above the upper canopy (Conover 2007). In my study, the moderate relationship between turbulence intensity and vegetation in forests may have occurred if some forests had a near-ground mixing zone and others did not. Regardless of the explanation for this pattern, my approach of taking ground-level airflow measurements likely overlooked some of the vegetation features most strongly influencing airflow in shrublands and forests. My study provides further support that airflow patterns in shrublands and forests are primarily influenced by large scale features, such as canopy characteristics and position relative to structural edges (see also Raynor 1971; Baldacchi & Meyers 1988; Amiro 1990; Stacey *et al.* 1994; Conover 2007).

In regards to vegetation features related to turbulence intensity in grasslands, high levels of horizontal concealment (which indirectly represents vegetation density), vegetation height, and vegetation roughness have all been shown to elevate the lower boundary of the mixing zone, and therefore the highest levels of turbulence intensity (Wilson *et al.* 1982; Amiro 1990; Shaw, Den Hartog & Neumann 1988). Because the lower boundary of the mixing zone in grasslands is roughly 3 cm above ground-level (Stull 2006), increasing vegetation density, height, and roughness likely elevated the most turbulent air closer to my sampling height of 25 cm.

OLFACTORY CONCEALMENT AND PREDATOR DETECTION

Turbulence intensity was the best predictor of egg survival in grasslands while visual vegetation features best predicted egg survival in forests and no forms of concealment predicted egg survival in shrublands. This differential importance of olfactory and visual variables could arise if predator foraging strategies are altered by the above-described differences in airflow dynamics among cover types. In grasslands, the preponderance of streamline airflow may facilitate olfactory tracking, and therefore increase the importance of olfactory concealment via turbulence. In the absence of turbulence, odour plumes are linear and predators need only detect an odourant and move upwind to locate the odorant source (David *et al.* 1982). In forests, I observed the lowest levels of turbulence and nearly flat airflow slope, factors which by themselves create ideal conditions for odour plume tracking. However, in most forests, which lack streamline airflow, infrequent injections of air from the upper canopy cause air at ground-level to move unpredictably and in multiple directions, thus tracking odourants upwind may often fail to lead predators to prey items (Elkington *et al.* 1987; Brady, Gibson & Packer 1989; Conover 2007). Likewise, the reduction of streamline airflow and frequent updrafts in shrublands compared to grasslands make odour plumes difficult to track. Olfactory predators in forests and shrublands may therefore be less likely to rely solely on olfaction, and instead, they may employ a dual detection approach combining olfactory and visual cues, with the latter used to pinpoint a prey item once it has been detected via olfaction.

IMPLICATIONS FOR ANIMAL ECOLOGY

My findings revealing variation in factors influencing olfactory concealment at multiple spatial scales, as well as potential survival implications of selecting for olfactory concealment, suggest several testable hypotheses related to animal habitat selection. Because turbulence intensity was related to egg survival in grasslands, I hypothesize that selection of locations with high turbulence intensity in this cover type could increase prey survival rates. My finding of strong relationships between local-scale vegetation features and turbulence intensity in grasslands indicates the possibility that animals could potentially select for olfactory concealment at a local-scale (i.e. 1-12 m). However, empirical evidence for active selection of olfactory concealment in grasslands remains limited. Sharp-tailed grouse (*Tympanuchus phasianellus*) have been shown to select grassland loafing locations with higher updraft and turbulence than random points (Conover & Borgo 2009), but other studies have found little or no support for olfactory habitat selection (Conover *et al.* 2010; Borgo & Conover 2016a, 2016b). I hypothesize that olfactory concealment could be especially important for grassland specialist species because streamline airflow in grasslands is generally favorable for predators to detect prey using odor cues.

My finding that olfactory concealment associated airflow varies by major vegetation type indicates that animals could also select for olfactory concealment at large spatial scales (e.g. patch- or landscape-scale); this would be especially pertinent to species with large home ranges or those that inhabit different vegetation types at different times of the day or year. I hypothesize that, all else being equal, animal selection for the shrubland cover type over grasslands favors olfactory concealment due to the higher airflow slopes and lack of streamline airflow at ground-level in shrublands. While no studies have attributed selection of shrub patches as a strategy to reduce olfactory detection, several studies of birds and mammals have attributed selection of shrub patches as a strategy to reduce predation risk (e.g. Huegel, Dahlgren & Gladfelter 1986; Giesen & Connelly 1993; Althoff, Storm & Dewalle 1997; Hiller 2007). Additionally, temporal studies of habitat use provide compelling evidence that shrubland cover also provides protection from harsh thermal conditions (Carroll *et al.* 2015; Tanner *et al.* 2016).

In forests, my findings that turbulence intensity is relatively low and airflow slopes are near zero indicates that forests would facilitate odour plume tracking; however, based on other studies it appears that odour tracking is often more difficult in forests (Elkington *et al.* 1987; Brady, Gibson & Packer 1989). Elkington *et al.* (1987) found that, in forests, as velocity decreased odour plumes became less linear and harder for gypsy moths (*Lymantria dispar*) to follow to a source, indicating that in forests airflow velocity may play an important role in olfactory concealment. Additionally, the frequency and strength of airflow injections from the forest canopy—which influences the straightness of odour plumes—is dependent on forest canopy characteristics (Stacey *et al.* 1994; Conover 2007). Thus, variation in airflow velocity and the consistency of airflow direction that are driven by canopy characteristics could influence olfactory concealment and possibly be important to forest-inhabiting animals. Further research is needed to understand the complex relationships between airflow dynamics, habitat selection, and olfactory concealment in forests.

Based on my findings, evolutionary theory, and the affect altering prey odour cues has on predator foraging (Hudson, Dobson & Newborn 1992; Conover 2007; Carthey, Bytheway & Banks 2011; Threlfall, Law & Banks 2013; Price & Banks 2016), I suspect that olfactory concealment is an important component of cover to prey and predator species, especially among grassland-inhabiting species. Nonetheless, further research with animals making cover selection decisions and having the potential to reap associated fitness-related benefits is needed to confirm whether animals perceive and actively select for olfactory concealment variables, such as turbulence and updraft. Additionally, because olfactory concealment is correlated with visual vegetation characteristics, and is also likely related to thermal cover (Hovick *et al.* 2014; Carroll *et al.* 2016), further research is required to disentangle how these different dimensions are interpreted during cover selection and how they independently and interactively convey fitness-related benefits. For example, animals could: (1) randomly occupy areas with olfactory concealment and receive fitness related benefits, (2) both directly select for and receive the benefit of olfactory concealment, (3) select visual or thermal cues such as grass height and/or temperature but instead receive a survival benefit due to the olfactory concealment that tall, cool vegetation provides, or (4) follow the selection strategies in either (1), (2) or (3) and receive a fitness benefit as a result of more than one concealment mechanisms. My egg survival experiment provides compelling evidence that, in cases where olfactory predators dominate, olfactory concealment could have a greater influence on survival than visual concealment. However, different patterns would likely arise when predator communities are dominated by visual predators or comprised of an equal mix of visual and olfactory predators (Perkins *et al.* 2014; Conover *et al.* 2010).

CONCLUSIONS

Here, I have provided a first approximation of an olfactory landscape across which prey species could potentially select cover to reduce the odour cues available to olfactory predators. I also provide experimental evidence suggesting that turbulence intensity, an airflow variable related to olfactory concealment, can influence prey survival and predator foraging success, factors that could have major implications for populations of predator and prey species and predator-prey interactions. I have illustrated strong relationships between olfactory and visual concealment variables, which suggests that apparent selection for visual concealment may in some cases actually reflect selection for olfactory concealment—a more ecologically relevant habitat feature for prey species depredated by olfactory predators. This finding has important implications for the interpretation of habitat selection studies, especially since these studies are often used to interpret species life histories and cover needs. Although I provide strong evidence for variation in olfactory habitat features, as well as potential survival benefits associated with increased olfactory concealment, further research is required to determine the degree to which animals actively select for olfactory concealment and receive its potential fitness-related benefits. Future research into olfactory habitat selection will have important implications for management of habitat and interpretation of animal behaviors, life histories, and individual, population, and community-level responses to anthropogenic disturbances.

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Tables and Figures

Table 1. Candidate variable set of plot scale and transect scale vegetation variables measured in 2015 and 2016 at randomly selected points on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

Predictor	Unit	Scale	Description
Grass height	cm	1 m^2	Measured from plot centered at sampling point
Vegetation height	cm	1 m^2	Measured from plot centered at sampling point
Transect height	cm	16 m	Average of maximum vegetation heights taken along transect
Vegetation roughness	cm	16 m	Standard deviation of maximum vegetation heights taken along transect
Transect non-vegetated	Percent	16 m	Average litter and bare cover along transect
Transect grass cover	Percent	16 m	Average grass cover along transect
Transect forb cover	Percent	16 m	Average forb cover along transect
Transect shrub cover	Percent	16 m	Average shrub cover along transect
Plot-scale non-vegetated	Percent	1 m^2	Litter and bare cover within plot centered at sampling point
Plot-scale grass cover	Percent	1 m^2	Grass cover within plot centered at sampling point
Plot-scale forb cover	Percent	1 m^2	Forb cover within plot centered at sampling point
Plot-scale shrub cover	Percent	1 m^2	Shrub cover within plot centered at sampling point
Horizontal concealment	Percent	4 m	Average of cover pole readings
Overhead concealment	Angle (0-90°)	Sample point	Average of angle of obstruction readings

Table 2. Model selection results for all univariate models evaluated in grassland, shrubland and forest cover types for the analysis of vegetation variables related to turbulence intensity on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA (2015–2016).

