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The nest predator community of grassland birds responds to agroecosystem habitat at multiple scales

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Nest predation is the leading cause of reproductive failure for grassland birds of conservation concern. Understanding variation in nest predation rates is complicated by the diverse assemblage of species known to prey on nests. As part of a long-term study of grassland bird ecology, we monitored populations of predators known to prey on grassland bird nests. We used information theoretic approach to examine the predator community's association with habitat at multiple scales, including local vegetation structure of grassland patches, spatial attributes of grassland patches (size and shape), and landscape composition surrounding grassland patches (land cover within 400 and 1600 m). Our results confirmed that nest predators respond to habitat at multiple scales and different predator species respond to habitat in different ways. The most informative habitat models we selected included variability in local vegetation (CV in the density of forbs), local patch (area and edge-to-interior ratio), and landscape within a 1600 m buffer around grasslands (percent of land covered by human structures and development). As a separate question, we asked if models that incorporated information from multiple scales simultaneously might improve the ability to explain variation in the predator community. Multi-scale models were not consistently superior to models derived from variables focused at a single spatial scale. Our results suggest that minimizing human development on and surrounding conservation land and the management of the vegetation structure on grassland fragments both may benefit grassland birds by decreasing the risk of nest predation.

The tallgrass prairie biome of the North American Great Plains is a critically endangered ecosystem, with $<2\%$ of the native ecosystem remaining (Noss et al. 1995, Hoekstra et al. 2005). Remaining grassland fragments in this area are isolated and embedded in a mosaic of habitat types including woodlots, human development, and agricultural fields. As the habitat has been altered, grassland birds have undergone precipitous population declines and are considered among the most threatened of groups of birds in North America (Knopf 1994, Peterjohn and Sauer 1999, Rich et al. 2004, Brennan and Kuvlesky 2005).

Nest predation is a leading cause of reproductive failure for most birds (Ricklefs 1969, Martin 1993) and can severely limit the ability of remaining habitat patches to sustain bird populations. While population declines of grassland birds are undoubtedly due to a variety of factors, including changes in wintering and migratory habitats, the ability of bird populations to recover is limited by low reproductive success resulting from nest predation. In the heavily agricultural areas of the former tallgrass prairie biome, grassland loss and fragmentation may increase predation risk by favoring habitat generalists such as raccoons *Procyon lotor*, coyotes *Canis latrans*, and garter snakes *Thamnophis* spp., which add to predation pressure from predators, such as ground squirrels *Spermophilus* spp., fox snakes *Elaphe vulpina*, and bull snakes *Pituophis catenifer* residing within the prairie fragments.

In studies focused on grassland birds, a diverse range of species have been responsible for nest predation, rather than one dominant species of specialist predator (Pietz and Granfors 2000, Renfrew and Ribic 2003, Thompson and Burhans 2003, Klug 2005). High predator diversity has contributed to an increased emphasis on the need to understand the entire guild of predators if we are to address the conservation implications of nest predation in grassland birds (Heske et al. 2001). However, there are few quantitative studies that include the entire predator community. Instead, most studies looking at the influence of habitat on nest predators focus on a narrow group or one species of predator (Chalfoun et al. 2002). Previous studies have focused on mid-sized mammals such as raccoons, canines, and skunks *Mephitis mephitis* (Dion et al. 1999, Heske et al. 1999, Dijak and Thompson 2000), bird predators such as brown-headed cowbirds *Molothrus ater* and corvids (Andrén 1992, Kosciuch and Sandercock 2008), and small mammals (Ackerman 2002, Bradley and Marzluff 2003).

Our study examined spatial variation in the entire community of nest predators as part of a long-term study of the ecology and reproductive success of dickcissels *Spiza americana.* Like many other grassland birds in North America, dickcissels have undergone significant population declines and are of conservation concern (Rich et al. 2004). High priority research needs for dickcissel conservation include information on nest predators and information on how landscape variables affect reproductive success (Partners in Flight – US 2005). In addition to the landscape scale, management and conservation decisions have been made at a variety of spatial scales such as local vegetation structure and the size and shape of the patch itself. Likewise, the ecology of nest predators can be influenced by habitat characteristics at multiple spatial scales. Therefore, we examined the relationship between nest predators and habitat at multiple scales (Bergin et al. 2000, Thompson et al. 2002, Kus et al. 2008) to better understand why predation risk might vary and to provide information for conservation at appropriate scales.

Our analyses were organized around three spatial scales. The finest spatial scale was the grassland patch where dickcissels were nesting and where we measured the abundance of nest predators. The habitat within a grassland patch was measured by vegetation composition and structure; hereafter the local vegetation scale (Table 1). Many habitat management activities take place at the local vegetation scale, especially in restored and heavily managed grassland fragments. We asked whether the average vegetation structure or the heterogeneity of that structure within the grassland was more informative for explaining variation in the predator community.

