

Examining the influence of landscape context on nest survival

By

VICTORIA SIMONSEN

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ABSTRACT

While the management and restoration of habitat is fundamentally viewed as the key method to conserve species of interest, local habitat management often fails to illicit desired responses in populations. Previous research indicates that landscape features beyond the local habitat scale are impacting the population dynamics of ring-necked pheasants (*Phasianus colchicus*), but the mechanism behind this response remains unknown. One possibility is that nest survival, which is primarily impacted by nest predation, is regulating pheasant responses to the landscape. We investigated the extent to which the land-use surrounding CRP fields impacted nest survival by studying the predation rates of 202 artificial nests on 12 CRP fields 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, while increasing fallowed ground decreased nest success. Our findings support theoretical and empirical evidence that nest predation rates are shaped by predator search efficacy, as changing the relative availability of suitable nesting habitat and alternative food source areas alters nest survival presumably by altering the search effort of potential nest predators. The similarities between the landscape relationships of predicted 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.

INTRODUCTION

Habitat restoration and management is a fundamental component of wildlife sciences and is often identified as the primary means of bolstering wildlife populations (Leopold 1933, Wiens 1994, Didier and Porter 1999, Sinclair et al. 2006). Consequently policy decisions and management actions of wildlife organizations are often focused on altering local vegetative conditions to meet the known habitat needs of species of management concern (Midwest Pheasant Study Group 2013). Unfortunately, while managers are highly successful in creating local habitat conditions with suitable vegetative structure and composition, habitat management too often fails to result in eliciting desired responses in wildlife populations and thus often 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 game birds (Patterson and Best 1996, Robertson 1996, Rogers 1999). Federal policy, state management plans, and the directives of non-governmental organizations often focus on local management actions (e.g., disking and interseeding, burning, or spraying) aimed at resetting vegetative succession with the expressed purpose of improving gamebird populations. While 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 ever increasing directives toward improving local habitat conditions (Midwest Pheasant Study Group 2013). Given the incredible 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, Clark et al. 1999, McCoy et al. 1999, Herkert et al. 2003, Henningsen and Best 2005, Winter et al. 2006, Rahmig et al. 2008). So while local grassland conditions clearly 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 1974, Robertson 1996); land-use practices and subsequent 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). As managers, accurately assessing the relationships between species and the surrounding landscape and land-use practices is therefore 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) has long been recognized to influence the local and regional abundance of pheasants (Midwest Pheasant Study Group 2013), and more recent evidence suggests that other land-cover types may act at a landscape scale to either facilitate (e.g., small grains) or constrain (e.g., trees) 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). Still 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 driving these patterns remain largely unknown.

Here we set out to test whether nest predation is a potential 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 therefore a key component of population dynamics for species with short lifespans such as pheasants (Martin 1995, Stephens et al. 2005). While 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, edge habitat) are also known to influence nest predation rates in grassland systems (Winter and Faaborg 1999, Madden et al. 2000, Riley and Schulz 2001, Stephens et al. 2005). More recent evidence suggests that factors acting at these or even larger spatial scales may ultimately limit grassland bird productivity (Clark et al. 1999, Herkert et al. 2003, Winter et al. 2006) and thereby population size. Using artificial nests, we asked whether landscape conditions driving patterns of nest success in CRP fields reflected landscape conditions predicted to shape populations of pheasants in Nebraska (Jorgensen et al. 2014).

STUDY AREA

The Southwestern Focus on Pheasant site located in Hitchcock and Hayes counties in southwest Nebraska provided the ideal study area for examining how landscape conditions drive local nest survival. The Focus on Pheasant area contains a multitude of CRP fields within a 1,062 square kilometer region that varies greatly in the diversity of land-cover types. Study sites consisted of twelve CRP fields ranging in size from 8.4 to 124.2 hectares and the surrounding landscapes within a two kilometer radius of the CRP field. A two kilometer buffer, an area an order of magnitude larger than an average female pheasant home range in the region (Williams et al. 2003, Fontaine unpublished data), was selected to ensure that the spatial scale was reflective of population not individual level ecological conditions of both predators and prey.