Top variables	K[a]	ΔAIC_c[b]	ωi[c]
Grassland			
Horizontal concealment	4	0.0	0.92
Grass height	4	5.82	0.05
Vegetation height	4	7.48	0.02
Transect height	4	12.07	0.00
Vegetation roughness	4	15.32	0.00
Transect non-vegetated	4	26.17	0.00
Null	3	27.48	0.00
Plot-scale non-vegetated	4	27.57	0.00
Shrubland			
Transect non-vegetated	4	0.00	0.33
Plot-scale non-vegetated	4	0.49	0.26
Horizontal concealment	4	1.05	0.20
Vegetation roughness	4	2.64	0.09
Plot-scale grass	4	3.39	0.06
Null	3	3.48	0.06
Forest			
Grass height	4	0.00	0.90
Plot-scale forb	4	5.06	0.07
Null	3	8.19	0.01
Horizontal concealment	4	9.24	0.01
Vegetation roughness	4	10.50	0.00

[a] Number of parameters in the model

[b] Difference in AIC_c value between model and the most strongly supported model

[c] AIC_c Weight - relative strength of support for model

Table 3. β ± SE estimates from univariate LMMs and Pearson's correlation coefficient (*r*) for all vegetation variables assessed in the analysis of vegetation variables related to turbulence intensity in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

Predictor	β ± SE	*r*
Grassland		
Horizontal concealment	0.002 ± 0.001	0.62
Grass height	0.002 ± 0.000	0.60
Vegetation height	0.002 ± 0.000	0.59
Transect height	0.002± 0.000	0.55
Roughness	0.005 ± 0.001	0.47
Transect non-vegetated	-0.002 ± 0.001	-0.25
Plot non-vegetated	-0.001 ± 0.001	-0.24
Shrubland		
Transect non-vegetated	-0.002 ± 0.001	-0.28
Plot-scale non-vegetated	-0.001 ± 0.001	-0.27
Horizontal concealment	0.002 ± 0.001	0.27
Vegetation roughness	-0.002 ± 0.001	-0.17
Plot-scale grass	0.001 ± 0.001	0.15
Forest		
Grass height	0.002 ± 0.000	0.42
Plot-scale forb	0.002 ± 0.001	0.38
Horizontal concealment	0.001 ± 0.001	0.16
Vegetation roughness	-0.000 ± 0.001	-0.03

Table 4. Model selection results for grassland, shrubland and forest cover types for the analysis relating olfactory and visual concealment to detection of a simulated prey item on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA (2015–2016).

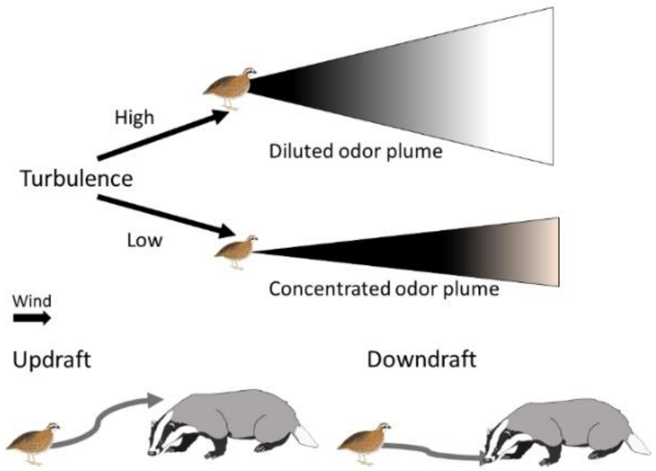
Model	K	ΔAIC_c	ωi
Grassland			
Turbulence intensity	3	0.00	0.29
Null	2	0.58	0.22
Horizontal concealment	3	1.11	0.17
Turbulence intensity + airflow slope	4	1.73	0.12
Overhead concealment	3	2.50	0.08
Airflow slope	3	2.80	0.07
Horizontal concealment + overhead concealment	4	3.70	0.05
Shrubland			
Null	2	0.00	0.39
Airflow slope	3	1.87	0.15
Horizontal concealment	3	2.30	0.12
Overhead concealment	3	2.33	0.12
Turbulence intensity	3	2.35	0.12
Turbulence intensity + airflow slope	4	4.10	0.05
Horizontal concealment + overhead concealment	4	4.89	0.03
Forest			
Horizontal concealment	3	0.00	0.34
Overhead concealment	3	0.13	0.31
Null	2	1.80	0.14
Horizontal concealment + overhead concealment	4	1.94	0.13
Airflow slope	3	4.30	0.04
Turbulence intensity	3	4.32	0.04
Turbulence intensity + airflow slope	4	7.02	0.01

[a] Number of parameters in the model

[b] Difference in AIC_c value between model and the most strongly supported model

[c] AIC_c Weight - relative strength of support for model

Figure 1. Conceptual diagram of relationships between turbulence intensity and airflow slope and olfactory concealment (Northern Bobwhite (*Colinus virginianus*) clip art from Clipart Kid (2016); American badger (*Taxidea taxus*) clip art from WorldArtsMe (2015)).



Clipart Kid. (2016) Flying quail clip art. [Clip art]. *Retrieved from* http://www.clipartkid.com/.

WorldArtsMe. (2015) Badger cartoon clip art. [Clip art]. *Retrieved from* http://worldartsme.com/.

Figure 2. Location of the study area on the McFarlin-Ingersoll ranch located in Inola, Oklahoma, USA.

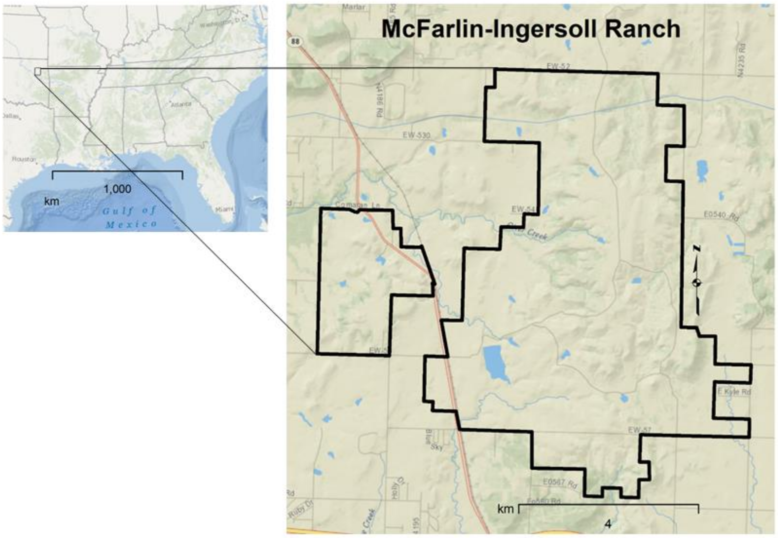
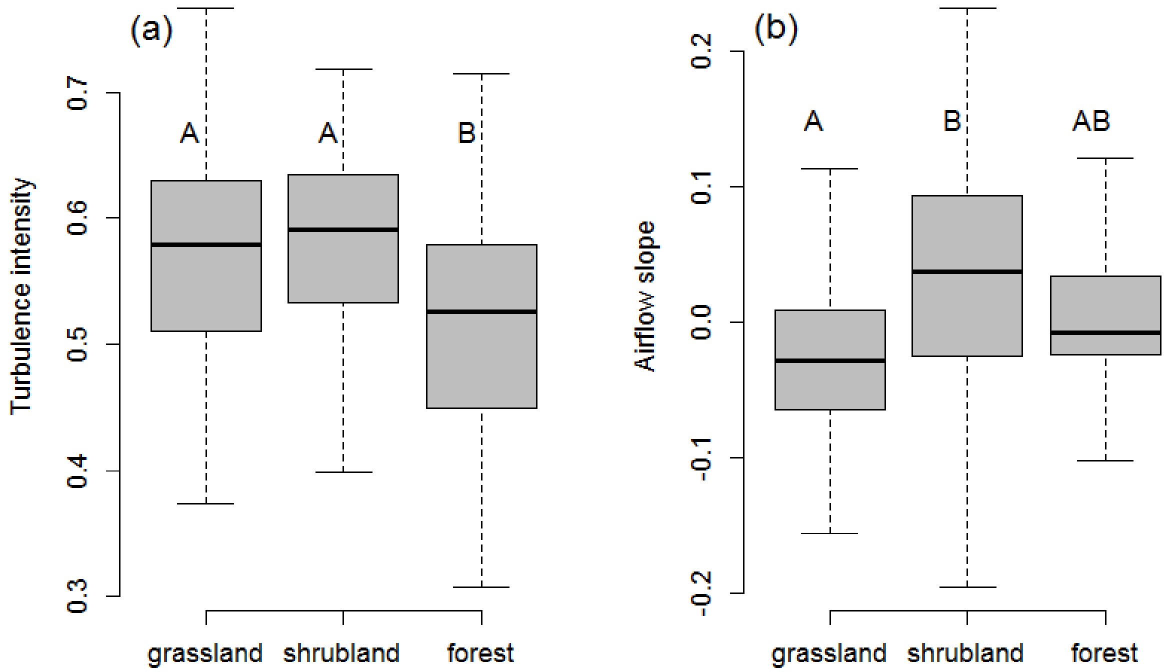


Figure 3. Mean and quartiles for (a) turbulence intensity and (b) airflow slope in grassland, shrubland, and forest cover types measured in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA. Letters indicate significant differences between vegetation cover types based on the results of a *post hoc* Tukey (HSD) test.



