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Simonsen, Victoria L. and Fontaine, Joseph J., "Landscape Context Influences Nest Survival in a Midwest Grassland" (2016). *Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications*. 226.
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Research Article

Landscape Context Influences Nest Survival in a Midwest Grassland

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ABSTRACT Although the management and restoration of habitat is the key method to conserve species of interest, local habitat management often fails to elicit desired responses in populations. Landscape features beyond the local habitat scale affect the population dynamics of ring-necked pheasants (*Phasianus colchicus*), but the mechanism behind this response is unknown. One possibility is that nest survival, which is primarily reduced by nest predation, is regulating pheasant responses to the landscape. We investigated the extent to which land use affected nest survival by studying 202 artificial nests on 12 Conservation Reserve Program (CRP) fields in Nebraska, USA with varying surrounding land-use practices. After running a hierarchical analysis of competing models, we found that predicted nest survival increased as the amount of CRP, winter wheat, and pastureland surrounding a CRP field increased, whereas increasing fallow fields was correlated with decreased nest success. Our findings support theoretical and empirical evidence that nest predation rates are shaped by predator search efficacy. Changing the relative availability of nesting habitat that potentially holds alternative prey sources in our study affected nest survival rates, possibly by altering the search area of opportunistic nest predators. The similarities between the landscape relationships that predict nest survival and landscape predictors of pheasant abundance indicate that nest survival may potentially act as the mechanism shaping population dynamics within an ever changing farmland ecosystem. We recommend that managers consider the land use surrounding areas under consideration for habitat improvement to enhance conservation investments. © 2016 The Wildlife Society.

KEY WORDS habitat, landscape context, nest predation, ring-necked pheasant, species distribution, success.

Habitat restoration and management is a fundamental component of wildlife sciences and is often identified as the primary means of increasing wildlife populations (Leopold 1933, Wiens 1995, Didier and Porter 1999, Sinclair et al. 2006). Consequently, policy decisions and management actions of wildlife organizations are often focused on altering local vegetation conditions to meet the habitat needs of species of management concern (Midwest Pheasant Study Group 2013). Unfortunately, although managers are highly successful in creating local habitat conditions with suitable vegetation structure and composition, habitat management too often fails to elicit desired responses in wildlife populations and falls short of management expectations (McCoy et al. 1999, Henningsen and Best 2005, Rahmig et al. 2008). In grassland and farmland ecosystems, for example, the management of early successional grasslands is identified as key to ensuring viable populations of upland gamebirds (Patterson and Best 1996, Robertson 1996, Rodgers 1999).

Federal policy, state management plans, and the directives of non-governmental organizations often focus on local management actions (e.g., discing and interseeding, burning, spraying) aimed at resetting succession with the expressed purpose of improving gamebird populations. Although there is certainly evidence that local grassland conditions affect populations of upland gamebirds (Davis 2005, Lusk and Koper 2013), populations of most gamebird species continue to decline despite increasing directives toward improving local habitat conditions (Nielson et al. 2006). Given the effort of wildlife managers, the economic costs to participating private landowners, and the increasing frustration of stakeholders, there is a need to identify why apparently suitable habitat management actions can fail to improve gamebird populations.

Increasingly, evidence suggests that ecological conditions acting beyond the scale of local management actions may limit management success (Robertson 1996, Rahmig et al. 2008). Although local grassland conditions affect grassland bird communities by altering habitat-selection decisions (Dieni and Jones 2003, Fisher and Davis 2010), population density (Haensly et al. 1987), survival (Davis 2005, Lusk and Koper 2013), and even productivity (Duebber and Kantrud

Received: 4 November 2015; Accepted: 29 February 2016

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1974, Robertson 1996), land-use practices and land cover beyond the local habitat patch can also influence the behaviors and life history of grassland birds (Best et al. 2001, Cunningham and Johnson 2006). For managers, accurately assessing the relationships between population responses and the surrounding landscape and land-use practices is a crucial component of management and conservation success (Guisan et al. 2006). For example, the availability of grasslands enrolled in the Conservation Reserve Program (CRP) influences the local and regional abundance of ring-necked pheasants (*Phasianus colchicus*; Midwest Pheasant Study Group 2013), and more recent evidence suggests that other land-cover types may act at a landscape scale to promote or constrain pheasant populations (Jorgensen et al. 2014). By recognizing how landscapes shape pheasant abundance, managers can direct management actions toward landscapes where the benefits of local management actions may be the greatest (Guisan et al. 2006).