At the next scale in our hierarchy, we measured the spatial attributes of the grassland patch itself; hereafter the local patch scale (Table 1). We evaluated models incorporating patch size and shape to ask what combination of variables was most informative for understanding the abundances of predators. Studying patch attributes reflected the conservation concerns about how nest predators respond to habitat fragmentation and habitat edge and is especially relevant to decisions related to the sizes of grassland restorations and how field boundaries are managed.

At the landscape scale we included information about land cover surrounding the grassland patches. We asked what types of land cover explained variation in the predator community and whether land cover in a narrow (400 m) or broad (1600 m) buffer around each site was most informative (Table 1). Our analyses encompassed the response of an entire community of predators where each species likely interacts with the landscape at a different spatial scale, ranging from mice, to raccoons, to migratory birds. Because our ultimate goal is to understand variation in the risk of predation from the entire predator community, rather than the abundance of any one species, we included models based on the same variables but measured at multiple buffer distances around the patch. We considered the 1600 m buffer to reflect the spatial extent necessary to encompass the broadest ranging predators, while a 400 m buffer might better reflect the ranges of smaller and less mobile predators.

At each of the three spatial scales, a set of models consisting of variables or combinations of variables emerged as being the most important in explaining predator communities. We then used model averaging to examine the direction and strength of associations among habitat variables in selected models and the individual types of predators in the predator community at each of the three spatial scales.

Table 1. Habitat variables used to develop models for explaining relative predator abundance. Models were evaluated using AIC_c (see text) to select the best candidate models.

Local vegetation
- Mean grass density
- Mean forb density
- Mean litter depth
- Mean max. veg. height
- Heterogeneity (CV) in litter depth
- Heterogeneity (CV) in max. veg. height
- Heterogeneity (CV) in grass density
- Heterogeneity (CV) in forb density

Local patch variables
- Area
- Edge-to-interior ratio

Landscape composition – in both 400 m and 1600 m radius buffer
- % Trees
- % Grassland
- % Crop
- % Wetlands
- % Development

Treating each spatial scale separately in our hierarchy provides information corresponding to management decisions occurring at multiple, distinct scales. For our final question we asked whether habitat variables at multiple scales provided more information about the predator community than data only at the local vegetation, local patch, or landscape scales.

Materials and methods

We conducted this study in eastern Nebraska and western Iowa, USA, in the Dissected Till Plains physiographic region (Fitzgerald and Pashley 2000). The native vegetation of this region was tallgrass prairie, but the landscape now consists of intensive agriculture interspersed with small parcels of remnant, restored or marginal grasslands. We monitored the predator communities at 36 grassland patches spread over an 815-km^2 area. Seventeen patches were monitored in both 2003 and 2004, and an additional six were used only in 2003 and 13 used only in 2004. The landscape surrounding the grassland patches was a mosaic of habitat types including row crop agriculture consisting mainly of corn and soybeans, human development such as housing and farm buildings, woodlots, forests, wetlands, water, grasslands, marginal grasslands within farms (terraces, waterways, ditches), and a small number of hayfields and pastures. Grassland patches were defined by landowners and managers and were distinct from neighboring patches based on habitat type or management regime. Grassland patches differed in their isolation, shape, and size and ranged from 1 to 50 ha. We used both public and private grasslands with varied management practices. We had 16 grasslands patches (1–9 ha) at agricultural farms, consisting of one Conservation Reserve Program (CRP) parcel, two switchgrass *Panicum virgatum* dominated stands set aside for wildlife by private landowners, and 13 patches consisting of agricultural terraces planted to cool season brome *Bromus* spp. surrounded by row crops. Private grasslands were characterized by no managed grazing and limited burning, though in some cases woody plants were removed manually or with herbicides. We used nine patches (7–50 ha) managed by Desoto National Wildlife Refuge and six patches (7–45 ha) managed by Boyer Chute National Wildlife Refuge. The refuge patches were restored grasslands managed with prescribed burning and no managed grazing. The dominant vegetation on the refuges ranged from primarily warm-season grasses to primarily cool-season grasses and varied in the density of forbs. We had three patches (4–28 ha) at the Allwine Prairie Preserve, a 30-yr old restored tallgrass prairie managed by the Univ. of Nebraska at Omaha and one patch (4 ha) at the Cuming City Cemetery Nature Preserve, a remnant native prairie managed by Dana College. The preserve grasslands were managed with prescribed burning and no managed grazing. Warm-season grasses were the dominant vegetation and the amount of forbs varied among patches at the preserve sites. All 36 sites, including those on the refuges and preserves, were surrounded by a mosaic of habitat types such as cropland, forest, grassland and wetland.

Surveys of the predator community

Based on previous studies of predators at grassland bird nests (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003) we established a priori that the suite of potential nest predators consisted of mid-sized mammals, small mammals, snakes, and avian predators. We used standard survey methods specific to each of these categories to establish the relative abundance of potential predators at each site in 2003 and 2004 (Parmelee and Fitch 1995, Ralph et al. 1995, Glennon et al. 2002, Kuehl and Clark 2002).

