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Effects of Native and Non-Native Grassland Plant Communities on Breeding Passerine Birds: Implications for Restoration of Northwest Bunchgrass Prairie

Patricia L. Kennedy,[1,2] Sandra J. DeBano,[3] Anne M. Bartuszevige,[1] and Andrea S. Lueders[1]

Abstract

One common problem encountered when restoring grasslands is the prominence of non-native plant species. It is unclear what effect non-native plants have on habitat quality of grassland passerines, which are among the most imperiled groups of birds. In 2004 and 2005, we compared patterns of avian reproduction and the mechanisms that might influence those patterns across a gradient of 13 grasslands in the Zumwalt Prairie in northeastern Oregon that vary in the degree of non-native plant cover (0.9–53.4%). We monitored the fate of 201 nests of all the breeding species in these pastures and found no association of percent non-native cover with nest densities, clutch size, productivity, nest survival, and nestling size. Regardless of the degree of non-native cover, birds primarily fed on Coleoptera, Orthoptera, and Araneae. But as percent non-native cover in the pastures increased, Orthoptera made up a greater proportion of diet and Coleoptera made up a smaller proportion. These diet switches were not the result of changes in terrestrial invertebrate abundance but may be related to decreases in percent bare ground associated with increasing cover of non-native vegetation. Measures of nest crypticity were not associated with cover of non-native vegetation, suggesting that predation risk may not increase with increased cover of non-native vegetation. Thus, the study results show that increased non-native cover is not associated with reduced food supplies or increased predation risk for nesting birds, supporting the growing body of evidence that grasslands with a mix of native and non-native vegetation can provide suitable habitat for native grassland breeding birds.

Key words: **avian reproduction, grassland birds, invasive plants, predation risk, terrestrial invertebrates.**

Introduction

The vast majority of grasslands have been eliminated or highly modified by a variety of human activities, including conversion to croplands, nonsustainable livestock management practices, encroachment by woody species, and invasion by non-native plants (Samson & Knopf 1994; Brennan & Kuvlesky 2005). Restoration of grasslands is a top conservation priority (Vickery et al. 1999; Samson et al. 2004; Ruprecht 2006), and one common problem in restoring these grasslands is the prominence of non-native plant species. However, it is unclear what effect non-native plants have on native vertebrates associated with these grasslands.

Ground-nesting passerines are one of the most prominent vertebrates in grasslands and are among the most imperiled groups of birds globally (Donald et al. 2001; Sauer et al. 2003; Thogmartin et al. 2006). Although many historical factors have impacted grassland passerine populations (Knopf 1994; Scheiman et al. 2003; Shrubb 2003), recent declines are likely due, at least in part, to factors reducing the habitat quality of remaining grassland habitats such as presence of non-native plants (Samson & Knopf 1994; Vickery et al. 1999; Scheiman et al. 2003).

Studies examining highly invaded grassland systems have found lower avian abundance and reproductive success compared to grasslands with moderate to high cover of native species (Scheiman et al. 2003; Lloyd & Martin 2005; Flanders et al. 2006). But other studies have found no differences in per capita fledging success between non-native and native grasslands (Jones & Bock 2005) or increasing nest survival associated with increasing cover of a non-native grass species at nests (Grant et al. 2006).

Not all invaded grasslands are monocultures dominated by a few species of non-native plants. The transformation of agriculture has released large areas of cultivation from use, the majority of which are currently in various stages of oldfield succession (Tatoni & Roche 1994; Benjamin

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[1] Department of Fisheries and Wildlife & Eastern Oregon Agricultural Research Center, Union Experiment Station, Oregon State University, PO Box E, Union, OR 97883, U.S.A.
[2] Address correspondence to P. L. Kennedy, email pat.kennedy@oregonstate.edu
[3] Department of Fisheries and Wildlife & Hermiston Agricultural Research and Extension Center, Oregon State University, PO Box 105, Hermiston, OR 97838, U.S.A.

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et al. 2005; Brennan & Kuvlesky 2005; Ruprecht 2006). Depending on the management regime, these habitats can be structurally similar to native prairie and have higher plant diversity than sites with monocultures of invasive species. Because vegetative structure is a better predictor of grassland bird habitat than floristics (Fletcher & Koford 2002; Scott et al. 2002; Jones & Bock 2005), oldfields and seeded rangelands may provide comparable nesting habitat to native prairie (McMaster et al. 2005).

Shifts in plant communities from native to non-native plants may affect nest predation levels by altering nest site quantity and quality (e.g., degree of concealment or predator access) and/or nest predator activity (e.g., density or behavior). Food availability also limits reproductive success of birds, typically by delaying or aborting nest initiation (Ortega et al. 2006), increasing starvation rates by reduced food abundance or foraging substrates (Maron & Lill 2005; Granbom & Smith 2006), and/or increasing predation risk from increased begging and/or reduced attentiveness of foraging adults (Dewey & Kennedy 2001; Zanette et al. 2003). Several studies comparing native grasslands versus those dominated by non-native vegetation suggest that food limitation may be an important mechanism in reducing grassland bird populations (Bock et al. 1986; Flanders et al. 2006; but see Jonas et al. 2002).

Understanding the mechanism by which non-native plant species impact bird populations will aid managers in choosing the most appropriate restoration technique. Depending on the mechanism responsible for declines, managers may be able to develop innovative techniques to improve habitat quality for birds that are less expensive and more feasible than removing non-native species and replanting with native species. These techniques might involve habitat restoration targeted at increasing nest crypticity or increasing the invertebrates preferred by grassland birds during the breeding season.

