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Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover

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Abstract Extremes in rangeland management, varying from too-frequent fire and intensive grazing to the suppression of both, threaten rangeland ecosystems worldwide. Intensive fire and grazing denude and homogenize vegetation whereas their suppression increases woody cover. Although habitat loss is implicated in grassland bird declines, degradation through intensive management or neglect also decreases breeding habitat and may reduce nesting success through increased rates of nest predation. Snakes are important nest predators, but little is known about how habitat use in snakes relates to predation risk for grassland birds nesting within tallgrass prairie subjected to different grazing and fire frequencies. We evaluated nest survival in the context of habitat used by nesting songbirds and two bird-eating snakes, the eastern yellowbelly racer *Coluber constrictor flaviventris* and Great Plains ratsnake *Pantherophis emoryi*. Daily nest survival rates decreased with increasing shrub cover and decreasing vegetation height, which characterize grasslands that have been neglected or intensively managed, respectively. Discriminant function analysis revealed that snake habitats were characterized by higher shrub cover, whereas successful nests were more likely to occur in areas with tall grass and forbs but reduced shrub cover. Because snakes often use shrub habitat, birds nesting in areas with increased shrub cover may be at higher risk of nest predation by snakes in addition to other predators known to use shrub habitat (e.g., mid-sized carnivores and avian predators). Depredated nests also occurred outside the discriminant space of the snakes, indicating that other predators (e.g., ground squirrels *Spermophilus* spp. and bullsnakes *Pituophis catenifer*) may be important in areas with denuded cover. Targeted removal of shrubs may increase nest success by minimizing the activity of nest predators attracted to shrub cover.

Keywords Fire · Grazing · Nest success · Predator–prey relationships · Tallgrass prairie

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Introduction

At a global scale, temperate grasslands have experienced severe habitat loss, fragmentation, and degradation (White et al. 2000). In North America, the estimated loss of grassland ecosystems has exceeded 80% (Samson and Knopf 1994). Less than 4% of tallgrass prairie remains, most of which is located in the Flint Hills of Kansas and Oklahoma (Knapp and Seastedt 1998). As a result of such extensive habitat loss, grassland birds have suffered the most widespread decline of any North American bird group (Brennan and Kuvlesky 2005; Sauer et al. 2004). While the effect of habitat loss on grassland birds is clear, habitat degradation through the intensive management of remaining grasslands is an additional concern, given that the conversion of grasslands to agriculture was mostly completed by the 1940s in the Midwestern United States (Waisanen and Bliss 2002). Degradation of grasslands results from extremes in management ranging from intensive fire and grazing to the suppression of both (Briggs

et al. 2005; With et al. 2008). For example, most of the Flint Hills is privately owned with management aimed at increasing livestock production, often to the detriment of native wildlife (Fuhlendorf and Engle 2001). In the Flint Hills, annual burns and early intensive grazing were adopted in the 1980s and make up 25% of managed grasslands in the region (With et al. 2008). Intensive use of fire and grazing dramatically reduces vegetation cover and homogenizes the landscape, thereby reducing breeding habitat for grassland birds (Robbins et al. 2002; With et al. 2008). At the other extreme, neglected grasslands rapidly become shrublands or savannas (Archer et al. 1995; Briggs et al. 2002), again rendering sites unsuitable for grassland obligates (Grant et al. 2004). Current land management thus does not resemble the historical disturbance regime where tallgrass prairie experienced two to three fires every 5 years followed by ungulates that would graze recently burned areas, producing a heterogeneous grassland mosaic (Collins and Gibson 1990).

By altering habitat and nesting cover, extremes in land management may increase the risk of nest predation by increasing the numerical or functional response of predators. For example, increased encounters between predators and nests may occur through increased abundance of predators or by changes in nest concealment that make nests easier to locate. Nest predation accounts for the majority of nest losses in many ecosystems (Martin 1993a; Ricklefs 1969), and in the Flint Hills >80% of all nest failures were attributed to predation (Rahmig et al. 2009; Sandercock et al. 2008). In particular, shrub cover may increase the abundance and activity of species known to deprecate grassland bird nests, such as snakes (Blouin-Demers and Weatherhead 2001a). Snakes have been documented as responsible for up to 90% of predation events in California sage scrub (Morrison and Bolger 2002) and 38–72% of deprecated nests in Missouri (Thompson et al. 1999; Thompson and Burhans 2003) and in Nebraska and Iowa (Klug 2005). Although snakes have been shown to be important predators of bird nests in many habitat types (Klug 2005; Weatherhead and Blouin-Demers 2004), few studies have examined the habitat use of snakes in relation to nest predation risk in birds (Sperry et al. 2009). Whether snakes actively search for nests or take nests through incidental encounters, nests in areas of high snake activity will be at greater risk of predation (Zimmerman 1984).

We compared habitat use of two snake species and five species of nesting songbirds within a landscape subjected to different fire and grazing treatments. The main questions we addressed were:

1. Do snakes use areas of shrub cover within the tallgrass prairie disproportionately to the availability of shrubs on the landscape?

2. Is nest survival lower for grassland birds nesting in or near shrub cover?

3. What degree of habitat overlap exists between nesting grassland birds and their snake predators?

Our aim is thus to achieve a better understanding of predation risk for grassland birds through an analysis of how snakes respond to habitat shaped by different management practices. Insights into snake habitat use can inform conservation efforts for grassland birds by gauging the plausibility of managing habitat features intensively used by predators.

