

**ASSESSING LOCAL AND LANDSCAPE CONSTRAINTS ON HABITAT
MANAGEMENT FOR GRASSLAND AND UPLAND BIRDS**

by

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ASSESSING LOCAL AND LANDSCAPE CONSTRAINTS ON HABITAT MANAGEMENT FOR GRASSLAND AND UPLAND BIRDS

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Species-habitat relationships are a central tenant to ecological theory and are critical in species management. Yet, despite a long-standing tradition of utilizing species-habitat relationships in both theoretical and applied ecology, there remains to be no clear predictors of how species relate to habitat. In order to further our understanding of the habitat selection process, we must begin to comprehend what spatial scales species form habitat decisions and what potential behavioral or life-history predictors underlie the scale of habitat decisions. During 2010-2012, I conducted point counts for grassland birds across Nebraska and assessed habitat relationships over multiple spatial scales to construct predictive species distribution models. Results indicated that landscape scale habitat variables drastically constrained or, alternatively, facilitated the positive effects of local land management for Ring-necked Pheasants. Hierarchical theory suggests that ecological processes function concurrently over multiple spatial scales and not all scales may be appropriate in determining species occurrence. I predicted that the spatial scale in which a species forms habitat decisions would correlate with body size, a predictor of life-history expression, if the scale is a function of how the species interacts with its environment. I tested this hypothesis on 10 obligate grassland bird species in Nebraska, USA. For seven species, I found evidence of a characteristic habitat selection scale, but no relationship to body mass. To quantify local habitat quality, a predictor of species

occurrence, I assessed the precision of five methods of measuring plant structure using ground-based imagery and processing techniques. I recorded standing herbaceous cover using digital imagery at two locations in a mixed-grass prairie. I compared the precision of the digital imagery vegetation analysis (DIVA) methods and quantified variability within each technique using the coefficient of variation. Vertical herbaceous cover estimates varied among DIVA techniques but the precision of four of the five techniques was consistently high. Overall, DIVA techniques are sufficient for measuring standing herbaceous cover and can adequately reduce measurement error associated with multiple observers.

DEDICATION

To my parents, for teaching a man to fish rather than feeding him for a day.

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Chapter 1: THE REALTOR'S DILEMMA: DOES THE NEIGHBORHOOD LIMIT CONSERVATION SUCCESS?

Abstract:

The loss of biodiversity is an ever-increasing threat. While habitat restoration is beneficial, management actions do not always demonstrate the desired outcome. Managers must understand why management actions fail; yet, past studies have focused on assessing habitat attributes at a single scale, and often fail to consider the importance of ecological mechanisms that act across scales. I located survey sites across southern Nebraska, USA and conducted point counts to estimate Ring-necked Pheasant abundance, an economically important species to the region, while simultaneously quantifying landscape effects using a geographic information system. I assessed habitat relationships using a Bayesian binomial-Poisson hierarchical model to construct predictive species distribution models of relative abundance meant to identify suitable areas for allocating limited management resources. Results indicated that landscape scale habitat variables severally constrained or, alternatively, facilitated the positive effects of local land management for Ring-necked Pheasants.

INTRODUCTION

Habitat restoration and management is a fundamental component of conservation science (Leopold 1933; Griffith 1989; Wiens 1994; Didier & Porter 1999; Sinclair 2006) and is routinely identified as the primary means to improve population viability for species of social-economic (Cowardin et al. 1995; Didier & Porter 1999; Connelly et al. 2000; Nielson et al. 2008) or conservation concern (Gibeau 1998; Kusak & Huber 1998; Miller et al. 2003). Although habitat management success is often measured by the ability to obtain a particular suite of vegetative structure and composition, ultimately success must be gauged by the population responses of target species. Unfortunately, despite our ability to routinely produce ‘suitable’ vegetative conditions, habitat management actions too often fail to meet the population expectations of managers (e.g., McCoy et al. 1999; Henningsen & Best 2005; Rahmig et al. 2008; Wrba et al. 2008). Understanding why populations fail to respond to apparently suitable habitat conditions represents a true conservation challenge which necessitates reconsidering the underlying mechanisms that drive species-habitat relationships.

Recognizing that individuals select among available habitats based on a set of environmental cues is fundamental to habitat selection theory, and therefore useful in predicting habitat suitability (Hilden 1965; James 1971). Utilizing conservation tools which translate ecological theory into spatial species-habitat relationships such as Species Distribution Models (SDMs) is therefore an effective population management strategy (Franklin 2009, Fletcher et al. 2010). Although habitat preferences have evolved to predict habitat suitability, the spatial scale at which individuals select and use habitat varies based on life history and mobility (Peters 1983; Rosenzweig 1991; Holling 1992).

Unfortunately, while many studies have demonstrated the importance of site-level habitat attributes (Wiens 1973; Patterson & Best 1996; Fisher & Davis 2010), many have failed to recognize that communities and other biological interactions are influenced by ecological factors across multiple spatial scales (Best et al. 2001; Turner et al. 2001; Cunningham & Johnson 2006). Ignoring the fact that ecological processes act across scales (Stephens et al. 2003) reduces the efficacy of habitat management and can drain limited financial and ecological resources, or worse, harm the species or community in consideration (*i.e.*, ecological trap; Robertson & Hutto 2006). Furthermore, public perception may change in concert with the success or failure of a management action, potentially dictating the future direction of policy and governance (Zinn et al. 1998; Bremner & Park 2007). To improve management efficacy, management plans must incorporate ecological mechanisms, particularly ecological factors that constrain management success, and do so at scales relevant to the biology of the species or communities of interest. Therefore, associating habitat variables with species occurrence or abundance on a spatial scale relevant to the species provides insight into how individuals make habitat decisions, and consequently, what constitutes suitable habitat (Rosenzweig 1991).

Effective conservation practices may be particularly important in highly altered systems, such as agro-ecosystems. Over the past 50 years, agro-ecosystems throughout Europe and North America have been increasingly exposed to land-use intensification and development, causing extensive losses in ecosystem functions and corresponding species declines (Stoate et al. 2001; Peterjohn 2003). Farmland and grassland birds, for example, have declined significantly over the past half century (Donald et al. 2006; Sauer

et al. 2011), and therefore are at the forefront of agro-ecosystem conservation. In North America, the Conservation Reserve Program (CRP) is one example of an agro-ecosystem conservation practice that is widely regarded to be beneficial to wildlife, including farmland birds (Peterjohn 2003; Giudice & Haroldson 2007; Nielson et al. 2008; Herkert 2009). Yet, despite significant successes surrounding the incorporation of CRP into the landscape, managers too often witness less-than-desirable management outcomes (McCoy et al. 1999; Rodgers 1999; Rahmig et al. 2008). The dynamic nature associated with agriculturally dominated landscapes makes for a perfect opportunity to explore species-habitat relationships and identify why farmland birds fail to respond to apparently suitable habitat improvements. To understand how farmland bird conservation efforts may be constrained, we must understand and address ecological interactions at both the land management level and in the surrounding landscape to ask the question: Is local habitat management constrained by the landscape habitat configuration and composition?

METHODS

STUDY SPECIES

Originally introduced to the United States in the early 1900's (Allen 1956), the Ring-necked Pheasant (*Phasianus colchicus*) prospered in the agro-ecosystems of the Midwest and Great Plains. Pheasant populations thrived in landscapes containing a diversity of crop types established over a variety of field sizes (Taylor et al. 1978). As pheasant populations grew, their importance as an upland game species increased throughout much of North America, providing prairie hunters a substitute for declining native grouse species. However, despite being a generalist and relatively resilient to

human disturbance, Ring-necked Pheasant populations have experienced significant declines over the past 50 years (Sauer et al. 2011). Given the social and economic value of Ring-necked Pheasants, the strong population decline has sparked intense research and conservation efforts from agencies and non-government organizations throughout the United States (Taylor et al. 1978; Perkins et al. 1997; Schmitz and Clark 1999; Smith et al. 1999; Leif 2005). Still, despite considerable efforts to conserve Ring-necked Pheasant populations, often management activities have proven unsuccessful (Leif 1994; Robertson 1996; Rodgers 1999) and may be inhibited by the surrounding landscape (Clark et al. 1999).

DATA COLLECTION AND PREPARATION

During April through July of 2010 – 2012, I conducted aural surveys ($n = 648$, 1161 and 1146) using a 500 m bounded distance sampling method (Blondel et al. 1981; Buckland et al. 2001) to estimate pheasant abundance at sites located throughout 17 counties in Nebraska (Fig. 1). Surveys began 15 minutes before sunrise and ended at 10:00 a.m., when aural detection rates are most consistent across all species (Hutto et al. 1986), and during which the maximum vocalization rate for Ring-necked Pheasants occurs (Luukkonen et al. 1997). All surveys were conducted at locations with a minimum of a quarter section (64 hectares) of contiguous grassland, the minimum habitat size assumed necessary to support viable Ring-necked Pheasant populations at a local scale (Clark et al. 1999). I randomly selected nine survey points at each site using a minimum spacing of 300 meters and sampled each point three times each season, leaving equally spaced time intervals between survey rounds. I recorded every individual seen or heard during a 3-minute period and used a laser range finder to measure distance from

observer to suspected location. Inclement weather, including fog, drizzle, prolonged rain, and wind greater than 20 km/h resulted in ending the survey prematurely.

Land cover variables were derived from a Nebraska Landcover layer with a 30 x 30 m resolution (Bishop et al. 2011). Individual habitat types were generalized into six cover classes which were predicted *a priori* to influence Ring-necked Pheasant populations (Conservation Reserve Program grasses, grass, trees, small grains, row crops, and wetlands) and reclassified into binary raster layers, where 1 is “habitat” and 0 is ‘non-habitat’. I implemented the Circular Focal Statistics Tool in ArcGIS 10.0 (ESRI, Redlands, California) to assess cover type at both a land management (1 km radius) and landscape scale (5 km radius), which is roughly equal to the dispersal distance of a Ring-necked Pheasant (Smith et al. 1999), and calculated the proportion of each land cover within the specified window size. I quantified the relative elevation in the surrounding area by deriving an elevation index from a Nebraska digital elevation model (DEM) with a 30 x 30 m resolution. The elevation index was equal to the standardized elevation of a township, where each individual raster cell was subtracted from the average elevation within a congressional township and was divided by the standard deviation of elevation within the political boundary.

Habitat and topographic variables were measured at spatial scales relevant to the managed area and the landscape surrounding the management area. Because there were differences in scale, all variables were standardized by subtracting the mean and dividing by the standard deviations from the mean (Bring 1994). In addition, standardizing variables helps improve model convergence and allowed for the direct comparison of parameter estimates (Royle & Dorazio 2008). Before including habitat and topographic

variables, I tested all variables for colinearity. Any two variables having a Person's correlation over 0.6 were determined to be highly significant and I eliminated one of the correlated variables from the model.

STATISTICAL MODEL

I modeled pheasant relative abundance (N_i) at each survey site (i) using a binomial-Poisson hierarchical model (Royle 2004; Royle and Darozio 2008; Kéry 2010; Kéry and Royle 2010). This model had the general form:

$$\begin{aligned} N_i &\sim \text{Poisson}(\lambda) \\ \log(\lambda) &= B_{k0} + B_1 X_1 + \dots + B_n X_n \\ B_k &\sim \text{Normal}(\mu_{B_0}, \sigma^2_{B_0}) \\ y_{ij} &\sim \text{Binomial}(N_i, p_{ij}) \\ \text{logit}(p_{ij}) &= A_0 + A_1 X_1 + \dots + A_n X_n \end{aligned}$$

which assumed a two-stage stochastic process. The first stochastic process relates to the ecological processes involved in distributing individuals throughout the landscape resulting in site specific abundance, N_i . I assumed that N_i was Poisson distributed which is an appropriate choice for count data (Zuur et al. 2007) and had a mean of λ . I included habitat and topographic variables in the linear predictor for ecological process using a log-link function for λ . Because survey locations were visited repeatedly and nested inside management area k , I added a random-intercept effect to account for potential spatial autocorrelation and variation among management areas (Zuur et al. 2007). The second stochastic process in the model is the observation process, where the actual numbers of individuals detected (y_{ij}) at site i during the j th survey was the product of a binomial distribution given that there were N_i individuals present at site i and a

probability of detecting those individuals p_{ij} (Kery 2010). I predicted that survey specific variables, time of day and Julian date, would influence the probability of detecting individuals and included them in the observation process using a logit-link function for p_{ij} . Peak vocalization-rates have been previously identified (Luukkonen et al. 1997); therefore I added a quadratic term for time of day to allow for non-linear relationships in detection probability (Luukkonen et al. 1997).

I ran the Bayesian analysis in WinBUGS (Lunn et al. 2000) using the R2WinBUGS package through the software R version 2.14.0 (R Development Core Team 2011). Three Markov Chain Monte Carlo (MCMC) simulation chains were used to calculate the posterior distribution with 35,000 iterations in each chain. Every 50th iteration was used to calculate the posterior distribution. I treated the first 5,000 iterations of the Markov Chain as a burn-in period and eliminated them from the calculation of the posterior distribution (Kery 2010). I visually inspected Markov Chains and used the Gelman-Rubic diagnostic, which compares within-chain and between-chain variability to determine model convergence (Brooks and Gelman 1998). Any parameter estimate with a Gelman-Rubic diagnostic below 1.1 was accepted as having successfully converged.

Model fit was assessed using a posterior predictive check using a Chi-squared discrepancy test (Gelman & Hill 2007; Kery 2010). I compared the lack of fit of the model fitted with the actual dataset with the lack of fit of a model fitted with replicated data generated from the parameter estimates obtained from the actual model. A Bayesian p-value was calculated to further assess model performance, which quantifies the

proportion of times the discrepancy measure for the replicated dataset is greater than the discrepancy measure for the actual dataset (Kery 2010).

DETERMINING SCALE

Habitat variables were measured using a spatial scale relevant to management (314 ha) and the landscape (7854 ha), determined by the average between-season dispersal distance of a Ring-necked Pheasant. Although previous studies have utilized various information-theoretic approaches (*i.e.*, AIC, BIC, DIC) to identify the spatial scales and cover types important in explaining species occupancy or abundance (Franklin 2009; Thogmartin et al. 2006), unfortunately they are controversial and may lack in performance when applied to a Bayesian hierarchical model (Spiegelhalter et al. 2002; Bolker et al. 2009; Ward 2008). Instead I used a hypothesis testing approach to build a final model, identifying which spatial scale habitat variables had the strongest influence on Ring-necked Pheasant distribution based on the parameter estimates (Gelman et al. 1995). I first modeled all of the variables measured at the management scale, created a second model with all of the variables measured at the landscape scale, and assessed which parameter estimates for a single habitat type better explained Ring-necked Pheasant abundance. The spatial scale at which the habitat variable had a stronger parameter estimate was included in the final model (Table 1). To allow for non-linear habitat relationships in the model, I added a quadratic term for all habitat variables measured within a 5km radius of the survey location. I assumed all of the effects within the final model were present, circumventing the use of an information-theoretic approach in model selection (Gelman & Hill 2007; Bolker et al. 2009).

SPATIAL MODELING AND VALIDATION

I created a predictive spatial model by combining geographic information systems (ArcGIS 10.0, Environmental Systems Research, Redlands, CA) grid layers of land cover classes and topographic variables based on their parameter estimates. Cover types and topographic variables were multiplied by the parameter estimates and un-standardized using the means and standard deviations of each variable in the ArcGIS Spatial Analyst calculator. The resulting weighted raster layers were summed together and added to the intercept, producing a species distribution model for Ring-necked Pheasants in Nebraska (Thogmartin et al. 2006).

In modeling Ring-necked Pheasant distributions and extrapolating beyond the study region, I recognized that habitat relationships did not make biological sense based on the biology of the species and the ecotypes of the region. In order to correct the species distribution model for Ring-necked Pheasants, I assumed that landscape variables may not adequately identify non-linear relationships and added an additional term (cubic term) for small grains and row crop. I identified the correction term by back-solving the equation with the assumption of zero Ring-necked Pheasants at 100 percent small grains or row crop agriculture in the surrounding landscape (Fig. 2; Best et al. 1995; Best et al. 2001). The resulting correction terms were added to a corrected species distribution model for Ring-necked Pheasants.

I validated the spatial models using an independent dataset. In 2012 I established 10 roadside transects outside of the main study area, each containing 15 survey locations, where each location was spaced roughly 5 km apart (Fig. 1). Because it was unlikely home range would significantly change during the breeding season (Leif 2005) and each

transect was visited three times, I used the maximum number of individuals detected over the three visits for each survey location as the observed dataset. I extracted values of both the fitted spatial model and “corrected” spatial model to the survey points of each transect using ArcGIS (Murray et al. 2008). I calculated Spearman’s rho statistics for rank correlation (r_s) between the observed dataset and the predicted datasets in using the statistical software program R. In order to visually inspect model performance, I used standardized observed abundance and standardized predicted abundance to fit a least-squares regression line and 95% confidence limits (Murray et al. 2008).

