Avian nest survival and snake abundance in restored and remnant grasslands in northwestern Iowa

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Avian nest survival and snake abundance in restored and remnant grasslands in northwestern Iowa

by

L. Embere Hall

A thesis submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Program of Study Committee:
Rolf R. Koford, Major Professor
Diane M. Debinski
Dave L. Otis

Iowa State University
Ames, Iowa
2005
This is to certify that the master's thesis of

L. Embere Hall

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy
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CHAPTER 1. GENERAL INTRODUCTION

Intensive agriculture in the Midwest has dramatically reduced the amount of grass on the landscape (Brennan and Kuvlesky 2005). Prior to European settlement in Iowa, for example, tallgrass prairie covered 79.5% of the state. Today less than 0.1% of the pre-settlement prairie remains (Smith 1998). Remaining patches of grassland are generally fragmented and imbedded in a matrix of row-crop agriculture. Consequently, native wildlife populations have declined (Christiansen 1981, Herkert 1995, Peterjohn and Sauer 1999).

Since settlement, at least 17 species of birds no longer nest in Iowa (Dinsmore 1981). Nearly 40% of all snake species native to Iowa are currently listed as endangered, threatened or of special concern (State of Iowa 2002, Knoot 2004).

In recent years federal initiatives such as the Conservation Reserve Program and the North American Waterfowl Management Plan (now part of the North American Bird Conservation Initiative) have provided incentives for large scale restoration of perennial grassland in agricultural landscapes (King and Savidge 1995, McCoy et al. 1999). These efforts have focused on creating suitable habitat for waterfowl (Batt et al. 1989), and consist of planting areas with only a few species of grasses and forbs (Fletcher and Koford 2002). Plantings typically do not achieve the biotic and structural diversity of native tallgrass prairies. While many studies have examined wildlife abundance and distribution in blocks of monotypic grass (Best et al. 1997, Johnson and Igl 2001, Phillips et al. 2004), little is known about how restored habitats function compared to remnant grasslands. With restoration efforts ongoing in the Midwest, it is important to understand how current restoration practices impact grassland-associated wildlife.
I studied the impacts of restoration on grassland birds and snakes in northwestern Iowa by examining two distinct, though interconnected, questions. First, I compared avian nest success on restored and remnant grasslands. Habitat restoration is one of the only strategies for conserving grassland bird populations (Vickery et al. 1999). Estimating demographic parameters of populations using both habitat types provides a way to effectively test the efficacy of restoration efforts (Marzluff and Ewing 2001). Second, I compared snake abundance near grass-road edges to abundance in the interior of restored grasslands. My snake survey method required the removal of vegetation and therefore intensive surveys were impractical on remnant prairies. Two species of snakes, plains garter snakes (*Thamnophis radix*) and common garter snakes (*T. sirtalis*) are documented grassland songbird nest predators (Thompson et al. 1999, Renfrew and Ribic 2003). Therefore, information on the distribution and abundance of snakes may help explain variation in grassland bird nest survival in highly fragmented agricultural landscapes. Despite population declines of some snake species in recent years (Christiansen 1981, Tennant 2003), little information exists on grassland snake habitat preferences. To my knowledge this is the first study that addresses the impact of road edges on grassland snake abundance.

My study provides information on the impacts of current restoration efforts on grassland-associated birds and snakes. Results from this study will help guide future efforts to develop high-quality habitat for grassland birds and snakes.

**Thesis organization**

This thesis is composed of two papers written for publication in peer-reviewed journals. Chapter 1 provides a general introduction to my thesis research. Chapter 2 examines variation in grassland bird nest success in restored and remnant grasslands in northwestern Iowa. Chapter 3 evaluates grassland snake abundance in relation to grass-road edges and
explores the influence of local and landscape factors on snake abundance in restored grasslands. Chapter 4 contains general conclusions from my thesis research. Data acquisition, statistical analysis and the preparation of this text were the responsibility of the candidate; Dr. Rolf R. Koford provided guidance and editorial advice.

**Literature Cited**


perspective. Auk 118: 24-34.


CHAPTER 2. AVIAN NEST SUCCESS IN RESTORED AND REMNANT GRASSLANDS IN NORTHWESTERN IOWA

A paper to be submitted to Studies in Avian Biology

L. Embere Hall and Rolf R. Koford

Abstract. In the Midwest, less than 1% of pre-settlement tallgrass prairie remains. Agencies and land managers have responded to this habitat loss with land acquisition and grassland restoration programs. Grassland restorations in the Midwest, however, frequently consist of planting areas with only a few species of grasses and forbs. These plantings often do not achieve the structural diversity of native prairies. Several studies have documented grassland-bird use in restored grasslands, yet little is known about how productivity in restored grasslands compares to remnant grasslands. With restoration ongoing in the Midwest, it is important to understand how current practices affect grassland-breeding birds. During the 2003 and 2004 breeding seasons, we located nests in 10 restored and 6 remnant grasslands in northwestern Iowa. Survival estimates were compared to examine the impact of current restoration efforts on local bird productivity. Dickcissels (Spiza americana), Bobolinks (Dolichonyx oryzivorus), Red-winged Blackbirds (Agelaius phoeniceus) and Clay-colored Sparrows (Spizella pallida) nested in both habitat types. We used logistic-exposure models and AIC model selection to examine variation in daily survival rates. Best-supported models included nest age, habitat type (restored grasslands vs. remnant prairies) and nest height (ground vs. above-ground), though the effects of both habitat type and nest height were weak. Results from our study indicate restored grasslands in highly fragmented agricultural landscapes can provide comparable habitat for grassland-breeding birds, even if the restoration efforts do not mirror native habitat conditions.
Key words: Iowa, Logistic-exposure models, grassland birds, nest survival, remnant prairie, restoration.

Population declines of grassland breeding birds are widely recognized (Herkert 1995, Peterjohn and Sauer 1999, Vickery and Herkert 2001, Brennan and Kuvlesky 2005). As a group, grassland birds have experienced the steepest, most geographically widespread declines of any behavioral or ecological guild of birds in North America (Knopf 1994). Habitat fragmentation, degradation and loss of native grasslands top the list of likely causes of the declines (Noss et al. 1995, Johnson and Igl 2001). In Iowa, for example, tallgrass prairie once covered 79.5% of the state; today less than 0.1% of the pre-settlement prairie remains (Smith 1998). In addition to the overwhelming loss of tallgrass prairie, most prairie remnants in Iowa are small and isolated from other perennial grass habitats (Smith 1981).

Similar to national trends, populations of grassland breeding birds in Iowa have declined. North American Breeding Bird Survey results for Iowa and the central Midwest indicate more than 70% of grassland birds in the region had significant negative population trends from 1966-2004 (Sauer et al. 2005). Bobolinks (Dolichonyx oryzivorus) and Dickcissels (Spiza americana), two species central to this study, showed steep negative population trends (Sauer et al. 2005).

In recent years federal initiatives such as the Conservation Reserve Program (CRP) and the North American Waterfowl Management Plan (now part of the North American Bird Conservation Initiative) have provided incentives for large-scale restoration of perennial grassland in agricultural landscapes (King and Savidge 1995, McCoy et al. 1999, Brennan and Kuvlesky 2005). Restoration efforts have focused on creating suitable waterfowl habitat, because grasslands in the Prairie Pothole Region are a major source for waterfowl breeding.
in North America (Batt et al. 1989). In Iowa, specifically, the Iowa Department of Natural Resources (IDNR) established a goal of protecting and enhancing 76,200ha of prairie pothole habitat in the northern part of the state (Zohrer 1999). Generally, the goal of restoration is to alter an ecosystem back to its original condition (Meffe and Carroll 1994), however, grassland restorations in the Midwest often consist of planting areas with a few species of grasses and forbs (Johnson and Igl 2001, Fletcher and Koford 2002). These plantings typically do not achieve the biotic and structural diversity of native prairies.

Since habitat restoration is one of the only strategies for conserving the tallgrass prairie ecosystem and the corresponding grassland bird populations (Vickery et al. 1999), it is important to understand whether or not Midwestern restoration efforts provide productive breeding habitat for grassland birds. Studies examining avian species richness on restored grasslands and native prairies have produced mixed results. Some have shown similar bird species richness on the two habitat types (Johnson and Igl 2001, Fletcher and Koford 2002) while others have indicated substantial differences (Wilson and Belcher 1989). While these studies provide insight into bird use of both habitat types, species richness and density can be misleading indicators of habitat quality (Van Horne 1983, Vickery et al. 1992, Hughes et al. 1999, Winter and Faaborg 1999). Just because a species is found in a specific habitat does not mean that it is breeding in that habitat. Marzluff and Ewing (2001) suggest that estimating demographic parameters of populations using both habitat types is a more biologically relevant approach to evaluation of the efficacy of restoration efforts.

The objectives of our study were to compare non-game grassland bird nest survival on restored and remnant tracts of prairie and to relate nest survival to local vegetation characteristics. The information gained from this study will help evaluate the impact of current grassland restoration efforts on grassland breeding bird populations.
METHODS

Study areas

Our study was conducted from 2003 - 2004 at the Spring Run Complex in northwestern Iowa and at 6 remnant prairie sites in the surrounding 6 counties. The study sites were located in the tallgrass prairie ecoregion.

