Effects of Suburban-Grassland Edges on the Distribution and Demography Of Grassland Bird Communities

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EFFECTS OF SUBURBAN-GRASSLAND EDGES ON THE DISTRIBUTION AND
DEMOGRAPHY OF GRASSLAND BIRD COMMUNITIES

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ABSTRACT

I examined the distribution and demography of avian communities in grasslands adjacent to and away from suburban developments on large natural areas in Boulder County, CO. Distributional edge effects occurred at all four study areas, where grassland-nesting species (*Pooecetes gramineus, Ammodramus savannarum*) utilized edge settings less than interior settings. Vegetation structure did not differ between edge and interior settings at any of the study areas, suggesting that birds chose to avoid edges based on other environmental selection cues. Predation rates on artificial nests were higher at edges on two of the four study areas. These two study areas had significantly lower vegetation structure compared to the others, suggesting that demographic edge effects may be magnified on areas with low vegetation structure. Although natural nests were scarce at edges, predation rates within these areas were 20% greater than interior settings. In addition, edge settings produced fewer fledglings per hectare than interior settings. Averaged across all study areas and species, natural nest predation rates were significantly greater on nests with low vegetation cover. This suggests that birds may experience higher predation rates in areas with low vegetation structure compared to areas with more dense vegetation. These results have important implications for the conservation and management of bird communities within suburban landscapes. Because certain species intrinsically avoid edge settings, edges should be minimized during the acquisition and development of natural areas. In addition, taller, ungrazed vegetation may provide more nest concealment from predators, thus increasing nesting success within edge settings.

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INTRODUCTION

As novel and enhanced threats to biological diversity are arising within increasingly anthropogenic landscapes, scientists must determine the biodiversity these areas can support (Daily 1997, Rosenzweig 2001) and the causal mechanisms altering their ecological patterns and processes (Balmford et al 1998). Anthropogenic landscapes include agricultural, rural, or urban settings, and can include the native habitat patches embedded within and adjacent to these areas. Improving conservation efforts within anthropogenic landscapes is important (Daily 1997, Gering and Blair 1999, Grimm et al. 2000) because: (1) ecosystem services (water purification, waste treatment, pollination, pest control) are often provided on the local scale within these human-dominated areas; (2) small native habitat patches within these landscapes are often more socially and economically feasible to conserve compared to large tracts of land; and (3) in many areas, few undisturbed tracts of land are likely to remain in the future.

Because anthropogenic landscapes are increasingly replacing native habitat areas, ecologists and land managers must establish methods of 'compensating' for additional habitat loss and degradation by making anthropogenic landscapes more inhabitable for a wider suite of species (Dale et al. 2000, Rosenzweig 2001). Although some species are readily able to adapt and persist within these landscapes (Daily et al. 2001), the potential exists to modify these areas to support a broader range of species (Rosenzweig 2001). When setting management objectives to improve habitat within an area, ecologists must first identify both the species' associations to particular habitat types and the species' response to alterations of their associated habitat (Knight 1998). Identifying these associations may elucidate the mechanisms or limiting factors that determine the abundance and distribution of a species. Once the mechanisms are identified, managers can then develop strategies to improve the landscape for a particular suite of species.

For a variety of reasons, birds can serve as a useful and important group for conservation strategies within anthropogenic landscapes. First, birds are charismatic organisms, capable of evoking concern from the general public for conservation purposes (Bock 1997). Second, birds may serve as useful indicators of environmental condition within a habitat (Bock 1997, Lawton and Gaston 2001). Specifically, as environmental conditions change within a season or over several seasons, bird abundance and composition may shift to reflect changes in habitat quality. Third, bird abundance and community composition can be easily quantified because birds are ubiquitous and highly visible. Fourth, birds have large area requirements compared to many

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other taxonomic groups; therefore, they may serve as functional "umbrella" species for the protection of other co-occurring species (Fleishman et al. 2001). Finally, birds are an important group for conservation efforts because they have experienced population declines throughout numerous ecosystems across North American and the world (Hagan and Johnston 1992, Vickery et al. 1992, Knopf 1994, Robinson et al. 1995).