Materials and methods

Study site

Our research was conducted at Konza Prairie Biological Station (KPBS; 3,487 ha) in the northern Flint Hills of Kansas (39°05′N, 96°35′W). Data collection occurred during the avian breeding season from June to August in 2006, 2007, and 2008. The KPBS is an experimental landscape designed to address the effects of grazing and fire on tallgrass prairie. Data collection for both snakes and bird nests initially occurred in eight focal watersheds that were either burned annually or every 4 years, and were either grazed or not by bison Bos bison. Radio-tracked snakes would occasionally move into other watersheds, however, and thus we ended up working in an additional eight watersheds, where we also encountered bird nests. In total, our study area covered 16 watersheds that encompassed a range of burn frequencies (1–20 years) and were either ungrazed or grazed by bison.

The KPBS exhibits a range of grassland habitats found in the Flint Hills including areas with shrub cover, areas dominated by C_4 prairie grasses, areas of increased forb density, and grazing lawns denuded of vegetation. Prairie grasses are found across the landscape with increased productivity in lowlands and areas that are not heavily grazed. The dominant grasses include big bluestem *Andropogon gerardii*, little bluestem *Schizachyrium scoparium*, Indian grass *Sorghastrum nutans*, and switchgrass *Panicum virgatum*. Shrubs include rough-leaved dogwood *Cornus drummondii*, sumac *Rhus* spp., prickly ash *Zanthoxylum americanum*, and eastern red cedar *Juniperus virginiana*. Although burning and grazing influence vegetation structure, a variety of habitats can still be found within individual watersheds on KPBS. For example, shrubs occur in lowlands and along rock outcrops within all watersheds as a function of variation in soil moisture, but are more prevalent in areas that are infrequently burned. Thus, habitat heterogeneity occurs at scales finer than the watershed.

Bird nests

We located nests of grassland birds by dragging a 30-m rope over the ground to flush incubating or brooding females, through behavioral observations of females, and via opportunistic encounters. Nest contents (number of eggs or young) were monitored every third day until the nest was successful or failed. We considered nests successful if they fledged at least one young, including young of the brood-parasitic brown-headed cowbird *Molothrus ater*, because our focus was on nest predation and not host productivity per se (i.e., it was unlikely to matter to the predator whether it consumed a cowbird or host chick). We considered nests successful if we observed parents alarm-calling and feeding fledglings nearby or found fecal droppings on the nest rim (where chicks perch prior to fledging). Only nests that were successful or depredated were included in the analysis whereas nests that failed due to weather or abandonment were excluded ($n = 14$).

Of the 156 nests that were depredated (70.3% of 222 total nests), 115 nests (73.7%) were found prematurely empty (before young could have fledged) but were otherwise completely intact. Although this evidence is consistent with snake predation, it does not rule out other species of predators that also cause minimal disturbance to the nest (Pietz and Granfors 2000). For example, brown-headed cowbirds have been known to remove both eggs and nestlings from a nest without laying eggs (Klug 2005). Although brown-headed cowbirds are abundant on KPBS, previous research did not find cowbirds to be a major source of nest loss (Sandercock et al. 2008). Cricetid rodents are ubiquitous on KPBS but usually leave eggshell fragments or nestling carcasses behind as evidence (Pietz and Granfors 2000). Long-term data sets on the abundance of vertebrates on KPBS have also shown that ground squirrels *Spermophilus* spp. are rare (KPBS-Long-Term Ecological Research (LTER) Program, CSM04; http://www.konza.ksu.edu/) and therefore not likely to have a significant impact on avian reproductive success. Mid-sized carnivores such as raccoons *Procyon lotor* also occur on KPBS, but at low densities and are mainly found in lowland gallery forests (Kaufman et al. 2005).

Because of the limitations of inferring the identity of predators from evidence left at the nest, we ran the analyses with all depredated nests regardless of predator type (Pietz and Granfors 2000). We present results from the analyses with all depredated nests to illustrate the full range of habitat conditions characterizing depredated nests, thus enabling us to pinpoint the habitat domain of the two most abundant snakes versus those of other potential predators. Although a high degree of habitat overlap between snakes and depredated bird nests does not prove that snakes are the culprit, it does provide a strong degree of association and

puts them at the scene, thus implicating them as likely nest predators.

Snake predators

Snakes were captured using coverboards (60×180-cm plywood sheets), drift fences with funnel traps, and through opportunistic encounters (Cavitt 2000a; Parmelee and Fitch 1995). We have focused on the eastern yellowbelly racer *Coluber constrictor flaviventris* (henceforth "*C. constrictor*") and the Great Plains ratsnake *Pantherophis emoryi* given their abundance on KPBS and known association with open grassland habitats (Wilgers and Horne 2006). *Coluber constrictor* and *P. emoryi* made up 47 and 27%, respectively, of all snakes captured ($n = 146$). Among the other snakes encountered, 10% were red-sided garter snakes *Thamnophis sirtalis*, 9% common kingsnakes *Lampropeltis getula*, 6% bullsnakes *Pituophis catenifer*, and 1% black ratsnakes *Elaphe obsoleta*. Although these snake species might also be nest predators, we did not find them in sufficient numbers for study, and thus assume their impact on grassland birds was minimal in comparison to *Coluber constrictor* and *P. emoryi*. *Coluber constrictor* has been documented depredating dickcissel *Spiza americana* nests on KPBS (Sandercock et al. 2008; personal observation), in old fields located in Missouri (Thompson et al. 1999; Winter 1999; Thompson and Burhans 2003) and restored grasslands in Nebraska and Iowa (Klug 2005). *Pantherophis emoryi* has been identified consuming golden-cheeked warbler *Dendroica chrysoparia* nests in the oak savannas of Fort Hood, TX (Stake 2001). In addition to video-documentation, the diets of *C. constrictor* and *P. emoryi* in Kansas (Fitch 1999) and on the KPBS (Cavitt 2000b) have been shown to include birds.