Mid-sized mammals

We measured the relative abundance of mid-sized mammals using two track stations placed at least 250 m apart at each grassland patch. Each track station was a one-meter diameter area of cleared vegetation, sprayed with glyphosate herbicide and covered with sand (Kuehl and Clark 2002). We placed a can of fish-flavored cat food perforated to act as an odor source but anchored to prevent mammals from gaining access to the food. For data collection, the sand was smoothed and left for two exposure nights. We identified tracks to species in the field based on Murie (1974). We surveyed each patch four times from June to August in 2003 and six times from May to August in 2004. Because precipitation obliterated tracks left in the sand, sample sizes of usable tracks at stations varied slightly among patches and years. Although we categorized raccoons, coyotes, striped skunks, Virginia opossums *Didelphis virginiana*, and domestic cats and dogs as potential nest predators, we only recorded raccoons as predators on nests at our sites (Klug 2005). For each patch and for each survey, we calculated a track index for raccoons by dividing the number of stations with tracks by the number of operating stations. For analysis, we used the average track index from the sampling periods at each grassland patch.

Small mammals

We measured the relative abundance of small mammals using ten track tubes at each grassland patch. Track tubes were placed 50 m apart and consisted of two 30-cm plastic gutters fastened together to form a tube (Glennon et al. 2002). Inkpads were placed at both ends and strips of contact paper created a track surface. For data collection we baited the tubes with trays containing a peanut butter and bird seed mixture and left them for two exposure nights. Tracks were identified by separating ground squirrels *Spermophilus* spp. from other cricetid rodents based on Murie (1974). We surveyed sites four times from June to August in 2003 and four times from May to August in 2004. For each sampling period we calculated an index of abundance by dividing the number of tubes with tracks by the number of operating tubes. Separate indices were calculated for ground squirrels and for cricetid rodents. We used a mean index from the four sampling periods in each year for analysis.

Snakes

We measured the relative abundance of snakes in each patch by using ten coverboards placed at 50 m intervals. Each coverboard was a 60 by 180 cm ply-wood sheet (Parmelee and Fitch 1995). We captured and identified all bird-eating snakes found under the boards. We surveyed sites six times from June to August in 2003 and 11 times from May to August in 2004. For each visit, we calculated an index of snake abundance by dividing the total number found by the number of boards checked. The index used only those species recorded on video as nest predators in the study area and included yellowbelly racers *Coluber constrictor*, red-sided garter snakes *Thamnophis sirtalis*, plains garter snakes *Thamnophis radix*, bullsnakes *Pituophis catenifer*, and fox snakes *Elaphe vulpina* (Klug 2005). We calculated a mean index for snake predators based on all surveys conducted at a site for analysis.

Birds

We measured the relative abundance of bird predators with 10-min point counts (Ralph et al. 1995). We did not adjust for distance from the observer and included all individuals observed from the point count because most of potential predators were observed either in flight or detected by sound beyond the boundaries of the patch. We conducted point counts in each grassland patch two times from May to June in both 2003 and 2004. Although we categorized blue jays *Cyanocitta cristata*, American crows *Corvus brachyrhynchos*, common grackles *Quiscalus quiscula*, brown-headed cowbirds, red-tailed hawks *Buteo jamaicensis*, and American kestrels *Falco sparverius* as potential nest predators (Andrén 1992, Pietz and Granfors 2000, Renfrew and Ribic 2003), we recorded only brown-headed cowbirds as actual predators on nests at our sites (Klug 2005). For each site, we calculated a mean relative abundance of brown-headed cowbirds by dividing the number of individuals present at a site by the total number of point counts conducted over the season.

Local vegetation scale

We measured local vegetation structure using the Wiens method (Rotenberry and Wiens 1980, Martin et al. 1997) by recording the number of times that grass or forbs contacted a 110-cm pole. Vertical vegetation structure was recorded at six (in 2003) or at nine (in 2004) randomly selected sampling locations within each grassland patch. We measured litter depth and the maximum vegetation height within a 5 cm radius of the pole at each sampling location. We calculated forb densities using the point-centered quarter method (Cottam and Curtis 1956), which has been effectively applied in other studies to measure plants at low density in grasslands (Rotenberry and Wiens 1980, Martin et al. 1997, Elzinga et al. 2001). Heterogeneity in vegetation structure for litter depth, vegetation height and vertical density were calculated using the coefficient of variation (CV) among the sampling points for each grassland patch (Table 1).

Local patch scale

We calculated the area and the edge-to-interior ratio with ortho-photo quadrangles in ArcGIS 8.1 (ESRI, Redlands, CA) by digitizing each grassland patch at a scale of 1:1500.