To our knowledge, no bird studies have compared patterns of reproduction and the mechanisms that might influence those patterns across a gradient of grasslands that vary in the degree of non-native species cover. We used this approach to determine whether:

(1) Reproductive performance of grassland birds is negatively associated with percent cover of non-native plants.
(2) Food availability is negatively associated with percent cover of non-native plants.
(3) Predation risk is positively associated with percent cover of non-native plants.

Methods

Study Area

We conducted this study during the 2004 and 2005 breeding seasons in the Zumwalt Prairie in northeastern Oregon. The Zumwalt Prairie (lat 117°3′N, long 45°31′W; Fig. 1) is one of the last, large relicts (approximately 65,000 ha) of the once extensive Idaho fescue (*Festuca idahoensis*)–dominated bunchgrass prairies of northwestern North America, which formerly covered approximately 800,000 ha in the northwestern United States and Canada (Tisdale 1982). After the prairie was opened to homesteading in the 1860s, livestock herds were confined by fences and cultivation was practiced (Black et al. 1998). Due to its dry and cold climate, homesteads were eventually abandoned and cultivation ceased except on the extreme southern areas of the prairie that are wetter and less rocky. Abandoned cultivated areas have been converted to rangeland for cattle production. Early homesteaders often planted these rangelands with non-native grasses (e.g., Smooth brome [*Bromus inermis*], Intermediate wheatgrass [*Thinopyrum intermedium*], and Timothy [*Phleum pratense*]), to enhance forage production. Today, the Zumwalt Prairie is mostly privately owned and used primarily for cattle production.

Pasture Selection

Prior to the 2004 field season, we selected pastures on The Nature Conservancy's (TNC) Zumwalt Prairie Preserve, the primary study area. Before TNC's purchase, the ranch had been grazed for 18 years by the same operator, who grazed pastures once per year for 30–60 days with low to moderate stocking rates. TNC continued this grazing regime (P. Shephard 2003, TNC, personal communication). We supplemented the eight TNC pastures with five other pastures on private lands. To identify comparable pastures to the TNC pastures, we obtained names of landowners from the Oregon State University Extension Service (J. Williams 2003, personal communication) who met the following criteria: (1) would allow ecological researchers access to their lands; (2) owned relatively flat grassland property that consisted of both grazed native prairie and grazed areas that were historically cultivated or seeded; (3) used similar pasture rotations and stocking rates; and (4) were not currently seeding or farming their pastures. All pastures were surrounded by prairie, and there was no woody vegetation surrounding any of the pastures that might cause an edge effect. We selected 13 pastures (Fig. 1) that varied in the degree to which they were invaded with non-native vegetation (Table 1). Pastures ranged in size from 15.3 to 108.6 ha ($\bar{X} = 47.1$ ha).

Vegetative Structure and Composition of Pastures

During July 2005, we conducted vegetation sampling to identify potential structural and compositional differences among pastures that might be associated with suitability of avian nesting habitat. We randomly placed three hundred and forty 1 × 1–m plots throughout the 13 pastures. The number of plots in each pasture was proportional to area, with the smallest pasture having 10 plots and the largest having 54. Only one pasture was an exception; TNC05 was one of the largest pastures, but

Figure 1. Locations of pastures ($n = 13$) sampled in the Zumwalt Prairie in northeastern Oregon during the 2004 and 2005 breeding seasons (except TNCO1, which was only sampled in 2004).

only 10 plots were sampled because it was heavily grazed just prior to vegetation sampling.

At each 1-m^2 plot, the percent cover of each species was recorded and placed into a cover class assignment: 0 = 0% cover, 1 = less than 1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–99%, and 8 = 99–100% (Mitchell et al. 1988; McCune & Grace 2002). Cover classes for total vegetation and each species were recorded separately. All plant taxonomy was based on the plant species list for the study area developed by TNC (http://conserveonline.org/workspaces/ZumwaltPrairieWorkspace/ZumPublic/Z). This plant list was based on Hitchcock and Cronquist (1973). In cases where a specific identification could not be made, the plants were grouped into generic categories. However, within generic categories, native and non-native species were kept separate. Annual forbs were difficult to identify to species and, thus, were grouped together. Vegetation height–density was measured

Table 1. Average (± SE) vegetation characteristics of the 13 pastures sampled in the study (statistical analysis results are in the footnotes).