Appendix

Appendix S1. Original land cover classification based on Oklahoma ecological systems classification, total area (ha), and reclassification of land cover on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

Ecological systems classification	Area	Reclassification
Osage Plains: tallgrass/prairie/pasture	2901.85	Grassland
Crosstimbers: pasture/prairie	2.46	Grassland
Ruderal deciduous shrubland and young woodland	359.71	Shrubland
Ruderal deciduous woodland	526.05	Shrubland
Ruderal eastern red cedar woodland and shrubland	0.18	Shrubland
South Central Interior: riparian shrubland and young woodland	70	Shrubland
Crosstimbers: post oak – blackjack oak slope forest	0.23	Forest
Crosstimbers: post oak forest	496.24	Forest
South Central Interior: bottomland hardwood forest	0.4	Forest
South Central Interior: riparian hardwood woodland	198.97	Forest
Eastern Great Plains: herbaceous wetland	3.02	Non-use
Open water	61.11	Non-use
Row crops	41.93	Non-use
South Central Interior: riparian herbaceous wetland	6.38	Non-use
Barren	1.5	Non-use
Urban low intensity	22.92	Non-use

Appendix S2. β and SE estimates, and 95% confidence intervals for analysis of vegetative cover type influence on turbulence intensity and airflow slope in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

Response	Cover type	β ± SE	95% CI
Turbulence intensity	Grassland	0.569 ± 0.018	0.504 – 0.633
	Shrubland	0.575 ± 0.019	0.508 – 0.642
	Forest	0.514 ± 0.015	0.485 – 0.543
Airflow slope	Grassland	-0.020 ± 0.015	-0.072 – 0.032
	Shrubland	0.023 ± 0.016	-0.031 – 0.076
	Forest	0.000 ± 0.012	-0.023 – 0.023

Figure S1. Turbulence intensity (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within grassland cover in 2015 and 2016 on the on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

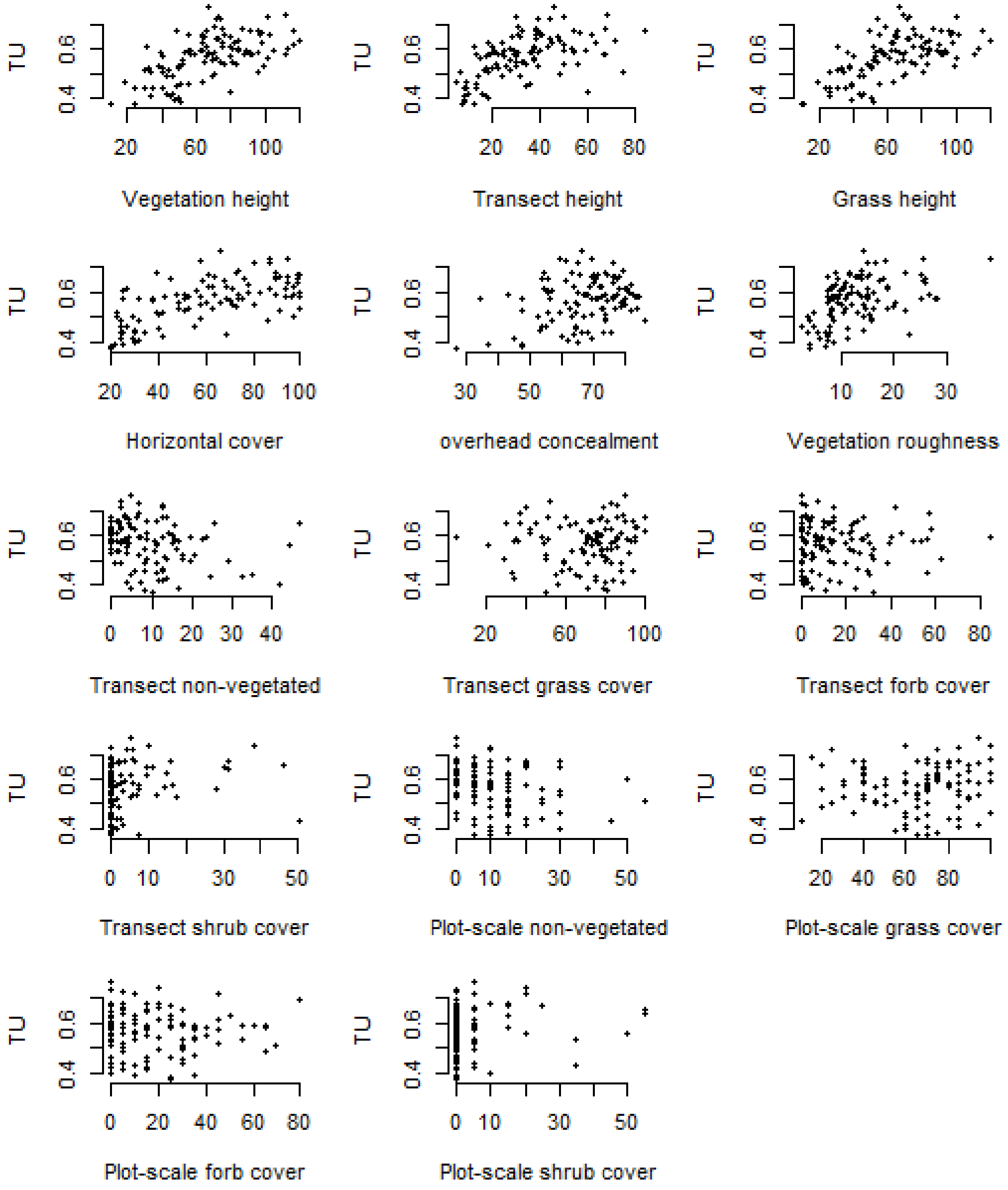


Figure S2. Turbulence intensity (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within shrubland cover in 2015 and 2016 on the on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

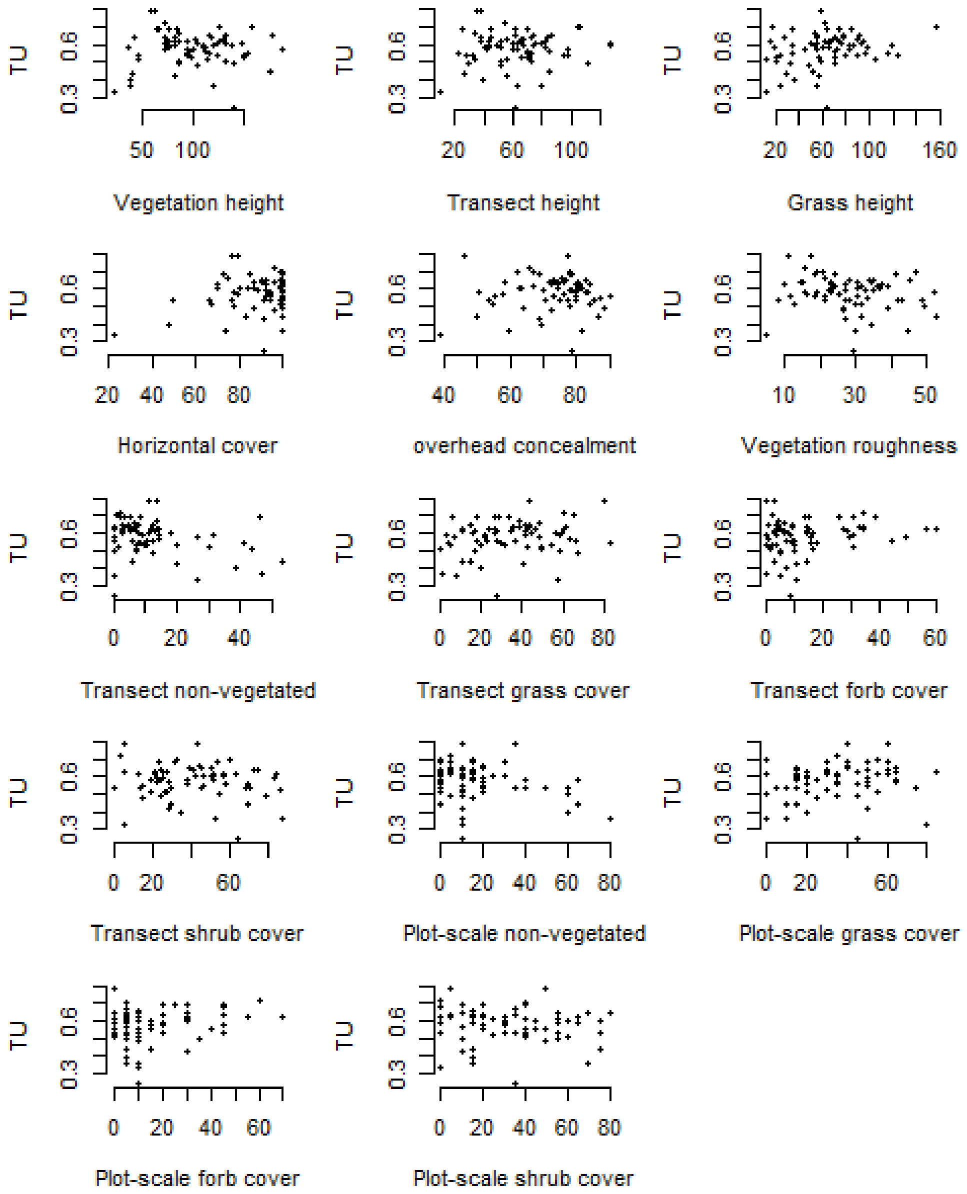


Figure S3. Turbulence intensity (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within forest cover in 2015 and 2016 on the on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