RESULTS

Of the seven topographic and habitat variables I investigated, the proportion of CRP and grass best explained the variability in pheasant abundance at the management scale (Fig. 3), with pheasant populations responding positively to each. In contrast, row crop agriculture, small grains and trees best explained the variability in pheasant abundance at the landscape scale (Fig. 4). With pheasant populations responding positively to the proportion of row crop and small grains in the landscape, but negatively to the amount of trees such that as few as 15% trees in the landscape severely limited the population (Fig. 5). When combined in the final model the landscape variables better predicted Ring-necked Pheasant abundance than local variables relevant to management actions (Table 1).

Overall the assessment of model fit for the Bayesian binomial-Poisson mixture model, which included a combination of variables quantified at local and landscape scales, indicated a well performing model (Bayesian P-value = 0.57). Visual assessment of the chi-squared discrepancy test indicated that the lack-of-fit of the fitted model was

comparable to the lack-of-fit of the replicated data generated from the parameter estimates.

Based on the corrected species distribution model, Ring-necked Pheasant populations were predicted to be most abundant in the southern and southwestern regions of Nebraska (Fig. 6). Concentrations of abundance also occurred around Alliance, Nebraska, located in the panhandle region of the state. Spearman's rho correlation statistics for the SDM based on the fitted model ($r_s = 0.60$) and the SDM based on the corrected habitat relationships ($r_s = 0.64$) indicated that both models adequately predicted pheasant abundance across Nebraska including outside the primary study area (Fig. 7). The mean and max values of the dataset used to fit the statistical model did not adequately account for the entire range of habitat in the landscape. By establishing non-linear relationships based on knowledge of pheasant biology, the "corrected" habitat relationships slightly improved the predictability of the species distribution model.

DISCUSSION

The influence of local habitat conditions, and thus habitat management on population viability and productivity is clear (Wiens 1973; Fisher & Davis 2010; Riley 1995; Eggebo et al. 2003; Nielson et al. 2008). However, while local conditions are obviously important, species are likely to respond to ecologically relevant conditions across multiple spatial scales (Hutto 1985; Holling 1992; Fletcher & Koford 2002; Stephens et al. 2003). For Ring-necked Pheasant, not only did I find that populations were responding to unique ecological conditions at different spatial scales, I clearly demonstrate the capability of large scale conditions to both facilitate and constrain local habitat benefits. For example, while it is not surprising that the availability of grassland

habitats at the local level had a positive influence on pheasant abundance (Fig. 3), the strength of these habitat relationships were significantly constrained by habitat relationships at the landscape scale (Fig. 5). Thus while several studies have previously suggested that local habitat management is critical for pheasant populations (Patterson & Best 1996; Eggebo et al. 2003), the “if you build it, they will come” approach, my findings show the benefits of these actions are constrained by presence of trees in the landscape and facilitated by the availability of row crop and small grains, at least to a point (Fig. 5).

The presence of small grains, for example, is widely known to influence breeding success of Ring-necked Pheasants (Robertson et al. 1993; Robertson 1996), often accounting for a significant proportion of productivity even when limited in availability in the landscape (Baxter & Wolf 1973). In agriculturally dominated landscapes where nesting habitat is significantly limited, the early green-up and ‘grass-like’ habitat created by small grains such as winter wheat may significantly increase breeding opportunities, a major factor limiting pheasant populations (Baxter & Wolfe 1973; Snyder 1984). Still while small grains are beneficial as nesting cover (Fig. 5), they have limited benefits for brood rearing as arthropod food resources are generally reduced by agriculture practices (Benton et al. 2002), and the winter cover afforded by grain stubble is significantly less than native warm season grasses (Lyon 1954, but see Rodgers 2002). Similar trade-offs are apparent for row crop habitats which produce ideal winter food resources (Fried 1940; Bogenschutz et al. 1995), but have limited benefits as breeding or winter cover (Lyon 1954; Best et al. 2001).

The inability of small grain and row crop cover classes to fulfill all the life history requirements of pheasants underlies my assumption that at some point the benefits associated with increasing dominance of agriculture in the landscape are offset by the costs, creating a normal distribution around some ideal availability of small grain and row crop. Based on the fitted relationships for row crop and small grain habitat types, the initial Ring-necked Pheasant SDM was inflated in areas where extremely high proportions of habitat existed in the landscape. This “run-away” regression error was largely an artifact of extrapolating beyond the study region, where extreme habitat values were not used in fitting the statistical model (Fig. 2). It is acknowledged that modeling the spatial distribution and abundance of species is largely an *ad hoc* process (Thogmartin et al. 2006) and by introducing habitat relationships based on the biology of the species, I was able to correct the fitted relationships for landscape variables and improve the performance of the SDM (Fig. 7). This approach bridges the gap between habitat suitability indices and regression-based species distribution modeling, where habitat suitability indices are largely based on *a priori* knowledge of the species of interest and expert opinion (Franklin 2009). It is widely held that probabilistic modeling is required in order to adequately model species distributions (Latimer et al. 2006); yet, I have demonstrated that by combining both a conceptual and empirical approach to species distribution modeling, we can predict species abundance and distribution based on known ecological trade-offs. Moreover, these trade-offs highlight the cross-scale interactions apparent in my model and demonstrates the importance of ecological processes which act across spatial scales.

An example of an ecological process that works across spatial scales and which is highlighted by the findings of my model is nest predation (e.g., Chalfoun & Martin 2007). Nest predation is the primary cause of reproductive failure for most birds (Ricklefs 1969; Martin 1995) and, thus, represents an important factor limiting pheasant populations. In the grassland ecosystems of Nebraska the primary nest predators limiting pheasant nest success are mesopredators (e.g., raccoon, skunk, possum) (Errington & Hamerstrom, Jr. 1937; Riley et al. 1998; Renfrew and Ribic 2003), most of which are limited by the availability of adequate winter and breeding habitats afforded by large trees (Chalfoun et al. 2002a; Chalfoun et al. 2002b; Disney et al. 2008). Thus while other studies have suggested that mature woody cover benefits pheasants (e.g., Leif 2005), I found that even limited woody cover in the landscape has strong negative consequence to pheasant populations (Fig. 4). This finding is likely driven by anthropogenic impacts to the landscape that alters predator-prey interactions, particularly predator search strategies. In highly altered and intensively managed agroecosystems nesting cover is generally limited, allowing highly mobile nest predators to converge and concentrate search effort (Mankin & Warner 1992). Thus even small increases in nest predator populations, mediated by small increases in woody cover, have detrimental and lasting impacts on pheasant populations. Improving nest success requires reducing nest predator populations (e.g., Garretson & Rohwer 2001; Rohwer et al. 2004), potentially by removing trees, or reducing nest predator efficacy (Emmering & Schmidt 2011). Indeed, the latter possibility likely underlies the positive impact of small grains in the landscape, which increase predator search area and likely nest dispersion, both of which reduce the positive feedback-loop inherent in predator search effort (Martin 1988). Clearly, the

complex factors driving nest success and consequently pheasant abundance are mediated by multiple ecological factors working across multiple scales.

The rate of decline in populations of grassland and farmland birds is alarming (Donald et al. 2006; Sauer et al. 2011); however despite increasing conservation efforts over the last thirty years, particularly local habitat management (Peterjohn 2003; Geudice & Haroldson 2007; Herkert 2009), most populations continue to decline. As conservation efforts are increasing perceived as failures (McCoy et al. 1999; Rodgers 1999; Rahmig et al. 2008), and sources of funding become more limited and increasingly coveted by alternative needs (Newburn et al. 2005; Possingham & Wilson 2005; Knight & Cowling 2007; Stephens et al. 2008), a loss of public support may underlie a reduction in future conservation efforts (Zinn et al. 1998; Bremner & Park 2007). To improve management efficacy and ensure the long-term sustainability of conservation, requires identifying the ecological factors that constrain management success. The importance of the landscape effects suggests that local land management is not likely the driving factor influencing pheasant populations. The high performance of the pheasant SDM supports this conclusion, as I was able to predict a completely independent dataset of observed pheasant numbers based on a model fitted from data collected only on managed lands (Fig. 7). By identifying and understanding how species select habitat and at what scales, I was better able to predict species distribution and pinpoint how populations may respond to management decisions on a local level. Although many species may respond to habitat characteristics at spatial scales too small to identify using GIS technology, here I demonstrated the importance of identifying spatial relationships in order to better

understand and predict species distribution and ultimately improve the management outcome for species responding to habitat beyond the boundaries of management area.

MANAGEMENT IMPLICATIONS

These findings contribute to our ability to effectively manage for Ring-necked Pheasant populations in Nebraska by increasing our understanding of how populations respond to management efforts. Assuming there are no other landscape features surrounding managed sites, pheasants responded positively to local habitat management such as CRP enrollment (Fig. 3). However, the landscape context surrounding management areas had drastic ramifications on the outcomes of local management efforts (Fig. 5). For instance, my findings demonstrate that areas in the landscape containing a high proportion of trees may in fact inhibit any benefits of local management efforts on Ring-necked Pheasants. Alternatively, managing habitat in areas suitable for Ring-necked Pheasant populations, such as in landscapes containing a high proportion of small grains, will enhance the benefits of local management (Fig. 5).

Understanding and accounting for potentially complex species-habitat relationships can be challenging. However, through the use of SDMs, managers can visually identify “hot-spots” that pin-point areas in the landscape that have the highest likelihood of a successful outcome given a management action, and thus potentially improving their success rate at maintaining and increasing species populations (Fig. 6). As conservation resources become increasingly limited, targeted prescribe management is necessary in order to get the most bang for the conservation dollar.

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TABLES AND FIGURES

Table 1. Parameter estimates of habitat and topographic variables measured at the management (1 km radius) and landscape scales (5 km radius), and the final model with habitat variables measured at both the management and landscape spatial scales.

Variable	Management scale estimates	Landscape scale estimates	Final model estimates	SD	95% credible interval		Final scale (km radius)
					2.5%	97.5%	
intercept	2.98	2.84	3.07	0.60	1.86	4.10	-
CRP	0.44	0.10	0.23	0.08	0.08	0.38	1.00
grass	0.39	0.22	0.13	0.08	-0.03	0.29	1.00
wetland	0.21	-0.22	-0.10	0.09	-0.28	0.06	5.00
trees	-0.11	-0.44	-0.55	0.13	-0.79	-0.27	5.00
trees ²	-	-	0.13	0.08	-0.02	0.29	5.00
row crop	0.46	0.65	0.51	0.18	0.16	0.87	5.00
row crop ²	-	-	-0.05	0.09	-0.22	0.15	5.00
small grains	0.22	0.42	0.45	0.14	0.18	0.72	5.00
small grains ²	-	-	-0.04	0.05	-0.14	0.06	5.00
elevation index	-0.09	-0.03	-0.07	0.05	-0.17	0.04	-
year	-0.09	-0.11	-0.16	0.13	-0.38	0.11	-

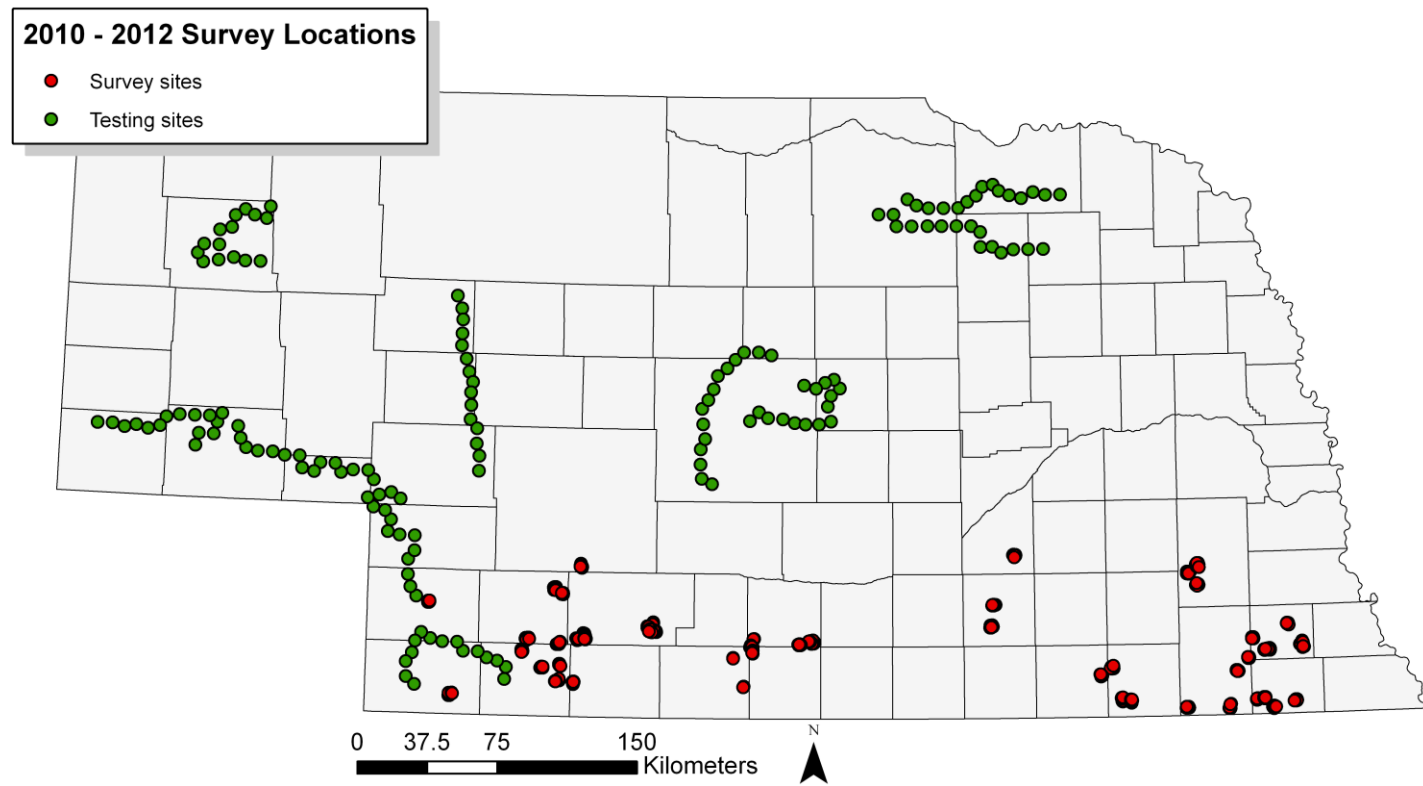


Figure 1. Ring-necked Pheasant abundance was recorded at 405 survey sites distributed throughout 45 state Wildlife Management Areas located in southern Nebraska (red points). Survey data was used to fit statistical models, which were validated using an independent testing dataset consisting of 150 survey sites evenly distributed across 10 road-transects (green points).

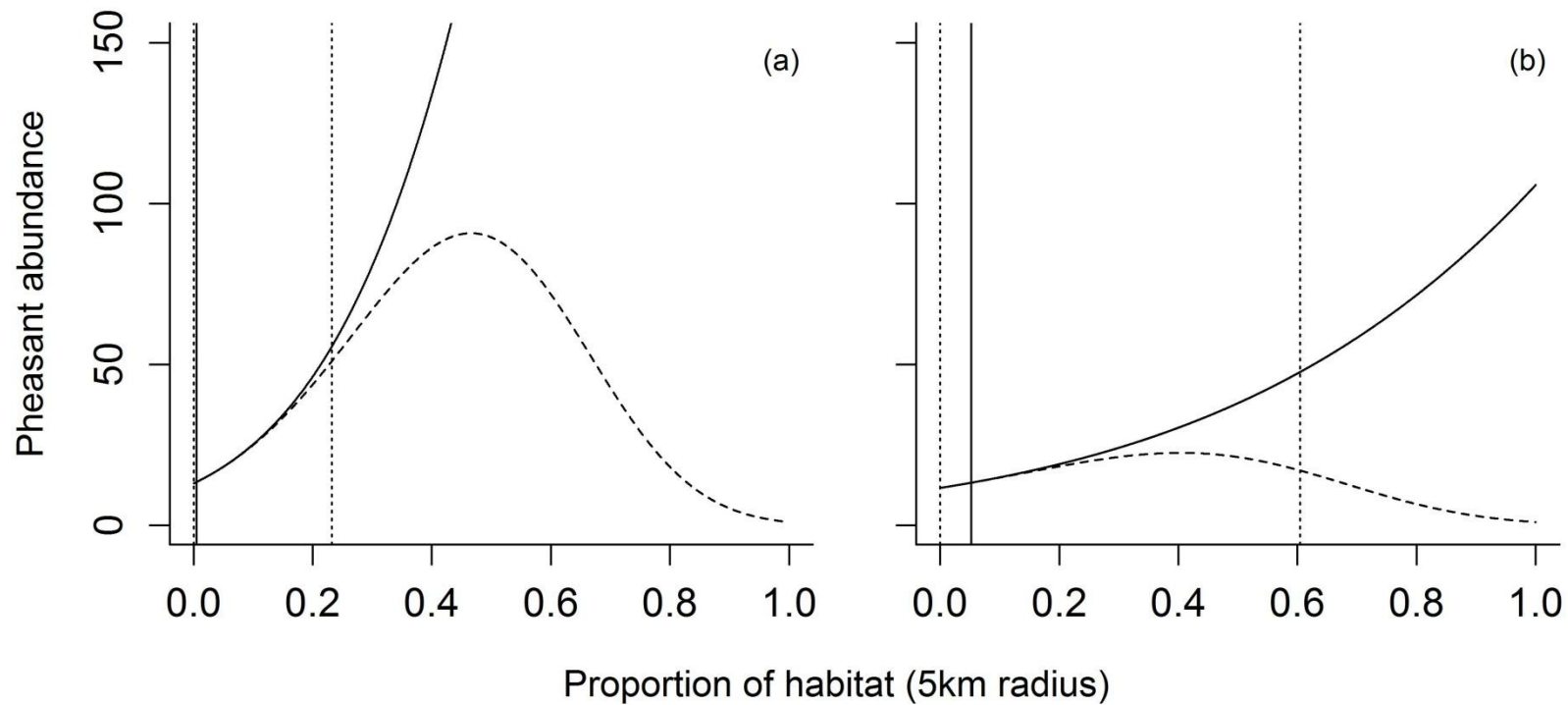


Figure 2. Fitted habitat relationships for Ring-necked Pheasants indicated a positive response to small grains (a) and row crops (b) in the landscape (dark line), but failed to predict pheasant response in areas containing a higher proportion of either cover class located outside of the study region. Vertical lines represent the minimum (dotted), mean (solid), maximum (dotted) values of the data used to fit relationships between Ring-necked Pheasant abundance and cover type. Assuming that too much row crop or small grains in the landscape would be detrimental to pheasants, dashed lines represent the corrected relationships used to create the final spatial model of Ring-necked Pheasant abundance in Nebraska.