We assessed habitat use by *C. constrictor* and *P. emoryi* by radio-tracking individual snakes. We fitted adult snakes weighing at least 100 g with temperature-sensitive radio-transmitters (5.0 g, 6–12 month battery life at 20°C; model SI-2T; Holohil Systems, Carp, ON, Canada). Radio-transmitters were implanted under the supervision of a veterinarian affiliated with the Kansas State University College of Veterinary Medicine, following standard procedures (Hardy and Greene 1999; Reinert and Cundall 1982). Other than one female *P. emoryi* that did not recover from surgery, implantation did not cause any major physiological or behavioral changes in the snakes. After implantation, we released snakes at the location of capture and tracked individuals every 24–48 h during the peak of the avian breeding season (June–August). We used a portable, radio-telemetry receiver (Challenger 2100; Advanced Telemetry Systems, Isanti, Minn.) to locate snakes between 0400 and 2400 hours to allow locations to be taken in the coolest and warmest parts of the day to fully

encompass the activity range of both a nocturnal (*P. emoryi*) and a diurnal (*C. constrictor*) snake. For each location, we recorded UTM coordinates with a handheld GPS, and flagged all locations for when we returned to measure local vegetation structure after the snake had moved (>100 m). We included locations that were used repeatedly by a single snake only once in the habitat overlap analysis.

Habitat categorization

To evaluate the use of shrub and grass habitat by snakes, we categorized the area surrounding each location (within 4 m) as either predominantly grass or shrub. We also selected a random point within 200 m (i.e., maximum breadth of summer home range for both *C. constrictor* and *P. emoryi*; unpublished data) of each snake location to measure habitat availability. We classified habitat at snake and random points as either predominantly grass or shrub based on visual observation in ArcMap 9.0 by referencing a remotely-sensed Quickbird image of the KPBS taken on 13 August 2007, which was pan-sharpened for a 1-m resolution. Shrub cover was unlikely to change substantially over the course of this study (i.e., 3 years); thus, the single image was sufficient for capturing the presence of shrub cover. Habitat characterization was carried out to identify habitat use of snakes using compositional analysis (see "Statistical analyses").

Habitat structure

To evaluate overlap between nesting songbirds and snakes, we measured habitat at bird nests ($n = 222$), *C. constrictor* locations ($n = 155$), and *P. emoryi* locations ($n = 128$). At each location, we measured vegetation structure within 30 m of the nest or snake location by averaging the readings at ten sampling points. We chose a maximum distance of 30 m to represent the foraging neighborhood of snakes, based on the estimated daily distance moved by *C. constrictor* (Fitch and Shirer 1971). Heterogeneity of habitat structure within grasslands has been shown to influence nest predation risk for grassland birds (Winter 1999; Churchwell et al. 2008). Thus, our analysis was conducted at the local scale (within 30 m of snake and bird locations).

We took one reading directly at the nest or snake location and nine additional readings at 3, 15, and 30 m from the location. The three points taken at each distance were at 120° from the first randomly chosen direction. We surveyed habitat an average of 7 days ($n = 222$, range = 0–30 days, SE = 0.4) after nest completion and an average of 13 days ($n = 283$, range = 1–30 days, SE = 0.6) after the snake had moved (i.e., >100 m from previous location).

We measured 12 structural variables at each point. Horizontal structure was measured with a Daubenmire frame (0.5 m × 0.5 m) to record percent vegetation cover including grass, forbs, and shrubs and to record percent ground cover including litter, bare ground, and rock. Vertical structure was assayed as both the height of the tallest vegetation within the Daubenmire frame, and by the visual obstruction reading of vegetation (i.e., biomass) in front of a 100-cm Robel pole placed perpendicular to the ground, with measurements taken in the four cardinal directions. We recorded litter depth as the average of four measurements taken at the corners of the Daubenmire frame. We used the coefficient of variation (CV) to capture heterogeneity in vegetative height, biomass, and litter depth. We tested for correlations among variables and dropped any variables that were highly correlated ($r > 0.6$). We excluded biomass (mean and CV) as it was positively correlated with vegetation height (mean, $r = 0.8$; CV, $r = 0.6$). We excluded percent bare ground as it was negatively correlated with both percent litter ($r = -0.9$) and litter depth ($r = -0.7$). We also excluded litter depth as it was positively correlated with percent litter ($r = 0.7$). Habitat structure was quantified to evaluate the daily survival rate (DSR) of nests as well as the overlap between bird nests and snake locations using discriminant function (DF) analysis (DFA; see "Statistical analyses").