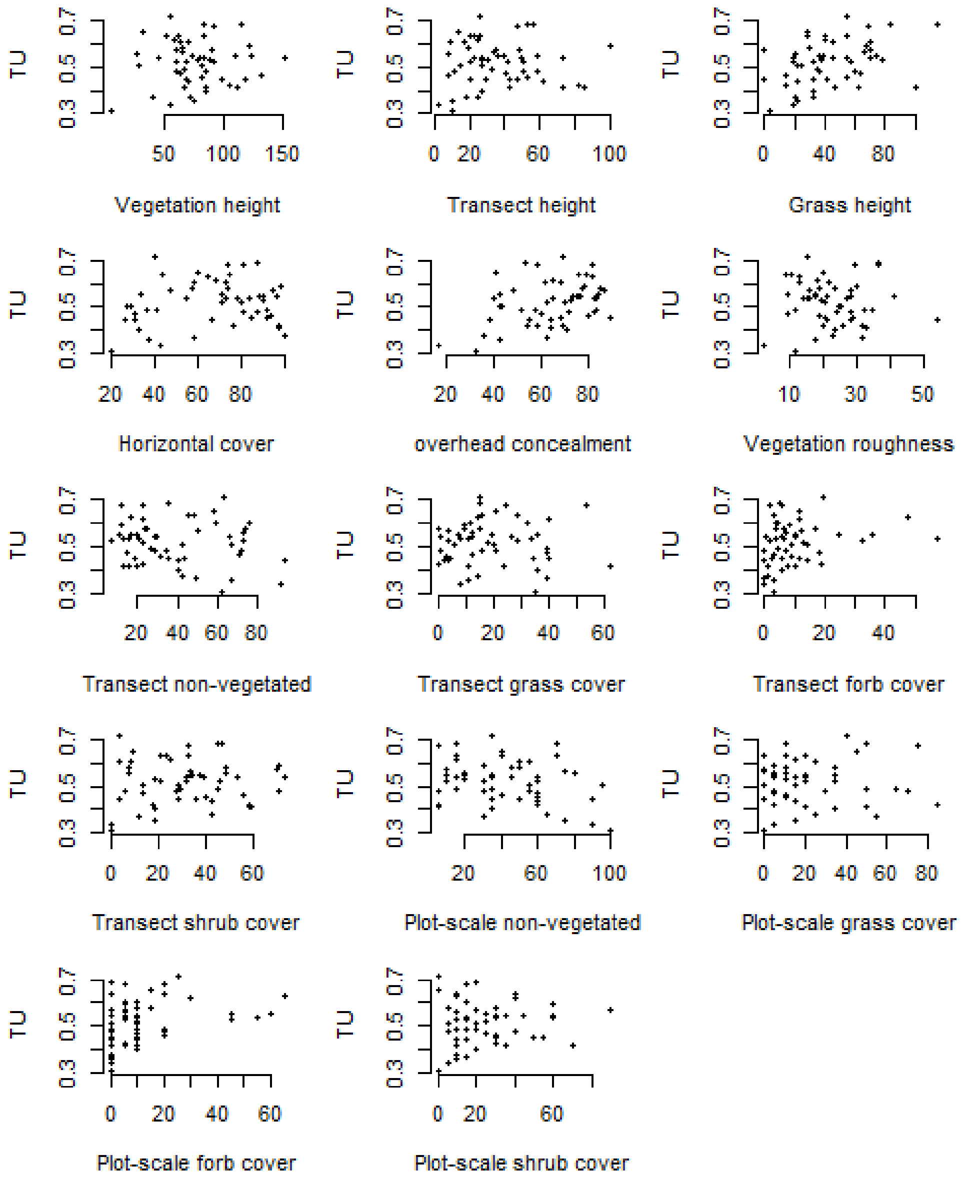


Figure S4. Airflow slope (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within grassland cover in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

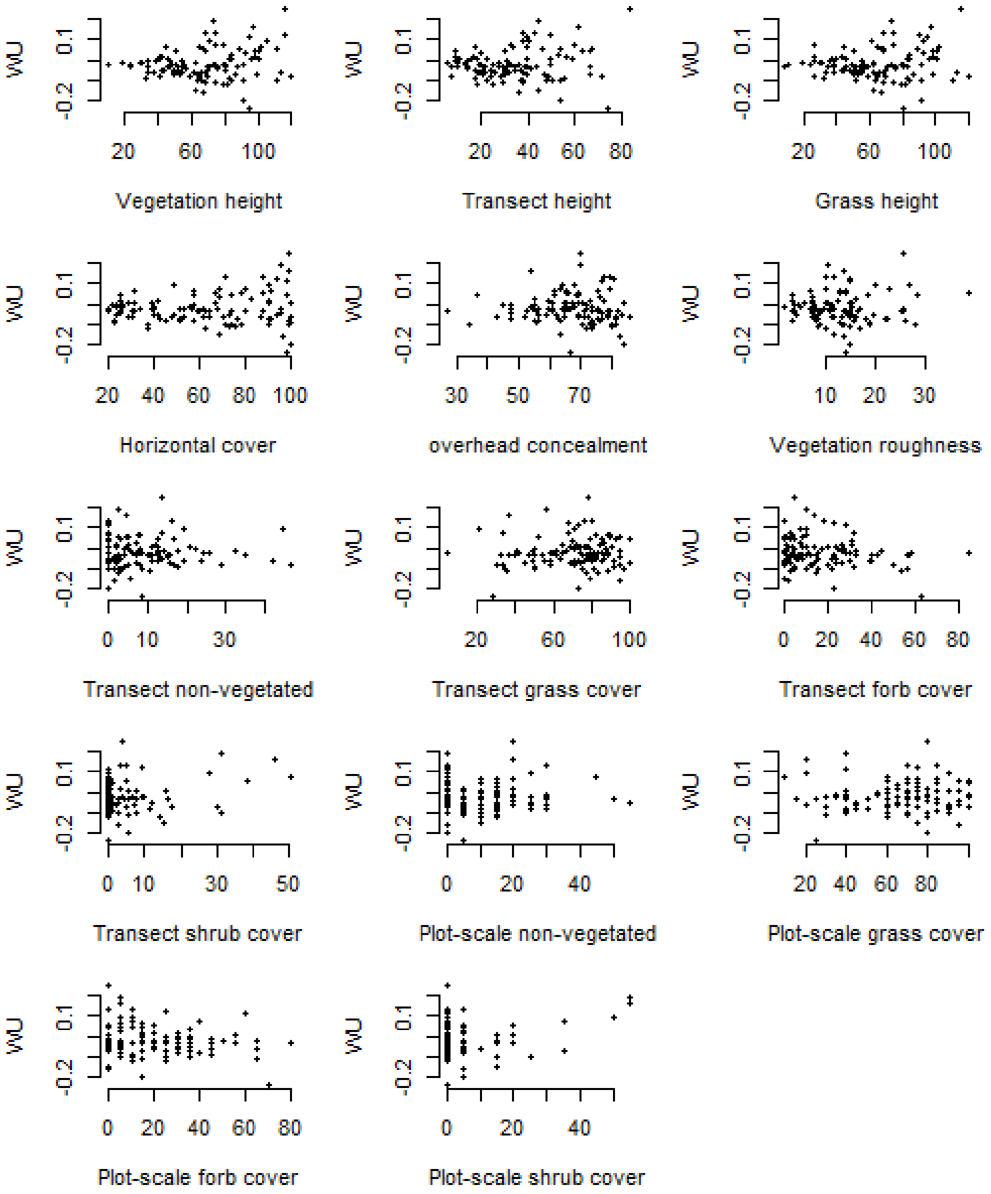


Figure S5. Airflow slope (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within shrubland cover in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

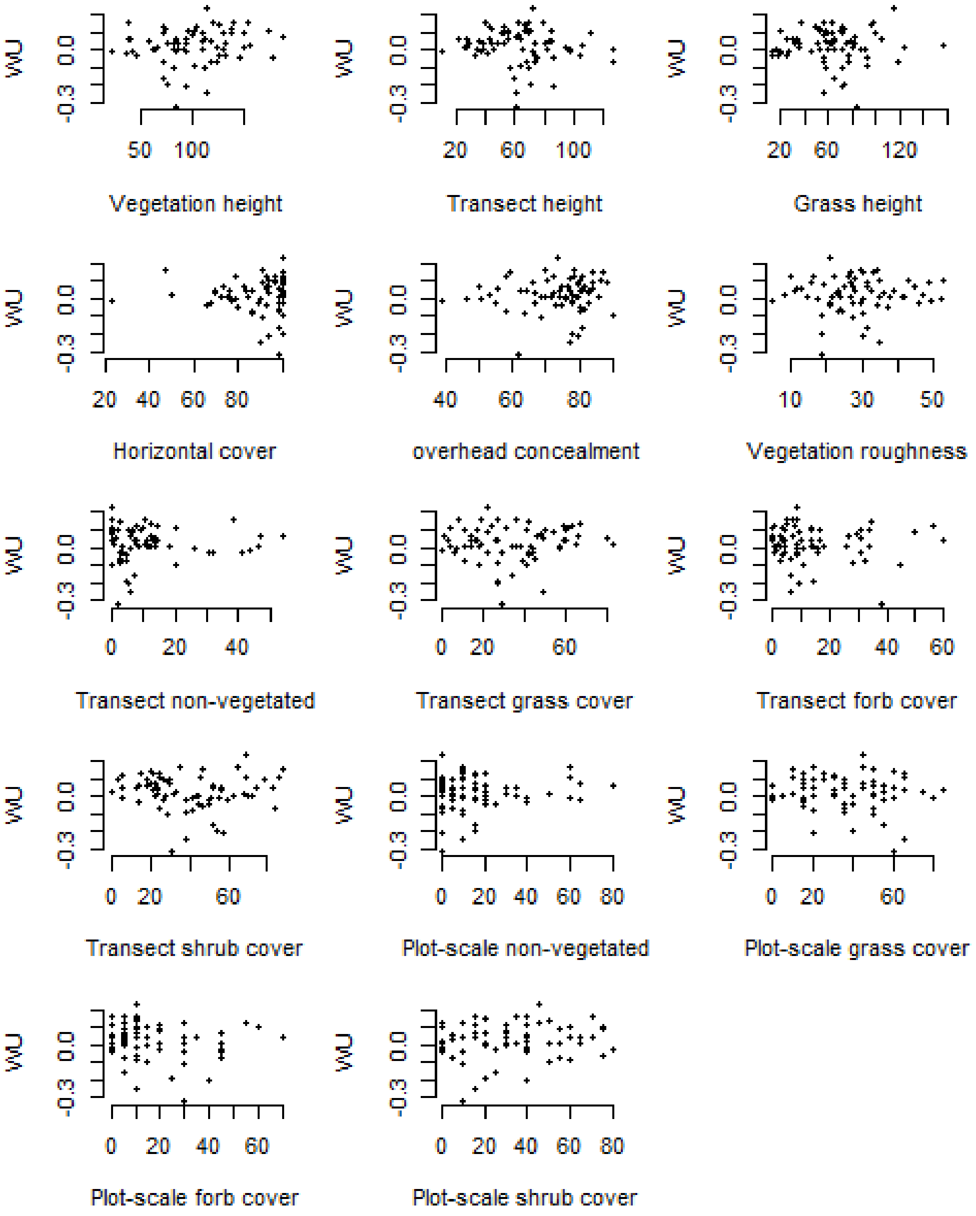
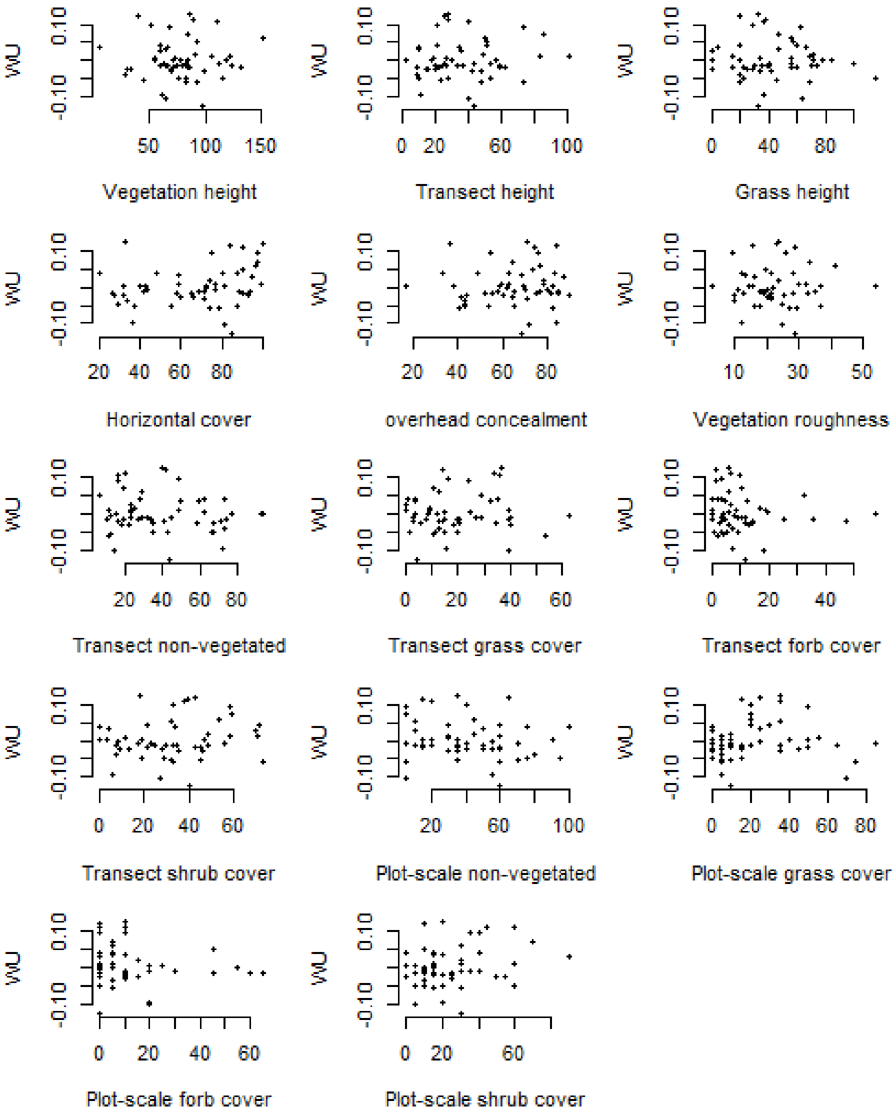