Site No.	*% Non-Native*[a]	*% Native*	*% Bare Ground*[b]	*% Litter*[c]	*Vegetation Height–Density*[d]
BUT01	24.1 (1.2)	17.7 (0.16)	36.8 (1.8)	34.3 (1.6)	0.83 (0.05)
BUT02	31.7 (1.9)	34.7 (2.0)	16.3 (0.81)	32.0 (1.3)	1.20 (0.06)
GOE01	0.9 (0.08)	57.9 (0.79)	33.5 (0.72)	23.0 (0.48)	0.57 (0.01)
GOE02	40.0 (1.6)	6.2 (0.57)	11.4 (1.1)	45.4 (1.6)	1.07 (0.03)
GOE03	40.1 (2.1)	32.3 (1.4)	16.4 (1.2)	27.9 (0.82)	1.31 (0.05)
TNC01	31.1 (1.2)	28.4 (1.2)	7.6 (0.74)	45.1 (0.97)	2.90 (0.06)
TNC02	4.9 (0.22)	57.5 (0.52)	17.7 (0.34)	17.6 (0.33)	1.30 (0.01)
TNC03	53.4 (1.0)	23.3 (0.5)	15.4 (0.22)	20.8 (0.18)	0.84 (0.01)
TNC04	6.1 (0.32)	53.7 (0.44)	25.2 (0.55)	26.1 (0.52)	1.46 (0.02)
TNC05	38.2 (2.5)	40.7 (2.7)	15.9 (1.3)	26.3 (1.2)	0.46 (0.02)
TNC06	19.1 (0.61)	46.0 (0.48)	24.1 (0.36)	25.7 (0.38)	1.25 (0.02)
TNC07	28.5 (0.71)	37.2 (0.9)	12.1 (0.35)	40.0 (0.77)	1.65 (0.03)
TNC10	9.2 (0.64)	55.7 (0.85)	30.6 (0.74)	19.9 (0.44)	1.58 (0.02)

[a] Pasture averages of percent native cover were negatively associated with pasture averages of percent non-native cover ($r^2 = 0.63$, $p = 0.001$).
[b] Pasture averages of percent bare ground were negatively associated with pasture averages of percent non-native cover ($r^2 = 0.38$, $p = 0.02$).
[c] Pasture averages of percent litter were not associated with pasture averages of percent non-native cover ($r^2 = 0.15$, $p = 0.19$).
[d] Pasture averages of vegetation height–density were not associated with pasture averages of percent non-native cover ($r^2 = 0.008$, $p = 0.77$).

at the center of each plot using a Robel pole (Robel et al. 1970), with one measurement made in each cardinal direction. These four measurements were averaged to create one Robel score for each plot.

Avian Reproductive Performance

Nest searching and monitoring occurred from 7 May to 31 July 2004 and 2 May to 11 August 2005. Nests were located using the rope-dragging technique, which involves dragging a weighted, 25-m rope stretched between two people over the ground, causing the incubating or brooding birds to flush from the nest. Nests were also located opportunistically during other field activities (e.g., nest checking), which occurred at equal frequency in all pastures. We avoided nest searching when it was raining or when temperatures or windchill indices were less than 7°C because nest searching during such conditions can negatively affect ground-nesting birds.

During 2004, we rope dragged each pasture three times (7 May to 8 June, 9 June to 1 July, and 6 to 19 July). The first sampling period commenced in both years when all species had begun to initiate nests (early May). The lack of success at finding any nests during exploratory searching bouts on 21–22 and 28 April 2005 corroborated this phenology. Nest searching ended at the predicted end of the breeding season, which was corroborated by the lack of many new nests found in the third sampling period in 2004 ($n = 9$). Based on the 2004 results, we only searched for nests during two sampling periods in 2005 (2 May to 8 June and 8 to 30 June).

When active nests (attended by two adults and containing a well-developed nest cup) were found, they were marked with surveyor flags (located 10 m and 30 m away from the nest in a random direction) and GPS coordinates to assist with relocation. We monitored the fate of each nest by visiting active nests every 2–5 days until the young fledged or the nest failed. In both years, nestlings were aged based on descriptions of nestling morphology from Wheelwright and Rising (1993), Lanyon (1994), Beason (1995), and Jones and Cornely (2002). We estimated age of nests located during incubation using the egg floatation angle (Westerkov 1950). We assigned each nest fate based on evidence at the nest and Breeding Bird Research and Monitoring Database (BBIRD) protocols (Martin et al. 1997).

During nest visits in 2005, we collected nestling morphometric data to estimate nestling growth trends as a function of pasture non-native cover. When a nest had recently hatched nestlings (1–2 days), two nestlings were randomly selected to mark (with nontoxic nail polish), measure, and remeasure on subsequent visits. Nestling measurements included mass, culmen length, and wing length.

Nestling Diet and Invertebrate Abundance

To determine if increasing non-native cover impacted nestling diet and abundance of potential prey, we examined (1) nestling fecal samples and (2) the abundance of invertebrates associated with the ground and vegetation. For nestling diet, we attempted to collect a fecal sac from each of the nestlings measured for growth rates. Nestlings often produce a fecal sac when handled. If the measured nestlings did not produce a fecal sac, other nestlings were handled to try to obtain additional samples. Fecal samples were stored in 95% ethanol until laboratory analysis.

In the laboratory, invertebrate fragments were removed from the diluted fecal samples, soaked in 70% ethanol for at least 5 minutes, and then soaked in 95% ethanol for 5 minutes. Fragments were then transferred to euparal essence for 5 minutes, mounted in euparal on glass slides, and allowed to cure for at least 3 days. Fragments were identified to the lowest taxonomic unit possible by comparison to local and regional reference collections and to drawings in taxonomic publications (Ralph et al. 1985). The number of each fragment type from different prey items was counted for each sample, and the number of prey items for each sample was estimated. If multiple fragments of one structure (e.g., a tibia) or if both a right and a left fragment of a paired structure (e.g., mandibles) of a particular taxon were found, we assumed the fragments belonged to one individual prey item. This technique thus provides a conservative estimate of the number of prey items (Ralph et al. 1985).