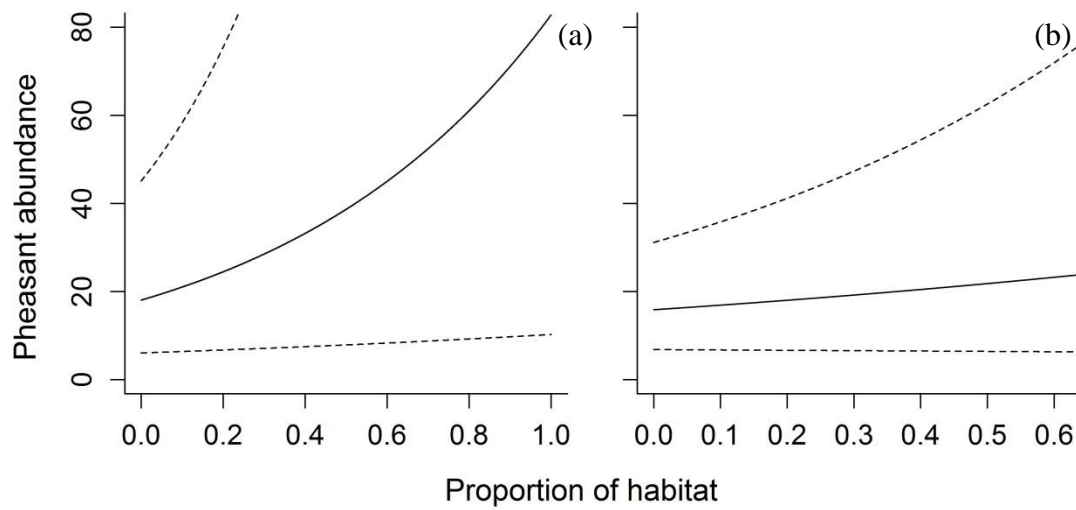


Figure 3. Ring-necked Pheasant populations respond positively to the proportion of CRP (a) and grassland habitat (b) at the local management level (1 km radius). Solid line represents habitat relationships and the dashed lines represent the 95% credible intervals.

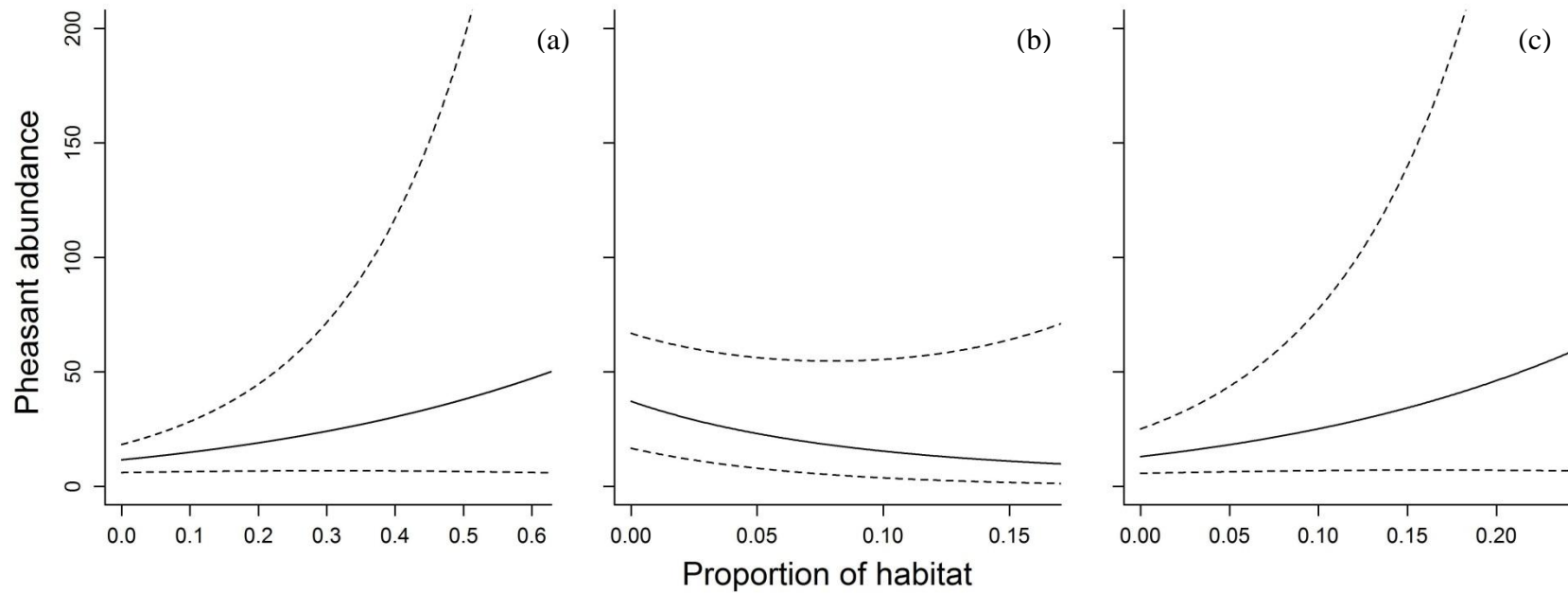


Figure 4. Ring-necked Pheasant populations respond positively to the proportion of row crop agriculture (a) and small grains (c) within the landscape (5 km radius), but negatively to the proportion of trees (b) in the landscape. Solid line represents habitat relationships and the dashed lines represent the 95% credible intervals.

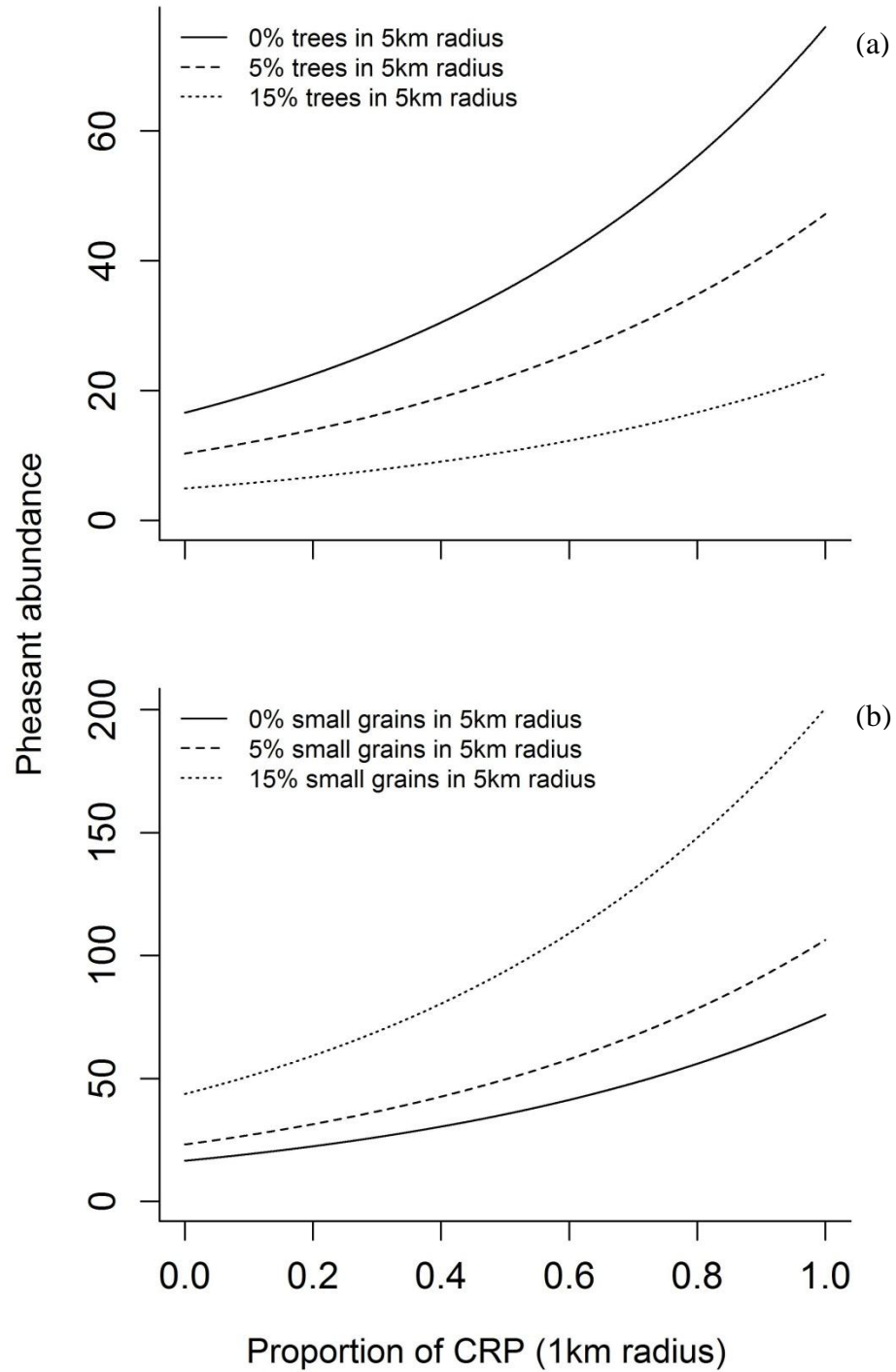


Figure 5. CRP enrollment increases pheasant abundance; however the benefits of CRP are inhibited by trees (a) in the surrounding landscape while aided by small grains (b).

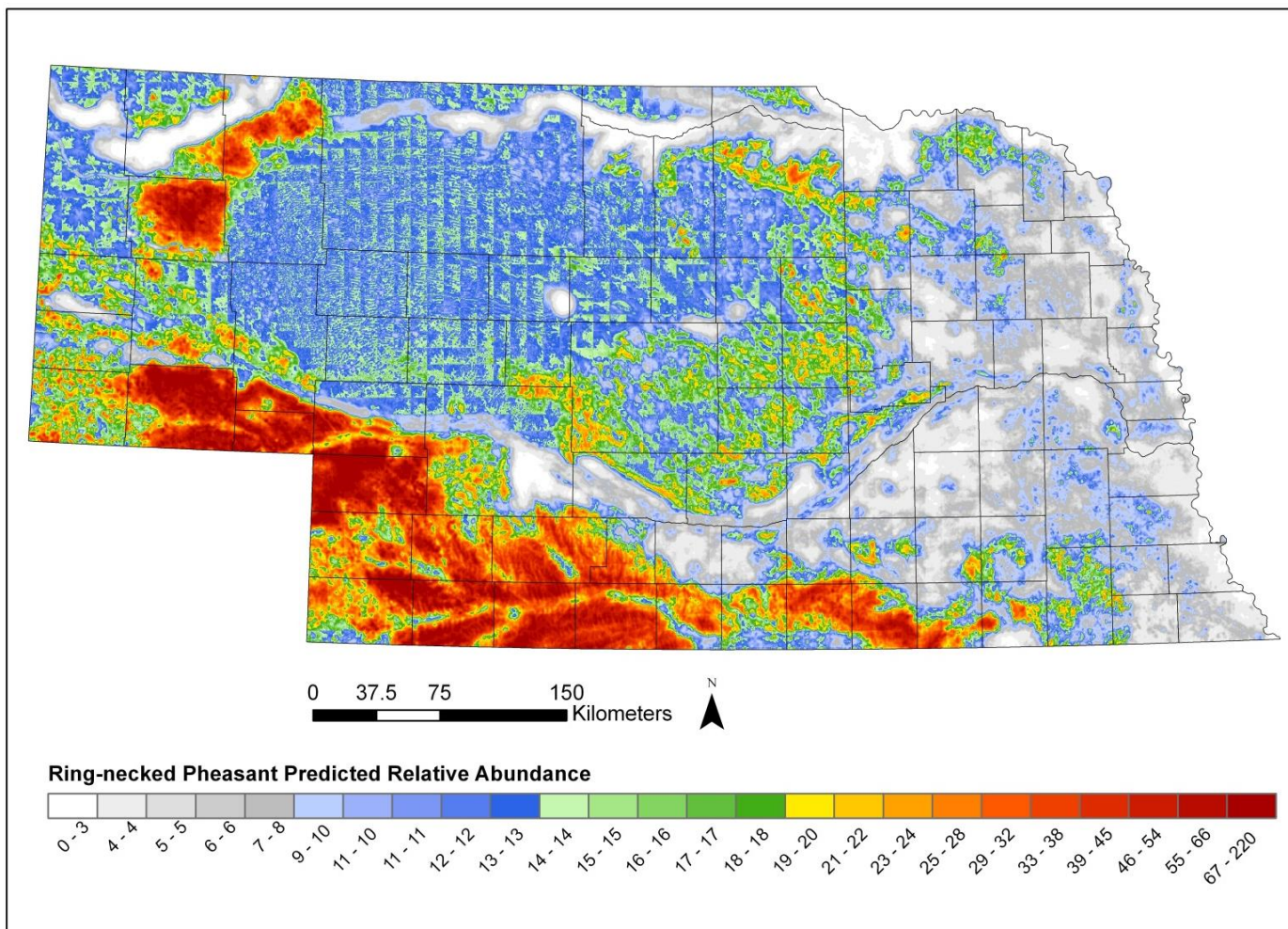


Figure 6. Predicted Ring-necked Pheasant species distribution model for Nebraska

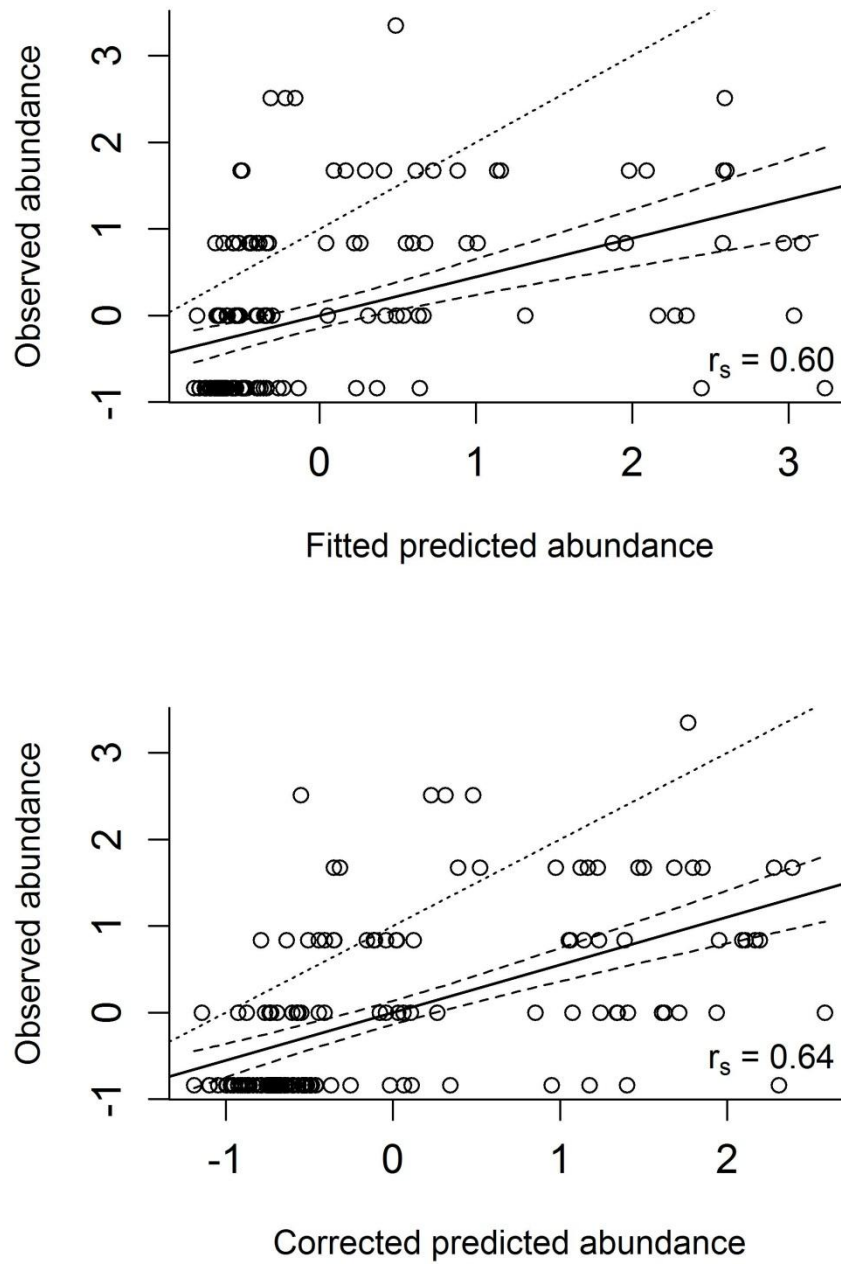


Figure 7. Standardized predicted values of Ring-necked Pheasant abundance compared to observed abundance indicated that both the original spatial model and the corrected spatial model perform well. The solid black line represents the fitted least-squares regression line and the two dashed lines represent the 95% confidence intervals. The dotted line on a 45 degree angle identified where a perfect fit would occur between predicted pheasant abundance and observed abundance.