Landscape scale

We digitized seven habitat types within a 1600 m buffer of each site with 1999 and 2003 ortho-photo quadrangles in ArcGIS 8.1 (ESRI, Redlands, CA) at a scale of 1:1500. We identified seven habitat categories: human development (residential, livestock), agricultural row crops, grassland (grazed pasture, hayfield, warm-season, cool-season, road ditches, waterways, terraces, and fence lines), trees (forest, riparian, woodlot, development, and savanna dominated by trees), wetland, water (rivers, streams, and lakes), and roads (highway, county, access, and driveway). We ground-truthed all areas for accuracy from 2004 to 2005. We computed landscape composition surrounding each site at 400 and 1600 m buffers from the perimeter of the site. We calculated landscape composition using the proportion of grassland, trees, wetland, row crops, and human development (Table 1).

Analysis framework

Our overall goal was to understand the relationship between variables describing habitat at multiple scales and a diverse community of nest predators. We used results of other studies to select habitat variables for each spatial scale that we considered, a priori, to be most important in explaining the predator community (Table 1). At the local vegetation scale, the variables used focused primarily on the average characteristics of the vegetation or on the variability in vegetation (measured by coefficients of variation, CV). These variables produced 30 models describing vegetation structure. We described the spatial characteristics of grassland patches by producing three models at the patch scale (area, edge-to-interior ratio, and area combined with edge-to-interior ratio). Landscape models were constructed for two buffer distances (400 and 1600 m radius) around each patch using five categories (% trees, % development, % cropland, % grassland, and % wetland). Landscape models did not mix variables measured at the different buffer sizes. We eliminated models that contained highly correlated variables ($r > 0.60$) to minimize redundant models (Tabachnick and Fidell 2007). At both buffer distances and in both years, percent crop was negatively correlated with percent trees and with percent grass and individual models did not contain more than one of these classes. Combinations of landscape variables resulted in 38 models. The models that best explained variation in the predator community were determined using Akaike's information criterion (AIC_c) corrected for small sample sizes (described in Statistical analyses). AIC_c was appropriate because it allowed us to examine how well various combinations of habitat variables explained the observed patterns of predator abundance at each scale.

Our study was set up to examine habitat relationships at three scales because treating each scale separately is most appropriate for informing conservation and management activities that are conducted at each scale. We also asked if combining information from multiple scales results in models that are more informative than single scale models. Our approach developed multi-scale models by forcing together the variables from the best models at each spatial scale. We then produced a competing set of models from these multi-scale models and the best single-scale models (Gehring and Swihart 2003). This approach deviated from the accepted approach of building models from a priori information. As a post hoc analysis we did not consider the weightings of the models produced by this process to be reliable relative to those from prior analyses. Thus, we limited our conclusions from this analysis to asking if there is consistent pattern of selecting single scale or multi-scale models.

Statistical analyses

Evaluation of models using AIC_c

We employed Akaike information criterion corrected for small sample sizes (AIC_c) to select the best models (Burnham and Anderson 1998). The value for AIC_c is,

$$AIC_c = -2\ln(\ell(\hat{\theta}|data)) + 2k + \frac{2k(k+1)}{N-k-1}$$

where $\ln(\ell\hat{\theta}|data)$ is the value of the maximized log-likelihood over the unknown parameters (θ), given the data and the model, k is the number of parameters, and N is the number of sites or sample size. To address model selection uncertainty, each alternative model was evaluated by the difference between the model AIC_c and the minimum AIC_c,

$$\Delta_i = AIC_{ci} - \min\ AIC_c$$

Models with $\Delta_i \leq 2$ were considered candidate models. Akaike weights (w_i) were the probability that model i was the best of all models being considered. We reported the adjusted-R^2 of each selected model as a diagnostic of model fit (Burnham and Anderson 1998).

We analyzed habitat models using the relative predator abundance as the dependent variables. Only predator taxa that were documented as actual predators on dickcissel nests at our study sites were included in the analyses (Klug 2005). The predator community was categorized into five types: raccoons, ground squirrels, cricetid rodents, snakes (five species observed taking nests), and brown-headed cowbirds. Although mink were documented as a nest predator on video, too few mink tracks were identified to include them as a predator category in the analysis.

We analyzed the relationship between habitat and the relative abundance of all predator types in the community simultaneously using multivariate general linear models (GLM) (SYSTAT ver. 11, SYSTAT Software, Chicago, IL) to conduct a multivariate analysis of variance. We standardized the data for each predator group to a mean of 0 and a standard deviation of 1 to compare among groups using a standard scale. Our data met assumptions of no outliers, homogeneity within the variance-covariance matrices (values were all within a factor of ten of each other), and the absence of multicollinearity of explanatory variables (Tabashnick and Fidell 2007). The sampling distributions for raccoons, ground squirrels, snakes and brown-headed cowbirds were skewed towards zero and did not meet assumptions of multivariate normality. However, the test is still considered robust when the assumption of multivariate normality is violated due to skew in the data and we chose not to transform the data to eliminate skew (Tabashnick and Fidell 2007). We analyzed predator data from 2003 and 2004 separately given that we had some, but not all, sites in both years. There were some differences in the means of predator abundance and local vegetation variables between the two years (Klug 2005). There were no differences between years in habitat variables at the patch or landscape scales.