We measured invertebrate abundance at 10 plots randomly selected from the vegetation plots in each of the 13 pastures during the peak period of avian reproduction (14 to 23 June 2005) using two methods, pitfall traps and vacuum sampling. Employing multiple sampling techniques helps control for any biases associated with a particular sampling method (Disney 1986) and allows for the collection of invertebrates from different microhabitats used by foraging passerines. One pitfall trap containing 75% ethanol was placed at each plot. We left the trap covered for 2 days to minimize any effects of disturbance from trap placement and then opened the trap for 1 week. We used a modified Troy-Bilt (Cleveland, OH, U.S.A.) 31 cc blower/vacuum (Stewart & Wright 1995; Harper & Guynn 1998) for 2 minutes at each plot to collect invertebrates associated with the vegetation and ground inside a bottomless frame box (0.75 × 0.75 × 0.75 m) covered with netting. The use of a leaf blower/vacuum has been found to be more efficient for grassland sampling than either sweep net sampling or traditional D-vac sampling (Stewart & Wright 1995; Buffington & Redak 1998). We identified invertebrates to the taxonomic resolution corresponding to the resolution of the fecal data.

Predation Risk

In 2005, we measured the following nest site characteristics that might influence nest crypticity: (1) vegetation height–density; (2) nest concealment; and (3) percent non-native cover at the nest. These measurements were collected after the nesting attempt was completed.

Vegetation height–density at the nest was measured using the Robel method, with the Robel pole placed directly in the nest cup. Nest concealment was measured by placing a 6.5-cm-diameter ball marked with a grid of 61 dots into the nest and recording the number of dots visible from a distance of 1 m directly above the nest (Nelson & Martin 1999). We measured vegetation composition of the nest sites by recording all plant species within 5 cm of the nest edge and estimated their respective percentages using ocular estimation.

Statistical Analyses

Pasture Composition and Structure. We converted cover class values to percentages by using the midpoint of the cover range for each cover class (e.g., a species placed in cover class 2 was assigned a percent cover of 3%). We used regression analysis to determine the relationship between pasture averages of percent cover of native versus non-native plant species. We predicted a negative relationship between native and non-native cover; notably, this relationship is not de facto because other types of nonplant cover (e.g., litter, bare ground) may weaken the relationship. We also regressed pasture averages of percent non-native cover versus vegetation height–density, percent bare ground, and percent litter (a measure of dead residual vegetation) to determine if pasture structure was associated with non-native cover.

Avian Reproductive Performance. Nest densities were estimated by measuring the area of each pasture using a GPS unit (Garmin Etrex Legend and Etrex Vista [Olathe, KS, U.S.A.] with an accuracy of 4–7 m) and ArcMap (version 9.x; ESRI 2007) and then dividing the total number of nests (found over the entire season) by the area. These nest densities are apparent densities because they were not adjusted for probability of detection. There were insufficient data to estimate apparent nest density by species, so we pooled the data across species and tested for year effects using a paired *t* test. Because clutch size and productivity (number of young fledged per successful nest) vary by species, we tested for species and year effects on these two parameters using a repeated measures analysis of variance (ANOVA). We used program MARK (version 4.3; White & Burnham 1999) to estimate daily nest survival (probability that a nest survives 1 day) from the fate monitoring data of all nests. Using MARK, nest survival can be modeled as a function of covariates without needing to partition the data (Jehle et al. 2004). We used MARK to estimate daily nest survival as a function of year, species, and pasture. Due to small sample sizes, we modeled each covariate separately. Regression analysis was used to determine the relationship between pasture-level averages of percent non-native cover and (1) apparent nest density; (2) clutch size; (3) productivity; and (4) nest survival.

Because nest failure rates were high, few nestlings were measured more than once. Thus, growth rates could not be estimated nor could the size of older nestlings be evaluated statistically. Sufficient measurement data were only available to estimate pasture averages of hatching morphometry for the Savannah Sparrow. Regression analysis was used to determine the relationship between pasture-level averages of percent non-native cover and (1) mass; (2) wing length; and (3) culmen of hatchling Savannah Sparrows.

Nestling Diet and Invertebrate Abundance. We used regression analyses to examine the relationship between pasture-level averages of percent non-native cover and pasture averages of (1) percentage of prey items in fecal samples and (2) abundance of invertebrates.

Predation Risk. Because we only had 1 year of nest site data, we used one-way ANOVAs to determine if pasture averages of vegetation height–density, concealment, and percent cover of non-native vegetation at the nest varied by bird species. Regression analysis was used to determine the relationship between average percent non-native cover of the pasture and pasture averages of each of the nest site characteristics. Due to sample size limitations, we did not test for the potential effect of within-season variation on nest site characteristics.

General Statistical Methods. With the exception of the nest survival analyses in program MARK, all analyses were conducted with SYSTAT (1997) and SAS (version 9.1; SAS Institute, Inc., 2004). Data were examined to determine if the residuals were normally distributed; percent exotic and Robel measurements for the pasture and the nest were log transformed before analyses. An alpha level of 0.05 was used as the criteria for statistical significance. All estimates of variance are standard errors.

Results

Pasture Vegetative Structure and Composition

The most common native grass species found on the prairie were Idaho fescue, Sandberg's bluegrass (*Poa secunda*), Prairie junegrass (*Koeleria macrantha*), One-spike oatgrass (*Danthonia unispicata*), and Bluebunch wheatgrass (*Pseudoroegneria spicata*). The most common native forb species were *Aster* sp., Western yarrow (*Achillea millefolium*), *Lupinus* sp., Prairie smoke (*Geum triflorum*), and *Potentilla* sp. The most common non-native grasses were Kentucky bluegrass (*Poa pratensis*), Timothy, Intermediate wheatgrass, and annual *Bromus* sp. non-native forbs were not found at cover values greater than 1%.