Chapter 2: ASSESSING RELATIONSHIPS OF BODY MASS AND SPATIAL SCALE: A BIRD'S EYE VIEW

Abstract:

Hierarchical theory suggests that ecological processes operate simultaneously over multiple spatial scales, and not all scales may be suitable in predicting species occurrence. Although past studies have demonstrated that the spatial scale at which species form habitat decisions is correlated with body size, habitat decisions are not exclusively based on ecological context, but rather indirect cues, predictive of the habitat condition. I assessed predictors of species characteristic selection scale by looking across a body size continuum of migratory birds. I hypothesized that the spatial scale at which a species forms habitat decisions is correlated with body size if the scale is a function of how the species interacts with its environment. I tested this hypothesis on 10 obligate grassland bird species in Nebraska, USA. For each species, I quantified habitat across 20 spatial scales and created models based on species occurrence and abundance to determine if a species characteristic selection scale exists. For seven species, I found evidence of a characteristic scale, but there was no relationship between the scale at which species form habitat decisions and body mass. My results also indicated that there is no relationship between species mobility and the species characteristic section scale.

INTRODUCTION

Predicting the distribution and abundance of species is a central tenant of biogeography with a longstanding history in both theoretical and applied ecology (Leopold 1933; MacArthur 1960; Brown 1984; Austin 2002; Elith & Leathwick 2009). The presence or absence of a species has obvious implications for understanding local community dynamics and subsequently ecosystem resilience (Holling 1973; Peterson et al. 1998), but unfortunately the processes that predict species distribution and abundance are complex and vary widely among species and environments (Van Dorp & Opdam 1987; Howell et al. 2000; Fisher & Davis 2010). For example, access to food, mates, refuge from predators, and appropriate climatic conditions clearly shape species occurrence (Whithman 1978; Rosenzweig 1991; Chase & Leibold 2003), but subtle differences in life-history expression, even among closely related species, may result in significant differences in species assemblages (Schoener 1974; Bonsall et al. 2004). Despite these challenges there continues to be an interest in developing overarching ‘rules’ that predict the presence or absence of a species across broad landscapes.

Among animal species, body size is highly correlated and predictive of life-history expression (Schoener 1974; Peters 1983; Brown & Maurer 1987; Holling 1992; Fisher et al. 2011), and therefore often used as a surrogate for the ecological processes that shape species occurrence and community composition (Werner & Gilliam 1984; Pyron 1999; Fisher et al. 2011). Geographical patterns between species size and distribution abound (Gaston & Blackburn 1996; Pyron 1999; Murray & Hose 2005; Fisher et al. 2011), but despite the presence of numerous body size ‘rules’ (Bergmann 1847; Yom-Tov and Nix 1986; Foster 1964; McNab 2010), predicting the occurrence of

individual species based on body size, and subsequent life-history expression, remains enigmatic. In part this may be due to how species perceive and respond to ecological conditions. Hierarchy theory suggest that ecological processes operate simultaneously at different spatial scales (Johnson 1980), and not all scales may be equal in determining species presence (Levin 1992). The presence of one species may be largely determined by landscape attributes such as patch size or connectivity (*i.e.*, Helzer 1999) while for other species, local vegetative structure may be the deterministic factor of habitat use (Wiens 1973; Patterson & Best 1996; Fisher and Davis 2010). The notion that one scale may better describe habitat selection for a species has been demonstrated across a wide range of taxa (Roland & Taylor 1997; Holland et al. 2004; Mowat 2006; Nams et al. 2006; Fisher et al. 2011) and is formally termed the *species characteristic selection scale* (Holland et al. 2004). Recent evidence suggests that like many other behavioral and life-history traits, the scale at which species make habitat decisions may be correlated with body size (Fisher et al. 2011). Clearly many of the ecological conditions that influence life-history expression after individuals select habitats are correlated with body size (Werner & Gilliam 1984; Lima 1986; Iriarte et al. 1990; Blanckenhorn 2000; McNab 2010); therefore finding a correlation between body size and species characteristic selection scale is not surprising. Still the generality of the relationship between body size and habitat decisions remains unclear as there are numerous exceptions to body size rules (McNab 2010). By considering the subtleties of the habitat decision process we may begin to understand why some species fail to follow the rules.

While ecological conditions such as predation risk or food availability generally scale with body size (Werner & Gilliam 1984; Lima 1986; Werner & Hall 1988; Chase &

Leibold 2003), habitat decisions are not solely based on ecological context (Whithman 1978; Rosenzweig 1981). For most species habitat selection decisions are manifested through indirect cues, that while predictive of ecological conditions, may act independently (Hildén 1965; James 1971; McGrath et al. 2008). When cues act independently from selection agents, the spatial scale at which species form habitat decisions may not be related to the scale at which ecological conditions shape life-history expression, but rather at the spatial scales of the cues that most easily predict those conditions. As such species characteristic selection scales may evolve uniquely for individual species based on the scale at which ecologically important selection agents act, the scale at which those selection agents are assessed, or some combination of the two. In any event it is likely that the correlation between body size and species characteristic selection scale is lost when body size is not associated with the ability to assess important sources of selection. If this assumption is true, then correlations between body size and the scale of habitat decision should be strongest for species that assess ecological conditions at the same spatial scale as the conditions act, and weakest for species that have the capability of assess conditions at markedly different scales. Unfortunately, for most species sensory scale and body size are likely highly correlated, as mobility, one indicator of sensory scale, is highly correlated with body size (Bowman et al. 2002; Jenkins et al. 2007). Thus identifying the mechanism underlying the species characteristic selection scale and the causation of outliers to the body size scale relationship has proven difficult.

Here I investigate predictors of species characteristic selection scale by taking advantage of a unique system that allows us to separate the scale of sources of selection

from the scale at which species can potentially assess ecological conditions. By looking across a body size continuum of migratory and non-migratory birds, some of which are clearly capable of assessing ecological conditions across a large range of spatial scales, independent of body mass (Hutto 1985; Wiens 1994; Stephens et al. 2003; Thogmartin et al. 2006; Cornell & Donovan 2010), we can independently assess the relationship between body size and habitat decisions. I predict that if the characteristic scale of species' habitat selection is a function of how a species interacts with its environment, then the scale of habitat decisions will increase as function of body size. However if the spatial scale of habitat selection is a function of the scale at which a species can assess these relationships, then I expect no correlation with body mass, but possibly a relationship with relative mobility.

METHODS

DATA COLLECTION

During April through July of 2010 – 2012, I recorded species abundance of grassland birds ($n = 648$, 1161 and 1146) throughout 17 counties in Nebraska, USA using a distance sampling method where the maximum detection distance was bounded at 500 m (Blondel et al. 1981; Buckland et al. 2001). Surveys began 15 minutes before sunrise and ended at 10:00 a.m., when aural detection rates are most consistent across all species (Hutto et al. 1986). Surveys were conducted along road transects ($n = 10$) and at points within wildlife management areas ($n = 45$). Road transects consisted of 15 stop locations, where each stop was spaced roughly 8 km apart. Wildlife management areas were selected based on having a minimum size of 64 hectares of contiguous grassland, a

common land unit in rural Nebraska, USA. I randomly selected nine survey points at each management area using a minimum spacing of 300 meters. Points in both the transects and wildlife management areas were sampled three times in random order during the course of the breeding season, leaving equally spaced time intervals between survey rounds. I recorded every individual seen or heard during a 3-minute period and used a Nikon Prostaff 550 Laser Rangefinder (Nikon, Melville, NY) to measure distance from observer. Inclement weather, including fog, drizzle, prolonged rain, and wind greater than 20 km/h resulted in ending the survey prematurely.

Land cover variables were derived from a landcover layer of Nebraska with a 30 x 30 m resolution (Bishop et al. 2011). Grassland and woodland habitat types, which are two cover classes that have been consistently reported to influence both occupancy and abundance for the range of species considered (Chapter 1, Patterson & Best 1996; Bakker et al. 2002; Buskirk & Willi 2004; Kelsey et al. 2006), were reclassified into binary raster datasets, where 1 is “habitat” and 0 is ‘non-habitat’. I implemented the Circular Focal Statistics Tool in ArcGIS 10.0 (ESRI, Redlands, California) to assess habitat at multiple spatial scales (250 m, 500 m, 750 m, 1000 m, 1250 m, 1500 m, 1750 m, 2000 m, 2250 m, 2500 m, 2750 m, 3000 m, 3250 m, 3500 m, 3750 m, 4000 m, 4250 m, 4500 m, 4750 m and 5000 m radii) and calculated the proportion of habitat within the specified window size. In order help with model convergence, all variables were standardized by subtracting the mean and dividing by the standard deviations from the mean (Bring 1994). For each spatial scale, I tested grassland and woodland habitat variables for collinearity prior to entering them into a model. I determined that any two variables

having a Person correlation coefficient greater-than or equal-to 0.6 were highly correlated and were not included within the same model.

STATISTICAL ANALYSIS

I modeled species occupancy and abundance, quantifying individual and population responses at each survey site in relation to the proportion of woodland and grassland habitat in the landscape. I used N-mixture models to model species abundance as a function of habitat (Royle 2004) and occupancy models to model the probability of a species occurring as a function of habitat (MacKenzie et al. 2005). All models were fitted using the statistical package ‘Unmarked’ (Fiske & Chandler 2011) supported through the software program R version 2.14.0 (R Development Core Team 2011).

Both the occupancy and N-mixture models break down a complex joint probability distribution for two processes, the detection process, and the ecological process, through a series of conditional probability distributions. I was primarily interested in the ecological process (*i.e.*, what is truly driving species occupancy or abundance), which distributes individuals throughout the landscape. I included grassland and woodland habitat variables in the linear predictor for ecological process using a log-link function in the N-mixture models or a logit-link function in the occupancy models. I added the respective quadratic term of each habitat variable in the linear predictor for every model in the model set to allow for non-linear species-habitat relationships. The year was added as a site-specific covariate for every model to account for annual variation. For each model set, I included a null model that contained year as the only site-specific covariate. I predicted that survey specific variables (*i.e.*, time of day and Julian date) would influence the probability of detecting individuals and included them in

the linear predictor for the observation process using a logit-link function (Royle 2004; MacKenzie et al. 2005). Peaks in song bird singing rates have previously been identified (Hutto 1986); therefore I added a quadratic term in for time of day to allow for non-linear relationships in detection.

DETERMINING SPATIAL SCALE

I ran 20 models per model set – one model set for each obligate grassland bird species – where each model in a candidate set included a single scale in which I measured grassland and woodland habitat cover. In order to identify which spatial scale best described the variation in species-habitat relationships, I used a model selection criterion, AICc, which included a correction factor to account for small sample size. The model with the lowest AICc score was considered the best-fit model (Burnham & Anderson 2002). I assumed that the species characteristic selection scale determined by the top-ranked model was the scale in which species began to form habitat selection decisions. For all obligate grassland birds in the study, the AICc weights calculated for each model were plotted against the spatial scale at which each model was fitted (following Fisher et al. 2011).

I used least-squares regression to test whether the spatial scale best supported based on AICc weights was a function of average female body mass or a species' mobility (Holling 1992; Fisher et al. 2011). For all species, average female body mass data was retrieved from The Birds of North America Online resource (Lanyon 1995; Yasukawa and Searcy 1995; Vickery 1996; Brennan 1999; Martin and Parrish 2000; Giudice and Ratti 2001; Temple 2002; Carey et al. 2008; Houston et al. 2011). I estimated migration distance for six of the 10 species by calculating the latitudinal

difference between the centroids of the species' breeding grounds and wintering grounds using the Haversine formula (Sinnott 1984). For the additional four species I obtained an estimate of migration or mean dispersal distance from the literature (Table 1). To visually quantify potential relationships with habitat selection, I plotted the species characteristic selection scale against body mass and migration distance.

RESULTS

I obtained adequate detections for 10 obligate grassland bird species throughout Nebraska. Resident species included Northern Bobwhite (*Colinus virginianus*) and Ring-necked Pheasant (*Phasianus colchicus*). I detected six short distance migrants, including Eastern Meadowlark (*Sturnella magna*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramus savannarum*), Lark Sparrow (*Chondestes grammacus*), Red-winged Blackbird (*Agelaius phoeniceus*) and Western Meadowlark (*Sturnella neglecta*). Dickcissel (*Spiza americana*) and Upland Sandpiper (*Bartramia longicauda*) made up the two long distance migrants.

Based on occupancy, multiple species had evident peaks in AICc weights, including Dickcissel, Eastern Meadowlark, Grasshopper Sparrow, Northern Bobwhite and Western Meadowlark with scales ranging from 250 m – 5000 m radii (Fig. 1). Field Sparrow and Lark Sparrow had less drastic peaks in AICc weights (AICc weight under 0.6), indicating less support for a single characteristic scale of habitat selection. There were two species, the Ring-necked Pheasant and Upland Sandpiper, that showed limited evidence for a characteristic scale and displayed a bimodal response pattern (Fig.1).

Based on abundance, there were seven species displaying strong response to a single spatial scale. Dickcissel, Eastern Meadowlark, Grasshopper Sparrow, Northern Bobwhite, Red-winged Blackbird, Ring-necked Pheasant and Western Meadowlark all had peak AICc weights above 0.8 for a specific spatial scale. A range of scales were attributed in explaining Upland Sandpiper and Lark Sparrow abundance (Fig. 2).

Between models of occurrence and abundance, several species responded to difference spatial scales (Table 2). For species where their characteristic selection scale changed based on the modeling approach, abundance tended to be explained by cover types measured at larger spatial scales (Table 2). In opposition to the predictions, there was not a significant correlation between species characteristic habitat selection and female body mass for both occupancy ($r^2 = 0.175$, $P = 0.127$) and abundance ($r^2 = 0.110$, $P = 0.184$; Figs. 3 & 4). I also found no significant relationships between the characteristic selection scale and migration for both occupancy ($r^2 = -0.009$, $P = 0.365$) and abundance models ($r^2 = -0.120$, $P = 0.859$; Figs. 5 & 6).

DISCUSSION

The exploration of a species characteristic selection scale has led to several conclusions. Of the 10 species I conducted analysis on, seven demonstrated evidence of a characteristic spatial scale of habitat selection in both occupancy and abundance (Figs. 1 & 2). Peaks in AICc weights at specific spatial scales suggests that a characteristic selection scale likely exists, a notion supported by various other studies (Holland et al. 2004; Mowat 2006; Nams et al. 2006; Fisher et al. 2011). Based on my results, several species responded to cover types at larger spatial extents when fitted using abundance

rather than occupancy as function of land cover (Figs. 1 & 2), which may be indicative of a species' population response to macro-habitat rather than an individual response to a habitat cue. In addition, the results support the concept that some scales are better suited at explaining ecological processes (Weins 1989; Levin 1992), solidifying the concept of scale dependency in habitat selection. Failing to consider the appropriate spatial scale when exploring ecological relationships can jeopardize a researcher's ability to reach conclusions and make inference based on the outcome of a study.

Although previous studies have stated the importance of landscape level habitat attributes on habitat selection for grassland birds (Bergin et al. 2000; Soderstrom & Part 2000; Ribic & Sample 2001; Bakker et al. 2002), many of which indicated that these species are particularly sensitive to fragmentation throughout the landscape (Cunningham & Johnson 2006), my results showed no evidence for any single characteristic selection scale universally important for all obligate grassland bird species. Even though multiple species may be responding to the same habitat features (*i.e.*, woody structure), species respond to the structure independently at various spatial extents (Soderstrom & Part 2000; Best et al. 2001; Ribic & Sample 2001; Cunningham & Johnson 2006). These results have strong implications to species conservation and management, where managing for one species may not provide adequate habitat at the appropriate spatial scale to support another. In regards to grassland birds, a species guild that has demonstrated drastic declines since European settlement (Samson & Knopf 1994; Herkert et al. 2003), careful consideration should be taken prior to managing grassland habitats, making certain that all species-habitat relationships and their respective characteristic selection scales are considered before implementing habitat management.