Figure S6. Airflow slope (y-axis) plotted against each vegetation predictor variable (x-axis) from points sampled within forest cover in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.



CHAPTER II

INFLUENCE OF OLFACTORY AND VISUAL CONCEALMENT AND WEATHERVARIABLES ON AVIAN NEST SITE SELECTION AND SUCCESS

Introduction

Animal habitat selection has major implications for survival, reproductive success, life-time fitness, and population-level processes, and habitat selection patterns are strongly influenced by environmental constraints and predator-prey interactions (Lima & Dill 1990; Martin 2001; Caro 2005). For birds, nest site selection is a key component of habitat selection influencing nest survival and reproductive output (Martin & Roper 1988; Martin 1993; Davis 2005). Birds invest substantial time and energy in selecting and defending nest locations because eggs and nestlings are highly sought after by many predator species. A substantial body of basic and applied ecology research has addressed nest site selection and nest success and predation because these processes have profound implications for predator and prey behaviour, life history evolution, and population management (Martin 1992, 1993; Clark & Shutler 1999).

Predators locate prey items, including nests, based on learned suites of sensory-based cues (i.e. search images; Nams 1991; Santisteban, Sieving & Avery 2002; Carthey, Bytheway & Banks 2011). These cues can be visual, thermal, aural, and/or olfactory, and evolutionary theory predicts that prey species should select habitat that minimizes the sensory cues used by dominant predator species (Van Valen 1973). Nest predator communities are often dominated by species that forage using olfactory cues (hereafter, olfactory predators; Burghardt 1966; Nams 1997; Slotnick 2001; Hughes, Price & Banks 2010; Threlfall, Law & Banks 2013). Therefore, nest site selection that increases olfactory concealment should increase nest survival, and potentially, enhance reproductive success and lifetime fitness. Despite the preponderance of olfactory predators, nearly all research into predation and habitat selection, including for avian nest site selection, has focused only on how habitat visually conceals prey.

Studies have begun to address how olfactory cues influence animal interactions, including predation. Alteration of prey odour cues can change predator behaviour and foraging success (Carthey, Bytheway & Banks 2011; Threlfall, Law & Banks 2013; Price & Banks 2016), which can have population-level implications. For example, red grouse (*Lagopus lagopus scotica*) with high parasite loads produce more odourants and experience higher depredation rates than lightly parasitized individuals, and this differential predation contributes to population stability for this species (Hudson, Dobson & Newborn 1992). Additionally, weather-related variables (e.g., wind speed and moisture) can influence detectability of prey odourants (Ruzicka & Conover 2011, 2012; Borgo & Conover 2015) and avian nest survival rates (Moynahan *et al.* 2007; Lehman *et al.* 2008; Webb *et al.* 2012). Nonetheless, few studies have systematically assessed the relative role of olfactory and visual habitat variables in influencing habitat selection decisions and the influence of those decisions on survival and reproductive output.

Olfactory concealment theory predicts that airflow patterns strongly influence the ability of predators to detect airborne odour cues (Conover 2007). Specifically, odour plumes generated by streamline airflow are linear and remain highly concentrated and easy to detect across long distances, whereas highly turbulent airflow (i.e. with variable direction and speed) creates broad, irregular, and rapidly diffusing odour plumes that are difficult to detect and track (Conover 2007). Additionally, updrafts elevate odour plumes above the detection height of ground-based predators, thus reducing the ground area over which odour plumes are detectable compared to plumes carried by parallel and downward-drafting airflow (Conover 2007). Turbulence and updraft are both influenced by surface features (e.g. topography, vegetation canopies, shelterbelts) (Stull 2006; Chapter 1) and are potentially selected for by prey species (Conover 2007). However, evidence is lacking for whether these airflow characteristics are incorporated into habitat selection decisions and influence survival and reproduction. The few studies addressing selection for olfactory concealment at avian nest sites have found selection for high levels of visual concealment (Conover *et al.* 2010; Borgo & Conover 2016*b*), and in one of these studies, lower turbulence was associated with successful nests, an unexpected finding (Borgo & Conover 2016*b*).

I examined the role of olfactory concealment in nest-site selection and nest success of grassland-nesting birds—a guild of conservation concern due the dramatic loss of grassland habitat and associated population declines of many bird species in North America (Hoekstra *et al.* 2005; Sauer *et al.* 2014; North American Bird Conservation Initiative 2016). My specific objectives were to: (1) assess whether birds select nest sites based on visual concealment and/or airflow characteristics that influence olfactory concealment and (2) assess the relative importance of visual concealment, as well as airflow and weather conditions associated with olfactory concealment, for influencing rates of nest survival. I hypothesize that in grasslands, birds select nest locations for both visual and olfactory concealment because of the dominance of olfactory predators and the many studies that have documented selection for visual concealment (e.g. Martin 1992; Weidinger 2002; Latif, Heath & Rotenberry 2012). In addition, I hypothesize that nest predation rate will be best predicted by factors influencing detection of prey odours (e.g. turbulence, updrafts, humidity and/or wind speed) because previous research indicates that olfactory predators are generally the most common species to depredate grassland bird nests (Pietz & Granfors 2000; Renfrew & Ribic 2003; Staller *et al.* 2005).

Materials and Methods

STUDY SYSTEM

I searched for and monitored nests of Northern Bobwhite (hereafter bobwhite) (*Colinus virginianus*) between May and August of 2015 and 2016; between May and July of 2016, I also searched for and monitored nests of Eastern Meadowlark (hereafter meadowlark) (*Sturnella magna*) and Grasshopper Sparrow (*Ammodramus savannarum*). All of these grassland-nesting species construct structurally similar dome-shaped nests made of dead grasses and forbs and placed in or near tussocks of bunchgrasses. Previous research indicates that the nest predator community for each species is dominated by olfactory predators (Pietz & granfors 2000; Renfrew & Ribic 2003; Staller *et al.* 2005), such as those in my study area listed below.

The study area was located on the 4,692-ha McFarlin-Ingersoll ranch, 45 km east of Tulsa, Oklahoma, USA (230 m elevation) (Fig. 1). Located within the central irregular plains ecoregion, the study area consists largely of tallgrass prairie pasture (~62% of area), with patches of forest (~15%) and shrubland (~20%) occurring near creeks and draws, on hillsides, and in low elevation areas. During the 2015 and 2016 nest monitoring periods, average daily temperature was 24°C and average daily maximum temperature was 30°C. Precipitation occurred on 45 of 123 days in 2015 (70 total cm) and 29 of 93 days in 2016 (31 total cm). Average daily dew point and relative humidity were 19°C and 77%, respectively (Brock *et al.* 1995; McPherson *et al.* 2007).