Non-native cover in the 13 pastures varied from 0.9 to 53.4%, and percent native cover was negatively related to percent non-native cover (Table 1). There were no significant relationships between percent non-native cover and vegetation height–density or percent litter (Table 1). However, there was a significant negative relationship between percent non-native cover and percent bare ground (Table 1).

Avian Reproductive Performance

During the three 2004 nest searching periods, we found 55, 35, and 9 nests, respectively. During the two 2005 nest searching periods, we found 45 and 56 nests, respectively. Nests of Savannah Sparrows (35 in 2004 and 41 in 2005), Western Meadowlarks (*Sturnella neglecta*; 33 in 2004 and 17 in 2005), Vesper Sparrows (*Pooecetes gramineus*; 16 in 2004 and 25 in 2005), and Horned Larks (*Eremophila alpestris*; 11 in 2004 and 15 in 2005) comprised 98.5% of all nests. Unless indicated otherwise, all species-level analyses described below are restricted to these four species.

Apparent nest densities did not vary significantly by year (2004: $\bar{X} = 14.8 \pm 1.6$ nests/100 ha; 2005: $\bar{X} = 17.1 \pm 2.1$ nests/100 ha; $t_{11} = 1.23$, $p = 0.25$). Average (across years) apparent nest density by pasture was not significantly related to average non-native cover of the pastures (Fig. 2a; $r^2 = 0.09$, $p = 0.32$, $n = 13$). Clutch sizes did not vary by year but there was significant variation among species (Table 2). Thus, separate regressions were conducted for each species (Table 2). There was no relationship between average (across years) clutch size by pasture and average non-native cover of pastures for any species (Table 2). Nest productivity did not vary by year ($F_{[1,26]} = 0.07$, $p = 0.79$) or species ($F_{[3,26]} = 1.82$, $p = 0.17$). Average (pooled across years and species) productivity by pasture was not associated with average non-native cover of the pastures (Fig. 2b; $r^2 = 0.16$, $p = 0.22$, $n = 11$).

Probability of daily nest survival did not vary by year (2004: $\bar{X} = 0.928$, 95% CI = 0.914–0.940, $n = 97$ nests; 2005: $\bar{X} = 0.942$, 95% CI = 0.930–0.951, $n = 94$ nests) or species (Horned Lark: $\bar{X} = 0.934$, 95% CI = 0.910–0.952, $n = 26$ nests; Savannah Sparrow: $\bar{X} = 0.935$, 95% CI = 0.921–0.947, $n = 73$ nests; Vesper Sparrow: $\bar{X} = 0.936$, 95% CI = 0.923–0.948, $n = 39$ nests; and Western Meadowlark: $\bar{X} = 0.937$, 95% CI = 0.916–0.953, $n = 49$ nests). There was also no association between pasture-level estimates of nest survival (pooled over year and species) and average percent non-native cover of the pastures (Fig. 2c; $r^2 = 0.01$, $p = 0.71$, $n = 13$).

Measurements of mass, wing length, and culmen length were obtained from 17 hatchling Savannah Sparrows found in eight pastures in 2005. Mass ($\bar{X} = 3.94 \pm 0.32$ g), wing length ($\bar{X} = 8.60 \pm 0.33$ mm), and culmen length ($\bar{X} = 2.68 \pm 0.08$ mm) were not associated with average non-native cover of the pastures (mass: $r^2 = 0.43$, $p = 0.08$, $n = 8$; wing length: $r^2 = 0.29$, $p = 0.17$, $n = 8$; and culmen length: $r^2 = 0.07$, $p = 0.53$, $n = 8$).

Nestling Diet and Food Availability

From 30 nests located in 10 pastures, we collected 43 fecal samples from five species of birds: 13 fecal samples were collected from Horned Larks, 13 from Vesper Sparrows, eight from Savannah Sparrows, seven from Western Meadowlarks, and two from Brewer's Blackbirds (*Euphagus cyanocephalus*). We estimated that 161 invertebrate specimens were present in the fecal samples, with the mean number of invertebrate specimens per sample being 3.8 ± 0.3.