Before developing strategies to improve anthropogenic areas to support avian populations, ecologists must first determine what factors or processes render birds sensitive to habitat modification within these areas. Many species have varying degrees of sensitivity to landscape alteration (With and King 2001, Fahrig 2001). Habitat fragmentation is a special case of landscape alteration (Collinge and Forman 1998) ubiquitous within anthropogenic landscapes. Fragmentation of habitat creates new boundaries or edges, where two distinct habitats are joined. Biological and physical conditions often are altered at edges, a phenomenon known as edge effect. Edge effects on bird communities can occur on many levels, depending on the biological or physical variable under study. In particular, the presence of an edge can affect both habitat selection (distributional edge effects) and demographic patterns (demographic edge effects) of bird populations (Winter et al. 2000).

Birds experience distributional edge effects when their selection of territories and/or nest sites is influenced by the presence of an edge. Territory and nest-site selection evolves when birds experience variations in fitness between different habitats (for territory choice) or microhabitats (for nest site choice), leading to a behavioral preference to choose a particular habitat/microhabitat type (Misenhelter and Rotenberry 2000). Although birds may acquire learned behaviors for selecting habitats, they possess strong genetic behavioral cues influencing territory and nest site selection. For example, Martin (1993b) reviewed the literature and found that most of the species he studied were nest site specialists for a certain substrate, suggesting that nest site choice is evolutionary conservative.

Distributional edge effects are a species-specific behavioral response; certain species will readily utilize edge settings, whereas other species will rarely forage or nest within these settings (Winter et al. 2000). This behavioral preference for a particular habitat may be genetically programmed to respond to multiple cues within the habitat, that include: proximate vegetation cues, food availability, and matrix type and/or quality (Marzluff 2002). Although bird behavior has been studied in great detail, particularly nest site selection and foraging behavior, less is

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known about cues affecting territory choice (Rolstad et al. 2000). Some avian species avoid edges when choosing territories, suggesting that either (1) ecological patterns serving as habitat selection cues (e.g., vegetation structure, food availability) differ between edge and interior settings; or (2) the structure or presence of an edge by itself may serve as a selection cue.

If a bird selects a territory in an edge setting, it may experience a demographic edge effect, where the fate of a nest is influenced by the presence of an edge. These edge effects may be due to multiple ecological processes differing between edge and interior, that include: nest predation, nest parasitism, and susceptibility to weather due to alterations in vegetation structure (Marzluff 2002). Although multiple causal mechanisms are possible, predation pressures typically are considered the main cause of demographic edge effects (Paton 1994, Jokimaki and Huhta 2000) because predation accounts for 80% of nesting failures on average (Ricklefs 1969, Martin 1993a,b, Major et al. 1994, Zanette and Jenkins 2000, Morrison and Bolger 2002).

In order for birds to experience demographic edge effects, they must first nest in edge settings. Where natural nests are rare at edges, investigators frequently have used artificial nests to quantify predation rates. Marzluff and Restini (1999) reviewed studies of predation pressures in forest fragments, and found that 23% of the studies used natural nests whereas 77% relied on artificial nests. However, it remains unclear how accurately artificial nest experiments simulate natural nest demographics (see Major and Kendal 1996 for review). In particular, many studies have placed high densities of artificial nests within 0-50m of the edge and concluded that increases in predation rates usually occur within this distance (see Patton 1994 for references and review), although the avian species associated with the habitat may rarely nest there. Thus, three key questions remain. (1) Which bird species nest within edge settings where they may experience demographic edge effects? (2) If a bird does nest in edge settings, will it preferentially nest in interior areas compared to edge areas? (3) If a bird nests in edge settings, are predation rates higher in these areas versus interior settings?