All of our reconstructed grassland sites (hereafter restored sites) were located at the Spring Run Complex. The Spring Run Complex is a 1620ha complex of reconstructed grasslands and wetlands in Dickinson County, Iowa. The Complex encompasses approximately 38.8km². This area includes both publicly owned land and privately owned farms. Despite the fragmented arrangement it is one of the largest remaining semi-contiguous prairie pothole complexes in Iowa. It comprises federal waterfowl production areas (WPA) and state wildlife management areas, which are managed for watershed protection and migratory waterfowl habitat. While most of the land is federally owned, it is managed by the IDNR. The IDNR began purchasing land in the Complex from willing sellers in the 1960’s, and continues to acquire properties today. Consequently the restoration progress on each tract is variable. Prior to purchase and restoration most tracts were used for row crop production. Current grassland management practices on the Complex include mowing, haying, grain plot farming and burning. Restored sites contained both warm-season and cool-season plantings, though cool-season species were by far most common. Warm-season plantings mostly consisted of switchgrass (*Panicum virgatum*). Cool-season plantings mostly consisted of smooth brome (*Bromus inermis*). Sweet clover (*Melilotus* spp.) and thistle (*Cirsium* spp.) were the dominant forbs, with few other forbs species occurring in the Complex.

Continuous tracts of remnant prairie were not available within the Spring Run Complex so we surveyed 6 publicly owned remnant prairies in the surrounding 6 counties;
Clay, Dickinson, Emmet, Osceola, Palo Alto and Kossuth. Five sites were managed by county conservation boards. One was managed by the IDNR. Remnant prairie sites (hereafter remnant sites) were natural prairies that had never been plowed or developed. They contained a high diversity of native warm season grasses and forbs, with some sites containing greater than 200 species. Current management practices on these sites include periodic burning and prairie seed harvest.

We surveyed all restored grasslands in the Complex that were greater than 10ha and that contained less than 50% wetland cover (n = 10). We surveyed 6 remnant sites in the surrounding area that satisfied the same criteria. With the exception of 1 remnant site, all sites were bordered by roads or by managed land (e.g. grazed pasture, row crop, etc.). One remnant site was bordered on 2 sides by a WPA planted to cool-season grasses. The remaining adjacent edge types on this site were grazed pasture and road. Aerial photographs taken in 2002 were used to quantify field size and percent wetland within each field. We surveyed a wide range of field sizes within each habitat type (restored grasslands: \( \bar{x} = 66.0, \) sd = ± 73.0ha; range = 12.7 - 248.6; remnant sites: \( \bar{x} = 51.2, \) sd = ± 29.0ha; range = 13.0 - 80.9). While highly variable, the range of plot sizes reflects the amount of available grassland habitat in the 6 county region.

Nest success

We located and monitored nests between 20 May and 9 August in 2003 and 2004. We divided our search time equally between both habitat types. We searched for nests of all grassland species, but focused our efforts on finding Bobolink and Dickcissel nests. Nests were located using a variety of techniques including systematic searches (Wiens 1969) and behavioral observations (Winter et al. 2003). We systematically searched sites by walking a pre-determined distance across a study plot carrying sweeping sticks. Sweeping sticks were
used to disturb the top of the vegetation. Birds, startled by the moving vegetation, flushed from their nests. We traversed each field walking parallel to each other, approximately 4m apart. We also located nests using behavioral observations. Behavioral cues such as chipping, flying short distances away from the observer, flushing close to the observer followed by a short flight, and carrying nest material, fecal sacs or food indicated that a nest might be nearby. The location of a potential nest site was marked with a short length of flagging tape. After marking a site we retreated several meters and tried to locate the nest when the bird returned. Nests were also found fortuitously, flushing birds while doing other research activities.

Once a nest was found we determined the location with a Global Positioning System (GPS) unit and placed a flag 2m north of the nest. Nests were monitored every 3 - 4 days. The monitoring interval was occasionally modified in individual cases to minimize nest disturbance and to check as close as possible to predicted hatch and fledge dates. During each nest check we recorded female presence/absence as well as the number and approximate age of the nest contents. Nests found during egg laying and incubation were aged using candlers (Lokemoen and Koford 1996). Nests containing nestlings were aged by comparing the nestlings to reference photographs illustrating daily development of altricial young. Precautionary methods, as described by Martin and Geupel (1993), were exercised to minimize human-induced mortality at nest sites.

A nest was considered successful if at least one nestling fledged. Evidence of success included feather sheaths and feces in the nest bowl, adults alarm calling or carrying food and the presence of fledglings. In some fields Bobolink nests were as little as 4 - 5m apart. Therefore it was sometimes difficult to determine which adult female was associated with a nest, and consequently difficult to determine the nest fate. However, as part of another
research objective we color banded many of the female Bobolinks for which we had nests. Having marked individuals helped us to determine if a female giving alarm calls was associated with a terminated nest.

We attributed nest failure to predation if the nest contents (eggs or nestlings) were removed. Failure was attributed to Brown-headed Cowbird (*Molothrus ater*) parasitism when nest abandonment occurred after a cowbird egg was deposited, or when only a cowbird nestling fledged. We considered weather the cause of failure when nests were found destroyed or abandoned after a storm. Finally nests were considered abandoned when the contents remained unchanged and no adults were present for two consecutive visits (Patterson and Best 1996).

Local vegetation measurement

Vegetation height, density and composition were recorded at each nest location to examine the relationship between nest survival and local habitat characteristics. Measurements were taken soon after a nest was no longer active. For each location, we measured vegetation using a method similar to Best et al. (1997). We measured vertical density by visual obstruction readings taken 4m from a Robel pole at a height of 1m above the ground (Robel et al. 1970). Four readings were taken at each nest location; one in each cardinal direction. The means of the measurements were used in analyses. We assessed canopy cover using a 20 x 50cm quadrat based on non-overlapping percentages (Daubenmire 1959). Canopy cover categories included: total (live + dead vegetation), litter, bare ground, standing live vegetation, standing dead vegetation, grass and forb. Cover was classified to the nearest 5 percent. To avoid biasing canopy cover estimates, we used the midpoints of these classes for analysis. We measured litter depth twice at each nest location, at opposite corners of the quadrat.
Statistical analyses

Vegetation characteristics

We used mixed-model analysis of variance (ANOVA) models to examine differences in vegetation structure between habitat types (PROC MIXED; SAS Institute 2001). We treated the mean of the vegetation metric as the response variable, site as a random effect and habitat type (restored or remnant) as the main explanatory variable. We used a year*type interaction to test for differential year effects. We chose sites that satisfied our area and percent wetland cover requirements. However, we treated site as a random effect because we had no reason to suspect that vegetation characteristics would be different on the studied sites, compared to other grassland sites of similar management, area and wetland cover in the landscape (sensu Fletcher and Koford 2002, Henningsen and Best 2005). Canopy cover estimates were transformed as needed to improve normality and homogeneity of variances; however untransformed means and errors are reported for ease of interpretation.

Nest survival

Logistic-exposure models (Shaffer 2004) were used to estimate nest survival on both habitat types. Similar to logistic regression, the logistic-exposure method models daily survival for any nest on a given day as a logistic function of the values of explanatory variables for the nest on that day. The method requires two assumptions. First, nests are assumed to survive independently. This assumption applies to all Mayfield-like estimators. Second, survival probabilities are assumed to be the same among nest-days with the same values of explanatory variables. The second assumption is much less restrictive than Mayfield's assumption, which is that daily survival rates are the same within and among nests (Mayfield 1975). Logistic-exposure models also allow the investigator to incorporate
categorical and continuous variables as well as time-specific effects (e.g., nest age). The observation unit for the model is a visitation interval, the time between individual nest visits.

We used PROC GENMOD (SAS Institute 2001) to estimate the regression coefficients in our logistic-exposure models (Shaffer 2004). We calculated predicted daily survival rates (DSR) and variances from the resulting logistic function.

Prior to analysis we developed a set of candidate models (Burnham and Anderson 2002) that included different sets of variables which we considered to be likely causes of variation in nest survival. These variables included nest height (on ground vs. above ground), nest age, habitat type (restored vs. remnant) and local vegetation metrics (percent forb cover and percent litter cover). We selected these variables based on the results of previous studies and on our own knowledge of grassland bird ecology.

We predicted that ground nests would be exposed to potentially different predator communities and therefore different predation pressure compared to above-ground nests (Burhans et al. 2002). Even though grouping nests into height categories does not directly account for species-level variation in survival, we felt that height categories were more biologically meaningful than individual species categories.

Nest survival rate can also vary with nest age (Ricklefs 1969, Patterson and Best 1996, Davis 2003). Predators may use parental activity to locate nests, causing daily survival to decline from incubation to fledging (Martin et al. 2000). Some studies, however, have also documented higher mortality during incubation (Zimmerman 1984, Winter 1999). We included linear and quadratic effects of nest age in our models. The quadratic nest-age effect allowed us to consider a non-linear relationship between nest survival and nest age. Age analyses were based on nest age at the interval midpoint.
Variation in nest survival between restored and remnant habitat was the focus of the study, so we included habitat type in our models.