To determine the number of acres dedicated to each land-use surrounding the study sites, we conducted visual surveys of the neighboring fields within the two kilometer radius of each study site. Land-use practices were recorded on aerial pictures and then digitized in Geospatial Information System (GIS) to create polygons that represented each field within the two kilometer buffer. The acres devoted to CRP, winter wheat, row crops (active corn and soybean), pastureland, and fallow fields were then calculated, with the total percent of the acres dedicated to each land-use practice used as predictor variables in subsequent models.

METHODS

Artificial Nests

Using artificial nests as a proxy to assess nest predation risk, we conducted two trials in the spring of 2013, one in May and one in June, each lasting 21 days, a period typical of the incubation period of pheasants in the region (Fontaine unpublished data). At each study site we randomly selected 6-8 locations within the field and created an artificial nest using grass collected from the surrounding area to resemble a pheasant nest in construction. To minimize the effects of nest site selection on nest predation rates, all nests were placed on the ground under the cover of little bluestem (*Schizachyrium scoparium*) and four brown chicken eggs were used as bait. Every 4 days, nests were checked to record depredation events. At five nests in each study sites we identified nest predators using Bushnell Trophy Cam HD game cameras attached to stakes and placed 30 centimeters off the ground and one meter 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, a new nest was created

in a new random location in the same field to maintain the nest density of the study site throughout the trial, as nest density of artificial and real nest is known to influence nest predation rates (Haensly et al. 1987, Martin 1988). At the end of the 21 day trial all nests were removed.

Artificial nests do not always adequately replicate real nests; therefore care must be paid to 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 are typical of the size, shape and color of pheasant eggs and therefore 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 an extensive literature on pheasant nest site selection (Clark et al. 1999, Matthews et al 2012). Any biases should be similar across study sites and therefore we assume that any observed differences in nest predation rates reflect 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 can have value (Fontaine et al. 2007). Real nests experience variance in nest site choice and hen activity which affect nest predation risk and can potentially conceal the effects of inherent environmental risk (Fontaine et al. 2007). Since we are primarily concerned with asking how landscape conditions influence nest survival, not hen behavior, using artificial nests we are better able to make accurate comparisons of how ecological conditions are acting at the landscape level.

Data Analysis

We were primarily interested in how landscape attributes affected nest success, but nest success is impacted by a wide variety of attributes. To account for sources of variation in nest success beyond landscape variables we used a hierarchical approach whereby we tested and built upon base models using Akaike's Information Criterion (AIC) to determine model fit at each step (Burnham and Anderson 1998, Symonds and Moussalli 2011). Given the seasonal patterns in nest success (Fields et al. 2006; Kerns et al. 2010; Decker et al. 2012, Lusk and Koper 2013) we first tested among four alternative models (null, Date, Trial, Date+Trial) to identify how trial period and date of nest creation affected survival rates. Next, because local vegetation characteristics influence nest survival (Davis 2005, Lusk and Koper 2013) we ran models to determine how the local environment affected nest survival. We used the cover and height covariates averaged from the estimates of each individual nest site, with the top model from the first analysis used as the null model for the second analysis. The last set of models involved the landscape covariates that were determined by the percent of each land-use practice within the two kilometer buffer around the CRP study sites along with the new null model, which was the top model from the second analysis. All models were ran in Program Mark (White and Burnham 1999, Dinsmore et al. 2002).

RESULTS

During the first trial, a total of 99 nests were placed in ten CRP fields. For the second trial, two additional CRP fields were added and 103 nests were placed in the 12 sites. There were a total of 84 depredation events recorded during the two trials, and the primary nest predators recorded included: raccoons (*Procyon lotor*), badgers (*Taxidea taxus*), and skunks

(*Mephitis mephitis*). Sites varied in surrounding land-use from 7-33 percent available nesting habitat in the surrounding landscape (i.e., a CRP field surrounded by additional CRP land and winter wheat; Table 1).