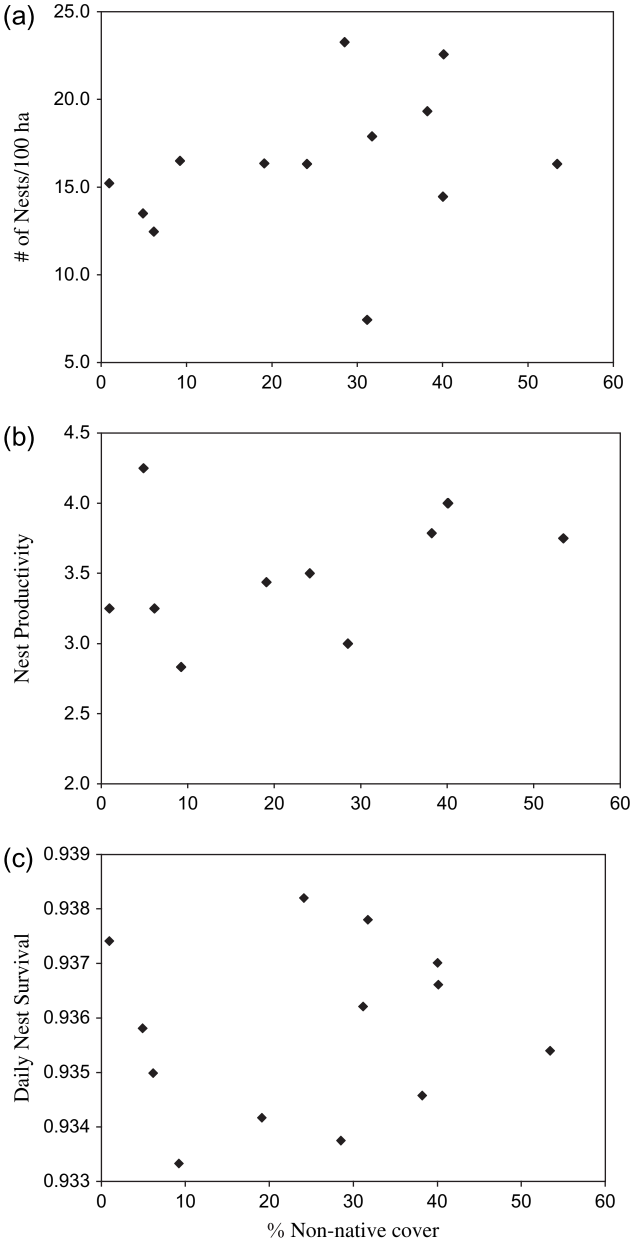

Figure 2. Relationship between average percent non-native cover of the pastures and (a) apparent nest density (unadjusted for detectability), (b) productivity, and (c) daily nest survival. Data are pooled over years and species. There are only 10 data points in Figure 2b and two pastures had equivalent average pasture productivity.

All specimens were identified to order or family. Of the 59 beetle specimens collected, 14 (approximately 24%) were identified to family (eight carabids and six

Table 2. Pasture-level averages ± SE (number of pastures) for clutch size and nest site characteristics, which varied by species[a] (statistical analysis results are in the footnotes).

	Species			
Nest Site Measurements (Units)	*Horned Lark*	*Savannah Sparrow*	*Vesper Sparrow*	*Western Meadowlark*
Clutch size (number of eggs)[b]	3.21 ± 0.13 (10)	3.87 ± 0.12 (11)	3.57 ± 0.15 (9)	4.88 ± 0.12 (11)
Vegetation height–density (dm)[c]	0.8 ± 0.13 (9)	1.3 ± 0.12 (9)	1.3 ± 0.07 (8)	1.6 ± 0.10 (6)
Concealment (number of dots exposed)[d]	43.9 ± 2.74 (9)	27.2 ± 2.71 (9)	27.6 ± 1.92 (8)	23.0 ± 5.57 (6)

[a] Clutch sizes were estimated in 2004 and 2005 but did not vary by year ($F_{[1,58]} = 0.23$, $p = 0.64$). Nest site characteristics were only measured in 2005. Clutch sizes ($F_{[3,58]} = 18.01$, $p < 0.001$), vegetation height–density at the nest ($F_{[3,31]} = 14.70$, $p < 0.001$), and nest concealment varied by species ($F_{[3,31]} = 7.88$, $p = 0.002$).

[b] There was no relationship between average (across years) clutch size by pasture and average non-native cover of pastures for any species (Horned Lark: $r^2 < 0.00$, $p = 0.99$; Savannah Sparrow: $r^2 = 0.29$, $p = 0.09$; Vesper Sparrow: $r^2 = 0.17$, $p = 0.27$; and Western Meadowlark: $r^2 < 0.00$, $p = 0.99$).

[c] Pasture-level averages of vegetation height–density at the nest were not associated with pasture-level averages of percent non-native cover: Horned Lark ($r^2 = 0.11$, $p = 0.38$); Savannah Sparrow ($r^2 = 0.02$, $p = 0.73$); Vesper Sparrow ($r^2 = 0.03$, $p = 0.66$); and Western Meadowlark ($r^2 = 0.10$, $p = 0.53$).

[d] Higher number of dots exposed indicates lower levels of concealment. Pasture-level averages of nest concealment were not associated with pasture-level averages of percent non-native cover: Horned Lark ($r^2 = 0.06$, $p = 0.51$); Savannah Sparrow ($r^2 = 0.14$, $p = 0.33$); Vesper Sparrow ($r^2 = 0.28$, $p = 0.17$); and Western Meadowlark ($r^2 = 0.04$, $p = 0.72$).

curculionids). None of the Orthoptera (51), Araneae (25), or Lepidoptera (12) was identified to family. All Hymenoptera (six) were Formicidae, all Hemiptera (five) were Miridae, and both Homoptera were Cicadellidae. For insects with complete metamorphosis (Lepidoptera, Coleoptera, and Hymenoptera), adult versus immature stages were distinguished. All Lepidoptera were larvae, all Hymenoptera were adults, and two of the 59 Coleoptera were larvae.