Statistical analyses

Our first objective was to evaluate if snakes occurred in grass or shrub habitat disproportionately to the availability of these habitats on the landscape. For each snake ($n = 12$ *C. constrictor* and $n = 15$ *P. emoryi*), we calculated habitat use as the proportion of snake locations in grass versus shrub habitat, where habitat availability was the proportion of random locations in grass or shrub habitat. We used compositional analysis to compare habitat use to availability (Aebischer et al. 1993). We compared the log ratios of the proportion of habitat used and the log ratios of the proportion of available habitat in separate analyses for *C. constrictor* and *P. emoryi* in SAS (SAS Institute, Cary, N.C.). We considered habitat use to be random if the log ratios of available and used habitat were approximately equal. If habitat use was non-random, we ranked habitat by comparing the pair-wise differences between matching log ratios.

To address our second objective as to which habitat variables best explained DSR, we used the review of the effects of management on grassland birds by Johnson et al. (2004) to identify habitat variables considered a priori to be important in explaining the reproductive success of grassland birds. We considered eight habitat variables using both the mean (% shrub, % grass, % forb, % litter, % rock,

and vegetation height) and CV (vegetation height and litter depth) after excluding biomass, CV biomass, and litter depth due to correlations with other variables as mentioned previously. We estimated DSR with the design matrix tools and the logit-link function in the nest survival model of Program MARK (Dinsmore et al. 2002). We calculated the variance in survival rates projected to a 20-day nesting cycle according to the delta method (Powell 2007). The encounter days were the number of days between the first and last day of nest monitoring. The variance inflation factor cannot be identified in the nest survival model in Program MARK and therefore overdispersion could not be tested (Dinsmore et al. 2002). For model selection, we used the Akaike information criterion adjusted for small sample sizes (AIC_c) and evaluated model fit based on differences in deviance, AIC_c values (ΔAIC_c) and Akaike weights (w_i; Guthery et al. 2005). After running the global model (all eight habitat variables), we evaluated the effect of each habitat variable by assessing if the slope coefficient (β) had a 95% confidence interval (CI) overlapping zero. We used the variables whose 95% CI for β did not overlap zero as a base for constructing models containing two habitat variables (13 models). We also included a constant model and eight single-variable habitat models. In addition, we included three categorical models to ensure that nesting success was not better explained by species, year, or treatment as opposed to habitat variables.

To evaluate our third objective as to the degree of habitat overlap between nesting grassland birds and snakes, we performed a multivariate analysis to compare the habitats associated with *C. constrictor* locations, *P. emoryi* locations, successful bird nests, and depredated bird nests. We used SAS (SAS Institute) to run a multivariate ANOVA (MANOVA) to determine if any significant differences existed among the four groups, followed by a DFA to identify the environmental variables contributing to differences among the groups. The DFA is a gradient analysis that allowed us to visualize the separation of depredated and successful nests in the context of snake habitat use.

Multivariate statistics come with assumptions that we considered in the analysis. Bartlett's modification of the likelihood ratio test indicated heterogeneity of the within-group covariance matrices ($\chi^2 = 487.7$, $P < 0.0001$). Although the homogeneity of covariance assumption is rarely met with ecological data, multivariate analyses can still have descriptive value (Blouin-Demers and Weatherhead 2001b). Numerous variables exhibited heteroscedacity and were log-transformed to meet the assumption of normality. The conclusions from the log-transformed analysis were not different from the analysis with the original data; we therefore report only the analyses based on non-transformed data. Finally, repeated measures on individual snakes violate the assumption of data independence in ANOVA, and radio-telemetry data are unlikely to represent a random sample. We could have taken the means of individual snakes to avoid potential bias, but this would have greatly reduced our sample sizes (i.e., 12 *C. constrictor* and 15 *P. emoryi*) and would not have captured the heterogeneity found within individuals, thus would have resulted in the loss of vital information about snake habitat use. The snakes with the most observations accounted for 11 and 10% of the total locations for *C. constrictor* and *P. emoryi*, respectively; thus, we view potential bias as minimal.

Results

Snake telemetry and habitat use

We monitored 27 snakes over three field seasons. For *C. constrictor*, we tagged eight females [snout–vent length (SVL), range = 66–81 cm, mean = 72 cm, SE = 1.9; mass, range = 122–256 g, mean = 160 g, SE = 15.8] and four males (SVL, range = 65–67 cm, mean = 66 cm, SE = 1.0; mass, range = 106–118 g, mean = 113 g, SE = 2.8). For *P. emoryi*, we tagged four females (SVL, range = 80–104 cm, mean = 91 cm, SE = 7.1; mass, range = 181–431 g, mean = 295 g, SE = 72.9) and 12 males (SVL, range = 74–105 cm, mean = 89 cm, SE = 3.0; mass, range = 137–348 g, mean = 236 g, SE = 19.5). We collected a total of 403 locations for *P. emoryi* and 374 locations for *C. constrictor*.

The use of habitats differed significantly from percent available for *C. constrictor* ($t = -2.67$, $P = 0.004$), which used shrub habitat more often than expected based on availability (Fig. 1). The proportion of *C. constrictor* locations found in shrub habitat averaged 46% ($n = 12$, SE = 0.09), which was significantly greater than 23% (SE = 0.05), the average proportion of random locations found in shrub habitat. For *P. emoryi*, the use of either habitat was not significantly different from percent available ($t = 0.328$, $P = 0.75$). The proportion of *P. emoryi* locations found in shrub habitat averaged 27% ($n = 12$, SE = 0.07), which was similar to 21% (SE = 0.04), the average proportion of random locations found in shrub habitat (Fig. 1).