For a select number of species, individuals showed little to no indication of a single spatial scale explaining habitat selection (Figs. 1 & 2). For these species, habitat selection may be explained by multiple scale-dependent habitat selection processes. Theory predicts that multiple spatial and temporal scales work collectively to determine how a species selects habitat (Hutto 1985; Holling 1992). In selecting a nesting site, a species may step down from selecting an area to settle, down to a suitable patch, and further downward to a nesting location with suitable foraging needs which in turn defines a territory (Holling 1992). This step-down approach to habitat selection may explain why certain species seem to respond to multiple spatial extents (Figs. 1 & 2). Furthermore, a species may respond to a cover class at one spatial extent and to another at a different scale (Chapter 1), which may explain the bimodal relationships of the species characteristic selection scale to the AICc weights for Ring-necked Pheasant and Upland Sandpiper (Fig. 1). Alternatively, a species portraying a multi-scalar response to habitat features may be merely an artifact of the landscape composition. If a species responds to a feature on the landscape at extremely large spatial scales, the multiple extents in which I measured the ecological process may not be independent from one another (Holling 1992). Self-similar landscapes may explain why Upland Sandpipers respond to grassland and woody structure over a gradient of spatial scales (Figs. 1 & 2), when in reality the scale-dependent processes of an animal of its size is likely to be explain by much larger spatial extents and at larger breaks, such as a log scale (*i.e.*, 10 m, 100 m, 1000 m, 10000 m). Other studies have supported this notion and indicating that migratory grassland birds potentially respond to landscape level processes out to 80,000 ha (Thogmartin et al. 2006).

I found no significant correlation between body size and a species' characteristic selection scale for either occupancy or abundance models (Figs. 3 & 4). Theory would predict that scale-dependent processes, such as territory size, dispersal, and migration, are relative to body mass and therefore correlated with the spatial extent in which a species selects habitat (Holling 1992). However, when species form habitat decisions based on indirect cues that act independently from the processes shaping life-history expression, they may perceive cues at larger spatial scales that are best suited for predicting local ecological conditions, as may be the case with migratory birds which travel extreme distances to and from breeding and wintering grounds on a bi-annual basis. My results support the notion that migratory birds perceive biological cues at spatial scales well beyond the bounds of the selection agents acting on life-history expression (Figs. 3 & 4), which are generally correlated with body size (Bowman et al. 2002; Jenkins et al. 2007).

Given that many grassland obligate bird species are highly mobile, some of which migrate over extreme distances (table 1), I anticipated that mobility would be a better predictor of a species' characteristic selection scale than body size. My results did not support this hypothesis as migration distance did not show any correlation with a species' characteristic selection scale (Figs. 5 & 6). Perhaps one explanation may be that the mobility represented by migratory birds is well beyond the 'perception' threshold indicative of habitat selection process such that any distance traveled outside that threshold does not impede or enhance their ability to perceive habitat cues. Furthermore, the lack of relationship between migration distance and a species' characteristic selection scale may be explained by hierarchical theory. For instance, theory predicts that a hierarchy of scales exists in which species form habitat decisions, and processes

occurring at smaller spatial scales are dependent on those occurring at large spatial extents (Weins 1973; Johnson 1980). For instance, the processes affecting a species choice to settle their home range is dependent on the processes that directed them to the breeding grounds during migration. Therefore by the time an individual reaches its breeding grounds, habitat selection decisions are being made at smaller spatial extents unexplained by migration distance.

My results demonstrate the potential significance of landscape composition on habitat selection and the variability in which species form habitat decisions. My results also suggest the importance of considering multiple species and how they may select areas for breeding prior to conservation management. In addition, migratory birds may not form habitat selection decisions in ways theory would predict, but rather on a species-specific basis. These decisions may be based on life-history, site fidelity, or other extrinsic factors such as conspecific attraction.

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TABLES AND FIGURES

Table 1. Migration distances as a measurement of mobility for each individual species determined by the latitudinal difference between the breeding and wintering grounds described in the references. Four of the 10 species had direct estimates of mobility obtained from their respective references.

Species	Distribution (Latitude)		Distance (km)	Source	
	Breeding	Wintering			
Dickcissel	39° 36' 12"N	8° 55' 34"N	3411.2	Temple 2002	*
Eastern Meadowlark	-	-	1000.0	Lanyon 1995	
Field Sparrow	43° 22' 32"N	31° 15' 51"N	1346.7	Carey et al. 2008	*
Grasshopper Sparrow	42° 02' 35"N	19° 54' 08"N	2461.9	Vickery 1996	*
Lark Sparrow	40° 58' 09"N	20° 08' 55"N	2315.1	Martin and Parrish 2000	*
Northern Bobwhite	-	-	3.0	Townsend et al. 2003	
Red-winged Blackbird	-	-	1000.0	Dolbeer 1982	
Ring-necked Pheasant	-	-	0.5	Smith et al. 1999	
Upland Sandpiper	44° 32' 12"N	24° 24' 18"S	7666.0	Skagen et al. 1999	*
Western Meadowlark	43° 38' 07"N	24° 13' 56"N	2157.5	Davis and Lanyon 2008	*

* Migration distance was calculated using the Haversine formula and the latitudinal difference between the estimated centroid of the breeding distribution and the centroid of the wintering distribution.

Table 2. Characteristic scales (radii) determined by modeling habitat in the surround landscape. Habitat was measured at 20 scales. The best-supporting model based on AICc weights among the 20 models determined the characteristic scale.

Species	Characteristic scales (meters)		Body mass (g)
	Occupancy	Abundance	
Dickcissel	250	250	25.2
Eastern Meadowlark	5000	5000	100.1
Field Sparrow	1000	1500	13
Grasshopper Sparrow	750	1000	17
Lark Sparrow	1250	5000	30.7
Northern Bobwhite	500	500	170
Red-winged Blackbird	1750	1750	43.8
Ring-necked Pheasant	3750	5000	917
Upland Sandpiper	1250	3000	164
Western Meadowlark	1000	1250	89.4

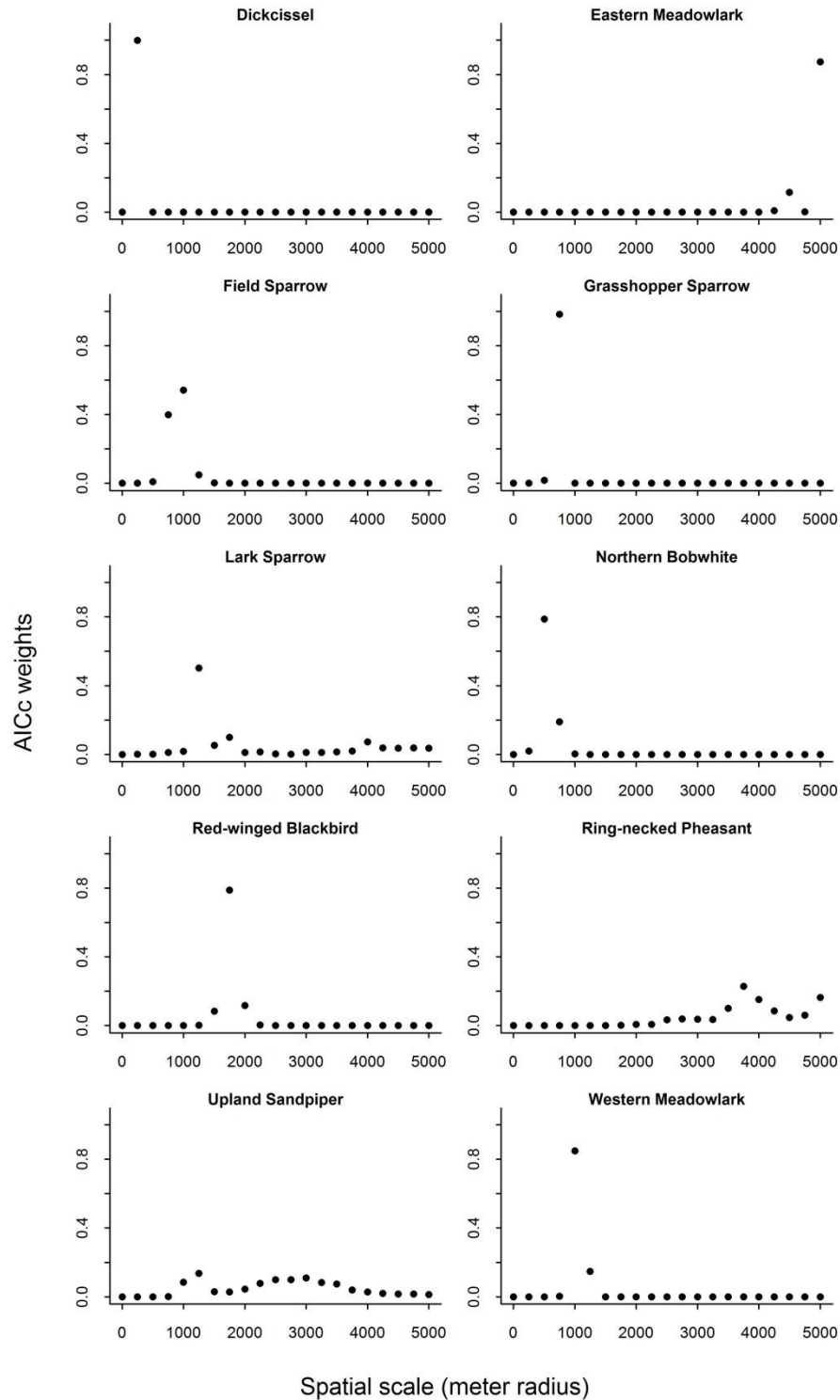


Figure 1. AICc weights of grassland bird occurrence for 10 species against cover types measured across 20 spatial scales (250 - 5000 m radii) around each survey site. The null model in each model set, which contains no cover class measurements, is represented at zero on the x-axis.

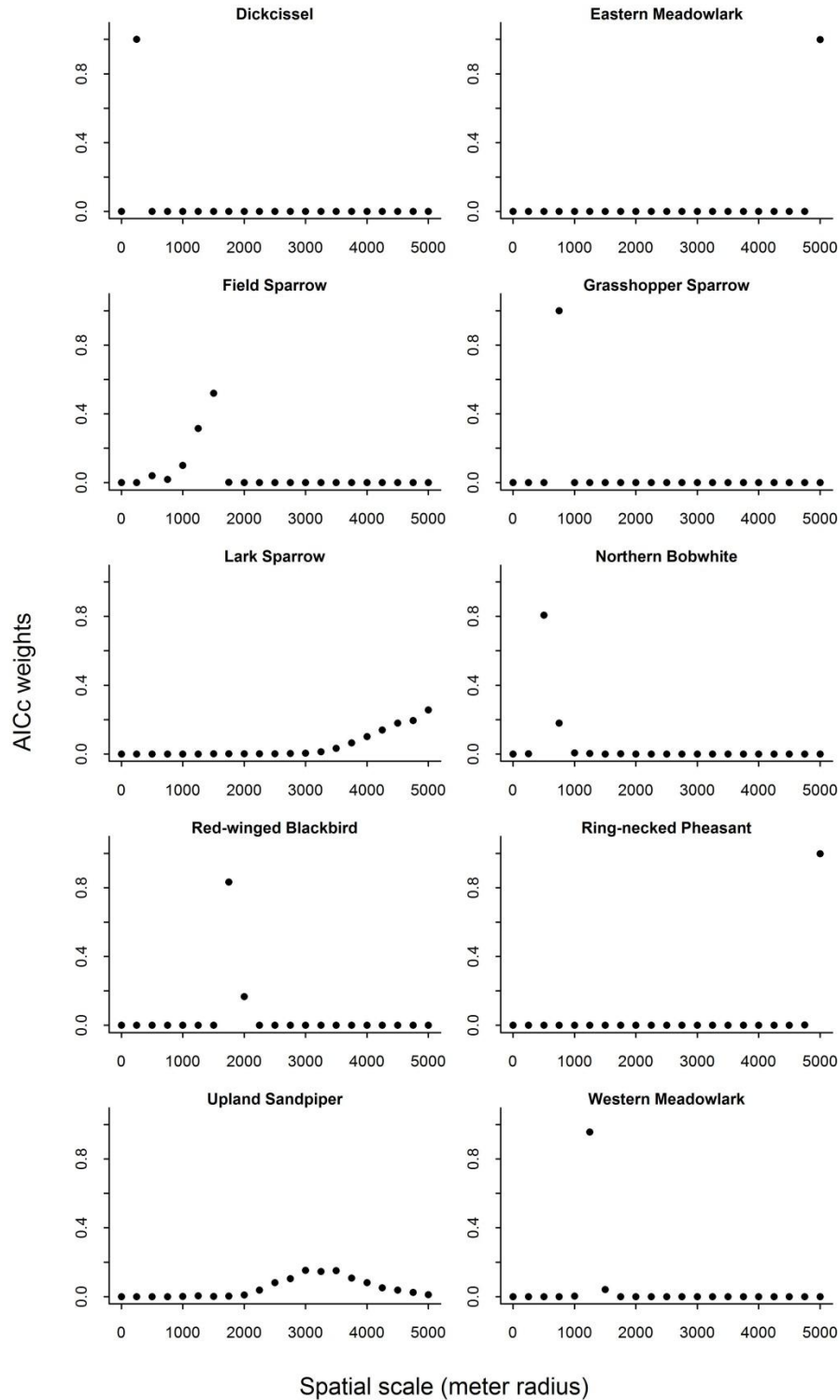


Figure 2. AICc weights of grassland bird abundance for 10 species against cover types measured across 20 spatial scales (250 - 5000 m radii) around each survey site. The null model in each model set, which contains no land cover measurements, is represented at zero on the x-axis.

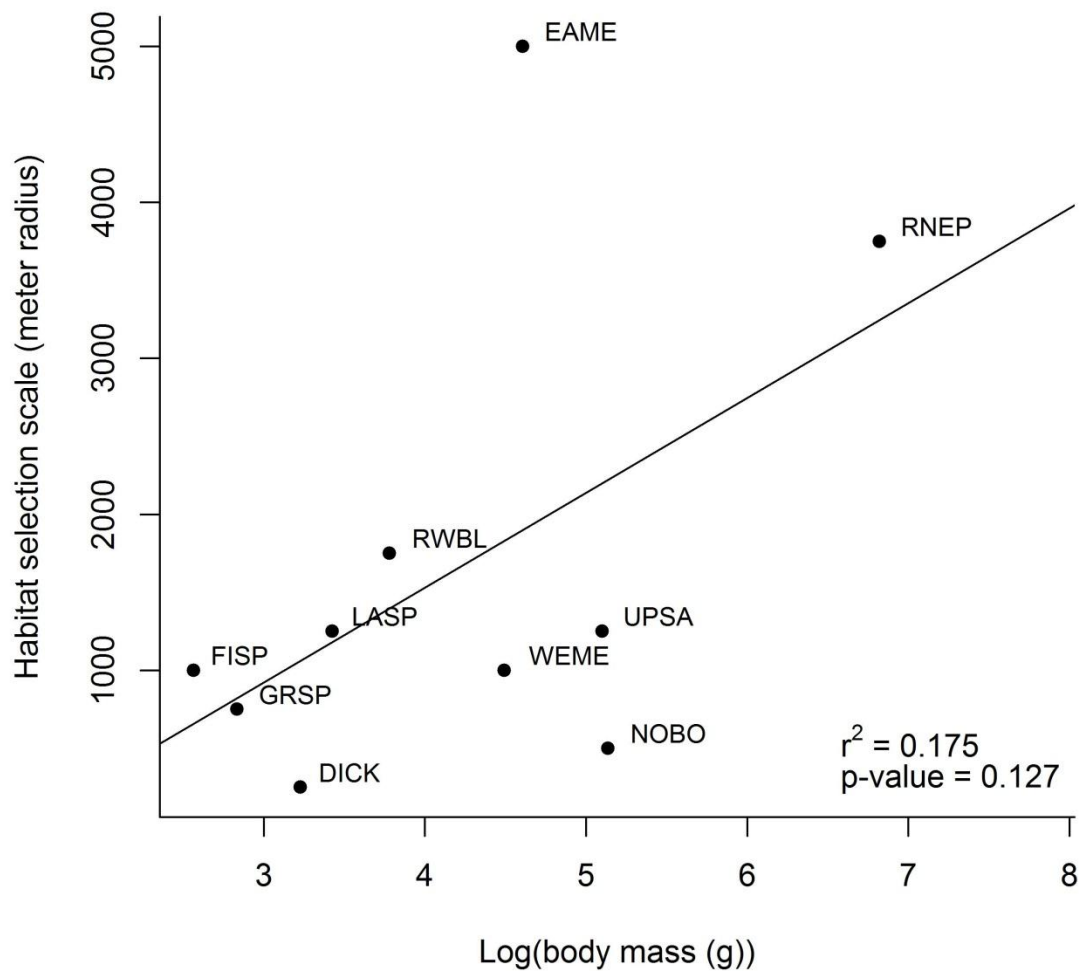


Figure 3. Characteristic scales, based on species occurrence, where not significantly correlated with female body mass. The spatial scale in which species respond to habitat (determined by AICc weight from occupancy models) modeled against the natural log of average female body mass of 10 species of grassland birds.