Only three orders of invertebrates were found in fecal samples in greater percentages than 10%. Coleoptera were the most common prey, making up 41.0 ± 5.0% of bird diets in each pasture; Orthoptera made up 27.5 ± 4.4%, and Araneae made up 17.2 ± 4.2%. Bird diet varied significantly with the percentage of non-native plant cover; as percent non-native cover increased, Orthoptera made up a greater percentage of bird diets (Fig. 3a; $r^2 = 0.55$, $p = 0.009$, $n = 11$) and Coleoptera made up a significantly smaller percentage (Fig. 3b; $r^2 = 0.36$, $p = 0.05$, $n = 11$). There was no statistically significant relationship between percent non-native plant cover and percentage of Araneae in bird diets ($r^2 = 0.03$, $p = 0.65$, $n = 11$).

We collected 16,448 invertebrates in pitfall samples, with four orders (Hymenoptera, Diptera, Coleoptera, and Araneae) making up more than 90% of individuals collected. On average, Hymenoptera made up 49.5 ± 4.3% of individuals collected in each pasture, Diptera made up 31.0 ± 3.6%, Coleoptera made up 8.0 ± 0.9%, and Araneae made up 5.2 ± 0.6%. All Hymenoptera collected in pitfall traps were ants. There were no significant relationships between the non-native cover of the pastures and the abundance of all invertebrates collected in pitfalls ($r^2 = 0.01$, $p = 0.74$, $n = 13$) or with the abundance of Hymenoptera ($r^2 = 0.25$, $p = 0.08$, $n = 13$), Diptera ($r^2 = 0.20$, $p = 0.11$, $n = 13$), Coleoptera ($r^2 = 0.02$, $p = 0.69$, $n = 13$), and Araneae ($r^2 = 0.01$, $p = 0.76$, $n = 13$).

We collected 6,382 invertebrates in vacuum samples, with five orders (Homoptera, Diptera, Hemiptera, Hymenoptera, and Orthoptera) making up more than 90% of individuals collected. Homoptera made up 41.5 ± 2.3% of individuals collected in each pasture, Diptera made up 20.9 ± 2.9%, Hemiptera made up 15.6 ± 2.3%, Hymenoptera made up 11.3 ± 2.2%, and Orthoptera made up 4.5 ± 2.0%. Hymenoptera collected in vacuum samples comprised ants (63%), wasps (34%), and bees (3%). There were no significant relationships between the

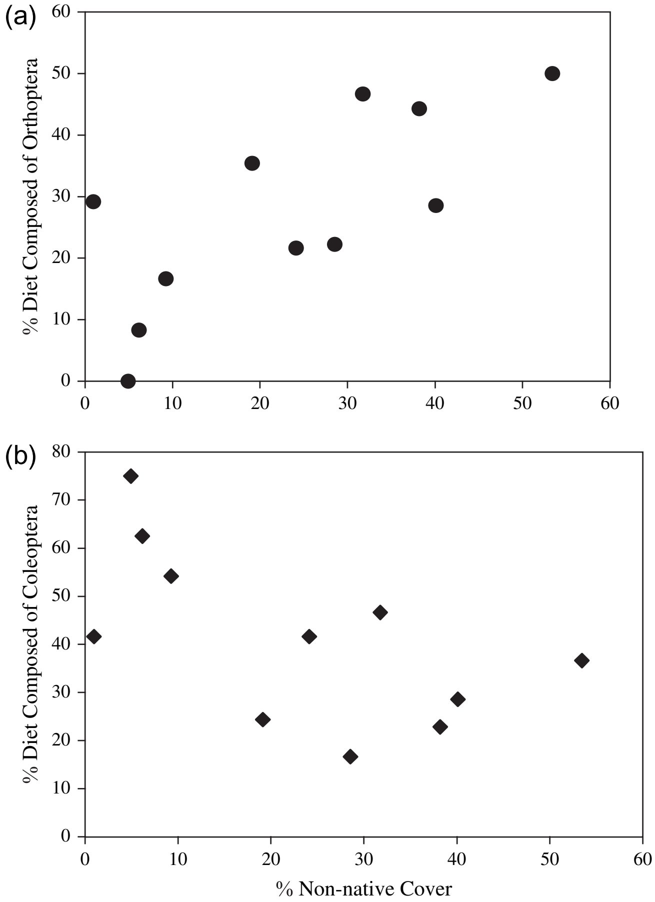

Figure 3. Relationship between average percent non-native plant cover of the pastures and (a) percent diet composed of Orthoptera and (b) percent diet composed of Coleoptera.

non-native plant cover and the abundance of all invertebrates collected in vacuum samples ($r^2 = 0.01$, $p = 0.88$, $n = 13$) or with the abundance of Homoptera ($r^2 = 0.02$, $p = 0.68$, $n = 13$), Diptera ($r^2 = 0.06$, $p = 0.44$, $n = 13$), Hemiptera ($r^2 = 0.03$, $p = 0.58$, $n = 13$), Hymenoptera ($r^2 = 0.01$, $p = 0.81$, $n = 13$), and Orthoptera ($r^2 = 0.02$, $p = 0.65$, $n = 13$).

Predation Risk

In 2005, we measured nest site characteristics at 32 nests located in 12 pastures. Because vegetation height–density at the nest and nest concealment varied by species (Table 2), separate regressions were conducted for each species. For each species, there was no relationship between percent non-native cover of the pastures and (1) vegetation height–density at the nest and (2) nest concealment (Table 2). Percent non-native cover at the nests did not vary by species ($F_{[3,31]} = 0.39$, $p = 0.76$, $n = 12$) and was positively associated with percent non-native cover of the pastures ($r^2 = 0.50$, $p = 0.01$, $n = 12$).