Avian nesting success

Over 3 years, we found 222 nests of five species of grassland songbirds: dickcissel (DICK; $n = 156$), grasshopper sparrow *Ammodramus savannarum* (GRSP; $n = 38$), lark sparrow *Chondestes grammacus* (LASP; $n = 19$), eastern meadowlark *Sturnella magna* (EAME; $n = 7$), and field
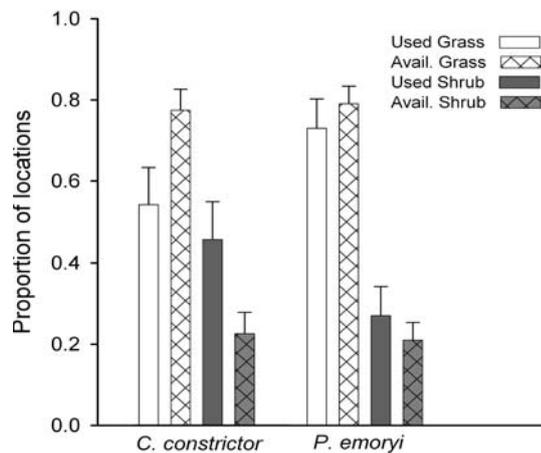
Fig. 1 The proportion of locations for *Coluber constrictor* and *Pantherophis emoryi* in grass habitat and shrub habitat as compared to the proportion of random locations in each habitat type on the Konza Prairie Biological Station (KPBS) 2006–2008. The mean and SE were calculated by averaging the proportions for *C. constrictor* ($n = 12$) and *P. emoryi* ($n = 12$). The total number of used and random locations was 374 and 403 for *C. constrictor* and *P. emoryi*, respectively. For *C. constrictor*, the number of random locations in shrubs was 94 (25.1%), and the number of used locations in shrubs was 183 (48.9%). For *P. emoryi*, the number of random locations in shrubs was 87 (21.5%), and the number of used locations in shrubs was 119 (29.5%). *Avail.* Available

sparrow *Spizella pusilla* (FISP; $n = 2$). Of the 222 nests, 66 fledged at least one young for an apparent nest survival rate of 29.7%. The DSR of nests was 0.915 ± 0.007, for an overall survival of $16.8 \pm 2.0\%$ when we extrapolated a 20-day nesting cycle for all five species. We monitored 90 nests in 2006, fifty-six in 2007, and seventy-six in 2008. The nests were found in nine treatments including annual burn and ungrazed (nests: DICK = 62, GRSP = 4, LASP = 6, FISP = 1, EAME = 1), annual burn and grazed (nests: DICK = 21, GRSP = 9, LASP = 7), 2-year burn and grazed (nests: DICK = 6), 2-year burn and ungrazed (nests: DICK = 2), 4-year burn and grazed (nests: DICK = 29, GRSP = 14, LASP = 3), 4-year burn and ungrazed (nests: DICK = 31, GRSP = 7, LASP = 1, EAME = 4, FISP = 1), 20-year burn and grazed (nests: DICK = 1, GRSP = 4), 20-year burn and ungrazed (nests: EAME = 2), and areas of no set burning or grazing treatment (nests: DICK = 4, LASP = 2). Out of the final models, the best model indicated that birds nesting in areas of increased vegetation height but decreased shrub cover had higher nest success (Table 1). The top model showed that the effect of percent shrub cover on nest survival was negative ($\beta = -0.30$, 95% CI $= -0.48$ to -0.12) and vegetation height was positive ($\beta = 0.32$, 95% CI $= 0.03$ to 0.41). As dickcissel nests made up 70% of the nest data set, we ran the DSR analysis in Program MARK with dickcissel nests only and the results did not change. Therefore, we present

Table 1 Models tested in Program MARK to predict daily survival rates of grassland birds on Konza Prairie Biological Station (KPBS) 2006–2008

Model	Deviance	k	AIC_c	ΔAIC_c[a]	w_i[b]
% Shrub, Veg. height	721.66	3	727.67	0.000	0.517
% Shrub	727.04	2	731.05	3.375	0.096
% Shrub, % Litter	725.56	3	731.58	3.905	0.073
% Shrub, CV Veg. height	725.72	3	731.73	4.059	0.068
% Shrub, % Grass	726.92	3	732.93	5.261	0.037
% Shrub, CV Litter depth	726.96	3	732.97	5.304	0.036
% Shrub, % Rock	726.97	3	732.99	5.318	0.036
% Shrub, % Forb	726.98	3	732.99	5.324	0.036
Constant	732.82	1	734.83	7.157	0.014
Global	717.51	9	735.61	7.943	0.010
Veg. height	731.74	2	735.74	8.072	0.009
% Litter	732.58	2	736.59	8.916	0.006
% Rock	732.80	2	736.81	9.138	0.005
CV Veg. height	732.81	2	736.82	9.149	0.005
% Grass	732.82	2	736.83	9.158	0.005
CV Litter depth	732.82	2	736.83	9.161	0.005
% Forb	732.82	2	736.83	9.161	0.005
Year	730.89	3	736.90	9.231	0.005
Species	727.20	5	737.23	9.564	0.004
Veg. height, % Forb	731.58	3	737.60	9.926	0.004
Veg. height, % Grass	731.61	3	737.62	9.951	0.004
Treatment	721.63	9	737.71	10.042	0.003
Veg. height, CV Litter depth	731.71	3	737.72	10.049	0.003
Veg. height, % Rock	731.73	3	737.74	10.073	0.003
Veg. height, % Litter	731.74	3	737.75	10.079	0.003
Veg. height, CV Veg. height	731.74	3	737.75	10.080	0.003

k Number of parameters, AIC_c Akaike's information criterion for small sample sizes, w_i Akaike weight, *Veg. height* vegetation height, *CV* coefficient of variation

[a] ΔAIC_c is the scaled value for AIC_c. Ascending ΔAIC_c ranks the candidate models

[b] w_i represents support for each model

the results including all grassland bird species because we are interested in nest predation by snakes on the entire community of grassland birds.