Model averaging

When more than one model was selected at a given scale, we asked if some habitat variables were found consistently in the selected models. We assumed that a variable found in multiple models was more important than a variable that appeared in only one selected model. We used the multivariate GLM to generate a standardized regression coefficient for each predator type and habitat variable which represented the relative strength and directionality of the association between the predator types and that habitat variable for a given model. To determine the overall direction of habitat effects on individual predator groups, we used model averaging of the parameter estimates of the selected models (Burnham and Anderson 1998). Model averaging allowed us to use the Akaike weight of each selected model to calculate a weighted mean and variance of a parameter estimate for each predator category.

Multiple-scale habitat models

To determine whether models describing habitat at multiple spatial scales were informative for explaining predator community composition, we combined scales by creating models made up of the best model selected at the individual spatial scales. We combined landscape and local patch variables by combining the variables from the best landscape model into the best local patch model. We also merged landscape and local vegetation variables by combining the variables from the best landscape model into the best local vegetation model. We then forced the best landscape-local patch model into the best local vegetation model to create a model with all three scales. The three multi-scale models were competed with the individual scale models to see if the multi-scale models better explained the variation in the predator community than single scale models. We compared AIC_c values of the best single-scale models (local vegetation only model, local patch only model, and landscape only model) with multi-scale models (landscape-local patch model, landscape-local vegetation model, and landscape-local patch-local vegetation model).

The Akaike weights (w_i) from the single scales are not directly comparable because the model sets for each scale were competed separately. Therefore, in our final question we directly competed the best models from each single scale, along with the multi-scale models. However, the multi-scale models were based on prior analyses at the single scales. Thus we do not present variables or coefficients with these results (Table 4) and consider this analysis as a way to ask about the benefits of multi-scale approaches in studying nest predators.

Results

Local vegetation scale

At the local vegetation scale we evaluated a set of 30 models for each year. In both 2003 and 2004, 11 of the competing models had a $\Delta AIC_c \leq 2$ (Table 2). Models describing the heterogeneity of vegetation were more likely to be selected as informative models explaining predator abundance than models describing the mean characteristics of vegetation. In 2003, seven of the selected models were based on variables describing variability in vegetation structure and only four were based on variables describing the mean characteristics. In 2004, nine of the selected models described vegetation variability and only two were based on models describing mean conditions (Table 2).

All of the variables measured were included in at least one selected model (Table 2). In 2003, CV of forb density occurred most frequently (in 4 selected models), while CV of grass density, CV of litter depth, and CV of maximum vegetation height each appear in two selected models. In 2004, CV of forb density appeared in five selected models and CV of grass density and CV of litter depth each appeared in four selected models (Table 2).

Patch scale

At the patch scale, we competed three models each year based on patch area, edge-to-interior ratio, and the combination of area and edge-to-interior ratio. In 2003, all three models were selected as equally informative for explaining variation in predator abundance, but all of these models had low explanatory power as indicated by the small adjusted R^2 values (Table 2). In 2004, area and the

Table 2. Candidate models for explaining the predator community at each of three scales in 2003 and 2004 are shown. Models with a Δ $AIC_c \leq 2$ are shown. Adjusted R^2 are reported as a diagnostic of absolute model fit (Burnham and Anderson 1998).

2003	Δ AIC_c	w_i	Adj R^2	2004	Δ AIC_c	w_i	Adj R^2
Local vegetation models				Local vegetation models			
Litter depth	0.00	0.17	0.35	CV forb density	0.00	0.11	0.38
CV forb density	0.13	0.16	0.26	CV grass density, CV forb density	0.68	0.08	0.52
CV litter depth	0.36	0.14	0.24	CV litter depth, CV forb density	0.89	0.07	0.49
Forb density	0.76	0.11	0.16	CV litter depth, CV grass, CV forb	1.24	0.06	0.72
CV maximum vegetation height	0.79	0.11	0.16	CV grass density	1.31	0.06	0.19
Grass density	0.84	0.11	0.18	CV max. veg. height, CV forb density	1.38	0.06	0.43
CV litter depth, CV forb density	0.97	0.10	0.50	CV litter depth	1.62	0.05	0.10
CV grass density	1.04	0.10	0.06	CV maximum vegetation height	1.83	0.04	0.09
Maximum vegetation height	1.61	0.07	0.00	Forb density	1.88	0.04	0.05
CV max. veg. height, CV forb density	1.66	0.07	0.30	CV litter depth, CV grass density	1.91	0.04	0.33
CV grass density, CV forb density	1.99	0.06	0.24	Grass density	1.94	0.04	0.08
Local patch models				Local patch models			
Edge-to-interior ratio	0.00	0.45	0.05	Patch area	0.00	0.51	0.59
Patch area	0.45	0.36	0.01	Area, edge-to-interior ratio	0.67	0.37	0.68
Area, edge-to-interior ratio	1.79	0.19	0.08				
Landscape composition models				Landscape composition models			
1600 m % development	0.00	0.17	0.85	1600 m % development	0.00	0.19	0.77
1600 m % development, % wetland	1.73	0.07	0.94	1600 m % development, % trees	0.70	0.13	0.87
1600 m % development, % grassland	1.88	0.06	0.87	1600 m % development, % cropland	1.65	0.08	0.76
				1600 m % development, % wetland	1.76	0.08	0.77