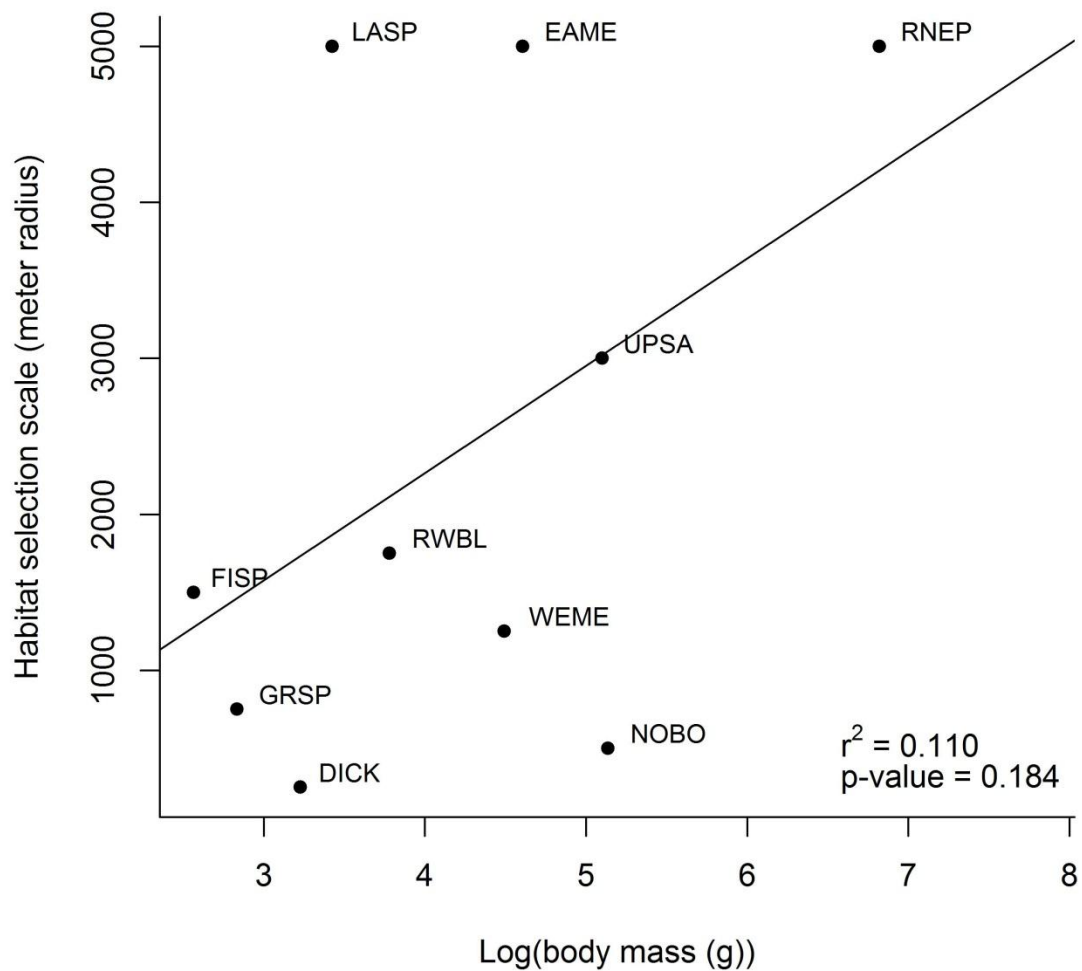


Figure 4. Characteristic scales, based on species abundance, were not significantly correlated with female body mass. The spatial scale in which species respond to habitat (determined by AICc weight from N-mixture models) modeled against the natural log of average female body mass of 10 species of grassland birds.

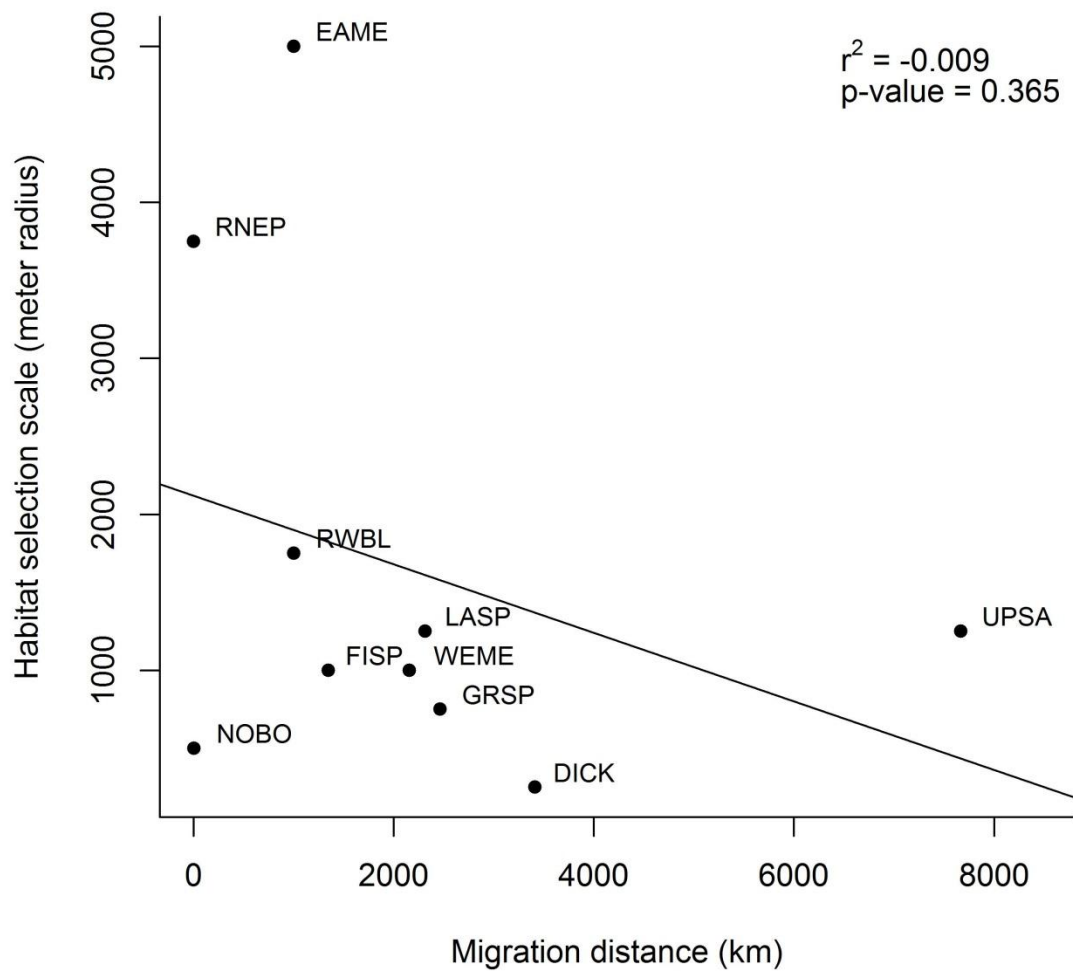


Figure 5. Characteristic scales, based on species occurrence, were not significantly correlated with migration distance. The spatial scale in which species respond to habitat (determined by AICc weight from occupancy models) modeled against estimated migration distance of 10 species of grassland birds.

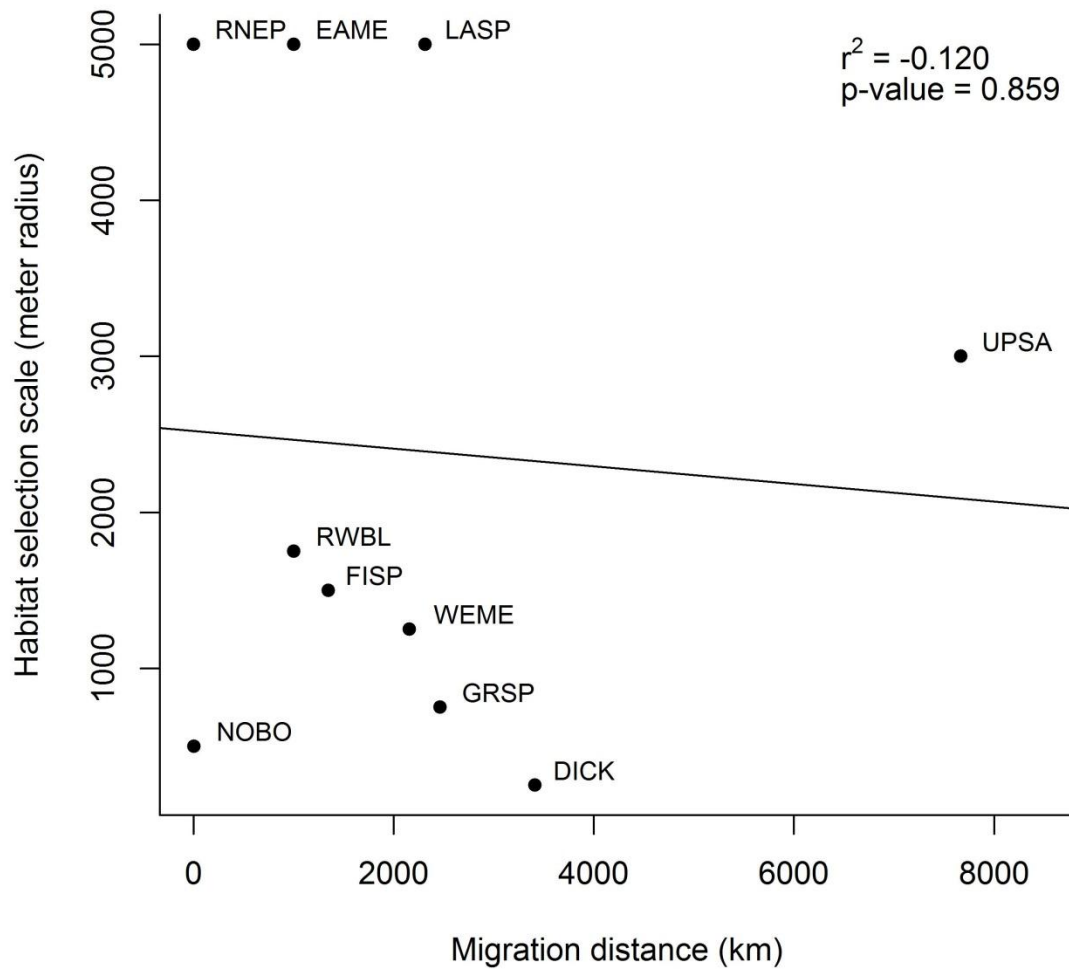


Figure 6. Characteristic scales, based on species abundance, were not significantly correlated with migration distance. The spatial scale in which species respond to habitat (determined by AICc weight from N-mixture models) modeled against the estimated migration distance of 10 species of grassland birds.

Chapter 3: CHOOSING A DIVA: A COMPARISON OF EMERGING DIGITAL IMAGERY VEGETATION ANALYSIS TECHNIQUES

Abstract:

Herbaceous plant structure plays an important role in shaping community composition and thus is widely measured to understand species-habitat relationships. However, traditional ocular techniques for estimating plant structure are subjective, and may introduce measurement error in study designs dependent upon multiple observers or multiple years of data collection. Fortunately, recent advances in digital imagery and processing techniques have led to new methods with the potential to eliminate measurement error, but the precision of these methods remains largely unknown. I assessed the precision of five methods of measuring plant structure using ground-based digital imagery and processing techniques. I recorded vertical herbaceous cover using digital imagery techniques at two distinct locations in a mixed-grass prairie. The precision of five ground-based digital imagery vegetation analysis (DIVA) methods for measuring plant structure was tested using a split-split plot analysis of covariance. Variability within each DIVA technique was estimated using coefficient of variation of mean percent cover. Vertical herbaceous cover estimates differed among DIVA techniques. Additionally, environmental conditions affected the vertical vegetation obstruction estimates for certain digital imagery methods, while other techniques were more adept to handle various conditions. Overall, visual obstruction values differed among techniques, but the precision of four of the five techniques were consistently high indicating that DIVA procedures are sufficient for measuring various heights and

densities of standing herbaceous cover. Moreover, digital imagery techniques can reduce measurement error associated with multiple observer standing herbaceous cover estimates, allowing for greater opportunity to detect patterns associated with vegetative structure.

INTRODUCTION

In terrestrial ecosystems, estimates of vegetative characteristics are an important means of predicting species-habitat relationships (Daubenmire 1959; Wiens 1969; Robel et al. 1970; Wiens 1973; Nudds 1977; Fisher & Davis 2010) with implications to how natural systems are managed (Catchpole & Wheeler 1992; Ganguli et al. 2000; Ammann & Nyberg 2005; Davies et al. 2008). Although collecting and weighing vegetation provides the most precise estimates of vegetative cover, it has limited application in large-scale ecological studies or when destructive sampling is not an option (Harmoney et al. 1997; Benkobi et al. 2000; Vermeire & Gillen 2001). As such, visual obstruction estimates are widely used to quantify plant structure (e.g., Robel et al. 1970) and are successful in a variety of systems (Robel et al. 1970; Ganguli et al. 2000; Vermeire & Gillen 2001; Vermeire et al. 2002; Uresk & Juntti 2008; Schmer et al. 2010; Toledo et al. 2010). Despite their ubiquity, traditional visual obstruction techniques that rely on ocular estimates are often criticized as being unstandardized (Fisher & Davis 2010) and subject to observer error that may mask important ecological patterns (Gotfryd & Hansell 1985; Collins & Becker 2001; Higgins 2005; Limb et al. 2007). A lack of confidence in traditional visual obstruction estimates has led to the development of new techniques using ground-based digital photography (Vanha-Majamaa et al. 2000; Boyd & Svejcar 2005; Limb et al. 2007; Carlyle et al. 2010). Rather than depending upon ocular estimates of vegetation density and structure, digital imagery vegetative analysis (DIVA) techniques often rely upon the ability of computer software to “count” the number of pixels in a digital photograph associated with vegetation and produce a digital estimate of visual obstruction. Analysis of digital imagery from satellite or aerial photography is a

long-standing and common practice in large-scale ecological studies (e.g., Lefsky et al. 2002; Welch et al. 2002; Horning et al. 2010), but DIVA has only recently gained favor as a means to differentiate small-scale vegetative variation (Booth et al. 2005; Booth et al. 2006; Luscier et al. 2006; Seefeldt & Booth 2006; Limb et al. 2007; Cagney et al. 2011). In theory, quantifying visual obstruction by means of digital processing could reduce observer error and increase the accuracy, precision and repeatability of visual obstruction estimates (Booth et al. 2005; Limb et al. 2007).

The DIVA technique has produced remarkably accurate and precise results relative to traditional methods such as the Robel Pole or the NuDDS cover board (Limb et al. 2007) and illustrates the potential for this new technique to become a common method for analyzing vegetative characteristics in ecology. Despite the apparent benefits, the interpretation and classification of digital imagery is susceptible to error from different sources, a number of which are novel in ecological study. For example, differences in cloud cover or overhead vegetation, date or time, and/or camera settings or sensor sensitivity among samples may alter the degree to which shadows and highlights occur, which potentially causes misclassified pixel values. Similarly, light conditions may influence the degree to which pixel values associated with vegetation merge with the backdrop. Such inconsistencies in reflectance can lead to misclassification of pixels by image processing software and severely reduce the accuracy and precision of estimates. Although previous examinations of DIVA techniques have explored the benefits of reduced observer error (e.g. Limb et al. 2007), the importance of other sources of error remain largely unknown. Moreover, the ever expanding number of image processing programs and processing techniques, each with varying levels of cost, effort required, and

degree of accuracy and precision, makes choosing a DIVA approach increasingly challenging. Determining which methods are acceptable and cost efficient is essential if DIVA techniques are to be widely implemented. Here I test five ground-based DIVA techniques to evaluate differences among methods in 1) estimates, 2) measurement error, and 3) time and cost.

METHODS

STUDY SYSTEM AND PHOTO STATIONS

I examined five visual obstruction digital imagery and processing techniques during November of 2010 in a mixed-grass prairie in Lincoln, Nebraska, U.S.A. The study site is located 358 m above sea level and has an average monthly precipitation range of 0.63 – 4.77 in annually. I constructed photo stations using 1 x 1 m backdrops constructed from tempered hardboard (0.476 cm thick, spray painted black) and white fiberglass reinforced wall paneling (Fig. 1). In order to capture sufficient variation in visual obstruction, I randomly placed two pairs of cover boards, each pair containing one black and one white board, in areas with variable grass height. Backdrops were secured vertically in a fixed position, facing south to maximize light exposure. A metal rod was driven into the ground, extending 1 m from the ground and positioned 4 m directly south of each board, creating a permanent reference point to stabilize the cameras (following Robel et al. 1970 and Limb et al. 2007).