Habitat overlap

When testing all four groups together, we found significant differences between the habitat associations of *C. constrictor*, *P. emoryi*, depredated nests, and successful nests (Wilk's $\lambda = 0.677$, $F_{45, 1447.5} = 4.52$, $P < 0.001$). The DFA produced two statistically significant DFs that collectively accounted for 97% of the variation (Table 2). Although the DFs are multivariate, we base our interpretation on the strength of the loadings (eigenvalue > 0.4) on particular variables and present the univariate differences

among groups for comparative purposes. The first DF ($F_{24, 1433.4} = 6.60$, $P < 0.001$) accounted for 59% of the variation and was loaded on percent shrub cover, vegetation height, heterogeneity of vegetation height, and percent litter cover (Table 2). The first DF could be interpreted as a gradient from open grassland to increased shrub cover and separated habitat used by snakes from that used by nesting songbirds (Table 3; Fig. 2). We did not expect complete overlap between snakes and birds because snakes use a variety of habitats and are not just concentrated at bird nest locations. The second DF ($F_{24, 1433.4} = 6.60$, $P < 0.001$) accounted for 38% of the variation and was loaded on vegetation height and rock cover (Table 2). We interpreted the second DF as a gradient from short vegetation with little rock cover to tall vegetation with abundant rock cover, which separated successful nests from depredated nests (DF2, $F_{1, 221} = 16.3$, $P < 0.001$), as well as the two snake species (DF2, $F_{1, 282} = 43.3$, $P < 0.001$; Table 3; Fig. 2).

Habitat used by *C. constrictor* was significantly different from that of successful nests along both DFs, with snake locations characterized by increased heterogeneity and taller vegetation due to shrubs (DF1: $F_{1, 220} = 49.5$, $P < 0.001$), and successful nests having taller vegetation related to grass and forbs (DF2: $F_{1, 220} = 31.9$, $P < 0.001$; Table 3; Fig. 2). Habitat used by *C. constrictor* was not significantly different from that of depredated nests along the second DF, as both were characterized by lower vegetation and rock cover (DF2: $F_{1, 310} = 3.5$, $P = 0.06$; Table 3). Habitat used by *P. emoryi* was significantly different from that of depredated nests along both DFs, having taller, shrubbier vegetation and more rock cover than that at depredated nest sites (DF1, $F_{1, 283} = 47.1$, $P < 0.0001$; DF2, $F_{1, 283} = 25.0$, $P < 0.001$; Tables 2, 3). *Coluber constrictor* and *P. emoryi* locations both had about 3 times the shrub cover of successful nests (Table 2). Depredated

nests, in turn, had 62% more shrub cover than successful nests (Table 2). Thus, nests in areas of increased shrub cover overlapped with habitat used by these two snake predators and suffered a higher rate of failure (Table 2).

Generalized linear distances were used to classify discriminant scores as belonging to one of the four groups through resubstitution (Table 3). Although groups may have been significantly different on average, individual discriminant scores may be classified into another group based on habitat characteristics. Only 9.1% of successful nests were misclassified as depredated, whereas 31.4% of depredated nests were misclassified as successful. For depredated nests, 25% were misclassified as *C. constrictor*, whereas only 16.7% of successful nests were misclassified as such. Of the depredated nests, 35.9% were misclassified as *P. emoryi* but only 4.6% of the successful nests were misclassified as *P. emoryi* (Table 3). Thus, 61% of depredated nests were misclassified as snake habitat, whereas only 21.3% of successful nests were misclassified as such, which indicates that substantial overlap occurs between habitats used by snakes and depredated nests.

Discussion

Nest predation is the major factor limiting reproductive success in grassland birds (Martin 1993b). A simultaneous assessment of habitat use by nesting songbirds and their nest predators thus contributes to a more comprehensive understanding of how habitat mediates nest predation risk in grassland birds. In this study, we were able to relate nest predation risk for grassland birds in tallgrass prairie to shrub habitat, which is also used extensively by snakes. We found that grassland birds achieved higher nesting success in areas with decreased shrub cover but increased vegetation height from grass and forbs. Other studies of nest predation in

Table 2 Univariate statistics (mean and SE) of each habitat variable used in the discriminant function (DF) analysis (*DFA*) to separate the four groups (successful nests, depredated nests, *Coluber constrictor*, and *Pantherophis emoryi*) and the pooled within-group correlations (DF1 and DF2) between measured variables to indicate the weighting of each variable on the DFs