We considered two local vegetation variables: percent forb cover and percent litter cover. Forb cover is often associated with Dickcissel and Bobolink abundance as well as nest site selection (Zimmerman 1971, Madden et al. 2000, Henningsen and Best 2005). Percent litter cover may influence the occurrence of snakes in grasslands. Fitch and Shirer (1971) found that snakes, when not active, were concealed under litter. Because snakes are grassland bird nest predators (Wheeler 1984, Thompson et al. 1999, Chalfoun et al. 2002), their occurrence may influence variation in nest survival.

To minimize problems with multicollinearity, we did not include strongly correlated variables in our models. Continuous variables were considered strongly correlated when Pearson correlation coefficients were $\geq 0.7$ (Quinn and Keough 2002, Ribic and Sample 2001). We used a two-step model selection process to model nest survival. First we ran 6 models that tested for evidence of nest-height and nest-age effects (hereafter Set-1 models). We suspected that nest height and nest age would influence nest survival independent of habitat type, so we modeled these factors first. We took the best model from the Set-1 models and added habitat type, vegetation variables (percent forb and percent litter cover) and interactions (habitat type*percent litter cover). Models in the second selection step are referred to as Set-2 models. We evaluated the degree of support for each of the models using Akaike's Information Criterion ($AIC_c$) corrected for small sample sizes and normalized Akaike weights (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered to have strong support. We used model-averaged parameter estimates to estimate daily survival probabilities, which allowed us to account for model selection uncertainty (Anderson et al. 2000). Goodness-of-fit of the best Set-2 model was evaluated using the decile method of
Hosmer and Lemeshow (1989). We examined goodness-of-fit for the best Set-2 model because we used this model to make inferences about the effects of vegetation, nest age and nest height on nest survival.

RESULTS

Vegetation characteristics

Vegetation composition and structure were different between habitat types. Percent forb cover was greater in remnant sites (Table 1). Remnant sites also had significantly higher percent total cover and percent live cover. Percent litter cover was significantly greater on restored sites. Litter depth was the only vegetation metric with a significant year*type interaction. It was greater on remnant sites in both years, but the magnitude of the difference varied substantially between years. In 2004 litter depth was significantly greater on remnant sites. In 2003 the difference was non significant.

Nest survival

We monitored 173 nests of 7 species for a total of 466 nest-visitation intervals. Two-hundred twenty six intervals were in remnant habitat, and 240 intervals were in restored habitat. The mean (+ se) interval length was 3.61 (+ 1.22) days. Predation was by far the primary cause of nest failure in both habitats (92% of nest failures were attributed to predation). American Goldfinches (Carduelis tristis), Bobolinks, Dickcissels and Red-winged Blackbirds (Agelaius phoeniceus) nested in both habitat types. We found Clay-colored Sparrow (Spizella pallida), Common Yellowthroat (Geothlypis trichas) and Song Sparrow (Melospiza melodia) nests only on remnant sites (Fig. 1). We recorded 206 intervals for ground nests and 260 intervals for above-ground nests. The only ground-nesting species was Bobolink. Above-ground nesting species included Common Yellowthroats, American
Goldfinches, Dickcissels, Clay-colored Sparrows, Red-winged Blackbirds and Song Sparrows.

The first set of models included effects of nest age and nest height. Two of the models in our candidate set of five models received substantial support (Table 2). The best fitting model included nest height, a linear effect of nest age and a quadratic effect of nest age. The next best model included nest height and a linear effect of nest age. Although the model containing only nest height and a linear effect of nest age was more parsimonious, we accepted the first model as the best model because it had the lowest $AIC_c$ value and the strongest Akaike weight.

The second set of models added local habitat variables to the best nest age and nest height model from the first model set. Again, two of the models in our candidate set of five received substantial support (Table 3). Only habitat type improved the best model from the first model set. The next-best model was simply the best model from Set-1. We accepted the model that included habitat type as the best model from Set-2 because it had the lowest $AIC_c$ value, the strongest Akaike weight and fit the data well ($\chi^2 = 3.2, P = 0.91$). When we calculated estimates of daily nest survival, however, we used model averaged parameter estimates to account for model selection uncertainty (Anderson et al. 2000).

The logistic regression equation for the best Set-2 model, using model averaged parameter estimates, appears below. One unconditional standard error (Burnham and Anderson 2002) appears in parenthesis below each parameter estimate:

$$\text{Logit}(\hat{S}) = 3.783 + (0.189)\text{habitat} + (0.407)\text{height} - (0.183)\text{age} + (0.004)\text{age}^2$$

$$\quad (0.716) \quad (0.241) \quad (0.210) \quad (0.088) \quad (0.003)$$
Parameter estimates for the covariates indicate increased daily nest survival in remnant habitat, increased daily survival for above-ground nests and generally declining daily survival as nests age.

Although parameter estimates and the associated standard errors indicate the direction and relative strength of effects, converting estimates to odds ratios facilitates additional interpretation. Linear nest age had the strongest association with nest survival (linear nest age odds ratio = 0.83, CL = 0.70, 0.99; quadratic nest age odds ratio = 1.0, CL = 0.99, 1.0; Fig. 2). The estimated odds of daily nest survival was greater in remnant sites than in restored sites (odds ratio = 1.21, CL = 0.72, 2.02). We acknowledge that the confidence interval for habitat type includes 1.0 and that there is not strong evidence of a habitat effect. The objective of our study, however, was to compare survival between habitat types. Therefore, we feel it is relevant to consider the result. Overall nest survival estimates (based on multiplying the estimated DSR for each day in the nesting cycle) were 31.7% in remnant habitat and 24.1% in restored habitat. The confidence interval for the odds of a nest height effect also included 1.0. The effect of nest height on nest survival was not the focus of the study; consequently we will not interpret the result.

DISCUSSION

Habitat-type effects

Nest survival tended to be higher in remnant sites, though the effect of habitat type was weak. Habitat type was included in the best Set-2 model, but had little weight of support over the best Set-1 model. Since nearly all of our nests (92%) failed due to predation, any difference in nest survival estimates between habitat types can be attributed almost entirely to differences in predation intensity. Remnant sites had significantly greater percent forb, live and total cover compared to restored sites. Vegetation structure and composition influences

Small mammal foraging behavior may be influenced by percent forb cover and vegetation structure. Dion et al. (2000) found that small mammals depredated simulated grassland songbird nests in low forb cover more frequently than did birds or mid-size mammals. Based on these results, we suspect small mammals likely predated nests more frequently on restored sites, which had significantly less forb cover.

Percent litter cover was significantly higher on restored sites. Grassland snakes may be more abundant in areas with greater litter cover because litter cover provides protection from predators and temperature extremes (Fitch and Shirer 1971, Rossman and Seigel 1996). Increased snake abundance may lead to higher grassland bird nest predation, causing lower nest survival on restored sites.

Our sites were embedded in highly fragmented agricultural landscapes where large patches of continuous grass cover were rare. Although we suspect that predator abundance varied between habitat types, predators may have been relatively abundant on all sites simply because little grassland habitat existed on the landscape. Differences in nest survival on native and exotic grasslands may be stronger in less fragmented landscapes (Lloyd and Martin 2005). Greater amounts of grass habitat may serve to reduce predator concentrations.

Nest-age effects

We found a strong effect of nest age on DSR. Survival generally declined from egg laying through fledging, independent of habitat type. We hypothesize that decreased daily survival rates as nests age are largely a function of activity at the nest. Movement and
vocalizations at the nest site may attract predators to the nest. Parental visits become more frequent as nests age (Lloyd and Martin 2005, Grant et al. 2005). Martin et al. (2000) videotaped nests of 10 open nesting species in high elevation forest drainages. They found that parents visited nests at higher rates during the nestling period than during incubation, though the magnitude of the difference in activity levels varied among species. Increased parental visits intensify activity at the nest, which may attract predators. In addition to parental visits, nestling activity may increase the conspicuousness of a nest. Young nestlings, especially, use begging calls to encourage feeding. These vocalizations may draw the attention of predators (Briskie et al. 1999, Holcomb 1972).

The rate of decline in daily survival rates becomes less steep around day 17 (Fig. 2). Older nestlings are generally more aware of the environment and are better able to control movement. Instead of vocalizing when predators approach, they sit quietly (Holcomb 1972, Grant et al. 2005). Older nestlings are also capable of withstanding weather extremes, such as cold temperatures, because of feathering and improved thermoregulation. Small rodents and snakes, which compose a substantial part of the grassland bird nest predator community (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003), may not be able to take larger nestlings (P. Pietz, pers. comm.). Finally, parents may defend older nests more vigorously because of greater investment (Montgomerie and Weatherhead 1988, Clark and Robertson 1981).