combination of area and edge-to-interior ratio were selected with $\Delta AIC_c \leq 2$ (Table 2).

Landscape scale

At the landscape scale we evaluated 38 models each year. Three models had a Δ $AIC_c \leq 2$ in 2003 and four models had a Δ $AIC_c \leq 2$ in 2004 (Table 2). Models were based either on land cover in a 400 m radius buffer or in a 1600 m radius buffer around each grassland. Only models based on land cover measured in the surrounding 1600 m were selected (Table 2). All selected models included the variable describing the percent of the landscape under human development (Table 2). The proportion of wetlands in the landscape appeared in one selected model in each year (Table 2).

Evaluation of coefficients using model averaging

Coefficients from selected models at each spatial scale were averaged to determine the direction and consistency of effects on predator types. The magnitude and direction of relationships between abundance and measurements of habitat varied among the predator types (Table 3). The 95% confidence intervals for the standardized coefficients did not over lap zero for 15 of the predator-habitat variable pairs (Table 3). Each of the five predator groups had at least one habitat coefficient with a 95% confidence interval that did not include zero. Likewise, for each of the three habitat scales we considered there were coefficients with 95% confidence intervals above or below zero (Table 3).

Evaluation of multiple-scale models

The best models selected at each scale were combined to create multi-scale models. These multi-scale models were competed against each other and against the best models at each single scale to ask if considering multiple scales simultaneously might be more informative for understanding the abundances of predators at different sites. In 2003, both single scale and multi-scale models were selected, with the landscape scale model being selected as the best model (Table 4). In 2004, only the multi-scale models were selected (Table 4).

Discussion

An understanding of nest success patterns for grassland birds requires an understanding of the entire community of nest predators especially in the in tallgrass prairie of North America where a single dominant nest predator has not been identified (Klug 2005). In contrast, most studies focus on the ecology of a single predator species or guild (Chalfoun et al. 2002). Single species investigations are important when the goal is to manipulate habitat to decrease one species of nest predator (Harding 2001), but in regions such as the Great Plains, the decrease of one predator may not be sufficient for increasing nesting success due to the wide diversity of predators and the interactions between nest predators. For example, both rodents and snakes are nest predators but the predatory relationship between the two may result in rodents acting as alternate prey for snakes (Ackerman 2002). Incorporating multiple predator species in a single analysis can detect cases where abundant populations of one nest predator may influence the occurrence of a second nest predator. In our study, the aim was to understand the relationships between the nest predator community and habitat variables measured at distinct spatial scales while addressing possible interactions among predator species.

Local vegetation scale

While ecological studies often focus on average conditions in patches, ample evidence from grasslands suggests

Table 3. Weighted means (±SE) of standardized model coefficients derived from model averaging for each type of nest predator and each habitat variable. Cells for variables that did not appear in selected models for a given year are blank. Coefficients where the 95% confidence interval does not overlap zero are in bold. Number of sites was 24 in 2003 and 30 in 2004.