Despite an increasing awareness that wildlife populations, and specifically upland gamebird populations, are in part regulated by landscape conditions, in many cases the ecological mechanism influencing these patterns remains unknown. Previous work has reported that pheasant populations positively respond to increasing proportions of CRP, grasslands, small grains crops (winter wheat and sorghum), and row crops (e.g., corn and soybeans) in the landscape (Jorgensen et al. 2014). We set out to test whether nest predation may be the mechanism regulating pheasant population responses to landscape conditions. Nest predation is the primary cause of reproductive failure for most bird species (Ricklefs 1969, Martin 1995) and a key component of population dynamics for species with short lifespans such as pheasants (Martin 1995, Stephens et al. 2005). Although local nest site characteristics are clearly important in regulating nest predation risk for grassland birds (Martin 1993, Chalfoun and Martin 2009), including pheasants (Eggebo et al. 2003), conditions at larger ecological scales (e.g., patch size, amount of grassland habitat) also influence nest predation rates in grassland systems (Winter and Faaborg 1999, Riley and Schulz 2001, Stephens et al. 2005). Our objectives were to assess whether landscape conditions surrounding a CRP field affect nest predation rates and reflect landscape conditions predicted to shape populations of pheasants in Nebraska.

STUDY AREA

The study took place in the Southwest Focus on Pheasants Area, a priority pheasant management area encompassing 1,062 km² of Hitchcock and Hayes counties, Nebraska. Lying on the transition between mixed- and short-grass prairies, the region consisted of flat to gently rolling topography, regularly interspersed by canyons. Elevation ranged from 650 m to 1,000 m, mean monthly temperature from -4°C to 24°C and annual precipitation averaged 50.5 cm (National Centers for Environmental Information, www.ncdc.noaa.gov, accessed March 2016). The mix of sandy and loamy soils and semiarid climate supported large

expanses of native rangelands and a diversity of irrigated and dryland crops including corn, soy, winter wheat, and sorghum. There were a number of CRP fields in the area also, generally dominated by native vegetation including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and a diversity of forbs. The diverse landscape matrix along with the high density of CRP fields provided an opportunity for us to select CRP study sites within landscapes ranging from predominately pastureland to primarily cropland (see Fig. S1, available online at www.onlinelibrary.wiley.com). Study sites consisted of 12 CRP fields ranging in size from 8.4 ha to 124.2 ha and the surrounding landscapes within a 2-km-radius of the CRP fields, which is an order of magnitude larger than an average female pheasant's home range in the region (Riley et al. 1998, Williams et al. 2003). We selected the 2-km-radius buffer to ensure that the spatial scale was reflective of population-level ecological conditions of predators and prey.

METHODS

Artificial Nests

Using artificial nests as a proxy to assess nest predation risk, we conducted 2 trials in spring 2013, 1 in May and 1 in June. Each trial lasted 21 days, a period representative of incubation for pheasants. At each study site, we placed 6–8 artificial nest bowls in randomly selected locations within the field. We formed artificial nest bowls using grass collected from the surrounding area to resemble a pheasant nest. To minimize the effects of nest site selection on nest predation rates, we placed all nests bowls on the ground under the cover of little bluestem and used 4 brown chicken eggs as bait. We did not use scent-masking methods because scent masks do not affect depredation rates (Donalby and Henke 2001). We checked nests every 4 days to record depredation events (broken eggs or eggs removed from the nest). At 5 nests in each study site, we identified nest predators using game cameras (Bushnell Trophy Cam HD; Bushnell Corporation, Overland Park, KS, USA) attached to stakes at a height of 30 cm and 1 m from the nest.