Our data indicated nest success in restored grasslands in highly fragmented agricultural landscapes was comparable to success in remnant sites, even when restoration efforts did not mirror native habitat conditions. Nest age had a strong negative effect on daily survival, independent of habitat type, suggesting that nest predation will affect nest survival regardless of vegetation structure within a habitat patch. Nest survival, however, is a limited
indicator of habitat quality; it does not account for within season survival of nestlings or the
effect of multiple nesting attempts (Van Horne 1983, Pease and Grzybowski 1995,
Woodworth 1999). Further research comparing seasonal fecundity and measures of nestling
fitness (sensu Lloyd and Martin 2005) in restored and remnant grasslands would enhance our
understanding of the effects of ongoing restoration efforts on grassland breeding birds in the
Midwest.

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TABLE 1. Vegetation characteristics of restored (n = 10) and remnant (n = 6) grasslands in northwestern Iowa, USA, 2003 and 2004, with treatment contrasts for habitat type (restored vs. remnant) and year effects.

<table>
<thead>
<tr>
<th>Vegetation Characteristic</th>
<th>Restored</th>
<th>Remnant</th>
<th>F&lt;sup&gt;a&lt;/sup&gt;</th>
<th>P</th>
<th>Year&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical density (dm)</td>
<td>5.8</td>
<td>5.5</td>
<td>0.51</td>
<td>0.490</td>
<td>0.736</td>
</tr>
<tr>
<td>Litter depth (mm)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>29.9</td>
<td>31.6</td>
<td>0.03</td>
<td>0.871</td>
<td>0.008</td>
</tr>
<tr>
<td>Litter depth (mm)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>33.2</td>
<td>49.1</td>
<td>19.9</td>
<td>0.001</td>
<td>---</td>
</tr>
<tr>
<td>Percent coverage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>80.6</td>
<td>88.4</td>
<td>6.52</td>
<td>0.027</td>
<td>0.490</td>
</tr>
<tr>
<td>Grass</td>
<td>70.4</td>
<td>34.1</td>
<td>2.10</td>
<td>&lt;0.001</td>
<td>0.384</td>
</tr>
<tr>
<td>Forb&lt;sup&gt;e&lt;/sup&gt;</td>
<td>9.3</td>
<td>53.7</td>
<td>140.42</td>
<td>&lt;0.001</td>
<td>0.912</td>
</tr>
<tr>
<td>Dead&lt;sup&gt;f&lt;/sup&gt;</td>
<td>16.2</td>
<td>6.9</td>
<td>7.61</td>
<td>0.019</td>
<td>0.817</td>
</tr>
<tr>
<td>Live&lt;sup&gt;f&lt;/sup&gt;</td>
<td>79.9</td>
<td>89.6</td>
<td>12.70</td>
<td>0.004</td>
<td>0.898</td>
</tr>
<tr>
<td>Litter</td>
<td>13.6</td>
<td>7.7</td>
<td>5.42</td>
<td>0.040</td>
<td>0.473</td>
</tr>
<tr>
<td>Bare ground&lt;sup&gt;f&lt;/sup&gt;</td>
<td>1.4</td>
<td>0.4</td>
<td>3.00</td>
<td>0.111</td>
<td>0.471</td>
</tr>
</tbody>
</table>

<sup>a</sup> Mixed-model ANOVAs were used to contrast means (df = 1, 14) between habitat types, with the vegetation metric as the response variable, type as the main explanatory variable and site as a random effect.

<sup>b</sup> Mixed-model ANOVAs were used to test for year to year differences.

<sup>c</sup> 2003.

<sup>d</sup> 2004.

<sup>e</sup> Arcsine square root transformed for analysis.

<sup>f</sup> Logit transformed for analysis.
TABLE 2. Set-1 Models. First set of *a priori* candidate models explaining nest success of grassland birds in northwestern Iowa, 2003 and 2004. Models include nest height and nest-age parameters. Number of parameters (*K*) in each model includes the intercept and each explanatory variable. Models with low $\Delta$AIC$_c$ values and high Akaike weights ($w_i$) have the most support.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest height + linear nest age + quadratic nest age</td>
<td>4</td>
<td>0.000</td>
<td>0.418</td>
</tr>
<tr>
<td>Nest height + linear nest age</td>
<td>3</td>
<td>1.303</td>
<td>0.246</td>
</tr>
<tr>
<td>Linear nest age + quadratic nest age</td>
<td>3</td>
<td>2.700</td>
<td>0.122</td>
</tr>
<tr>
<td>Nest height$^a$</td>
<td>2</td>
<td>3.260</td>
<td>0.092</td>
</tr>
<tr>
<td>Linear nest age</td>
<td>2</td>
<td>4.599</td>
<td>0.047</td>
</tr>
<tr>
<td>Constant survival</td>
<td>1</td>
<td>9.320</td>
<td>0.004</td>
</tr>
</tbody>
</table>

$^a$ Ground vs. above-ground nests.
TABLE 3. Set-2 Models. Second set of *a priori* candidate models explaining nest success of grassland birds in northwestern Iowa, 2003 and 2004. Models include the addition of habitat type and vegetation variables to the best model from the first model set (Table 1). Number of parameters (K) in each model includes the intercept and each explanatory variable. Models with low \( \Delta AIC_c \) values and high Akaike weights \( (w_i) \) have the most support.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>( \Delta AIC_c )</th>
<th>( w_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Best Set-1 model + habitat type^a</td>
<td>5</td>
<td>0.000</td>
<td>0.439</td>
</tr>
<tr>
<td>Best Set-1 model</td>
<td>4</td>
<td>0.489</td>
<td>0.344</td>
</tr>
<tr>
<td>Best Set-1 model + habitat type + vegetation^b</td>
<td>7</td>
<td>3.336</td>
<td>0.083</td>
</tr>
<tr>
<td>Best Set-1 model + habitat type + vegetation + interaction^c</td>
<td>8</td>
<td>3.405</td>
<td>0.080</td>
</tr>
<tr>
<td>Best Set-1 model + vegetation</td>
<td>6</td>
<td>4.160</td>
<td>0.055</td>
</tr>
</tbody>
</table>

^a Restored vs. remnant grasslands.  
^b Percent forb cover and percent litter cover.  
^c Habitat type*percent litter cover.
FIGURE LEGENDS

FIGURE 1. Number of nest visitation intervals for bird species in remnant (n = 6) and restored (n = 10) grasslands in northwestern Iowa, USA, 2003 and 2004.

FIGURE 2. Predicted rate of success (calculated from the logistic regression equation from the best Set-1 model) for grassland-bird nests in northwestern Iowa, USA, 2003 and 2004. Nest height was included in the model, but the effect was negligible and was ignored for the purposes of this figure.
FIGURE 1.
FIGURE 2.
APPENDIX. Estimated nest survival on 6 remnant and 10 restored grasslands in northwestern Iowa, USA, 2003 and 2004.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat type</th>
<th>Total nests(^a)</th>
<th>Parameter estimate(^b)</th>
<th>se</th>
<th>Estimated DSR(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anderson</td>
<td>remnant</td>
<td>25</td>
<td>0.343</td>
<td>1.066</td>
<td>0.953</td>
</tr>
<tr>
<td>Cayler</td>
<td>remnant</td>
<td>32</td>
<td>0.030</td>
<td>1.053</td>
<td>0.937</td>
</tr>
<tr>
<td>Kirchner</td>
<td>remnant</td>
<td>7</td>
<td>-2.341</td>
<td>1.265</td>
<td>0.581</td>
</tr>
<tr>
<td>Stinson</td>
<td>remnant</td>
<td>4</td>
<td>-0.568</td>
<td>1.497</td>
<td>0.891</td>
</tr>
<tr>
<td>Telford</td>
<td>remnant</td>
<td>4</td>
<td>-0.734</td>
<td>1.294</td>
<td>0.874</td>
</tr>
<tr>
<td>Wolters</td>
<td>remnant</td>
<td>5</td>
<td>0.033</td>
<td>1.326</td>
<td>0.912</td>
</tr>
<tr>
<td>Capner</td>
<td>restored</td>
<td>17</td>
<td>-1.286</td>
<td>1.091</td>
<td>0.800</td>
</tr>
<tr>
<td>Graff</td>
<td>restored</td>
<td>6</td>
<td>-1.099</td>
<td>1.228</td>
<td>0.828</td>
</tr>
<tr>
<td>Jones</td>
<td>restored</td>
<td>9</td>
<td>-0.197</td>
<td>1.137</td>
<td>0.922</td>
</tr>
<tr>
<td>Korey-Holber</td>
<td>restored</td>
<td>5</td>
<td>0.349</td>
<td>1.459</td>
<td>0.953</td>
</tr>
<tr>
<td>Lair</td>
<td>restored</td>
<td>34</td>
<td>-0.011</td>
<td>1.056</td>
<td>0.934</td>
</tr>
<tr>
<td>Mk</td>
<td>restored</td>
<td>5</td>
<td>-0.696</td>
<td>1.284</td>
<td>0.878</td>
</tr>
<tr>
<td>Savard</td>
<td>restored</td>
<td>3</td>
<td>-0.565</td>
<td>1.763</td>
<td>0.743</td>
</tr>
<tr>
<td>Seeman</td>
<td>restored</td>
<td>7</td>
<td>-0.675</td>
<td>1.143</td>
<td>0.880</td>
</tr>
<tr>
<td>South Lair</td>
<td>restored</td>
<td>7</td>
<td>-0.309</td>
<td>1.122</td>
<td>0.914</td>
</tr>
<tr>
<td>Wolthius</td>
<td>restored</td>
<td>3</td>
<td>0.000</td>
<td>0.000</td>
<td>0.935</td>
</tr>
</tbody>
</table>