Variable	Successful nests ($n = 66$)	Depredated nests ($n = 156$)	*C. constrictor* ($n = 155$)	*P. emoryi* ($n = 128$)	Eigenvalue[a]	
					DF1	DF2
% Shrub	5.81 (1.08)	9.40 (1.00)	18.71 (1.68)	17.64 (1.80)	*0.660*	−0.111
% Litter	47.12 (3.92)	45.47 (2.59)	58.46 (1.91)	57.25 (2.44)	*0.457*	0.006
% Rock	12.35 (1.62)	10.79 (0.88)	8.67 (0.65)	14.09 (1.33)	−0.012	*0.486*
% Grass	44.41 (2.08)	45.99 (1.62)	46.24 (1.18)	48.01 (1.50)	0.110	0.063
% Forb	35.25 (1.59)	33.92 (1.07)	31.43 (1.10)	32.86 (1.20)	−0.192	0.130
Veg. height	77.61 (2.71)	72.06 (1.68)	77.38 (1.84)	87.63 (2.51)	*0.379*	*0.517*
CV Veg. height	0.25 (0.02)	0.28 (0.01)	0.36 (0.02)	0.36 (0.02)	*0.569*	−0.066
CV Litter depth	0.86 (0.09)	0.81 (0.05)	0.86 (0.03)	0.88 (0.04)	0.080	0.075

[a] Eigenvalues >0.4 are in *italics*

Table 3 The generalized squared distances[a] between the four group centroids and the associated statistical significance including the multivariate ANOVA and ANOVA for each DF as well as the percentage of discriminant scores classified into each of the four groups[b] [successful bird nests (S), depredated bird nests (D), C. constrictor locations (C), and P. emoryi locations (P)] on KPBS 2006–2008

	Depredated					C. constrictor					P. emoryi				
	Distance	% Classified	F	df	P	Distance	% Classified	F	df	P	Distance	% Classified	F	df	P
Successful			11.0	2,219	<0.001			35.1	2,218	<0.001			25.7	2,191	<0.001
DF1	S–D = 28.2	S–D = 9.1	2.5	1,221	0.12	S–C = 27.7	S–C = 16.7	49.5	1,220	<0.001	S–P = 30.0	S–P = 4.6	51.4	1,193	<0.001
DF2	D–S = 27.5	D–S = 31.4	16.3	1,221	<0.001	C–S = 31.8	C–S = 17.4	31.9	1,220	<0.001	P–S = 30.0	P–S = 17.2	0.3	1,193	0.57
Depredated								24.9	2,308	<0.001			32.9	2,281	<0.001
DF1						D–C = 27.1	D–C = 25.0	46.7	1,310	<0.001	D–P = 27.6	D–P = 35.9	47.1	1,283	<0.001
DF2						C–D = 28.5	C–D = 9.7	3.5	1,310	0.06	P–D = 28.8	P–D = 10.2	25.0	1,283	<0.001
C. constrictor													22.2	2,280	<0.001
DF1											C–P = 29.1	C–P = 9.7	0.1	1,282	0.73
DF2											P–C = 27.5	P–C = 27.3	43.3	1,282	<0.001

[a] Generalized squared distances for each group (S–S = 26.51, D–D = 27.60, C–C = 26.23, P–P = 28.58)

[b] Percent of discriminant scores correctly classified into each group (S–S = 69.7, D–D = 35.9, C–C = 63.2, P–P = 45.3)

grassland birds have found a positive correlation between vegetation height and survival rate (Davis 2005; Winter 1999) possibly due to greater nest concealment or interference with predator search strategies. Although shrubs can provide cover for nests, we have shown that shrubs are heavily used by snakes (i.e., C. constrictor) and may contribute to increased predation pressure.

Snakes may use shrub habitat because it affords cover and increased structural heterogeneity, which may provide protection from predators (Wilgers and Horne 2007), a favorable thermal environment (Blouin-Demers and Weatherhead 2001a), or higher prey densities (Carfagno et al. 2006). Studies in the tropics have shown that snakes are attracted to shrubby edges because of an increased density of small mammals (Heard et al. 2004), but studies in temperate regions have not shown the same relationship, possibly due to greater prey diversity or because thermoregulatory needs place a greater constraint on habitat selection (Carfagno et al. 2006). We have anecdotal evidence that snakes may be using shrubs to reach higher body temperatures to aid in digestion. For example, we observed a C. constrictor consuming a large meal of dickcissel nestlings and subsequently moving to a higher position in a dogwood shrub. We also found that snakes had higher body temperatures ($+1.5°C$) when higher up in shrub habitat compared to grass habitat (unpublished data), which again suggests that snakes may use shrubs for thermoregulation. Regardless of why snakes use shrubs, birds nesting in or near shrubs will have a higher likelihood of being encountered by a snake.