After a nest was depredated, or the 21 days of the trial concluded, we measured the vegetation structure and cover of each nest site according to BBIRD Field Protocol (Martin et al. 1997). If a nest was depredated before the 21 days of the trial concluded, we placed a new nest in a new random location in the same field to maintain the nest density of the study site throughout the trial because nest density of artificial and real nests influences nest predation rates (Haensly et al. 1987, Martin 1988). At the end of the 21-day trial, we removed all nests.

Artificial nests do not always adequately replicate real nests; therefore, researchers must carefully consider how they are used and the assumptions surrounding their use (Major and Kendal 1996, Moore and Robinson 2004, Fontaine et al. 2007). To improve experimental validity, we designed nests to replicate pheasant nests in size, shape, substrate, and material, and monitored nests to ensure that the artificial nest

predator community represented known pheasant nest predators (Riley and Schulz 2001, Frey et al. 2003, Moore and Robinson 2004, Thompson and Burhans 2004). Additionally, the eggs used were typical of the size, shape, and color of pheasant eggs and did not limit our predator community (Major and Kendal 1996). We chose sites for artificial nests that mimicked real nests as closely as possible based on experience in the system and extensive literature review on pheasant nest site selection (Clark et al. 1999, Matthews et al. 2012). Any biases should be similar across our study sites and, therefore, we assumed that any observed differences in nest predation rates reflected inherent differences in risk. Finally, we are not suggesting that artificial nests represent real nests (Sieving and Willson 1998); however, for examinations of environmental risk, artificial nests have value (Fontaine et al. 2007). Real nests vary by site choice and female activity, which affect nest predation risk and can potentially conceal the effects of inherent environmental risk (Fontaine et al. 2007). Because we were primarily concerned with assessing how landscape conditions influence nest survival, not female behavior, artificial nests allow for more accurate comparisons of how ecological conditions are acting at the landscape level.

Land-Use Surveys

To determine the number of hectares dedicated to each land use surrounding the study sites, we conducted visual surveys of neighboring fields within the 2-km radius of each study site. We waited to conduct the surveys until the second trial period to ensure proper land-use identification. We recorded land-use practices on aerial images during surveys and then digitized boundaries in ArcMap (ESRI, Redlands, CA, USA) to create polygons that represented each field within the 2-km buffer. We calculated the area devoted to CRP, winter wheat, row crops (active corn and soybean), pastureland, and fallow fields (unplowed fields left idle since harvest), and used the total proportion of the area dedicated to each land-use practice as predictor variables in subsequent models.

Data Analysis

We were primarily interested in how landscape attributes affected nest success, but nest success is affected by a wide variety of attributes. To account for sources of variation in

nest success beyond landscape variables, we incorporated covariates into the models in a hierarchical manner whereby we tested and built upon base models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) to determine model fit at each step (Burnham and Anderson 1998, Stephens et al. 2005, Symonds and Moussalli 2011). Given seasonal patterns in nest success (Fields et al. 2006, Kerns et al. 2010, Decker et al. 2012, Lusk and Koper 2013), we first tested 4 alternative models (null, date, trial, date + trial) to account for seasonal variation in nest survival. The covariates in these models were the trial period (trial) and Julian date of nest placement (date). Next, because local vegetation characteristics influence nest survival (Davis 2005, Lusk and Koper 2013), we ran a second set of 4 models to account for variation in nest success as a result of the local environment. We used the averages of the 5 estimates of visual cover (cover) and height of vegetation (height) that we measured at each nest as covariates for individual nest sites, with the top model from the first analysis used as the null model for the second analysis.