After accounting for seasonal (Table 2a), and local habitat conditions (Table 2b) the landscape variables that best accounted for nest success included CRP, Wheat, Pasture, and Fallow (Table 2c); however, because the model including row crop was within two Delta AIC of the top model, we model averaged the top two models (Table 3; Burnham and Anderson 1998, Symonds and Moussalli 2011). Nest success increased with increasing CRP, wheat, and pasture in the landscape, but decreased with increases in the percentage of area in fallow (Figure 1).

DISCUSSION

The results of our study indicate that the landscape matrix surrounding nesting sites does influence nest success independent of local habitat features (Figure 1). Previous studies have shown that the size, pattern, and abundance of the nesting habitat patches within the landscape matrix affect nest survival (Haensly et al. 1987, Clark et al. 1999, Stephens et al. 2005), so it is not unexpected that different land-use practices would impact the survival rates of nests within CRP fields. However, looking into the specific effect of land-use practices on nest survival rates allows us to better understand how the landscape matrix is impacting nest success and thus pheasant abundance.

The strong positive relationship between the proportion of CRP and winter wheat in the landscape and nest survival rates (Figure 1a,b) was not unexpected. Increasing CRP and winter wheat in the landscape increases the availability of alternative suitable nesting habitat on the landscape (Midwest Pheasant Study Group 2013), and in doing so may decrease nest density.

Although we attempted to control for nest density by maintaining a consistent number of artificial nests in each of our study sites; our nests were meant to mimic real pheasant nests, therefore it is possible that the overall nest density (real and artificial nests) in CRP fields surrounded by a matrix dominated by CRP or winter wheat may be relatively low. Nest density has important implications for both predator efficiency and predator search image as indicated by the positive feedback between prey density and predation rates found in many predator-prey systems (Nams 1997, McKinely and Hein 2012), including nest predation (Martin 1988). Changes in nest density alter the probability that a predator, many of which remain opportunistic nest predators unless behaviorally impacted by arbitrarily discovering high nesting densities, will actively search for nests (Martin 1988, Lariviere and Messier 1998). In a landscape dominated by CRP and winter wheat, real pheasant nests are likely dispersed across a larger landscape, decreasing encounter rates with potential nest predators and inhibiting the functional response of the predator community on real nests, as well as the artificial nests we used to assess nest predation risk.

The strong negative relationship between the proportion of fallow fields in the landscape and nest survival rates (Figure 1d) may be further evidence that landscape level changes in land-use alter nest predation rates by affecting nesting density and the subsequent functional response of the predator community. Fallow fields are not suitable nesting habitat, and therefore increasing the proportion of fallow fields in the landscape does not allow for a decrease in nest density on our study sites, and may actually increase nesting density as birds crowd into the remaining limited nesting habitat. Still, although the surrounding land-use practices may affect nesting density within a site, which clearly has the capacity to alter nest predation rates, it is the behavioral response of opportunistic nest predators that shape predation risk. The importance of

understanding predator behavior is highlighted by the differences we found between how the presence of fallow fields and pasturelands in the landscape affect nest predation rates (Figure 1c,d). Like fallow fields, pasturelands are not preferred nesting habitat for pheasants (Midwest Pheasant Study Group 2013), but opposite of the pattern we found with fallow fields, increasing the proportion of pastureland in the landscape actually decreases nest predation rates. So why is there a difference in the effect of these two land-use practices assuming that their implications for nesting density are the same? The answer likely has to do with the alternative food resources they provide potential nest predators. In addition to not being suitable nesting habitat, fallow fields hold few alternative prey for nest predators. As the landscape matrix is increasingly dominated by fallow fields, nest predators likely spend more time foraging in the remaining habitat, in our case CRP fields. The increasing preference for foraging where pheasants nest, then leads 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, diluting the foraging focus of predator populations on the landscape, and positively impacting the survival rates of pheasant nests within suitable nesting habitats. 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.