Other potential nest predators also occur in the system. For example, raccoons may also preferentially forage in shrubby habitats (Newbury and Nelson 2007), thus compounding predation pressure on bird nests in shrubby areas if the effect of additional predators is additive. Depredated nests outside the snake habitat space may be attributable to another type of predator, such as bullsnakes or ground squirrels, which prefer short vegetation, as might be found in intensively grazed and burned sites (Kaufman and Fleharty 1974; Fitch 1999). The region in discriminant space consisting only of successful nests could be viewed as habitat with a low risk of predation. The low-risk area was characterized by tall vegetation but low shrub cover. On KPBS, this type of vegetation is found in watersheds with annual burning and low-density grazing. Elsewhere in the Flint Hills, tall vegetation and low shrub cover is likely to be attained in native prairie hayfields, which have late-season haying, and in season-long grazed pastures that are stocked at half the density of pastures that are annually burned and double-stocked (Rahmig et al. 2009). Several grassland birds (dickcissel, grasshopper sparrow and eastern meadowlark) were found to have higher reproductive success in hayfields than in grazed grassland in the Flint
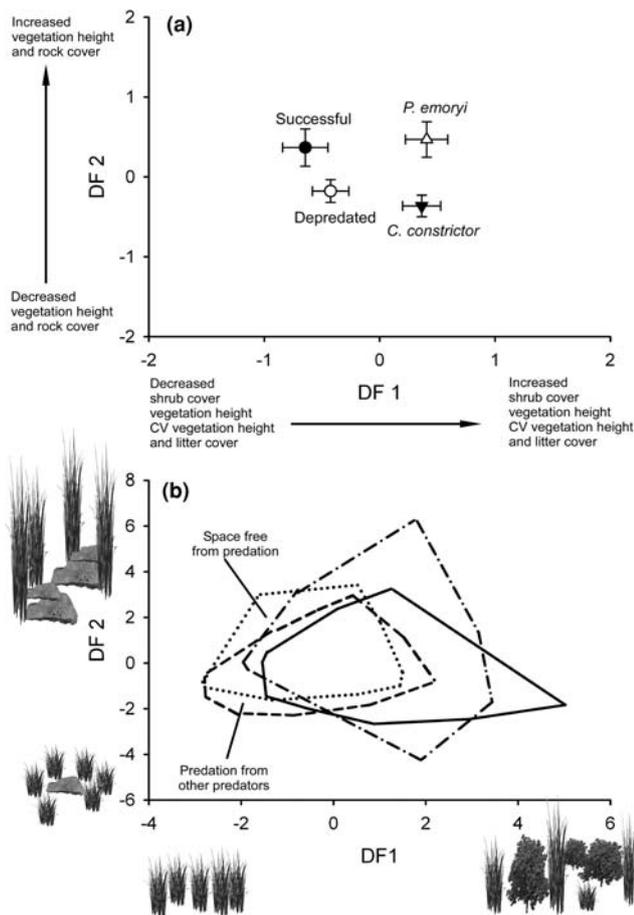
811

Fig. 2 Habitat gradients in the analysis of habitat use by grassland birds and two species of snake predators on the KPBS 2006–2008. **a** Group centroids and SEs on the significant discriminant axes for successful nests, depredated nests, and locations of *C. constrictor*, and *P. emoryi*. **b** Outline of discriminant scores for each group: successful nests (*dotted*), depredated nests (*dashed*), *C. constrictor* locations (*solid*), and *P. emoryi* locations (*dashed/dotted*). *DF* Discriminant function, *CV* coefficient of variation

Hills (Rahmig et al. 2009; With et al. 2008), perhaps as a consequence of lower predation pressure in hayfields relative to other managed grasslands.

Rangeland management in the Flint Hills, which involves widespread grazing and annual burning, has reduced tallgrass vegetation to a stature akin to that of the shortgrass steppe of the western Great Plains. At the other extreme, fire suppression, particularly around centers of urban growth (exurban development), is spurring woody encroachment. In both cases, reductions in vegetative cover and the promotion of woody invasives are predicted to lead to increased predation risk for nesting grassland birds by predators such as snakes, which may explain the inordinately high rates of nest predation and reproductive failure experienced by grassland birds in the Flint Hills region (Rahmig et al. 2009; With et al. 2008). Therefore, any increase in the survival rate of nests through reductions in

predation could help increase reproductive success and alleviate declines in grassland bird populations, which are estimated to be declining by 3–29% annually in the Flint Hills (With et al. 2008).

The primary focus of grassland bird conservation is usually on either the restoration of grasslands or the management of existing grasslands to improve habitat quality. In regions such as the Flint Hills, where much of the grassland is under private land ownership and management is mainly commodity driven (e.g., for the benefit of livestock production), opportunities for altering land-management practices are limited. Elsewhere, such as in areas of exurban development, it may not be possible to restore burning and grazing to halt shrub invasion. Once shrubs become established, however, burning and grazing may no longer be sufficient in any case, and mechanical removal is necessary (Briggs et al. 2005). Thus, one alternative might be the strategic removal of shrubs and trees to mediate nest predation risk in areas where woody invasion is of particular concern. In our system, shrub cover should be reduced or maintained to encompass no more than 5% of the total area (i.e., the average shrub cover at successful nests), which may require only a small reduction in existing shrub cover, given that the average shrub cover at depredated nests was ~10% (Table 2). Thus, relatively small changes in the amount of shrubs might significantly reduce predation risk on nests of grassland birds, although this needs to be tested through future experimental research.

Although removal of shrub habitat may aid in the recovery of grassland birds, it could also remove habitat that may be necessary for sustaining snake populations, which are equally valuable components of the endangered tallgrass prairie. Conversely, if snake populations can be sustained without shrub cover, the removal of shrubs may simply spread snake activity across the landscape endangering a broader range of nests. Future research should thus examine the effect of shrub removal on snake habitat use and density in addition to nest survival (a before–after comparison), especially given the labor and expense of manually removing shrubs and trees. In addition, the removal of shrubs not only impacts individual predators but interactions between the suite of predators known to use shrubs (e.g., mid-sized carnivores, snakes, and brownheaded cowbirds). Therefore, future studies analyzing the experimental removal of shrubs should consider the impact on the abundance and activity of multiple predators as well as their interactions (Klug et al. 2009).

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