The last set of models assessed the landscape covariates. Our methods of recording land use led to the collection of a suite of potentially correlated, partially redundant covariates reflecting various characteristics of land cover (Graham 2003). To avoid multi-collinearity (Tabachnick and Fidell 2007), which can limit the accuracy of regression models (Brauner and Shacham 1998), we excluded predictor variables that were correlated with each other (i.e., $|r| > 0.7$; Green 1979, Dormann et al. 2013). Of collinear pairs, our selection criteria preferred variables in the following sequence: 1) ecologically relevant; 2) feasible to collect; 3) measured with low error; and 4) closer to the mechanism (Harrell 2001, Austin 2002). Therefore, our models in the third analysis included the proportion of CRP, winter wheat, pastureland, corn and soybean cropland, and fallow land within the CRP field and the 2-km buffer as covariates, as well as the size of the CRP study site. We ran each unique combination of these 6 covariates with the new null model, which was the top model from the second analysis. We ran all models in Program MARK (White and Burnham 1999, Dinsmore et al. 2002).

Table 1. Area of each study site (ha), total area of the study site and 2-km-radius buffer (ha), and percent of each of the land-use type within a 2-km-radius buffer in southwestern Nebraska, 2013.

Study site	Area (ha)	Area studied (ha)	% CRP	% wheat	% pasture	% row	% fallow
1	31.9	1,760.3	9	12	32	11	13
2	16.1	1,651.8	20	0	38	29	4
3	42.1	1,849.9	16	12	33	12	4
4	124.2	2,354.4	7	20	28	20	17
5	49.6	1,873.2	10	9	49	11	0
6	58.8	1,972.2	10	13	44	7	8
7	50.8	2,128.2	7	11	38	28	6
8	50.5	1,943.5	4	4	41	19	5
9	8.4	1,502.9	8	14	7	30	18
10	61.9	1,955.2	2	6	34	10	9
11	32.7	1,815.0	19	4	6	23	5
12	59.2	1,925.2	15	18	12	18	3

Table 2. Models with respective Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c , model weight (w), model likelihood, number of parameters (K), and deviance used to examine survival of artificial ring-necked pheasant nests in southwestern Nebraska, USA, 2013. Our first set of models accounted for temporal variation in nest survival using the covariates of Julian date of nest placement (date) and trial period (trial). The second set accounted for local habitat conditions using the covariates average percent visual cover of the nest (cover) and average height of vegetation (height). Finally, we examined the influence of 5 different land-use types on nest survival using the proportion of the 2-km-radius buffer dedicated to Conservation Reserve Program fields (CRP), pastureland (pasture), winter wheat fields (wheat), corn and soybean fields (row), and fallow fields (fallow). We also incorporated the size of the study site (field) into the third analysis to account for variation in the size of the CRP fields. Because of the large number of models in the third analysis, we only listed the top 10.

Analysis and covariates	AIC_c	ΔAIC_c	w	Likelihood	K	Deviance
Temporal variation						
Date + trial	494.74	0.00	1.00	1.00	3	488.73
Null	517.16	22.41	0.00	0.00	1	515.15
Trial	517.42	22.67	0.00	0.00	2	513.41
Day	519.16	24.41	0.00	0.00	2	151.15
Local habitat conditions						
Trial + date + cover + height	491.87	0.00	0.44	1.00	5	481.85
Trial + date + cover	492.81	0.93	0.28	0.62	4	484.79
Trial + date + height	493.91	2.04	0.16	0.36	4	485.90
Date + trial	494.74	2.87	0.11	0.24	3	488.74
Landscape						
Trial + date + cover + height + CRP + wheat + pasture + fallow	429.05	0.00	0.31	1.00	9	410.98
Trial + date + cover + height + CRP + wheat + pasture + fallow + field	430.00	0.95	0.19	0.62	10	409.92
Trial + date + cover + height + CRP + wheat + pasture + row + fallow	431.03	1.98	0.11	0.37	10	410.95
Trial + date + cover + height + wheat + pasture + row + fallow + field	432.01	2.96	0.07	0.22	11	409.91
Trial + date + cover + height + wheat + pasture + fallow	432.87	3.81	0.04	0.14	8	416.81
Trial + date + cover + height + wheat + pasture + row + fallow	433.78	4.73	0.02	0.09	9	415.71
Trial + date + cover + height + CRP + wheat + pasture + field	433.82	4.77	0.02	0.09	9	415.75
Trial + date + cover + height + CRP + pasture + field	434.37	5.31	0.02	0.07	8	418.31
Trial + date + cover + height + wheat + fallow	434.67	5.61	0.01	0.06	7	420.62
Trial + date + cover + height + CRP + wheat + pasture + fallow + field	434.75	5.70	0.01	0.05	9	416.69