I recorded digital images of the standing vegetation in front of the backdrops using four Polaroid® t1031, 10.0 megapixel digital cameras (one camera for each observer) with standardized settings at each of the four photo stations over a two week

period. The locations of the backdrops and the four photo stations remained constant for the duration of the study. Because the vegetation was in senescence the amount of vegetation within the confines of the backdrop was assumed to remain constant throughout the two week period. Four observers visited each photo station 21 times, taking a total of 84 photos. Visits were distributed evenly throughout the day in order to measure the influence of lighting and temporal conditions on estimates. I recorded time of day, wind speed and cloud cover. Images were imported into Adobe Photoshop® CS3 (Adobe Systems Inc, San Jose, CA, US) and cropped such that only the 1 x 1 m backboard was visible in the image (as outlined by Limb et al. 2007).

IMAGE PROCESSING

Image processing was completed using three software programs, Adobe Photoshop® (Adobe Systems Inc, San Jose, CA, US), Intelligent Perception Pixcavator® (Intelligent Perception Co., Huntington, WV, US), and GNU Image Manipulation Program® (GIMP) (Kimball & Mattis 2006, an open-source software package). A total of five DIVA techniques were analyzed: Grid, Photo Training, Threshold, GIMP, and Pixcavator. For each technique I estimated the per photo effort based on time and cost of analyzing 100 photos.

GRID

Using Adobe Photoshop®, I overlaid an evenly spaced 50 x 50 lattice grid on each image and visually determined the number of cells that contained >50% vegetation present (similar to cover board estimates; Jones 1968). Visual obstruction was estimated as the number of cells containing >50% vegetation divided by the total number of cells.

Because of the large degree of time and effort required, I sampled a random subset of 11 of the 21 images per backdrop for a total of 55 images.

THRESHOLD

I followed the threshold method as outlined by Limb et al. (2007), with the addition of using both white and black boards as backdrops. Using the Adobe Photoshop® software threshold function, images were converted to binary form (i.e., either 1 or 0) based on a standardized luminance threshold value of 128, such that all pixels above 128 were converted to white, and all pixels below 128 were converted to black. Photos containing white backdrops converted vegetation to black pixels, while photos with black backdrops converted vegetation to white pixels (Fig. 2). I obtained the percent vegetative cover by placing the cursor over the center of the histogram window in Adobe Photoshop® and recorded the percentage of black pixels comprising the image. For images containing black backdrops, the histogram window provided the inverse of percent vegetative cover; therefore I subtracted the value from 1 in order to obtain the percent cover estimates.

PHOTO TRAINING

I utilized a photo training technique to account for potential variability associated with temporal and environmental factors, which may have inadvertently caused the threshold approach to convert vegetation to the same pixel values as the backdrop, potentially introducing measurement error into the analysis. I used the replace color tool in Adobe Photoshop® to classify, or train the program to identify which pixel values in each photo were associated with vegetation, and which ranges were associated with the backdrop. In order to train the program with minimum effort, I limited the sampling to

five photos randomly chosen from each photo station. With larger photosets, it may be advantageous to include additional photos in a subset in order to sufficiently train the program to differentiate unique vegetation samples from the backdrop. To begin the training process, I selected a photo from one of the photo subsets for each station and imported it into Adobe Photoshop®. With the replace color tool window open and the fuzziness value set to 30 (the fuzziness value sets the degree of tolerance in which the pixel values similar to the values selected will be included in the selection process), I selected vegetation using the eyedropper tool, highlighting areas in the image associated with the value range specific to the vegetation. I selected the remaining vegetation in the photo that was not currently highlighted by using the eyedropper plus tool, accumulating additional color ranges to the selection (Fig. 3). Areas where the backdrop was inadvertently included in the selection were corrected with the eyedropper minus tool by clicking on the region of the image where the error occurred, deselecting the specific pixel value range associated with the backdrop. Once all of the vegetation was included in the selection, I moved the lightness adjustment bar to the left, turning all of the pixels containing value ranges associated with vegetation to black. After all of the vegetation in each image was completely black, the replace color settings were saved to a separate folder as a layer mask. I imported a new photo into Adobe Photoshop® and reopened the replace color tool window. Within the window, the previous layer mask was imported and applied to the current photo by selecting load file. Any unselected pixel values associated with vegetation were added to the previous selection by employing the eyedropper plus tool. Once all of the vegetation in the image was selected and turned black, I resaved the new layer mask containing the newly added pixel values, replacing

the previous file. The procedure for the backdrop was identical except that lightness adjustment bar was moved to the right, ensuring that the pixels comprising the backdrop were completely white. Thus, I ended up with two layer masks, one to classify the backdrop and one to classify the vegetation. The entire process was identical for the black backdrops with the exception that I classified the vegetation as white and the board as black.

Once the layer masks were constructed, I imported a cropped image into Adobe Photoshop® and opened the actions panel. An action is simply a means of applying a technique to an image using a prerecorded series of commands. To create an action, I clicked the ‘record actions’ button in the actions panel. Once the action was recording, I preceded with analysis. I loaded and applied the “replace board” and “replace vegetation” layer masks to the photo via the replace color tool window. I implemented the threshold tool, with a standardized luminance threshold value of 128, to classify any remaining pixel values within the RGB range to black or white. The image was saved to a new folder and closed out of Adobe Photoshop®. I clicked the stop recording button in the action panel, completing the training process. I repeated the procedure creating two actions, one for the white boards and one for the black boards. A droplet was created using the appropriate action for each board color (A droplet enables the user to “drop” entire folders containing multiple images onto the icon, processing each image using an action). For each backdrop color, a new folder was made and filled with the appropriate cropped images. I dropped each folder of cropped images onto their respective droplet, enabling the program to repeat the analysis for every photo within the folder, saving them in binary format to a designated location. I imported each binary photo into Adobe

Photoshop® and recorded the percentage of black pixels utilizing the histogram window (similar to Limb et al. 2007), indicating the percentage of vegetative cover in the image. For images containing black backdrops, the histogram window provided the inverse of percent vegetative cover; therefore I subtracted these values from 1 in order to obtain the percent vegetative cover estimates (Fig. 3).

GIMP

Carlyle et al. (2010) devised a vegetative cover assessment method using the open source image program GNU Image Manipulation Program® (Kimball & Mattis 2006), which I modified to fit the study design. Using the color select tool on each individual image, I selected all pixels that matched the cover board. Different lighting conditions caused the cover board in each image to have a range of black or white hues, so I utilized a similarity threshold of 40.0 (Carlyle et al. 2010) and employed the add to selection option by selecting multiple pixel values in each image. The number of selected pixels was then subtracted from the total number of pixels in each image, resulting in the number of pixels representing vegetation. Visual obstruction was calculated for each image as the ratio of vegetation pixels to total pixels.

PIXCAVATOR

The last approach I tested used Pixcavator IA Standard Edition. Pixcavator identifies edges and objects in images based on changes in value of each pixel. Cropped photos of the black backdrop were selected in the Analysis tab and analyzed in the Green color channel using a Shrink factor of 3 to allow for faster processing. In the Output tab, the settings were reduced to zero for the object size, maximal contrast, border contrast, average contrast, and the intensity, light adjustments. The variable setting was the

Intensity, dark adjustment (Intensity, dark sets the threshold at which all objects are separated into light and dark categories). This value was increased or decreased until the pieces of vegetation were identified as light colored objects or there was enough “false vegetation” to make up for the real vegetation not identified as light. Because Pixcavator analyzes images based on pixel values that are displayed using an RGB presentation, some areas of the board are counted as light objects (e.g. glare). I called this “false vegetation” and tried to minimize its occurrence. The Hide contours and Display channel buttons were helpful when determining when the Intensity, dark was appropriate. When an acceptable level had been reached, the percentage of the total area of dark objects was given in the Review summary section of the output. I recorded the Intensity, dark value and total area of dark objects. The total vegetation coverage was obtained by subtracting the area of dark objects from 100. In some cases, it was necessary to analyze half of a picture at a time in order to reduce the total number of objects within an image. Photos containing the white backdrops were analyzed in a similar manner with the exception that vegetation cover was the total dark area, thus there was no need to subtract from 100.

STATISTICAL ANALYSES

In analyzing the data, my goal was to quantify the variation within DIVA techniques and compare among each. Thus, the variability within each DIVA technique was estimated using coefficient of variation (CV) of mean percent cover. The coefficient of variation is a normalized measure of dispersion from the mean ($CV = \text{standard deviation}/\text{mean}$), which is a particularly useful measurement when comparing the dispersion of two or more variables when their means are substantially different (Shahbaba 2012). For each survey location, a CV of percent obstruction was calculated

for each board color within the analysis technique. CV values were plotted and visually inspected to compare precision among DIVA techniques.

The measurement variability among DIVA techniques and locations was tested using a split-split plot analysis of covariance (Pinheiro & Bates 2000; Pinheiro et al. 2012). Prior to analysis, I assessed normality and applied an arcsine square root transformation on percent cover to help normalize the response variable (normality was met; Gotelli & Ellison 2004). In the model, each black and white board combination was treated as a block, where board color and DIVA technique were considered to be the split-plot and split-split plot respectively.

I considered the Grid method as the null DIVA technique, which has previously been credited by other studies using similar methods to successfully quantify vegetation structure (Jones 1968; Peterson & Cooper 1987; Maxson & Riggs 1996; Coates & Delehanty 2010; Fisher & Davis 2010). I used a random intercept model parameterization at each of the block, split-plot, and split-split plot levels to account for the nesting of the experimental design (Pinheiro & Bates 2000). Because board color (split-plot) and DIVA technique (split-split plot) were nested as random effects inside block, I was also able to consider them as fixed effects in trial models to test for systematic differences in percent cover (Pinheiro & Bates 2000). I added environmental and temporal variables to the model as fixed effects, specifying time of day, wind speed, and Julian date as continuous variables and cloud cover as a factor with three levels (sunny, partly sunny, and cloudy). I included two-way interactions between DIVA techniques and environmental and temporal conditions. Non-significant terms and interactions from trial models were excluded from the final model. Post-hoc two-way

comparisons of DIVA techniques were conducted using Tukey's honest significance test (Hothorn et al. 2008). All statistical analyses were done using R (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

The DIVA techniques provided different estimates of percent cover, even after accounting for nested effects in the study design (DIVA: $F_{4,12}=22.34$, $P<0.001$).

Environmental effects of cloud cover did not have an effect on percent cover estimates (cloud cover: $F_{2,350}=2.15$, $P=0.12$), but the interaction between DIVA technique and cloud cover was statistically significant (DIVA * cloud cover: $F_{8,350}=2.05$, $P=0.04$; Table 1).

Of the five DIVA techniques, the Threshold method had the lowest mean percent cover estimate after accounting for variation in the random and fixed effects, and differed significantly from the other methods, but there were no differences among the other four methods (Table 2; Fig. 4).

Within each DIVA technique, the Threshold method performed the worst, with the highest averaged CV values of 27.87% and 58.56% for the black and white backdrops respectively. The Pixcavator method had the lowest average CV values of 5.74% and 5.65% for the black and white backdrops (Fig. 5). Levels of variation (CV) did differ among cover estimates from the Photo Training, Pixcavator, GIMP, and Grid methods, but each performed better than the Threshold method, with average CV values below 20% (Fig. 5).

Cost of the software packages varied significantly by DIVA technique (Table 3). Of the five techniques, the GIMP and the Grid methods were the most cost effective, utilizing open-source software packages such as the GNU Image Manipulation Program. The Photo Training technique was the most expensive method, costing roughly \$700 (USD) for the full Adobe Photoshop license. However, a month-to-month license can be purchased from Adobe for a more economical approach (\$49 per month).

Field measurements and photo cropping were rapid, about 90 seconds per photo, but the per photo processing time based on a batch size of 100 photos varied greatly among DIVA techniques (Photo Training ~0.6 sec.; Threshold 1 min.; GIMP 1-3 min.; Pixcavator 2-3 min.; Grid 10-15 min.).

DISCUSSION

Although visual obstruction estimates varied among the five image processing techniques in the study (Fig. 4), all but the Threshold technique measured visual obstruction consistently, regardless of backdrop color or vegetation height (Fig. 5). Low measurement variation is ideal for multi-year studies, eliminating the variability associated with multiple observers and ocular estimation. However, DIVA estimates were sensitive to lighting conditions as noted by the significant effects of the interaction between DIVA technique and cloud cover, which may lead to the high CV values for some approaches (Fig. 5). Shadows increase measurement variation by introducing overlap between vegetation and backdrop pixel values. Using a set value for the threshold function within the Adobe Threshold technique made it especially sensitive to lighting conditions as overexposed photos were prone to misclassify vegetation as non-

vegetation on white backboards and underexposed photos were prone to misclassify the backboard as vegetation. The similar but opposite pattern occurred if the backboard was black instead of white. The level of error associated with the threshold technique is somewhat surprising given that others have found it reliably predicts clipped herbaceous biomass (Limb et al. 2007), but the previous work controlled for environmental and temporal variation by recording all images in “rapid sequential order” (Limb et al. 2007), an approach which is highly impractical in field studies. Because the analysis was done across a range of conditions, the use of a set threshold caused pixel values associated with vegetation (or the backdrop) to shift back and forth over this value, increasing the measurement error (Fig. 5). Other image processing techniques, such as the Pixcavator, Photo Training, and GIMP methods, were better equipped to handle variable light conditions by allowing the user to correct for the level of exposure.

Tradeoffs between precision and processing time are important to consider when choosing any sampling method as available time and resources may limit processing choices. Fortunately, with the exception of the threshold technique all the DIVA methods I tested were relatively precise, enabling users to focus on the time and costs constraints associated with each methodology. Not surprisingly, at up to 15 minutes per photo, the Grid method was the most time consuming, but it was also the easiest of the techniques to explain to personnel. Moreover, although I used Adobe Photoshop, this method could be implemented in a variety of software packages, some of which are inexpensive or even free (*i.e.*, Adobe Photoshop Elements 10; GNU Image Manipulation Program (GIMP); PhotoScape Image Editing Software 3.5). The Pixcavator method was considerably faster (2-3 minutes per photo), but did require more time to learn and is

dependent on a for-cost software package (Intelligent Perception Pixcavator®, \$29/mo). The Threshold and GIMP techniques were faster yet, averaging 1 min per photo, but low precision made the Threshold technique undesirable. By contrast, the GIMP technique was precise and also the least expensive of the DIVA methods as the GNU Image Manipulation Program® is available online as a free, open-source software package. Maybe the most interesting of the DIVAs from a logistics perspective was the Photo Training technique. Although it was dependent on costly software (Adobe Photoshop CS5®, ~\$700), by automating the photo analysis process and utilizing batch-processing techniques, the Adobe Photo Training method took considerably less time and was capable of making precise estimates of percent cover at a rate of 100 photos per minute. Automation enabled the software to analyze the entire folder of cropped photos in a matter of seconds, making it convenient for the investigator to quickly open the image in Adobe Photoshop®, click on the histogram and identify the percent cover. The capability to analyze numerous photos rapidly may be particularly advantageous for large studies, but it is important to note that less expensive versions of Photoshop (Adobe Photoshop Elements 10, ~\$100) do not have the capability to allow the user to record “actions” for batch processing which adds considerable time to processing large numbers of photos.

In addition to processing approaches, field implementation is also important to successfully record visual obstruction. The size, shape and construction of backdrops must be considered prior to field work. A black or white 1 x 1 m board was sufficient for the study design and was capable of quantifying a range of vegetation heights associated with mixed-grass prairie. In other systems it may be more appropriate to use smaller or larger board sizes depending on vegetation height and the variation in height among

samples. Rigidity is also important, as a rigid backdrop can be propped upright on a set of posts, enabling the investigator to quickly move to and from each survey plot. In addition, a rigid backdrop minimizes shadows caused by sagging of the top edge and is capable of surviving being carried through thick vegetation over a course of multiple field seasons. A white fiberglass reinforced wall paneling was excellent at maintaining its structural integrity throughout the investigation and was completely waterproof. On the other hand, tempered hardboard was more prone to warping when wet and dried repeatedly. Other studies have used bed sheeting (Limb et al. 2007) or painted plywood (Boyd & Svejcar 2005) as effective backdrops, but these may be more or less mobile depending on the type of vegetation.

The techniques outlined in this study are a sample of the potential ways to analyze visual obstruction using digital processing techniques (see Booth et al. 2005; Booth et al. 2006; Lusnier et al. 2006; Seefeldt & Booth 2006; Cagney et al. 2001), of which many are suitable for estimating vegetation quickly and effectively. My results suggest that the multiple techniques assessed in this study are sufficient for measuring visual obstruction in a variety of grassland ecosystems. By using DIVA techniques to estimate visual obstruction, error commonly associated with multiple observer visual obstruction estimates can be reduced greatly. Minimizing variation will allow greater opportunity to detect patterns associated with vegetative structure and increase the power of a study.

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TABLES AND FIGURES

Table 1. A split-split plot analysis of covariance (ANCOVA) table.