\(^a\) All active nests monitored within sites.
\(^b\) Logistic-exposure models were used to calculate parameter estimates for all sites.
\(^c\) Estimated daily survival rates (DSR) were calculated by solving the logistic regression equation from a logistic-exposure model that included parameter estimates for each site.
CHAPTER 3. GRASSLAND SNAKE HABITAT USE AND RESPONSE TO ROAD EDGES IN A FRAGMENTED LANDSCAPE

A paper to be submitted to Biological Conservation

L. Embere Hall and Rolf R. Koford

Abstract

Intensive agriculture in the Midwest has reduced the amount of grass on the landscape and increased the amount of edge in remaining grassland patches. Little is known about grassland snake habitat associations and responses to edge in fragmented agricultural landscapes, despite population declines in some grassland-associated species. We examined the effect of edges on snake abundance in 8 restored grassland sites in northwestern Iowa by comparing snake abundance in the interior of patches to abundance within 100m of a road edge. Additionally, we evaluated the effects of local habitat characteristics and landscape composition on grassland snake abundance. Through the use of artificial shelters, we captured 694 individuals of four species during 16 survey weeks. Sixty-six percent of the captures were plains garter snakes (*Thamnophis radix*). We found no significant difference between interior and edge snake abundance, indicating that grassland snake abundance is not influenced by road edges at the scale we measured. Distance to nearest farmstead was the only habitat-structure variable significantly related to snake abundance. Garter snakes, smooth brown snakes (*Storeria dekayi*) and smooth green snakes (*Opheodrys vernalis*) were less abundant closer to farmsteads. Results of this study will help researchers and land managers better understand grassland snake habitat use. Information on habitat use is crucial to maintaining declining populations of grassland snakes in fragmented landscapes.

**Keywords:** Edges; Grasslands; Road; Snakes; *Thamnophis radix*
1. Introduction

Intensive agriculture in the Midwest has dramatically reduced the amount of grass on the landscape (King and Savidge 1995, McCoy et al. 1999, Brennan and Kuvlesky 2005). In Iowa, for example, tallgrass prairie once covered 79.5% of the state. Today less than 0.1% of the pre-settlement prairie remains (Smith 1998). Remaining patches of grassland are generally fragmented and embedded in a matrix of row-crop agriculture. Fragmentation not only transforms large expanses of grassland into smaller, isolated patches, it increases the amount of edge on the landscape (Laurance and Yensen 1991). Grassland loss and fragmentation have been implicated in population declines of many species, especially grassland birds (Herkert 1994, Johnson and Igl 2001). Consequently, most studies that examine the influence of edges on grassland fauna focus on bird abundance and nest survival (Wiens 1994, Pasitschniak-Arts and Messier 1995, Helzer and Jelinski 1999, Winter and Faaborg 1999, Herkert et al. 2003, Fletcher and Koford 2003, Henningsen and Best 2005), as well as on nest predator movement and distribution (Bider 1968, Pasitschniak-Arts and Messier 1998, Heske et al. 1999, Kuehl and Clark 2002, Phillips et al. 2004).

Relatively little work has addressed grassland snake responses to edge, despite the fact that populations of some species have declined substantially in recent years (Christiansen 1981, Christiansen and Bailey 1990, Tennant 2003). In Iowa, 10 snake species are listed on the State Endangered, Threatened and Special Concern species lists (State of Iowa 2002). Six of the 10 species are associated with grasslands (Christiansen 1981). Studies that directly examine snake response to habitat edges are based primarily on work in fragmented forests (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001a, Chalfoun et al. 2002; but see Keller and Heske 2000 and Shine et al. 2004). Unlike
grassland edges, forest edges may be attractive to snakes because they are exposed to greater sunlight than the forest interior (Blouin-Demers and Weatherhead 2001b). Increased sunlight exposure facilitates thermoregulation in snakes (Huey et al. 1989). Grassland edges probably do not present similar variation in thermal gradient because they lack substantial changes in canopy cover and illumination, compared to the interior.

In the absence of an attractive thermal gradient, it is possible that grassland snakes avoid edges. There is some evidence that snakes may be sensitive to patch area (Hager 1998, Robinson et al. 1992, Kjoss and Litvaitis 2001a, Knoot 2004). Because smaller patches have a greater perimeter to area ratio (Levenson 1981), edge avoidance may explain apparent area sensitivity in some species.

We examined the abundance of snakes in the edge and interior of restored grasslands in northwestern Iowa. We compared relative snake abundance (number of snakes per transect) in the interior of our plots to relative abundance in the edges, which we defined as grassy habitat within 100m of a two-lane gravel road. We studied road edges because, like many regions dominated by row-crop agriculture, this was the most abundant edge type adjoining tracts of grassland in the landscape. Several studies have recorded grassland bird edge avoidance within 100m of various edge types, including grass-road edges (Bollinger and Gavin 2004, Fletcher and Koford 2003). Since snakes are documented grassland bird nest predators (Renfrew and Ribic 2003, Bryan and Best 1994), variation in snake abundance in the edge and interior of grassland blocks might also help explain edge avoidance in some species of grassland birds.

Differences in abundance by site-type (edge vs. interior) would indicate that snakes are likely responding to grass-road edges in one of three ways. Snakes may avoid edges (Sullivan 2000, Shine et al. 2004), be attracted to edges (Weatherhead and Charland 1985) or
experience higher mortality in edges. It is also possible that snakes are attracted to edges and simultaneously experience higher mortality in edges. To further explain variation in snake abundance, we also examined the influence of vegetation structure and landscape composition on the relative number of snakes captured. To our knowledge this is the first study that directly examines the effects of road edges on grassland snake abundance.

2. Methods

2.1 Description of study areas

Our study was conducted from 1 May - 21 August 2004 at the Spring Run Complex in northwestern Iowa. The Complex is located in the Des Moines Lobe landform region and is part of the southern end of the Prairie Pothole Region. Most of the land is rolling with numerous ponds and marshes that cluster in low areas (Prior 1991).

The Spring Run Complex is a 1620ha complex of restored grasslands and wetlands in Dickinson County, Iowa. The Complex encompasses approximately 38.8km². This area includes both publicly owned land and privately owned farms. Despite the fragmented arrangement it is one of the largest remaining semi-contiguous prairie pothole complexes in Iowa. It comprises federal waterfowl production areas (WPAs) and state wildlife management areas, which are managed for watershed protection and migratory waterfowl habitat. While most of the land is federally owned, it is managed by the Iowa Department of Natural Resources (IDNR). The IDNR began purchasing land in the Complex from willing sellers in the 1960’s, and continues to acquire properties today. Prior to purchase and restoration most tracts were used for row crop production. Current grassland management practices on the complex include mowing, haying, grain plot farming and burning. Sites
contained both warm-season and cool-season plantings, though cool-season species were most common. Smooth brome (*Bromus inermis*) and sweet clover (*Melilotus* spp.) were the dominant grass and forb species, respectively. We surveyed all reconstructed grasslands in the Complex that were greater than 10ha, and included at least 4ha of contiguous grass cover (*n* = 10). Four hectares of grass cover was large enough to accommodate two 200m x 100m snake-survey transects.

### 2.2 Snake Surveys

We compared snake abundance in the edge and interior of all survey sites that were bordered on at least one side by a two-lane gravel road and could accommodate a minimum of one 200m x 100m transect in the edge and one in the interior (*n* = 8). Edge and interior transects were apportioned according to the area of each site-type on each study site. We installed 17 transects in edge habitat and 18 transects in interior habitat. We placed five additional transects in the interior of two sites that were not bordered by roads, but that satisfied our minimum area requirement. Data from these transects were used in analyses that examined the effects of vegetation characteristics and habitat structure on snake abundance, but were not included in the edge and interior comparisons.

We used artificial shelters and mark-recapture methods (Fitch 1987) to estimate snake abundance and species richness. We surveyed snakes from 1 May - 21 August, 2004. We constructed artificial shelters of 0.64cm thick sheets of oriented strand board, cut to either 1.22 x 1.22m sections or 0.91 x 0.91m sections. Each snake-survey transect comprised five boards. One board on each transect measured 0.91 x 0.91m; the rest were 1.22 x 1.22m. Each shelter was placed a random distance (0 - 50m) from the centerline of the transect, at intervals of 50m along the 200m transect. We alternated sides of the centerline for each
successive shelter (Knoot 2004); therefore boards were ≥ 50m apart. The vegetation under each board was clipped to approximately 5.0 cm so that observers could more easily see snakes during surveys. Boards were installed in mid April to allow them to weather before we began surveys (Knoot 2004).