RESULTS

During the first trial, we placed 99 nests in 10 CRP fields. For the second trial, we added 2 additional CRP fields and placed 103 nests in 12 sites. There were 84 depredation events during the 2 trials for a nest success rate of 41.6%, which is similar to nest success rates found in real pheasant nests (Clark et al. 1999: 39.8–53.8%, Matthews et al. 2012: 28–47%). In addition, the nest predators we recorded were all known pheasant nest predators including raccoons (*Procyon lotor*; 15 nests), American badgers (*Taxidea taxus*; 8 nests), and striped skunks (*Mephitis mephitis*; 4 nests; Snyder 1984, Clark et al. 1999). Sites varied in surrounding land use from 7–33% nesting habitat within the 2-km-radius buffer (i.e., a CRP field surrounded by additional CRP and winter wheat fields; Table 1).

After accounting for seasonal and local habitat conditions, 3 models in the third group of models resulted in $\Delta AIC_c < 2$ (Table 2). The top model included the variables trial, date, cover, height, percent CRP, percent wheat, percent pasture, and percent fallow as accounting for variation in nest success (Table 2). The second and third models included all the variables from the first model with the addition of field size in the second best model, and percent row crop in the third best model. However, both the field size and row crop variables were relatively uninformative because of small beta values (0.005 and -0.38 , respectively) and confidence intervals that overlapped 0. Therefore, we focused on the top model because it was the most parsimonious model to explain variation (Arnold 2010) with nest success increasing with increasing CRP, wheat, and pasture in the surrounding

landscape but decreasing with increasing fallow land in the area (Table 3; Fig. 1).

DISCUSSION

The landscape matrix surrounding nesting sites influenced the success of artificial ground nests independent of local habitat features (Fig. 1). Previous studies have reported that the abundance and proximity of habitats (e.g., grasslands, croplands, wetlands) at the landscape scale can affect the nest survival of several grassland nesting species (Greenwood

Table 3. Model parameter estimates from the top model of survival rates for artificial ring-necked pheasant nests in southwestern Nebraska, USA, 2013. Covariates included in this model that accounted for variation in temporal and local habitat conditions were the Julian date of nest placement (date), trial period (trial), average percent visual cover of the nest (cover), and the average height of vegetation (height). The 4 landscape covariates included in this model were the proportion of the 2-km-radius buffer dedicated to Conservation Reserve Program fields (CRP), pastureland (pasture), winter wheat fields (wheat), and fallow fields (fallow).

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
Trial	-0.75	0.82	-2.36	0.87
Date	-0.01	0.02	-0.06	0.03
Cover	-0.01	0.01	-0.04	0.01
Height	0.01	0.01	0.00	0.03
CRP*	7.84	3.37	1.23	14.45
Wheat*	12.50	3.41	5.81	19.18
Pasture*	4.49	1.50	1.56	7.42
Fallow*	-13.33	4.81	-22.75	-3.91

* Variables that possess 95% confidence intervals that do not overlap zero.