	Raccoon		Ground squirrel		Cricetid rodent		Snake		Brown-headed cowbird	
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Vegetation scale										
Mean forb density	0.44 ± 0.22	−0.26 ± 0.19	−0.06 ± 0.25	−0.21 ± 0.19	0.20 ± 0.25	0.18 ± 0.19	0.13 ± 0.25	0.22 ± 0.19	−0.27 ± 0.24	−0.09 ± 0.19
Mean grass density	−0.43 ± 0.23	0.13 ± 0.19	−0.03 ± 0.25	0.16 ± 0.19	0.05 ± 0.25	−0.14 ± 0.19	−0.32 ± 0.24	−0.34 ± 0.18	0.11 ± 0.25	−0.10 ± 0.19
Mean litter depth	−0.20 ± 0.24		−0.03 ± 0.25		−0.16 ± 0.25		**−0.57 ± 0.20**		0.35 ± 0.23	
Mean max. height	0.21 ± 0.24		−0.02 ± 0.25		−0.10 ± 0.25		−0.20 ± 0.25		0.07 ± 0.25	
CV forb density	−0.15 ± 0.25	**−0.54 ± 0.19**	−0.44 ± 0.23	−0.16 ± 0.19	−0.34 ± 0.23	−0.30 ± 0.18	−0.24 ± 0.25	0.28 ± 0.18	−0.35 ± 0.23	−0.05 ± 0.20
CV grass density	0.34 ± 0.24	0.06 ± 0.17	−0.25 ± 0.23	**−0.36 ± 0.18**	0.22 ± 0.24	0.15 ± 0.18	−0.08 ± 0.25	**0.42 ± 0.17**	−0.15 ± 0.24	0.04 ± 0.20
CV litter depth	0.23 ± 0.25	−0.30 ± 0.17	0.11 ± 0.24	**0.33 ± 0.04**	−0.03 ± 0.22	**0.29 ± 0.04**	0.23 ± 0.25	**0.09 ± 0.04**	0.10 ± 0.23	−0.00 ± 0.05
CV max. height	**0.48 ± 0.22**	−0.24 ± 0.17	−0.13 ± 0.25	−0.14 ± 0.19	0.19 ± 0.18	0.31 ± 0.18	−0.21 ± 0.22	0.10 ± 0.19	−0.02 ± 0.17	0.07 ± 0.19
Patch scale										
Area	−0.19 ± 0.25	−0.35 ± 0.18	−0.19 ± 0.15	−0.06 ± 0.19	−0.20 ± 0.16	0.26 ± 0.18	−0.12 ± 0.15	−0.02 ± 0.19	−0.26 ± 0.16	**0.74 ± 0.14**
Edge-to-interior	−0.25 ± 0.24	0.06 ± 0.18	−0.18 ± 0.25	−0.34 ± 0.19	−0.36 ± 0.24	**0.39 ± 0.18**	−0.27 ± 0.24	−0.13 ± 0.19	0.14 ± 0.25	0.17 ± 0.13
Landscape scale										
% Development	0.20 ± 0.24	0.09 ± 0.19	**0.74 ± 0.17**	**0.84 ± 0.10**	0.17 ± 0.24	−0.32 ± 0.18	0.08 ± 0.25	−0.23 ± 0.19	**0.60 ± 0.20**	0.06 ± 0.19
% Grassland	0.17 ± 0.25		0.05 ± 0.18		0.42 ± 0.23		−0.14 ± 0.26		0.04 ± 0.20	
% Wetland	**0.48 ± 0.23**	−0.11 ± 0.19	0.06 ± 0.17	0.03 ± 0.11	0.14 ± 0.25	0.24 ± 0.18	−0.00 ± 0.26	0.17 ± 0.19	−0.19 ± 0.20	−0.11 ± 0.19
% Trees		0.31 ± 0.19		**0.25 ± 0.10**		−0.20 ± 0.18		−0.19 ± 0.19		0.14 ± 0.19
% Cropland		−0.15 ± 0.19		−0.14 ± 0.11		0.19 ± 0.18		0.07 ± 0.19		−0.20 ± 0.19

Table 4. Candidate model selection with a Δ AIC$_c \leq 2$ from a set of models consisting of the best models from each of the three spatial scales (Table 2) and multi-scale models creating by forcing the variables from the best single scale models into new models.

Scales included in models – 2003	Δ AIC$_c$	w_i	Scales included in models – 2004	Δ AIC$_c$	w_i
Landscape	0.00	0.29	Vegetation + Patch + Landscape	0.00	0.54
Vegetation + Landscape	0.21	0.26	Patch + Landscape	1.91	0.21
Patch + Landscape	1.48	0.14			
Vegetation	1.93	0.11			

that habitat heterogeneity may be at least as important for wildlife (Zimmerman 1982, Johnson et al. 2004, Weatherhead and Blouin-Demers 2004). The fact that models based on the coefficients of variation for habitat variables are more likely to be selected than those based on the means for the same variables supports the idea that the nest predator community is responding to habitat heterogeneity in grasslands (Table 2).

While the selected models explained differences in the overall predator community, our ability to modify predation risk via habitat management will be improved with a more specific knowledge of the one-to-one relationship between individual predator types and specific habitat variables. As expected, different predator species respond to different measures of habitat quality and in different ways (Table 3). Greater variability in forb density was associated with lower densities of most nest predators, although the 95% confidence intervals for most of species overlap zero. The importance of forbs in explaining nest predators is consistent with other aspects of grassland bird ecology where increased nest success (Johnson et al. 2004) and fledgling survival (Berkeley et al. 2007) are linked to increased forbs.