Observers surveyed each transect weekly (Fellers and Drost 1994) by checking for snakes under each board. Due to logistical constraints associated with installing the transects, 4 sites were not surveyed for the entire 16-week sampling period. Once a snake was captured, we clipped a unique pattern of scutes to identify individual snakes for purposes of mark-recapture estimation (Fitch 1987). We recorded the snout-to-vent length, soil moisture and weather conditions for each capture. Soil moisture was measured under the board where the snake was captured. Weather conditions were also recorded at the capture site. Edge and interior transects on the same plot were surveyed on the same day each week to minimize variation in capture rates due to weather related factors.

2.3 Transect-level measurements

Vegetation measurements were taken once on each transect, between 3 August and 21 August 2004. We quantified vegetation height, density and composition at each transect to examine the relationship between snake abundance and local habitat characteristics. We measured vegetation at the center of the interval between each board (e.g., between board 1 and board 2) on each transect for a total of 4 vegetation sample locations per transect. Vegetation measurements at the sample locations were averaged to obtain the mean of each vegetation variable for each transect. For each sample location, we measured vegetation using a method similar to Best et al. (1997). We measured vertical density by visual obstruction readings taken 4 m from a Robel pole at a height of 1 m above the ground (Robel
et al. 1970). Four readings were taken at each sample location; one in each cardinal direction. We estimated canopy cover using a 20 x 50cm quadrat based on non-overlapping percentages (Daubenmire 1959). Canopy cover categories included: total (live+ dead vegetation), litter, bare ground, standing live vegetation, standing dead vegetation, grass and forb. Cover was classified to the nearest five percent. We measured litter depth twice at each location, at opposite corners of the quadrat. Because foundations, old wells and out-buildings associated with farmsteads can provide suitable snake hibernacula (Vogt 1981), we recorded the distance to the nearest farmstead from the mid point of each transect using a Geographic Information System (GIS) and color infrared orthophotos.

2.4 Landscape-level measurements

We used color infrared orthophotos taken in April 2002 to quantify the landscape structure surrounding our 10 study sites. We digitized land use patterns within a 1.5km buffer from the center of each site using a GIS. We quantified land use categories that we considered likely to influence grassland snake abundance. These metrics included percent herbaceous block cover (pasture, alfalfa fields, Conservation Reserve Program fields, and WPAs) and percent wetland cover. We evaluated percent herbaceous cover in the landscape because snakes may prefer large blocks of grassy habitat, compared to small blocks. Knoot (2004) found that the frequency of occurrence of 3 species of grassland snakes was positively influenced by grassed waterway width. Robinson et al. (1992) also found that the abundance of some snake species increased with increasing patch size. Percent wetland cover in the landscape may be important because grassland snakes prey on invertebrates, fish, earthworms and amphibians associated with wetlands (Ernst and Barbour 1989, Vogt 1981, Oliver 1955). A 1.5km buffer from the center of each site encompassed most grassland snake
movement estimates (Kjoss and Litvaitis 2001a, Fitch 1999, Ernst and Barbour 1989, Oliver 1955; but see Gregory and Stewart 1975), and exceeded the boundaries of all of our survey sites.

2.5 Statistical Analyses

2.5.1 Edge vs. interior

We used mixed-model analyses of variance (ANOVAs) to examine differences in vegetation structure and composition between site-types (PROC MIXED; SAS Institute 2003). We treated the vegetation metric as the response variable, site as a random effect and site-type as the main explanatory variable. Canopy cover estimates were transformed as needed to improve normality and homogeneity of variances; however untransformed means and errors are reported for ease of interpretation. We measured vegetation at each edge and interior transect; therefore the vegetation comparison analysis is based on 35 sample points within 8 sites.

We used mixed-model, repeated measures ANOVAs (PROC GLMMIX; SAS Institute 2003) to examine the difference in relative snake abundance by site-type. Snake counts were assumed to follow a Poisson distribution (McCullagh and Nelder 1983). The GLMMIX procedure allowed us to fit a model with both fixed and random effects to data that followed a Poisson distribution. We treated the number of snakes captured per week on the edge and interior of each site as the response variable and used the log of the number of transects in each site-type as an offset variable. Use of transect number as an offset in the model effectively allowed us to model snake density (number of snakes captured per week in each site-type / number of transects in each site-type). We considered site and site*site-type as random effects, week as the repeated measure, and week and site-type as the main
explanatory variables. Snakes captured multiple times were counted only once in analyses, and were associated with the site-type in which they were most frequently observed. We chose sites within the Spring Run Complex that satisfied our area and edge-type criteria. However, we treated site as a random effect because we had no reason to suspect that snakes would respond to edges differently on the selected sites, compared to other grassland sites of similar area and edge structure in the landscape (sensu Fletcher and Koford 2002, Henningsen and Best 2005).

2.5.2 Vegetation, landscape composition and snake abundance

We used multiple-regression models to examine the relationship between vegetation composition, distance to nearest farmstead and snake abundance on 40 transects (hereafter transect-level analyses). Snake abundance was natural-log transformed to meet assumptions of normality and homogeneity of variances. Untransformed counts are reported for ease of interpretation. We included data from 35 transects from the eight sites in the blocked edge vs. interior design, plus data from the five transects placed in only the interior of two other study sites. We also used multiple-regression models to examine the relationship between landscape composition and snake abundance. Landscape-level variables included percent wetland cover and percent herbaceous block cover within a 1.5km radius from the center of each site. Ten landscapes were included in these analyses. At both the transect level and the landscape level we evaluated the abundance of three groups of snakes. The first group included all snake species. The second group included only garter snakes (Thamnophis spp.), and the third included only brown (Storeria dekayi) and smooth green snakes (Ophiodrys vernalis). Common garter snakes (T. sirtalis) and plains garter snakes (T. radix) were combined in analyses because they have similar habitat use, activity patterns, thermal biology
and diets (Dalrymple and Reichenbach 1981). Brown and green snakes were combined because of similar habitat use and diet (Oliver 1955).

To minimize problems with multicollinearity in both the transect-level and landscape-level analyses, we did not include strongly correlated variables in our models. Variables were considered strongly correlated when Pearson correlation coefficients were \( \geq 0.7 \) (Quinn and Keough 2002, Ribic and Sample 2001).

3. Results

We captured 694 individuals of four species during 16 survey weeks on all survey sites. Sixty-six percent of the captures were plains garter snakes. We recaptured 23.1% of the 694 individuals at least once. We captured 614 individuals on the eight sites used to compare edge and interior snake abundance (Table 1). Total snake captures peaked in mid-June. After the peak, captures generally declined throughout the remainder of the sampling period (Fig. 1).

3.1 Edge vs. interior

Vegetation structure and composition on edge and interior transects were similar. Percent total cover and litter depth were higher in the edge and showed the strongest differences by site-type of all vegetation variables (Table 2). However, these differences were non-significant.

There was no significant difference in relative snake abundance by site-type \((F = 1.9, df = 1, 7, P = 0.226)\). The coefficient for site-type was negative, however, indicating that interior abundance was estimated to be greater than edge abundance. While snake abundance
was not significantly different between site-types, 44.2% more snakes per transect were captured in the interior than in the edge over the entire 16-week sampling period. This percent difference reflects the total number of edge snakes per transect subtracted from the total number of interior snakes per transect, and does not account for the paired sampling design. Sites with high interior snake abundance often had correspondingly high edge snake abundance (Table 3), resulting in small site-level differences in relative snake abundance. We captured the same four species in both site-types; therefore there was no difference in edge and interior species richness.

3.2 Transect-level and landscape-level models

Our transect-level models, which considered vegetation composition and distance to nearest farmstead, had low predictive power; $R^2$ values ranged from 0.129 - 0.134. Distance to nearest farmstead was the only transect-level variable that significantly influenced snake abundance (Table 3). The coefficient for distance to nearest farmstead was positive for both garter snakes, and brown and green snakes combined, indicating that both groups of snakes were positively associated with distance to farmstead. In other words, snakes were more abundant farther from farmsteads. Garter snake abundance was also positively related to percent cover of grass, litter and bare ground. Garter snakes were associated negatively with vertical density and litter depth. As expected, brown snakes and green snakes showed somewhat different habitat associations. Brown and green snake abundance was related positively to vertical density, litter depth and percent ground cover. They were associated negatively with percent litter and grass cover.

On the landscape level, neither percent wetland cover or percent herbaceous block cover were associated significantly with snake abundance (Table 4). Both groups of snakes
responded positively to percent wetland cover. Brown and green snakes were also associated positively with percent herbaceous block cover, but garter snakes showed a slight negative relationship. Predictive power of the landscape-level models was comparable to that of the transect-level models.

4. Discussion

4.1 Edge vs. interior

We found no significant evidence that grassland snakes were more abundant in the interior of grassy plots, compared to the edges. This indicates that grass-road edges in highly fragmented landscapes may not influence the distribution and abundance of the four species we encountered. While several studies have addressed snake response to forest fragmentation and forest-field edges (Weatherhead and Charland 1985, Keller and Heske 2000, Blouin-Demers and Weatherhead 2001b, Calfoun et al. 2002) to our knowledge this is the first study that directly examines the impact of road edges on grassland snake abundance.