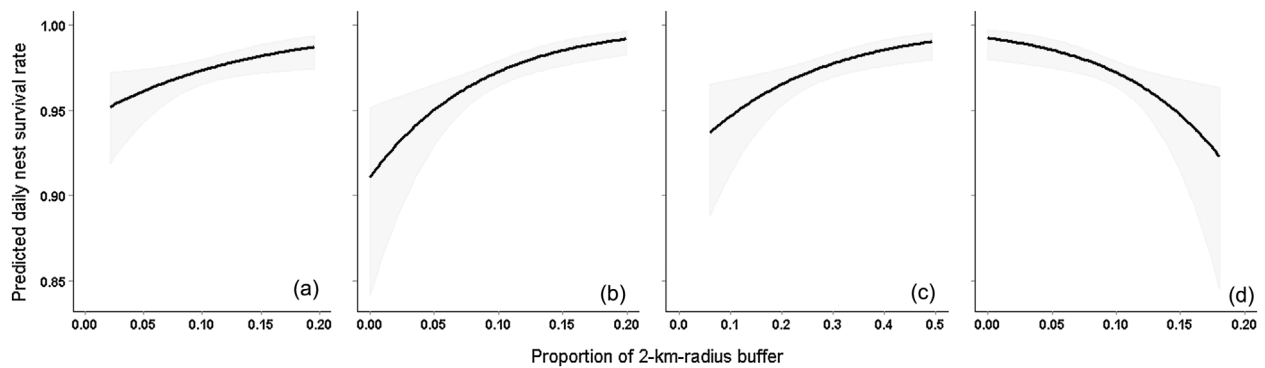


Figure 1. Landscape context influences nest success. Increasing the proportion of (a) Conservation Reserve Program, (b) winter wheat, and (c) pasture surrounding where a nest is found increases survival, while more fallow (d) ground decreases nest survival. Graphs are based on Program MARK analysis of the change in predicted daily nest survival rates (and 95% CIs) of artificial ring-necked pheasant nests in southwestern Nebraska, USA, 2013 in relation to changes in the proportion of the surrounding 2-km landscape that is dedicated to each land-use practice.

et al. 1995, Clark et al. 1999, Reynolds et al. 2001, Stephens et al. 2005). However, because our experimental design eliminated variation in depredation caused by differences in nest site selection and behavior, we were able to examine how specific land use in the landscape matrix can affect the inherent risk of nest predation within a CRP field.

The strong positive relationship between the proportion of CRP and winter wheat in the landscape and nest survival rates (Fig. 1a and b) was not unexpected. Increasing CRP and winter wheat in the landscape increases the availability of nesting habitat (Snyder 1984, Midwest Pheasant Study Group 2013), which can positively affect nest survival rates (Clark et al. 1999). Research indicates that landscape features can influence the foraging patterns of nest predators (Phillips et al. 2003). Our research supports previous speculation that by increasing the amount of nesting habitat within the landscape, predator foraging efficiency can be reduced by increasing the amount of area available for predators to search (Phillips et al. 2003, Stephens et al. 2005). This may be important for nest success because in grassland ecosystems most nest predators are mesopredators that do not actively search for nests unless behaviorally affected by arbitrarily discovering high nesting densities (Martin 1988, Lariviere and Messier 1998, Riley et al. 1998). Therefore, by increasing the total area available for predators to search, the likelihood of predators encountering nests and initiating a functional response to actively search for nests may decrease.

When looking at the impacts of fallow fields and pasturelands, the relationships are not as straight forward (Fig. 1c and d). Neither fallow fields nor pasturelands are pheasant nesting habitats in this area (Midwest Pheasant Study Group 2013). So, why is there a difference in the effect of these 2 land-use practices? The answer likely has to do with the alternative food resources they provide potential nest predators. In addition to not being pheasant nesting habitat, fallow fields hold few alternative prey for nest predators. As the landscape matrix becomes increasingly dominated by fallow fields, nest predators likely spend more time foraging in the remaining habitat, in our case CRP

fields (Jackson et al. 1975). Increased predator foraging where pheasants nest could then lead to a higher probability of opportunistic predators incidentally discovering nests, even if searching for nests was not the primary foraging behavior. In contrast, pasturelands hold a diversity of alternative prey for potential nest predators that can serve to dilute the foraging focus of predator populations across a greater portion of the landscape. These alternative prey sources positively affect the survival rates of pheasant nests within nesting habitats, as long as the predator population does not increase in response to greater prey abundance (Clark et al. 1999). Thus, depending on the landscape conditions, the relative densities at a site level of both predators and prey are likely shifting and altering predation risk for any individual nest (Reynolds et al. 2001).