The primary land use is cow-calf domestic cattle (*Bos tauras*) production, and during the 2015–2016 study period, there was an average stocking rate of 3.1 hectares per animal unit (ha/AU). Common grassland vegetation included little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and big bluestem (*Andropogon gerardi*); common forbs included southern ragweed (*Ambrosia bidentate*), western ragweed (*Ambrosia psilostachya*), common yarrow (*Achillea millefolium*), and antelope-horn milkweed (*Asclepias viridis*). Frequently observed olfactory predators included coyote (*Canis latrans*), Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), northern raccoon (*Procyon lotor*), nine-banded armadillo (*Dasypus novemcinctus*), eastern wood rat (*Neotoma floridana*), and several snake species. Independent of the objectives of my study, supplemental feeding— intended for bobwhite and white-tailed deer (*Odocoileus virginianus*)—occurred throughout the year; twelve self-dispensing corn-grain (*Zea mays*) feeders and 30 self-dispensing sorghum-grain (*Sorghum bicolor*) feeders were spaced throughout the study area. All corn-grain feeders were >1 km from monitored nests; however, sorghum-grain feeders were commonly <0.5 km from nests. The study area is also used annually from October to April for occasional competition bird-dog trials during which roughly 1200 captive-reared bobwhite are released. To distinguish these captive-reared birds from wild-hatched bobwhite, leg bands with unique numeric codes were attached to all released bobwhite in 2015 and 2016. However, some wild bobwhite presumably bred with captive-raised birds prior to the onset of my study (DeVos & Speake 1995); therefore, an unknown proportion of the bobwhite nests I monitored may have represented birds with a mix of wild and captive-reared provenance.

DATA COLLECTION

Nest location and monitoring

Between 1 February and 15 July 2015 and 2016, I captured bobwhite with funnel traps, and to all wild (i.e. unbanded) birds, I attached a leg band and 6 g VHF radio-collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). I monitored bobwhite for nesting activity with radio-telemetry on a daily basis between April and July; all bobwhite nests were found by searching areas where bobwhite were repeatedly observed at the same location. To locate meadowlark and grasshopper sparrow nests in 2016, I selected grassland areas with appropriate vegetation structure for these species (Fisher & Davis 2010; Hovick *et al.* 2015), and 2-3 observers simultaneously walked parallel ~250 m transects spaced 1 m apart from 0800 – 1200. When birds were flushed, I visually searched the general area for a nest. All nest locations were marked with a handheld GPS unit, and nests were monitored every 1–3 days until completion. Nests were considered successful if ≥ 1 nestling fledged and failed if no nestlings fledged. I confirmed nests as successful by checking the nest on or after the estimated fledging date and observing fledglings or parental agitation and/or defense behaviours near the nest. All animal capture and handling procedures were approved by The Institutional Animal Care and Use Committee at Oklahoma State University (IACUC; Protocol No. AG-14-25).

Collection of habitat variables influencing olfactory and visual concealment

Measurement of all habitat variables was conducted at nest sites and random points between 1000 and 1700 from 16 April to 21 August 2015 and 2016 on days when ambient wind speeds were between 7–24 km/hour. This range of wind speeds is representative of average conditions experienced in the study area and contains the range of wind speeds thought to correspond to favorable conditions for olfactory detection (Brock *et al.* 1995; McPherson *et al.* 2007; Ruzicka & Conover 2011). To avoid disturbing active nests, I measured habitat at all nests immediately after completion, and random points were measured throughout the nesting season. Random points were selected under a stratified random sampling scheme also used for a complementary study of multi-scale variation in olfactory concealment variables (Chapter 1). In that study, clusters of 3 points each were randomly located in grassland, shrubland, and forest cover types; however, for the current study I only used the grassland points (110 total points from 40 clusters). Points within clusters were ≥50 m apart and clusters were ≥ 100 m apart.

To characterize olfactory concealment at all nest sites and random points, I used a sonic anemometer (CSAT3, Campbell Scientific, Utah, USA) to measure airflow velocity in three dimensions, with measurements taken every second for 30 minutes at a height of 25 cm above ground. All metrics used for analysis were based on averaging all readings over the entire 30 minute period. I used a camera tripod to mount and level the anemometer, and to prevent the structure of the anemometer and tripod from influencing measurements, I faced the anemometer into the direction of the wind. Airflow measurements corresponded to a u,v,w coordinate system where the u-axis was parallel to a horizontal plane aligned with the direction of the wind, the v-axis was parallel to a horizontal plane and perpendicular to the u-axis, and the w-axis was vertical. For each point, velocity (U) was calculated as the square root of $u^2 + v^2$. Turbulence (T) was calculated as the standard deviation of U; however, because T is positively correlated to U, I used turbulence intensity (TU; calculated as T/U) in my analyses. TU is a measure of airflow variability per unit area and is therefore an ecologically meaningful metric to characterize how odour plumes disperse over space (Conover 2007). To characterize the tendency for air to rise or fall relative to distance from an odour source, I first calculated average velocity on the w-axis (W), and then divided by U to calculate airflow slope (WU). Airflow slope provides an index for the horizontal distance over which an odour plume remains within a range of height detectable to ground-based predators. This variable is therefore more ecologically meaningful than strength or frequency of updraft (or downdraft).

At each point I also quantified visual concealment variables, including grass height, horizontal concealment and overhead concealment. Grass height can be an important habitat feature selected for by birds and has previously been related to visual, olfactory and thermal aspects of habitat selection and concealment (Conover 2007, Hovick et al. 2014; Chapter 1). Grass height was recorded at the tallest blade/stem of grass in a 1 m^2 plot centered at the sample point. To measure horizontal concealment, I visually estimated percent visual obstruction starting at ground level in 20% increments (e.g., 0-20%, 21-40%, etc.) for each of four 10 cm-tall segments on a 2.5 cm-width cover pole (similar to Griffith and Youtie 1988). Observations were taken from a height of 1 m and a horizontal distance of 4 m in each cardinal direction, and all obstruction estimates for each point were averaged to generate an index of horizontal concealment within 40 cm of ground-level. To measure overhead concealment, I used the angle of obstruction method (AOB) (Kopp *et al.* 1988). For AOB, a pole and digital level are used to record the angle in the vertical plane (0–90°, starting at 90° straight above the point) at which a direct line of sight from 1.5 m to ground level is first obstructed (90° indicates complete obstruction). This measurement was repeated at each cardinal and sub-cardinal direction ($n = 8$) and averaged to provide an index of concealment from above, a measurement relevant to microclimate (i.e. overhead concealment relates to shade) and detection by avian predators (Kopp *et al.* 1988; Carroll *et al*. 2016).

Collection of weather variables influencing olfactory concealment

For each day that habitat measurement was conducted, weather data were accessed from the Oklahoma Mesonet database for a weather station in Inola, Oklahoma, 7.5 km southeast of the study area (Brock *et al.* 1995; McPherson *et al.* 2007). Variables compiled included several measurements of moisture: soil moisture for the top 5 cm (hereafter soil moisture), percent relative air humidity (hereafter humidity), and daily precipitation (hereafter precipitation)—which was also used to create a variable reflecting a 1-day lag effect of precipitation (i.e. amount of precipitation the previous day; hereafter previous day precipitation). Increased moisture has been shown to increase nest predation rates due to birds emitting more odourants and thus increasing odour cues available to predators (Conover 2007; Lehman *et al.* 2008; Ruzicka & Conover 2012). Further, some studies have shown a lag effect of precipitation one day after a rain event (Moynahan *et al.* 2007; Webb *et al.* 2012). In addition to moisture variables, I also extracted a single wind speed variable: wind speed at 2 m above ground-level. Wind disperses odour plumes, and the rate of odour dispersal has been shown to influence predation rates (Ruzicka & Conover 2012; Webb *et al.* 2012). I tested whether the above variables were related to nest success (see following sub-section); when the time between nest monitoring visits (hereafter exposure period) was >1 day, I averaged all weather variables over the exposure period.

STATISTICAL ANALYSES

Across both years, I found 32 bobwhite nests, and in 2016 I found 11 grasshopper sparrow and 14 meadowlark nests (57 total nests). Of these, I only measured habitat characteristics at 50 nests (26 bobwhite, 13 meadowlark, and 11 grasshopper sparrow nests) because the vegetative structure at the remaining 7 nests was severely altered by livestock. For the nest survival analysis, I also removed nests that did not survive through at least one exposure period, a requirement of the logistic exposure modeling approach (Shaffer 2004), and I also removed abandoned nests because they were not relevant to an evaluation of nest predation. After implementing these steps, 44 nests remained for the nest survival analysis (21 bobwhite, 12 meadowlark, and 11 grasshopper sparrow nests). For both nest site selection and nest survival analyses, all nests were pooled due to sample size constraints and to allow general assessment of the role of olfaction in the nesting ecology of ground-nesting birds in grasslands.

All analyses were conducted in R Version 3.2.2 (R Core Team 2015). To assess whether birds select nest sites for olfactory and/or visual concealment, I compared habitat variables between nest sites (*n* = 50) and random sites (*n* = 110) using linear mixed models (LMMs; lmer function in package lme4) with species as a random-effect (variable slope only) to account for similarities within species. For each habitat variable—including grass height, overhead concealment, horizontal concealment, turbulence intensity, and airflow slope—I defined a model with the habitat variable as the response variable and point type (nest or random un-used) as a fixed-effect. I assessed significance of habitat variables by using a likelihood ratio test comparing each above model to a null model (significance determined at $\alpha = 0.05$).

To assess the relative importance of visual concealment, as well as airflow and weather conditions associated with olfactory concealment in predicting daily nest survival probability, I used generalized linear mixed models (GLMMs; glmer function in package lme4) with a binomial error distribution and the logistic exposure link function (Shaffer 2004). This nest survival modeling approach accommodates temporally varying predictor variables (e.g. precipitation and wind speed), and the link function takes into account the length of the exposure period when calculating daily survival probabilities. For each category of potential predictor variables—visual concealment, olfactory concealment and weather—I created candidate models of univariate and additive models based on the above-described support from the literature. All models were compared, along with a null model, using Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002). Assessment of model support was based on ΔAIC_c values (ΔAIC_c values 0 – 2 indicating strong relative support), AIC_c weights, and model support relative to the null model.