Artificial shelters are an effective snake-capture method, especially in areas with little natural cover (Fitch 1992, Parmelee and Fitch 1995, Kjoss and Litvaitis 2001b). The temperature under plywood shelters is cooler during peak ambient air temperatures and warmer when the ambient air temperatures are cool (Engelstoft and Ovaska 2000). Snakes are attracted to shelters because of the changed thermal gradient and because shelters provide protection in the form of cover (Parmelee and Fitch 1995). Like most sampling methods, however, artificial shelters are not without bias. Engelstoft and Ovaska (2000) suggest that the portion of the snake population using artificial cover may not be representative of the population as a whole. Factors that influence thermal preferences in snakes, such as food
ingestion, reproductive condition and ecdysis may affect the likelihood that snakes use cover. These potential sampling biases, while valid, do not impact the results of our study. We compared habitat use in two very similar habitat types which were exposed to the same weather conditions and illumination. We have no reason to suspect that the shelters attracted different species or size classes of snakes differently in the edge as compared to the interior.

Vegetation structure and composition were similar between edge and interior transects. Variation in vegetation structure can affect the snake community by influencing food supply (Warren et al. 1987), cover (Shine and Fitzgerald 1996) and microclimatic factors such as soil temperature and moisture (Cavitt 2000). Given that the vegetation structure was similar in both site-types, the edge and interior may provide essentially the same habitat and resources. All four snake species captured during the study are associated with moist conditions, likely because of increased prey availability (Vogt 1981, Fitch 1999). Wetlands were abundant in both sites-types, indicating that prey resources likely were plentiful regardless of location. In the absence of a strong difference in resource availability, snake abundance is likely to be similar in both site-types.

Prior to the study, we suspected that variation in snake abundance might result from high predation risk along grass-road edges. Road surfaces can provide attractive basking sites for snakes because reduced canopy cover promotes high incident radiation compared to the surrounding habitat (Gokula 1997; but see Shine et al. 2004). If snakes are attracted to sun warmed roads, then we might expect higher mortality in snakes using edge habitat due to road kills (Ernst and Barbour 1989), and depredation by species foraging along the edges of grass patches (Phillips et al. 2004). Snakes using the interior are less likely to encounter a road, and therefore might be less vulnerable to edge related mortality. We observed several Thamnophis spp. dead on the road (DOR) at our study sites. All DORs appeared to have been
run over by passing vehicles. When a DOR was found, we looked for evidence of clipped scutes to determine if the snake had been captured earlier in the study. Unfortunately, most DORs were too mangled and desiccated to tell if they had been marked. While we did not attempt to quantify the impact of road mortality, other studies have documented large numbers of road kill snakes (Gokula 1997, Sullivan 2000). Because we found no difference in abundance between site-types, we conclude that higher predation risk along edges, either from vehicular traffic or from predators foraging along edges, did not significantly impact the relative abundance of snakes on our study sites.

Bonnet et al. (1999) suggest that snakes are most vulnerable to predation during long-distance movements. Small summer home range estimates for both garter snakes (0.74ha, Fitch 1999) and brown snakes (<1.5ha; Kjoss and Litvaitis 2001a) indicate that daily movements are short. Based on a multi-year mark-recapture study using artificial shelters, Fitch (1999) found that common garter snakes move short distances on a daily basis, with relatively few movements exceeding 300m. If movements generally are short during the summer months, perhaps snakes in both site-types experience relatively low mortality, resulting in similar abundances.

While we found no evidence of higher mortality in edges, we can not discount the possibility that snakes avoid road edges (Sullivan 2000). Shine et al. (2004) found that common garter snakes typically changed their direction of movement when they encountered a limestone gravel road. Snakes are more vulnerable to predation in habitats with low cover (Shine and Fitzgerald 1996) and may avoid open spaces (Fitch and Shirer 1971). Edge-avoidance would be difficult to detect with our dataset, especially if the behavior is apparent only within a few meters of the road (Shine et al. 2004). We defined edge as grassy habitat within 100m of a road. Each artificial shelter was placed a random distance from the
centerline of the transect, alternating sides of the centerline with each successive shelter. Consequently, few shelters were directly adjacent to the road edge. If snake response to road edges is limited to a few meters on either side of the road, abundance measured in the edge, as we defined it, would not be impacted by edge-avoidance.

4.2 Vegetation, landscape composition and snake abundance

Distance to nearest farmstead was the only transect-level variable that significantly influenced snake abundance. Snakes were more abundant farther from farmsteads. This was unexpected, since farmsteads may provide suitable hibernacula (Vogt 1981) and hibernacula are important to the persistence of snakes in temperate regions (Burbrink et al. 1998). We classified both farm buildings and residential housing as farmsteads. Residential housing may not provide potential hibernacula to the same degree as outbuildings and old wells associated with farmsteads (Vogt 1981). Additionally, snakes may experience higher mortality in residential areas due to deliberate killing by humans (Bonnet et al. 1999) and mowing mortality (Dickman 1987). Grass surrounding residential housing is generally shorter than un-mowed prairie grasses. Short grass may provide snakes with little protective cover from predators. Of 53 farmsteads digitized in our landscapes, 32 represented non farm residences. The negative association between grassland snakes and distance to nearest farmstead likely reflects reduced snake abundance near residential housing.

Both our transect-level models and our landscape-level models had low predictive power, indicating that snakes may not be responding to the vegetation and landscape characteristics we measured. Rossman et al. (1996) suggest that snake habitat selection is complex, involving aspects of vegetation structure, availability of thermal sites and prey abundance. Snakes may respond more to suitable hibernacula sites and prey availability than
to vegetation composition (Keller and Heske 2000). Garter snakes, in particular, use diverse hibernacula sites including mammal burrows (Ernst and Barbour 1989), deserted ant mounds, rock crevices, building foundations (Vogt 1981), limestone outcrops (Fitch 1999) and abandoned railroad ties (Keller and Heske 2000). Our models may not have captured variability in suitable hibernacula sites or prey abundance, resulting in low predictive power.

Our study was simply observational, and examined the correlations between snake abundance and habitat structure. Explanations for habitat selection must be tested through rigorous experimental studies (Reinert 1993). While the relationships between habitat structure and snake abundance have been studied extensively in forest-dwelling snakes (Weatherhead and Charland 1985, Durner and Gates 1993, Chalfoun et al. 2002), data are lacking for grassland associated snakes. Our data indicate that snakes are not sensitive to grass-road edges at the scale we measured, though we can not discount the possibility that snakes may avoid edges. Further research on the snake behavior near roads is needed (sensu Shine et al. 2004) before we can fully understand the effects of road edges on grassland snakes. We expect that studies of snake abundance within a few meters of roads may reveal different patterns. Given the intensive nature of road systems in agricultural ecosystems, it is important to understand how road edges effect grassland snake populations. Understanding the effects of road edges is a crucial step toward understanding snake ecology and habitat use in fragmented agricultural landscapes.

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Table 1
Mean (SE) abundance of snakes captured in the edge and interior of 8 restored grasslands in northwestern Iowa, USA, 2004.

<table>
<thead>
<tr>
<th>Snake Species</th>
<th>Edge</th>
<th>Interior</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total captures (%)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Abundance&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>SE</td>
</tr>
<tr>
<td>Brown snake</td>
<td>49 (42.2)</td>
<td>2.83</td>
</tr>
<tr>
<td></td>
<td>1.06</td>
<td></td>
</tr>
<tr>
<td>Common garter snake</td>
<td>39 (54.9)</td>
<td>1.81</td>
</tr>
<tr>
<td></td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Plains garter snake</td>
<td>154 (36.5)</td>
<td>8.58</td>
</tr>
<tr>
<td></td>
<td>2.05</td>
<td></td>
</tr>
<tr>
<td>Smooth green snake</td>
<td>1 (20)</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>Total snakes</td>
<td>243 (39.6)</td>
<td>13.27</td>
</tr>
<tr>
<td></td>
<td>2.66</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Percent of total captures by site-type. Snakes captured multiple times were included only once.

<sup>b</sup> Number of snakes per transect.
Table 2
Vegetation characteristics (mean and SE) of 8 restored grasslands in northwestern Iowa, USA, 2004, with treatment contrasts for site-type.