Variable	Numerator <i>df</i>	Denominator <i>df</i>	F-value	p-value
intercept	1	350	32.2098	<.0001
DIVA technique	4	12	22.34465	<.0001
cloud cover	2	350	2.15094	0.1179
DIVA technique:cloud cover	8	350	2.05396	0.0397

Table 2. A Tukey *post-hoc* multiple comparison test indicates that the Threshold method provides significantly different estimates of percent vegetative cover when compared to the rest of the DIVA techniques.

Comparison	Estimate	Std. Error	z value	value	Pr(> z)
GIMP - Grid	0.04653	0.04729	0.984	0.04653	0.863
Pix - Grid	0.01167	0.04729	0.247	0.01167	0.999
Thresh - Grid	-0.30311	0.04729	-6.41	-0.30311	<0.001
Train - Grid	0.08229	0.04729	1.74	0.08229	0.409
Pix - GIMP	-0.03486	0.04546	-0.767	-0.03486	0.94
Thresh - GIMP	-0.34964	0.04546	-7.692	-0.34964	<0.001
Train - GIMP	0.03576	0.04546	0.787	0.03576	0.935
Thresh - Pix	-0.31478	0.04546	-6.925	-0.31478	<0.001
Train - Pix	0.07062	0.04546	1.554	0.07062	0.527
Train - Thresh	0.3854	0.04546	8.478	0.3854	<0.001

Table 3. The software packages options and estimated costs (U.S. Dollars, February 2012), as well as the processing time of the five digital imagery vegetation analysis (DIVA) techniques.

DIVA Technique	Software Options	Software Cost	Minutes per 100 photos	Batch processing
GIMP	GNU Image Manipulation Program	\$0	100	No
Grid	Adobe Photoshop Elements 10	\$0	1500	No
	GNU Image Manipulation Program	\$0		No
	PhotoScape Image Editing Software 3.5	\$100		No
Photo Training	Adobe Photoshop CS5	\$700*	~ 1	Yes
Pixcavator	Intelligent Perception Pixcavator	\$300*	200	No
Threshold	Adobe Photoshop Elements 10	\$100	100	No
	Adobe Photoshop CS5	\$700*		Yes

*Monthly license available



Figure 1. An example showing the metal rod placement and backdrop set-up for a digital imagery vegetation analysis.

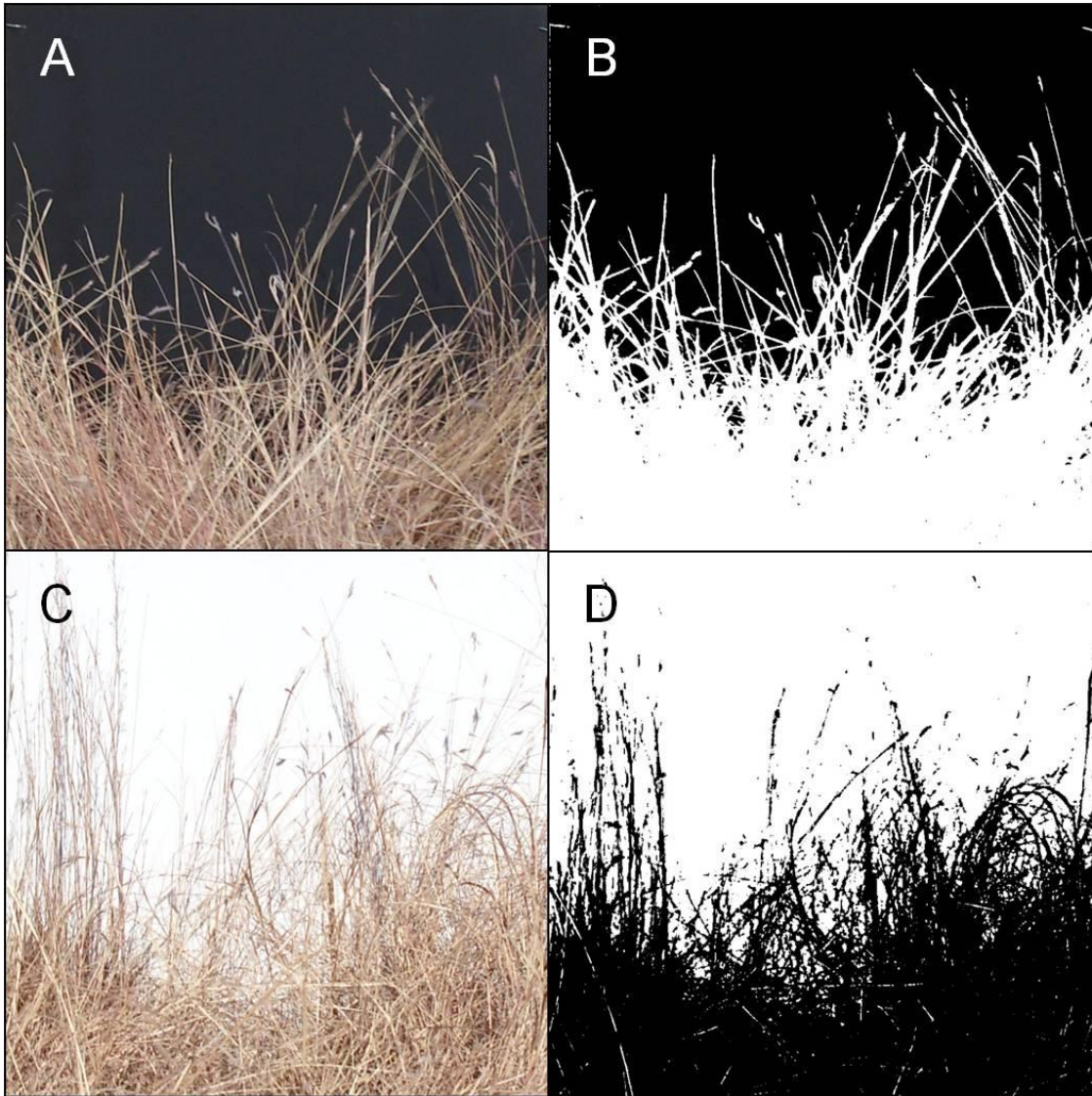


Figure 2. An example of two digital images, black backdrop (A) and white backdrop (C), and their respective binary images (B and D) which were converted using digital imagery vegetation analysis (DIVA) techniques.

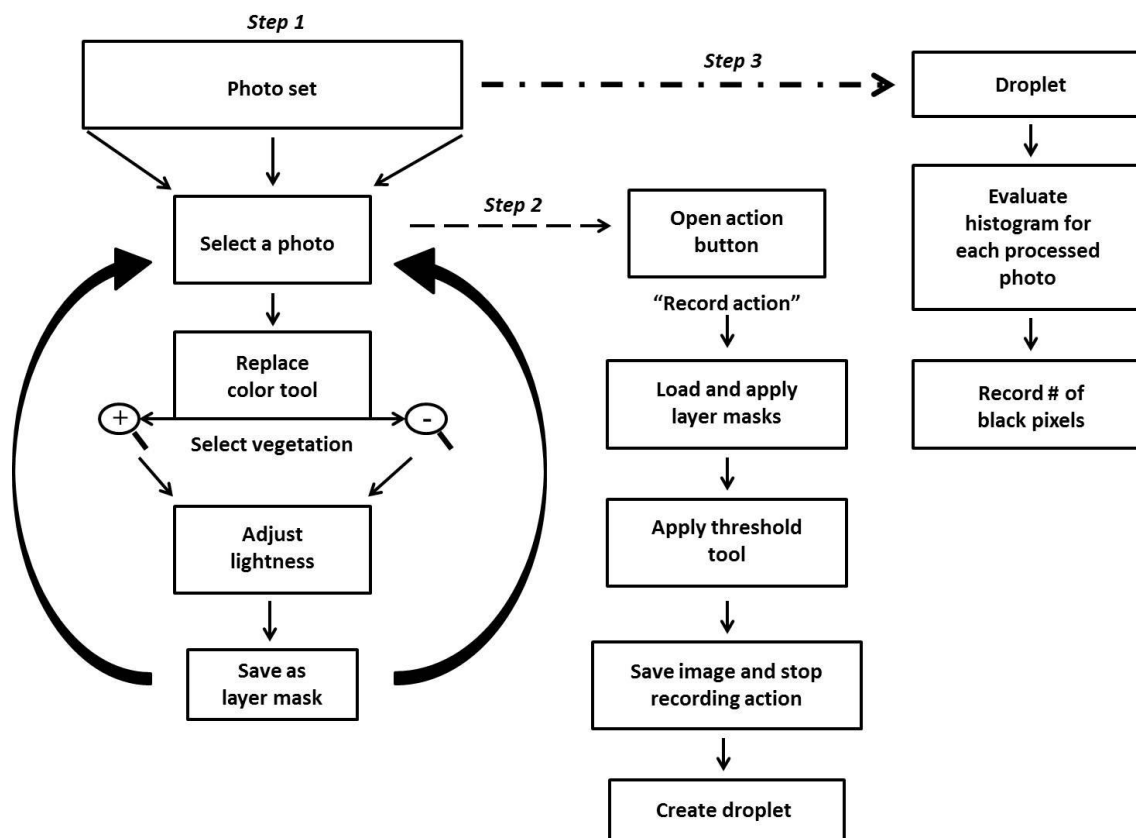


Figure 3. The flowchart describes the process of creating a layer mask, adjusting the image and developing a droplet for batch processing while using the photo training technique to estimate percent vegetative cover. Readers may refer to Adobe Photoshop's help document for additional instruction on the *replace color* tool, recording *actions*, and developing *droplets*.

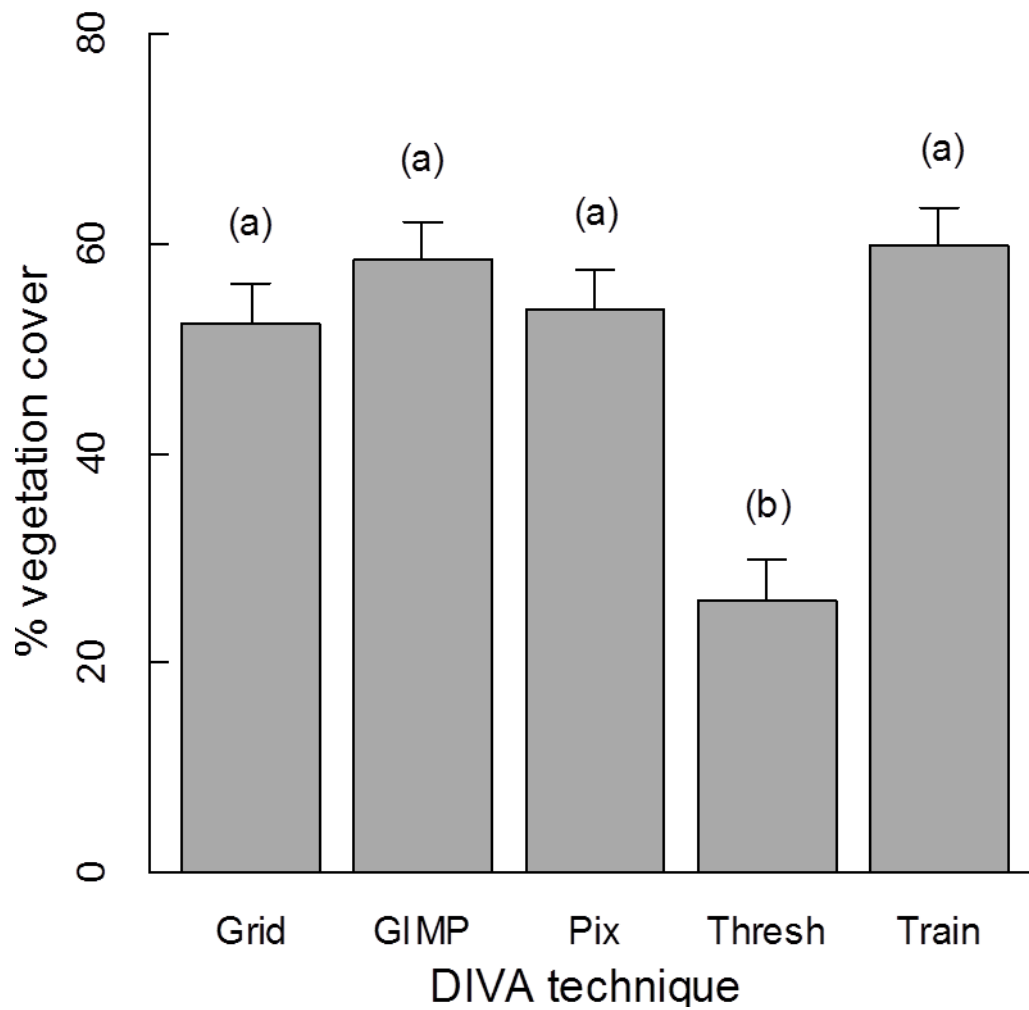


Figure 4. Percent vegetation cover estimates differed among the digital imagery vegetation analysis (DIVA) techniques. Columns represent the estimated marginal means after controlling for nested random effects in the study design and variation in cloud cover. Columns denoted by different letters are significantly different at the 0.05 level according to a Tukey *post-hoc* multiple comparison test.

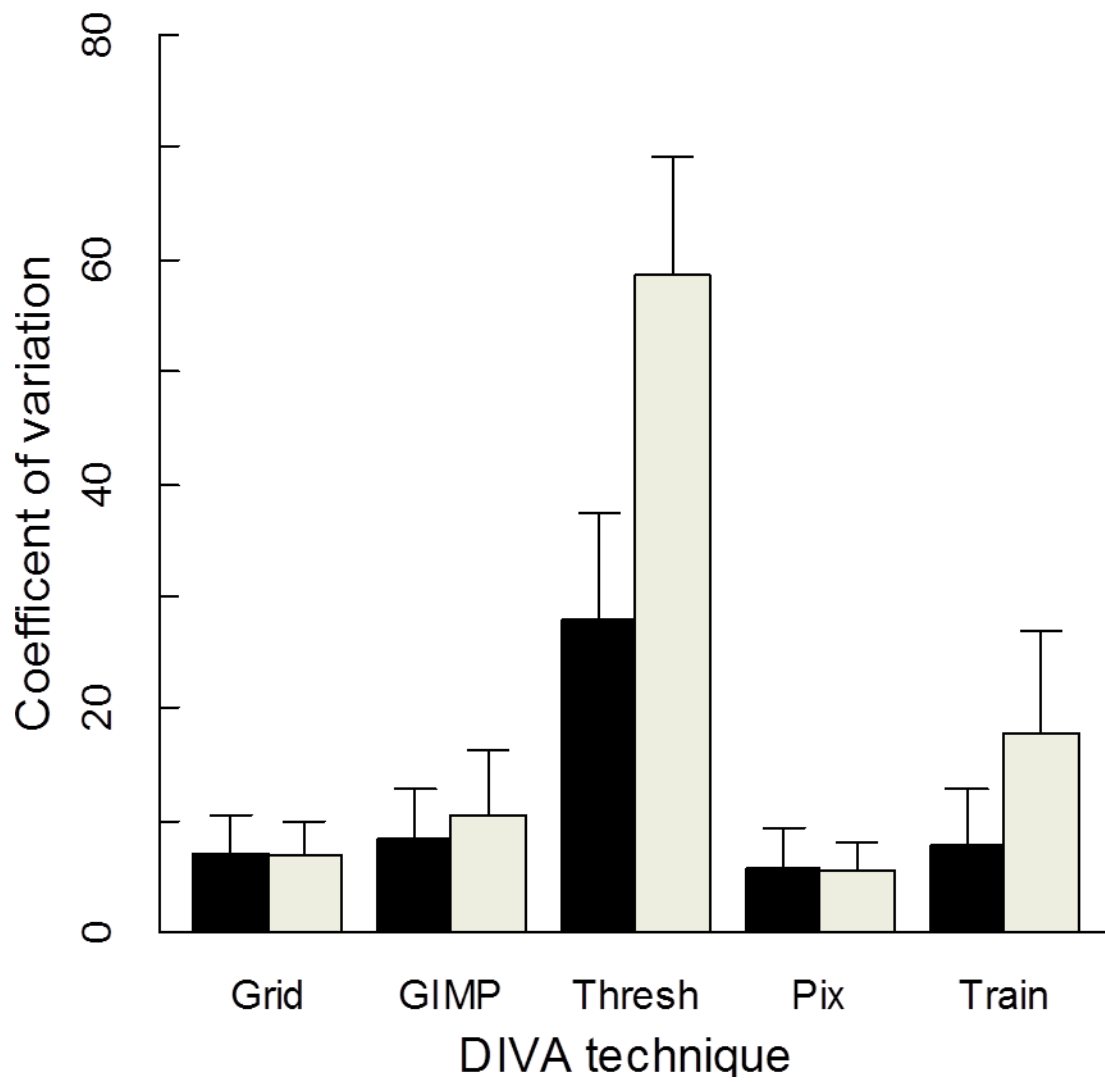


Figure 5. The amount of variation within the Threshold method was considerable and differed between digital imagery vegetation analysis (DIVA) techniques and backdrop colors. Columns represent the coefficient of variation (CV) in percent vegetative cover estimates for each DIVA technique and backdrop color (black bars = black backdrop, grey bars= white backdrop).