Results

NEST SITE SELECTION

Likelihood ratio tests relative to the null model indicated that turbulence intensity, airflow slope, horizontal concealment, and grass height were not significantly different between nest sites and random points ($\chi^2 \leq 2.66$, df = 1, $p \geq 0.10$); however, the difference in turbulence intensity was nearly significant ($p = 0.10$), with turbulence intensity marginally greater at nest sites (see Fig. 1a and Appendix S1). Overhead concealment ($\chi^2 = 9.13$, df = 1, $p < 0.01$) was significantly greater at nest sites (β±SE = 77.26 ± 1.45) compared to random sites (β±SE = 67.00 ± 1.79).

DAILY NEST SURVIVAL MODELING

A total of 44 nests (21 bobwhite, 12 meadowlark, and 11 grasshopper sparrow nests) were used to model daily nest survival, and of these, 10 nests (2 bobwhite, 7 meadowlark, and 1 grasshopper sparrow nest) were successful. Because I removed abandoned nests (i.e. included nests were either successful or depredated), survival rates directly reflect probability of surviving depredation. Average daily survival rate estimated from the null model (all following daily survival rate estimates include ± standard error [SE]) was 0.916 ± 0.001.

To assess the relative importance of visual concealment, as well as airflow and weather conditions associated with olfactory concealment in influencing daily nest survival probability, I evaluated 18 candidate models (1 null model, 3 visual concealment models, 3 olfactory concealment models, and 11 weather models; Table 1). Of these, four weather models, but no olfactory or visual concealment models, were strongly supported ($\Delta AIC_c < 2$), clearly indicating that weather variables most strongly influenced daily survival rate (Table 1). The top model ($\Delta AIC_c = 0.0$, $\omega i = 0.26$) contained precipitation; this variable was positively associated with daily nest survival ($\beta = 1.001 \pm 0.576$), and the model indicated a 0.895 ± 0.020 chance of nest survival on days with no precipitation compared to a 0.999 ± 0.016 chance of nest survival on days with 5 cm of precipitation. The second best model ($\Delta AIC_c = 0.9$, $\omega i = 0.16$) contained humidity, and this variable was positively associated with nest survival ($\beta = 0.079 \pm 0.033$). The third best model ($\Delta AIC_c = 1.2$, $\omega i = 0.14$) included both precipitation and previous day precipitation ($\beta = 0.221 \pm 0.265$). The fourth best model ($\Delta AIC_c = 2.0$, $\omega i = 0.09$) included both humidity and wind speed ($\beta = 0.033 \pm 0.035$). Precipitation and humidity were the only variables in more than one top-ranked model suggesting additional importance for these predictors of daily nest survival. Furthermore, standard errors of the β coefficient for wind speed and previous day precipitation overlapped zero, indicating a weak effect size of these variables, and these variables also appear to be “uninformative” based on ΔAIC_c values falling within 2 Δ_i units from the simpler nested models (Arnold 2010).

Discussion

Few studies have evaluated the relative role of visual concealment, as well as airflow and weather conditions associated with olfactory concealment in influencing animal habitat selection and population vital rates. In this study, I found that ground-nesting birds in grasslands select nest sites for overhead visual concealment, but there was no clear evidence of selection for turbulence intensity or airflow slope, variables associated with olfactory concealment. As described in detail below, overhead concealment could provide multiple benefits to prey species, including both visual and thermal concealment. I also found that weather variables related to moisture, specifically precipitation and relative humidity, had the greatest influence on nest survival. Although turbulence intensity and airflow slope did not predict nest survival, precipitation and humidity could potentially influence olfactory detection of nest sites by predators.

NEST SITE SELECTION

Contrary to my hypothesis that ground-nesting birds in grasslands would select nest sites for factors influencing both visual and olfactory concealment, I found that only overhead concealment was selected for among the variables I measured. I measured overhead concealment to provide an index of nest concealment from nest-depredating birds, which in some cases are important nest predators (Erikstad, Blom & Myrberget 1982; Dinkins *et al.* 2016). Overhead concealment and other habitat characteristics thought to influence nest detection by avian predators (e.g. proximity to potential perch locations) have been shown to be selected for at nest sites and to influence nest survival (Clark & Shutler 1999; Conover *et al.* 2010; Borgo & Conover 2016*a*). However, selection for overhead concealment has typically only been documented for bird species that construct open-cup nests and not for species that build dome-shaped nests, including the 3 bird species in my study. Additionally, studies using cameras to identify nest predators of grassland birds have found little if any depredation by avian predators (Pietz & Granfors 2000; Renfrew

& Ribic 2003; Staller *et al.* 2005). Therefore, it is unlikely that selection for overhead concealment reflected an attempt to avoid visual detection by avian predators.

Although overhead cover could in some cases prevent visual detection of nests by mammalian predators, I surmise that overhead concealment in my study area reflects a different mechanism of protection for ground-nesting birds, especially since the dominant predators in my study area rely primarily on olfactory detection (Pietz & granfors 2000; Renfrew & Ribic 2003; Staller *et al.* 2005). Previous studies indicate that increasing overhead concealment is associated with cooler microclimates (Carroll *et al.* 2016) and that cooler conditions can be selected for and influence survival at nests of ground-nesting birds (Hovick *et al.* 2014; Carroll *et al.* 2015a, Grisham *et al.* 2016). Selection for relatively cooler microclimates allows individuals and their nests to avoid lethal summer temperatures, and this strategy of avoiding extreme heat is likely important in my study area where daily temperatures exceeded 30°C on 91 days during the 2015 and 2016 nesting seasons. Therefore, high temperatures may have plausibly driven selection for high levels of overhead concealment due to the shade and cooler conditions it provides.

Although selection for thermal cover may be especially important in subtropical grassland ecosystems such as my study area, there is no evidence that a tradeoff exists between thermal cover and other types of concealment. Indeed, vegetation could provide multiple mechanisms of protection. For example, tall vegetation has variously been associated with cooler temperatures (Hovick *et al.* 2014; Carroll *et al.* 2016), high levels of visual concealment (Ganguli *et al.* 2000; Unpublished data D.T.F), and high levels of turbulence intensity (Chapter 1), which is positively correlated with olfactory concealment. In many cases, these different dimensions of cover are therefore likely to be confounded. I hypothesize that birds and other animals could simultaneously select habitat for more than one of these components of concealment, for example, to both reduce the risk of detection by olfactory predators and to moderate high temperatures. Further research is needed to isolate which habitat feature(s) (e.g. olfactory, thermal and visual) are selected for under various environmental conditions and with varying predator community compositions and to identify which combinations of the above habitat cover mechanisms confer fitness related benefits in these different contexts.

Turbulence intensity was not significantly different between nest sites and random points. However, because this relationship was nearly significant ($p = 0.10$) even with a relatively limited sample size of nests ($n = 50$), further research should address whether turbulence intensity influences nest survival via its influence on olfactory concealment. Grassland-nesting birds in particular would be expected to select habitat based on the olfactory concealment it provides because: (1) nest predator communities in grasslands are often dominated by olfactory predators, (2) alteration of odour cues can reduce foraging efficiency of olfactory predators (Carthey, Bytheway & Banks 2011; Threlfall, Law & Banks 2013; Price & Banks 2016), (3) high levels of turbulence intensity have been shown to decrease the probability that olfactory predators detect a simulated prey item in the same grasslands used for the current study (Chapter 1), and (4) the only other study evaluating potential selection for turbulence intensity at grassland nest sites also found a nearly significant higher level of turbulence intensity at nest sites compared to random points despite also being limited by a relatively small sample size of nests (Conover *et al.* 2010).

NEST SURVIVAL

I observed high rates of nest predation, which likely reflects a high density of nest predators in my study area and could also partially be an artifact of my relatively small sample size of nests. Although I did not directly observe nest depredation events, olfactory predators, including Virginia opossum, nine-banded armadillo, striped skunk, eastern wood rat and several snake species, were frequently observed in the same areas where nests were located. Additionally, snakes were found in recently depredated nests on two occasions.

Average daily precipitation and relative humidity during the exposure period were the best predictors of daily nest survival. Contrary to the expectation under olfactory concealment theory (Conover 2007), these moisture-related variables were positively associated with daily nest survival. Previous research indicates that the effect of daily precipitation on nest survival is likely context-dependent, with some studies finding nests more likely to survive on days with precipitation (Pleasant, Dabert & Mitchell 2003; Moynahan *et al.* 2007; Rader *et al.* 2007; Conrey *et al.* 2016), and others finding survival to be less likely on days with precipitation (Dinsmore, White & Knopf 2002; Lehman *et al.* 2008; Webb *et al.* 2012; Dinkins *et al.* 2016). During periods of high moisture, water molecules are thought to displace odourants from surface binding sites (e.g., vegetation at bed sites, eggs, feathers and fur of prey) and thus increase available odour cues and predator foraging efficiency (i.e. the moisture-facilitated depredation hypothesis; Conover 2007).

Although some studies have provided empirical support for the moisture-facilitated depredation hypothesis (Ruzicka & Conover 2012; Borgo & Conover 2015), explanations for a positive effect of precipitation on nest success are less certain.