Given the presumed ability of the landscape to dilute the density of predators and prey at the site level, a reasonable expectation might be that a landscape with an abundance of alternative foraging habitat and nesting habitat may hold the greatest reproductive potential for pheasants. However, even under this scenario, there are constraints that may help define the landscapes that provide optimal nesting conditions. For example, assuming CRP provides ideal nesting conditions and supports an abundance of alternative prey, increasing CRP in the landscape would presumably have the greatest benefit to nest success. However, our model suggests that the landscape availability of winter wheat, not CRP, has the strongest effect on nest success within a site. Although this may simply represent an artifact of sampling, there are reasons to expect additional benefits to site-specific nest success from having winter wheat in the surrounding landscape as opposed to CRP.

Even in systems where nest predation is high, predator population dynamics such as over-winter survival are primarily determined by the availability of other food resources. So, although the availability of alternative prey may have some benefits in diluting nest predation risk (Vander Lee et al. 1999), the same prey may also support a larger and more stable permanent over-wintering predator community. Winter wheat and other annual crops have a

limited prey community when compared to grasslands such as CRP (Kaufman and Kaufman 1997), particularly in the winter (Kaufman and Kaufman 1990). Therefore, a landscape dominated by winter wheat would presumably support a more limited predator community (Clark et al. 1999).

The similarities between the relationships of our estimates of daily nest success rates and land-use practices (Fig. 1) and the positive relationships pheasant abundance has with the proportion of CRP, grasslands, and small grains in the landscape (Jorgensen et al. 2014) suggest that nest survival may be the mechanism underlying regional differences in pheasant abundance. Because of the variation real nests experience in female activity and site choice, we are unable to definitively determine that the land-use matrix influencing predator behavior and the inherent predation risk of nesting habitats are the mechanisms behind pheasant population distributions. However, the similarities between the relationships of our estimates of daily nest success and the relationships of pheasant abundance to land-use practices suggest that further research examining the connection between land use and real nest survival would be beneficial (Jorgensen et al. 2014). By determining whether nest predators and nesting success are the mechanisms driving population distributions, managers would be able to better understand and predict how populations may respond to management efforts (Jorgensen et al. 2014).

MANAGEMENT IMPLICATIONS

Although local habitat quality is an important component of habitat management, our findings suggest that the surrounding landscape matrix plays a critical role in shaping ecological processes that affect management outcomes. Whether or not land use in the surrounding landscape will work cooperatively with or against conservation efforts could affect the overall potential of habitat management efforts. Our research suggests that CRP placed within landscapes with higher proportions of winter wheat, additional CRP, and pastureland that also have fewer fallow fields in the surrounding matrix will promote higher productivity, through decreasing predator efficacy, than CRP created in less beneficial landscapes. By including landscape variables in the evaluation process, wildlife managers can focus management efforts on areas that have greater potential to reach management goals with less cost.

ACKNOWLEDGMENTS

We thank L. N. Messinger, J. A. Laskowski, E. F. Stuber, and L. A. Powell for comments and support and the many private landowners that allowed us access to their properties. Funding was provided by a Federal Aid in Wildlife Restoration Project (W-98-R) administered by the Nebraska Game and Parks Commission, with additional support provided by the University of Nebraska–Lincoln Undergraduate Creative Activities and Research Experience program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The Nebraska Cooperative Fish and

Wildlife Research Unit is supported by a cooperative agreement among the U.S. Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska, the U.S. Fish and Wildlife Service, and the Wildlife Management Institute.

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Associate Editor: Timothy Fulbright.

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