<table>
<thead>
<tr>
<th>Vegetation Characteristic</th>
<th>Edge</th>
<th>Interior</th>
<th>Edge</th>
<th>Interior</th>
<th>$F^a$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical density (dm)</td>
<td>4.2</td>
<td>0.2</td>
<td>3.8</td>
<td>0.2</td>
<td>2.44</td>
<td>0.162</td>
</tr>
<tr>
<td>Litter depth (mm)</td>
<td>35.7</td>
<td>3.6</td>
<td>26.9</td>
<td>3.6</td>
<td>4.8</td>
<td>0.065</td>
</tr>
<tr>
<td>Percent coverage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>84.2</td>
<td>2.4</td>
<td>79.1</td>
<td>2.3</td>
<td>3.6</td>
<td>0.099</td>
</tr>
<tr>
<td>Grass</td>
<td>73.5</td>
<td>3.6</td>
<td>69.5</td>
<td>3.5</td>
<td>0.7</td>
<td>0.444</td>
</tr>
<tr>
<td>Forb$^b$</td>
<td>8.8</td>
<td>2.1</td>
<td>6.8</td>
<td>2.1</td>
<td>0.7</td>
<td>0.434</td>
</tr>
<tr>
<td>Dead$^c$</td>
<td>12.9</td>
<td>2.7</td>
<td>19.5</td>
<td>2.7</td>
<td>0.8</td>
<td>0.394</td>
</tr>
<tr>
<td>Live$^c$</td>
<td>83.4</td>
<td>2.8</td>
<td>76.6</td>
<td>2.7</td>
<td>1.0</td>
<td>0.343</td>
</tr>
<tr>
<td>Litter</td>
<td>10.2</td>
<td>1.7</td>
<td>10.9</td>
<td>1.7</td>
<td>0.1</td>
<td>0.784</td>
</tr>
<tr>
<td>Bare ground$^c$</td>
<td>2.7</td>
<td>1.6</td>
<td>5.2</td>
<td>1.6</td>
<td>0.1</td>
<td>0.818</td>
</tr>
</tbody>
</table>

$^a$ Repeated measures, mixed-model ANOVAs were used to contrast means between site-types, with the vegetation metric as the response variable, site as a random effect and site-type as the main explanatory variable.

$^b$ Arcsine square root transformed for analysis.

$^c$ Logit transformed for analysis.
Table 3
Difference between grassland snake abundance in the edge and interior of 8 restored grassland sites in northwestern Iowa, USA, 2004.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total relative snake abundance&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Difference&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Edge</td>
<td>Interior</td>
</tr>
<tr>
<td>Capner</td>
<td>18.0</td>
<td>18.0</td>
</tr>
<tr>
<td>Cayler</td>
<td>5.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Lair</td>
<td>25.3</td>
<td>32.0</td>
</tr>
<tr>
<td>Main</td>
<td>19.3</td>
<td>26.0</td>
</tr>
<tr>
<td>McBreen</td>
<td>5.0</td>
<td>8.0</td>
</tr>
<tr>
<td>South Lair</td>
<td>6.0</td>
<td>31.5</td>
</tr>
<tr>
<td>Savard</td>
<td>13.0</td>
<td>24.0</td>
</tr>
<tr>
<td>Seeman</td>
<td>14.5</td>
<td>11.0</td>
</tr>
</tbody>
</table>

<sup>a</sup> Total number of snakes captured during a 16-week sampling period, divided by the number of transects in each site-type.

<sup>b</sup> Total relative interior snake abundance subtracted from total relative edge snake abundance.
Table 4
Coefficients (SE) for all transect-level variables in multiple-regression models explaining snake abundance on 40 transects in 10 restored grasslands in northwestern Iowa, USA, 2004.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dfarm</th>
<th>Vertd</th>
<th>Litter</th>
<th>Covlit</th>
<th>Grass</th>
<th>Covgmd</th>
</tr>
</thead>
<tbody>
<tr>
<td>All snakes</td>
<td>0.001*</td>
<td>0.000</td>
<td>-0.022</td>
<td>0.126</td>
<td>-0.002</td>
<td>0.009</td>
</tr>
<tr>
<td>Garter snakes</td>
<td>0.001*</td>
<td>0.001</td>
<td>-0.074</td>
<td>0.168</td>
<td>-0.006</td>
<td>0.013</td>
</tr>
<tr>
<td>Brown and green snakes</td>
<td>0.001*</td>
<td>0.001</td>
<td>0.066</td>
<td>0.172</td>
<td>0.006</td>
<td>0.013</td>
</tr>
</tbody>
</table>

* Transect-level variables included: Dfarm = distance to nearest farmstead (m), Vertd = vertical density (dm), Litter = litter depth (mm), Covlit = exposed litter cover (%), Grass = grass cover (%), Covgmd = exposed bare ground (%).

* P < 0.05
Table 5
Coefficients (SE) for all landscape-level variables used in multiple-regression models explaining snake abundance on 10 restored grassland landscapes in northwestern Iowa, USA, 2004.

<table>
<thead>
<tr>
<th>Species</th>
<th>Landscape-level Variables$^a$</th>
<th>$\beta$</th>
<th>SE</th>
<th>$\beta$</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>All snakes</td>
<td>Ptwet</td>
<td>0.041</td>
<td>0.035</td>
<td>0.007</td>
<td>0.014</td>
</tr>
<tr>
<td>Garter snakes</td>
<td>Ptgrass</td>
<td>0.059</td>
<td>0.038</td>
<td>-0.007</td>
<td>0.015</td>
</tr>
<tr>
<td>Brown and green snakes</td>
<td>Ptwet</td>
<td>0.031</td>
<td>0.037</td>
<td>0.020</td>
<td>0.014</td>
</tr>
</tbody>
</table>

$^a$ Landscape-level variables included: Ptwet = wetland cover (%), Ptgrass = grass cover (%).

* $P < 0.05
Figure legends

Figure 1 Total captures of all species on 35 transects in 8 restored grasslands in northwestern Iowa, USA, 2004. Snakes captured multiple times were counted only once.
Figure 1
CHAPTER 4. GENERAL CONCLUSIONS

Avian nest success in restored and remnant grasslands in northwestern Iowa-- We monitored 173 nests of 7 species for a total of 466 nest visitation intervals in 6 remnant and 10 restored grasslands. Two-hundred twenty six intervals were in remnant habitat, and 240 intervals were in restored habitat. American goldfinches (*Carduelis tristis*), bobolinks (*Dolichonyx oryzivorus*), dickcissels (*Spiza americana*) and red-winged blackbirds (*Agelaius phoeniceus*) nested in both habitat types. We found clay-colored sparrow (*Spizella pallida*), common yellowthroat (*Geothlypis trichas*) and song sparrow (*Melospiza melodia*) nests only on remnant sites. Predation was the primary cause of nest failure in both habitats, with 92% of nest failures attributed to predation.

Our results indicated nest survival in remnant prairies tended to be higher, but the effect of type was extremely weak. The best model, which included habitat type in addition to nest age and nest location effects, had little weight of support over the more parsimonious model which included only nest age and nest location. Overall, nest age had a strong negative effect on daily survival rates. The strength of the effect lessened towards the end of the nesting cycle likely due to changes in nestling size and behavior (Holcomb 1972, Grant et al. 2005).

Our data indicated that restoring grasslands in highly fragmented agricultural landscapes can provide suitable habitat for grassland-breeding birds, even if the restoration efforts do not mirror native habitat conditions. Nest age had a negative effect on daily nest survival, indicating that nest predation will affect nest survival regardless of vegetation structure within a habitat patch. Grassland nests are depredated by a diverse suite of predators (Pietz and Granfors 2000, Renfrew and Ribic 2003), many of which are abundant
in fragmented landscapes. I suspect that predation rates in severely fragmented agricultural landscapes will be high even if the vegetation structure within patches is similar to native prairie. My results indicate that current restoration practices provide similar quality breeding habitat for grassland birds.

*Grassland snake habitat use and response to road edges in a fragmented landscape*--We captured 694 individuals of 4 species during 16 survey weeks on 10 restored grassland sites. Sixty-six percent of the captures were plains garter snakes (*Thamnophis radix*). Smooth green snakes (*Opheodrys vernalis*), a species of special concern in Iowa (State of Iowa 2002), were found on 2 sites. The presence of smooth green snakes suggests that restored grasslands provide suitable habitat for this species, which has experienced substantial population declines due to habitat loss in much of its eastern and central range (Christiansen and Bailey 1990, Tennant 2003).

Our transect-level and landscape-level models of snake abundance had low predictive power, indicating snakes may not be responding to the vegetation and landscape characteristics we measured. Distance to nearest farmstead was the only variable that significantly influenced snake abundance, with snakes being more abundant farther from farmsteads. Garter snakes (*Thamnophis spp.*), and brown (*Storeria dekayi*) and green snakes showed somewhat different habitat associations. Vertical density, for example, was associated positively with brown and green snake abundance, and negatively with garter snake abundance. While the transect-level and landscape-level variables we examined did not influence snake abundance significantly, species-specific responses to habitat structure indicate management decisions should consider the entire suite of snake species present when attempting to maximize the value of grasslands for snake species.
We found no significant evidence that grassland snakes abundance was different in the interior of grassy plots, as compared to the edges. This indicates that grass-road edges in highly fragmented landscapes may not influence the distribution and abundance of the 4 species we encountered. Vegetation structure and composition were similar in the edge and interior. Variation in vegetation structure can affect the snake community by influencing food supply, cover, and microclimatic factors such as soil temperature and moisture (Cavitt 2000). In the absence strong differences in habitat structure or resource availability, snake abundance is likely to be similar in both site-types. While we found no indication that grassland snake abundance is affected by proximity to roads, we can not discount the possibility that snakes avoid road edges (Shine et al. 2004), especially if avoidance behavior is evident only at the immediate road edge. Given the intensive nature of road systems in agricultural ecosystems, it is important to understand how road edges effect grassland snake populations. Understanding the effects of road edges is a crucial step toward understanding snake ecology and habitat use in fragmented agricultural landscapes.

**Literature Cited**


Pietz, P.J., and D.A. Granfors. 2000. Identifying predators and fates of grassland


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