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 both alternative foraging habitat and suitable nesting habitat may hold the greatest reproductive potential for pheasants. Still even under this scenario there are constraints that may help define the landscapes that provide optimal nesting conditions. For example, assuming CRP provides

both 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 also support an over wintering predator community. Winter wheat has a limited prey community when compared to grasslands such as CRP (Kaufman and Kaufman 1997), particularly in the winter (Kaufman and Kaufman 1990), and therefore a landscape dominated by winter wheat would presumably support a more limited predator community. That winter wheat has a greater impact on predicted nest success suggests that predator community, and the behaviors predators express, ultimately must be considered in concert when assessing the landscape implications of land-use practices on pheasant nest success. To improve our understanding of nest predation and how it varies across landscapes further, we must strive to tease apart factors impacting the three main influences of predation risk: predator abundance, habitat structure, and predator and prey behavior (Fontaine et al. 2007). Future research should focus on identifying the species composition of predator communities and the density of predators across landscapes.

MANAGEMENT IMPLICATIONS

When avian populations decline, significant focus is placed upon improving nest success by decreasing nest predation (Fisk 2010). Managing nest predators directly can significantly improve reproductive success, but is generally cost prohibitive and requires continued action to maintain the benefits (Vander Lee et al. 1999, Riley and Schulz 2001). Moreover, the impact of managing predators is often limited because of the inherent difficulty in removing some predators, such as snakes, and the potential for alternative predator guilds to compensate for the removal of the primary predators (Palmer et al 2005, Ellis-Felege et al. 2012). Improving nesting habitat has an advantage over predator management because the benefits are longer lasting and more cost effective (Duebbert and Kantrud 1974, Frey et al. 2003, Palmer et al 2005, Benson et al. 2010). A common method to improve nest survival is to improve local habitat conditions, but focusing on local habitat features has failed to meet the expectations of managers repeatedly (McCoy et al. 1999, Henningsen and Best 2005, Rahmig et al. 2008). Understanding the multi-scale nature of avian habitat use and realizing the important role that the landscape matrix plays in population dynamics is critical for land managers to successfully accomplish goals (Best et al. 2001).

The similarities between the relationships of our estimates of daily nest success and land-use practices (Figure 1) and the relationships between pheasant abundance and land-use practices (Jorgensen et al. 2014) suggest that nest survival maybe the mechanism underlying regional differences in pheasant abundance. Predation shapes nearly all aspects of prey life history and behavior (Cote and Sutherland 1997), and nest predation is particularly important in regulating avian populations (Martin 1993). Nest predation is one of the most important parameters in the population dynamics of grassland-nesting species (Stephens et al. 2005) and our research indicates that nest predation risk is not only an important factor in ring-necked pheasant

population dynamics, but may ultimately define the distribution of the species. So while we cannot rule out that landscape conditions have direct impacts on pheasant populations (i.e., food resources, winter habitat), it is reasonable that the landscape effects we are seeing manifested in pheasant populations are nest predator mediated. Land-use conditions clearly alter predator distribution and abundance (Cote and Sutherland 1997, Keuhl and Clark 2002). It would appear that nest survival, and thereby pheasant population viability, relies heavily on landscape features that limit the probability of exposure to predators.

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FIGURES AND TABLES

Table 1: This table summarizes the area of each study site along with the percent of the two kilometer surrounding landscape dedicated the five land-uses focused on in this study:

Conservation Reserve Program (CRP), winter wheat (wheat), pasture, row (row crops including corn and soybeans), and fallow fields.