Moynahan (2007) documented a positive effect of precipitation on daily nest survival despite depredation rates increasing the day following precipitation events. The author hypothesized that parental nest attendance was high and predator activity was low during precipitation events and that nest attendance was low and predator activity was high on the days following precipitation events. Despite this explanation, there is no evidence that olfactory predators reduce foraging activity during precipitation events (Vickery & Bider 1981; Cresswell & Harris 1988), and moreover, I found no support for the effect of previous-day precipitation in my nest survival analysis. An alternative explanation is that, during a precipitation event, a pulse of odourants is released from many biotic sources (e.g., potential prey items) and abiotic sources (e.g. previously used loafing/bedding sites, trails, and nests), and that olfactory predators are "swamped" by this odour pulse and unable to distinguish between biotic and abiotic odour cues, thus increasing prey survival. Experimental studies support that broad emission of odourants from multiple abiotic sources increases prey survival (Carthey, Bytheway & Banks 2011; Price & Banks 2016). Regardless of the mechanism for the positive association between precipitation and nest survival, my findings are broadly consistent with other studies that indicate weather can have large impacts on population vital rates (Morrison & Bolger 2002; Grisham *et al.* 2016; Conrey *et al.* 2016).

CONCLUSIONS

Predation and the constraints of weather, which includes long-term variation, averages, and extremes events, broadly influences animal habitat selection, survival, and reproductive output (Parmesan, Root & Willig 2000; Caro 2005; Tanner *et al.* 2016). My results further illustrate how vegetation and weather variables influence nest site selection and survival, respectively, for a suite of ground-nesting birds in grasslands. The pattern of nest site selection documented here, specifically selection for high levels of overhead concealment, likely reflects a strategy used to cope with extreme heat. This finding reinforces other studies illustrating that habitat can be selected to mitigate thermal extremes (Hovick *et al.* 2014; Carroll *et al.* 2015*a*, 2016; Tanner *et al.* 2016). Understanding how animals use space to increase resilience against extreme heat is especially important in light of anthropogenic global change, and this area of inquiry is a frontier of ecology and conservation research.

While habitat selection can help mitigate the effect of weather extremes, these phenomena cannot be entirely avoided by animals, and extremes such as prolonged drought intense rainfall events, and intense heat, can strongly influence animal behavior, reproduction and population dynamics (Mörschel & Klein 1997; Parmesan, Root & Willig 2000; Albright 2010, Grisham *et al.* 2016). In support of the importance of weather, I found that precipitation and relative humidity had the greatest influence on nest success. I hypothesize that both precipitation and humidity could indirectly mediate nest predation by olfactory predators by causing large amounts of both prey-related and non-prey-related odorants to swamp predators and reduce detectability of prey. The role olfaction plays in influencing nest success—a key area of inquiry for this study—hinges on the accuracy of this hypothesis, and further research is required to assess the strength of odour plumes released from abiotic surfaces during high moisture conditions and how this affects predator foraging efficiency and prey survival. Nonetheless, because weather can have large impacts on animal communities; it is important to understand the mechanism(s) (e.g. moisture-facilitated depredation, reduced food availability, lack of protective cover, etc.) through which animal communities are impacted by weather and the strategies animals use to mitigate adverse effects.

Understanding which dimensions of habitat are actively selected for by animals and which dimensions confer fitness related benefits requires ecologists to adopt a mechanistic approach to studying habitat. As hypothesized here, weather characteristics can indirectly influence survival through predation (Weseloh 1988; Yasué, Quinn & Cresswell 2003; Conrey *et al.* 2016); in these circumstances, habitat selection strategies that reduce the risk of predation also have potential to mitigate effects of adverse weather. Selection for olfactory concealment is one potential mechanism that could be used to mitigate the effects of weather patterns that facilitate olfactory-based foraging. Further research that identifies the mechanisms by which weather mediates reproductive success—as well as research that parses apart mechanisms of habitat concealment—will have major conservation implications because it will facilitate: (1) identification of animal populations susceptible to extreme weather, (2) prediction and prevention of land cover changes likely to reduce species resilience to extreme weather, and (3) management for and conservation of the aspects of habitat (i.e. visual, olfactory, thermal) that are used in animal habitat selection and that provide mitigation against extreme weather events.

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Tables and Figures

Table 1. Model selection results for analysis of the influence of olfactory concealment, visual concealment, and weather variables on daily nest survival of ground-nesting birds in grasslands on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA (2015 and 2016).

Model type	Model	K^a	$\Delta AIC_c{}^b$	ωi^c
Weather	Precipitation	3	0.0	0.26
Weather	Humidity	3	0.9	0.16
Weather	Precipitation + previous day precipitation	4	1.2	0.14
Weather	Humidity + wind speed	4	2.0	0.09
Weather	Precipitation + wind speed	4	2.1	0.09
Weather	Precipitation + previous day precipitation + wind speed	5	3.3	0.05
Visual	Vertical concealment	3	3.5	0.05
Visual	Overhead concealment + horizontal concealment	4	3.9	0.04
Weather	previous day precipitation	3	4.5	0.03
Null	Null	2	4.9	0.02
Visual	Turbulence intensity	3	5.3	0.02
Weather	previous day precipitation + wind speed	4	6.5	0.01
Visual	Horizontal cover	3	6.7	0.01
Weather	Wind speed	3	6.7	
Olfactory	Airflow slope	3	6.8	0.01
Olfactory	Turbulence intensity + airflow slope	4	6.9	0.01
Weather	Soil moisture	3	6.9	0.01
Weather	Soil moisture + wind speed	4	8.8	0.00

[a] Number of parameters in the model

[b] Difference in AIC_c value between model and the most strongly supported model

[c] AIC_c Weight - relative strength of support for model

Fig. 1 Location of the study area on the McFarlin-Ingersoll ranch located in Inola, Oklahoma, USA.

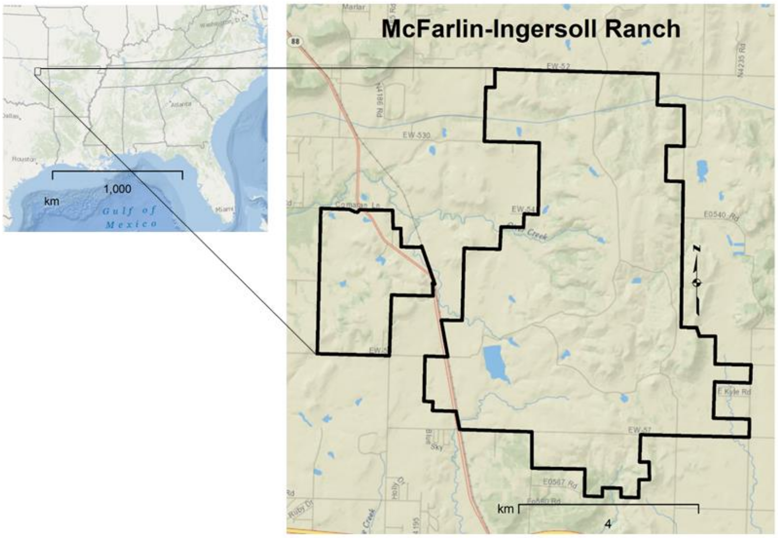
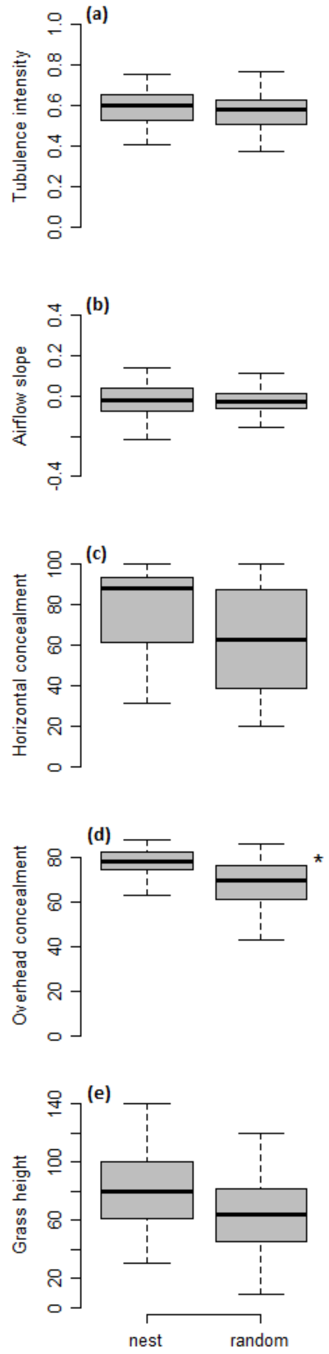


Fig. 2 Mean and quartiles for (a) turbulence intensity, (b) airflow slope, (c) horizontal concealment, (d) overhead concealment and (e) grass height at nest sites and random grassland sites measured in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA. * indicates a significant difference between nest sites and random sites.



Appendix

Appendix S1. Parameter estimates from linear mixed models and results of likelihood ratio tests for analysis of nest site selection by ground-nesting birds in grasslands in 2015 and 2016 on the McFarlin-Ingersoll ranch, Inola, Oklahoma, USA.

Characteristic	Nest β ± SE	Random β ± SE	χ^2	*P*-value
Olfactory				
Turbulence intensity	0.59 ± 0.01	0.57 ± 0.01	2.66	0.10
Airflow slope	-0.02 ± 0.02	-0.02 ± 0.02	0.15	0.70
Visual				
Horizontal concealment	74.00 ± 11.17	61.67 ± 21.66	0.69	0.41
Overhead concealment	77.26 ± 1.45	67.00 ± 1.79	9.13	0.00
Grass height	74.82 ± 12.28	64.17 ± 23.97	0.42	0.52

VITA

Dillon T. Fogarty

Candidate for the Degree of

Master of Science

Thesis: ASSESMENT OF OLFACTORY CONCEALMENT RELATED TO HABITAT SELECTION BY TERRESTRIAL ANIMALS

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in December, 2016.

Completed the requirements for the Bachelor of Science in Biology at Bemidji State University, Bemidji, Minnesota in 2013.

Experience:

Graduate Research Assistant – Oklahoma State University, Dept. of Natural Resource Ecology and Management (2014–2016)

Wildlife Technician – Minnesota Department of Natural Resources (2014)

Wildlife Technician – South Dakota Game Fish and Parks (2013–2014)

Professional Memberships:

The Wildlife Society (Since 2011)
Ecological Society of America (Since 2016)
American Ornithologists Union (Since 2016)