The results of model averaging for the local vegetation models could be used to generate hypotheses by predicting how the predator abundances will change with habitat variables. For example, management to increase the heterogeneity of forbs should decrease the abundance of predators. Likewise, results of model averaging generated predictions that increasing the heterogeneity in grass density should decrease the numbers of ground squirrels but might lead to an increase in snake abundance. In our study, interpretation of causal effects is especially complex due to possible interactions among predator taxa. Based on our results, it is not possible to determine if the higher probability of both snakes and rodents at sites with greater variability in litter depth reflects independent habitat preferences or if an increase in rodents may attract snakes. Therefore the results from the model averaging are best interpreted as forming the basis for hypotheses and predictions, rather than as clear management recommendations.

Patch scale

The set of variables we selected to describe the local patch resulted in three possible models including patch size, edge-to-interior ratio, and the two variables combined (Table 2). The single variable models appeared as the best models because the selection criteria favor models with fewer variables. Although patch attributes did not differ significantly between sites used in 2003 and 2004 ($p > 0.45$), only the results from 2004 support our a priori selection of these variables based on numerous other studies of patch attributes (Helzer and Jelinski 1999, Sovada et al. 2000, Horn et al. 2005). Thus, the importance of the size and shape of a grassland patch will rely on the predator composition as well as on the dynamic nature of predator populations over time. For example, patch attributes may be important in the years when far-ranging predators such as raccoons have high populations (e.g. in 2004), whereas patch attributes may be less important when predators of limited dispersal such as ground squirrels make up the majority of the predator community.

Landscape scale

The models based on land-cover in a 1600 m buffer around the grasslands were selected as being informative for explaining the variation in the nest predator community in both years of the study (Table 2). The importance of land cover at this relatively large spatial scale on the nest predator community is consistent with studies of habitat use (Bakermans and Rodewald 2006), nest success (Kurki and Lindén 1995, Driscoll et al. 2005, Tewksbury et al. 2006), and nest predators (Andrén 1992, Rodewald and Yahner 2001, Chalfoun et al. 2002); all of which highlight the importance of the land-cover composition for birds in highly heterogeneous landscapes such as where our study was conducted (Kus et al. 2008).

At the landscape scale, the best models in both years were based on the single variable describing the percent of land developed with human structures. The percent development variable appeared consistently in every candidate model retained with a Δ AIC$_c \leq 2$ (Table 2). An increase in the percent development was associated with more nest predators for each case where averaged coefficients differed from zero. Therefore, it appears that ground squirrels and brown-headed cowbirds are not negatively impacted by human development and can become an increasing threat to nesting birds as agricultural lands surrounding grassland patches are converted to human structures. The negative influence of increased human development and decreased native habitat for birds has been recognized (Friesen et al. 1995, Marzluff et al. 2007), but in our study human structures tend to displace barren, agricultural land and not the grasslands used by birds and their nest predators. While we expected development to impact wildlife, it is surprising that percent development is so important in a landscape that has been almost entirely converted to human use and highlights the importance of the intensity and nature of human development on predator communities. The negative effect of human structures in the landscape on nest success supports concerns about the proliferation of "acreages" and subdivision of agricultural land for suburbs (Klug 2005).

Evaluation of multiple-scale models

We have shown that most species respond to their environment at multiple scales, however, predicting the abundance of organisms using information from multiple scales may or may not be an efficient approach. Our approach evaluated the importance of multiple scales by asking if the best model at a single scale would be improved by adding the best models from other scales. When we competed the single scale models with the multi-scale models, the results were not consistent. In 2004, two multi-scale models were selected as being more effective in describing the predator community than the best models at single scales (Table 4). However, in 2003, the simple landscape scale model was superior to any of the multi-scale models and vegetation scale model was also selected. The inconsistency in our results provides only mixed support for the advocating a multi-scale approach to understanding predator communities (Dijak and Thompson 2000, Chalfoun et al. 2002, Kuehl and Clark 2002, Gehring and Swihart 2003) and nest predation in birds (Donovan et al. 1997, Tewksbury et al. 1998, Bergin et al. 2000, Heske et al. 2001).

Conservation implications

Nest predation rates are an important concern for management of grassland birds. However, the diversity of species responsible for nest predation complicates any management response. Our research suggests that the nest predator community responds to habitat variables at multiple scales. While several variables emerge as consistent predictors of the predator community, individual predator species respond in different ways to those variables. Any action taken to manage predators separately should be done with caution because a decrease in one predator may not result in an increase in nesting success. For example, raccoons were detected at higher rates in 2004 but these differences were not related to nest predation rates on dickcissels, indicating that raccoons are not the sole driving force behind decreased nest success (Klug 2005).

Management is also complicated when predator species may themselves be of conservation concern. Snakes were the most common predators of bird nests at the wildlife refuges, but management recommendations are difficult due to overlap in habitat preferences between grassland birds and their snake predators (Klug 2005). The snakes documented consuming bird nests are also native members of the grassland community and may be legitimate targets of conservation efforts. Additional information about snake and bird interactions, as well as interactions among groups of predators, under various landscapes and management designations may be valuable in helping establish management practices that minimize nest predation while maintaining populations of native predators.

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