Discussion

Although the 13 pastures measured in this study varied floristically, they were structurally similar based on the vegetation height–density measurement, which is commonly used to determine habitat structure for breeding grassland birds. The lack of structural differences in the pasture-level vegetation suggests that non-native species do not necessarily substantially change the structural nature of the plant communities from the functional perspective of a breeding bird. This is likely due to the fact that most of the non-native species are perennial grasses and are a mixture of rhizomatous and caespitose growth forms. In addition, the common sod-forming non-native grasses found in this system (e.g., Kentucky bluegrass) did not produce the extreme amounts of litter documented in more mesic conditions. High amounts of litter have been negatively associated with abundance and reproduction of grassland birds (Wilson & Belcher 1989; Nenneman 2003).

We documented that vegetative structure of the pastures at the end of the nesting season does not vary with non-native cover but structure may differ earlier in the season and thus may influence avian settlement patterns. We did not evaluate vegetative structural differences early in the season, but Lloyd and Martin (2005), who conducted the only study on this topic, found no difference in settlement patterns of chestnut-collared longspurs nesting in monocultures of crested wheatgrass as compared with native prairie in Montana.

Our results suggest that percent cover of non-natives in the pastures sampled was not associated with any measure of avian reproduction. These data support the results of other investigators who have found that small to moderate amounts of non-native cover do not influence productivity of grassland birds (Wilson & Belcher 1989; Schneider 1998; Grant et al. 2004, 2006). Negative impacts on reproduction may not occur in this area until the level of non-native cover exceeds some threshold not sampled in our study (>55%). Negative effects of non-native species on breeding habitat selection, nesting densities, and reproduction of grassland birds have been documented when percent non-native cover is greater than 95% (Davis & Duncan 1999; Lloyd & Martin 2005; Flanders et al. 2006), but the extent to which this effect occurs in less invaded systems is unknown.

Similar to Jonas et al. (2002), we failed to find strong differences in total invertebrate abundance related to the cover of non-native plants. However, the diet switches we documented suggest that food access may vary as a function of non-native cover. Percent bare ground decreased with increasing cover of non-native vegetation. As bare ground decreased, ground-active Coleoptera may have become less visible and thus, birds switched to Orthoptera, an insect order that is often gleaned from vegetation. We cannot evaluate this hypothesis with our data, but future investigations could test this hypothesis by experimentally manipulating percent bare ground near nests and monitoring feeding behavior and diet preferences of nesting adults.

Differences in invertebrate abundance may have occurred at finer levels of taxonomic resolution than we detected. Our taxonomic resolution of the invertebrate abundance data was dictated by the resolution of the fecal samples. Fecal samples are an excellent, non-invasive method for identifying avian consumption patterns, but specimens are at least partially digested, and identification beyond the ordinal level is difficult. Future research should obtain diet data with techniques that result in prey being identified prior to digestion (e.g., video cameras at nests [Pietz & Granfors 2000], throat ligatures [Orians 1966; Post & Greenlaw 2006], or emetics [Díaz 1989; Valera et al. 2005]).

The nest evidence suggested that predation was the primary cause of nest failures in this system (38.3% of the nests for which fate could be determined [$n = 150$] failed due to predation), but nest crypticity was not associated with non-native cover of the pastures. The influence of non-native cover on predator abundance and activity, the other important components of predation risk, is unknown and poorly studied.

Our results have important implications for restoration activities aimed at conservation of grassland birds. Our data support the growing body of evidence that grasslands with a mix of native and non-native vegetation can provide suitable habitat for nesting grassland breeding birds, at least in low or moderately invaded systems. Vegetation structure may be the key attribute that determines the ultimate impact of non-native plants on birds, and managers concerned about the quality of bird habitat should potentially focus on invading plant species that differ strongly in structure from native species. Food limitation may not be a major concern in these systems; we found no evidence that non-native plant species decreased the abundance of invertebrates that serve as prey for birds. As indicated by several other investigators, grassland restoration efforts do not need to mirror native conditions to provide suitable nesting habitat (Davis & Duncan 1999; Fletcher & Koford 2002). As noted by Ewel and Putz (2004) and Lugo (2004), eradication of non-native species in ecosystem restoration is not always cost-effective and some non-native species can be tolerated.

The results of this study highlight several important areas of future research. There is a need for large-scale experiments in which the degree of non-native cover can be directly manipulated and treatments randomly assigned. Our study and the other cited investigations are limited in inference because of their observational nature. Finally, it is unclear what the long-term trajectory of passively restored grasslands will be in this system. Seven of the 13 pastures sampled in this study were cultivated or seeded for forage production within the past 20–60 years but contain moderate amounts of native cover, suggesting that there is some degree of natural recovery (to our knowledge, no active prairie restoration activities have occurred). Conversely, none of the pastures were devoid of non-native species, suggesting that these cultivated areas and seeded rangelands may be a source of non-native species. Thus, further research is needed to track the long-term trajectory of invasion versus self-restoration in passively restored grasslands.

Implications for Practice

- Grasslands with low to moderate levels of non-native cover can provide suitable habitat for nesting grassland breeding birds.
- Grassland restoration efforts targeted at enhancing habitat suitability for grassland birds do not need to mirror native conditions to provide suitable nesting habitat.
- Managers should pay particular attention to the physical structure of invading non-native plant species; if the structure of invading species differs strongly from native plant species in the area, the effect on nesting grassland birds should be monitored closely.

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