Study site	Area (ha)	Total area studied (ha)	Percent CRP	Percent wheat	Percent pasture	Percent row	Percent fallow
By	31.9	1760.3	9	12	32	11	13
Gues	16.1	1651.8	20	0	38	29	4
Knos	42.1	1849.9	16	12	33	12	4
Knos 2	124.2	2354.4	7	20	28	20	17
Knos NW	49.6	1873.2	10	9	49	11	0
Knos W	58.8	1972.2	10	13	44	7	8
Kol	50.8	2128.2	7	11	38	28	6
Kor	50.5	1943.5	4	4	41	19	5
Kot	8.4	1502.9	8	14	7	30	18
Leag	61.9	1955.2	2	6	34	10	9
Olm	32.7	1815.0	19	4	6	23	5
Wertz	59.2	1925.2	15	18	12	18	3

Table 2a: Models with respective Akaike's Information Criteria (AIC), delta AIC, AIC weight, model likelihood, number of parameters, and deviance from the temporal analysis.

Covariates	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
Day+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

Table 2b: Models with respective Akaike's Information Criteria (AIC), delta AIC, AIC weight, model likelihood, number of parameters, and deviance from the local habitat conditions analysis.

Covariates	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
Trial+Day+Cover+Height	491.87	0.00	0.44	1.00	5	481.85
Trial+Day+Cover	492.81	0.93	0.28	0.62	4	484.79
Trial+Day+Height	493.91	2.04	0.16	0.36	4	485.90
Day+Trial	494.74	0.00	1.00	1.00	3	488.73
Null	517.16	22.41	0.00	0.00	1	515.15

Table 2c: Models with respective Akaike's Information Criteria (AIC), delta AIC, AIC weight, model likelihood, number of parameters, and deviance from the landscape habitat analysis.

Covariates	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
Trial+Day+Cover+Height+CRP+Wheat+Pasture+Fallow	429.05	0.00	0.55	1.00	9	410.98
Trial+Day+Cover+Height+CRP+Wheat+Pasture+Row+Fallow	231.03	1.98	0.20	0.37	10	410.95
Trial+Day+Cover+Height+Wheat+Pasture+Fallow	432.87	3.81	0.08	0.14	8	416.81
Trial+Day+Cover+Height+Wheat+Pasture+Row+Fallow	433.78	4.73	0.05	0.09	9	415.71
Trial+Day+Cover+Height+Wheat+Fallow	434.67	5.61	0.03	0.06	7	420.62
Trial+Day+Cover+Height+CRP+Wheat+Pasture	435.59	6.54	0.02	0.03	8	419.54
Trial+Day+Cover+Height+CRP+Wheat+Pasture+Row	436.10	7.04	0.01	0.02	9	418.03
Trial+Day+Cover+Height+CRP+Wheat+Fallow	436.17	7.11	0.01	0.02	8	420.11
Trial+Day+Cover+Height+Wheat+Row+Fallow	436.65	7.59	0.01	0.02	8	420.59
Trial+Day+Cover+Height+CRP+Wheat+Row+Fallow	437.39	8.34	0.00	0.01	9	419.33

Table 3: Averaged model parameter estimates from the top two models (with $\Delta AIC < 2$).
 Variables that possess 95% confidence intervals not overlapping zero are denoted by (*).

Variable	Estimate	Standard Error	Lower 95% CI	Upper 95% CI
Trial	-0.7435	0.6876	-2.0913	0.6042
Day	-0.0127	0.1181	-0.2443	0.2188
Cover	0.0147	0.0726	-0.1276	0.1569
Height	-0.0131	0.0871	-0.1838	0.1577
CRP*	7.9182	1.4232	5.1287	10.7077
Wheat*	12.4758	1.3963	9.7391	15.2125
Pasture*	4.4738	0.9256	2.6596	6.2880
Fallow*	-13.2372	1.6871	-16.5438	-9.9305

Figure 1: The relationships between land-use in the surrounding two kilometer landscape and the predicted daily nest survival rate indicate that the landscape does impact nest survival. The graphs below are based upon Program Mark analysis of the change in predicted daily nest survival rates in relation to changes in the proportion of the surrounding two kilometer landscape that is dedicated to Conservation Reserve Program (a), winter wheat (b), pastureland (c), and fallow fields (d).