Although demographic edge effects have been implicated as a general cause of avian population declines in fragmented habitats across North America (cited in Patton 1994), recent reviews suggest that these effects are study-specific phenomena (Marluff and Restini 1999, Lahti 2001). Lahti (2001) reviewed 54 studies of nest predation in edge versus interior landscape settings, and found that only 13 studies demonstrated increases in nest predation in edge, 31 studies had no increase in nest predation, and 10 studies had increases in some treatments but not

others. Because nest predation is a function of predator abundance and behavior in a specific area (Marzluff and Restini 1999), understanding the predator community on a site-by-site basis may be more predictive of avian population demographics than attempts to generalize avian responses as a function of edge (Donovan et al. 1997).

Grasslands have been lost and modified more than any other type of terrestrial ecosystem (Vickery et al. 1999, Nias 2001), and they are predicted to experience the most significant losses in biodiversity within the next century, along with Mediterranean climate regions (Sala et al. 2000). Grassland bird populations have suffered substantial declines as a result of habitat loss and landscape alteration (Peterjohn and Sauer 1993, Knopf 1994, Herkert 1995, 1997, Winter and Faaborg 1999). Peterjohn and Sauer (1999) reviewed North American breeding bird population trends from 1966-1996, finding that only 3 of 25 grassland species increased significantly within this 30-year period, whereas 13 species decreased significantly, and 9 species had non-significant trends. Knopf (1994:251) concluded that grassland birds have experienced greater "declines than any other behavioral or ecological guild" of birds in North America, primarily as a result of agricultural conversion.

Although the majority of grassland habitat loss and degradation has been a result of agricultural conversion in the past, urban and suburban sprawl are becoming increasing forms of habitat modification within these ecosystems. Urban encroachment into grasslands creates geometrical configurations conducive to studying the response of avian populations and communities to edge settings. In addition, natural areas surrounded by a matrix of development and agriculture are important for conservation efforts to protect diversity within a landscape. Although some species forage and nest in housing developments and agricultural areas, edge-sensitive species may rely on native or semi-native habitat parcels as a last refuge for population persistence within anthropogenic landscapes.

City of Boulder, Colorado, has a unique system of natural areas, known as Open Space lands, surrounding and embedded within the city (Figure 1). Boulder Open Space lands support a rich variety of native grassland songbirds; however, abundances of most of these species are reduced on grassland parcels adjacent to urban and suburban developments. Bock et al. (1999) measured bird composition and abundance between grassland areas located either near suburban edges or >200m away from edges on Boulder Open Space grasslands. Most native grassland birds (e.g., grasshopper sparrow, *Ammodramus savannarum;* vesper sparrow, *Pooecetes*

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gramineus; western meadowlark, *Sturnella neglecta;* lark sparrow, *Chondestes grammacus*) were more common away from the suburban edges, whereas a variety of suburban-nesting birds foraged more frequently in grasslands at the suburban edges (e.g., American robin, *Turdus migratorius;* house sparrow, *Passer domesticus*). Within the grassland-nesting group, grasshopper sparrows were the most sensitive to edge settings, followed by vesper sparrows and western meadowlarks, respectively, suggesting a species-specific response to edge sensitivity. Bock et al. (1999) concluded that there is a need to identify the reasons why most grassland birds are relatively scarce at existing edges in order to develop land management strategies designed to minimize or compensate for these effects.

The purpose of the present study was to determine the presence and magnitude of suburban edge effects on the distribution and demography of grassland bird species on City of Boulder Open Space grasslands, and to identify possible factors responsible for them. First, I repeated the work of Bock et al. (1999) to determine the magnitude of distributional edge effects on grassland bird abundances across an additional set of five study areas. Second, I measured the distribution and density of nests between edge and interior landscape settings. Third, I quantified demographic edge effects within these landscapes using both natural and artificial nests. Finally, I analyzed vegetation characteristics of study areas and nest sites to determine if they were related to either the distribution or demographics of the grassland birds under study.

Specific objectives of this study were to determine the following:

(1) if native bird abundances were lower at edges than in grassland interiors;

(2) if native birds preferentially nested away from edges;

(3) if natural and artificial nest predation rates were higher at edges;

(4) if vegetation structure differed between edge and interior; and

(5) if vegetation structure within a study area and at nest sites affected nest fate.

Answers to these questions should help land managers in Boulder and elsewhere to improve the quality of habitat for grassland birds within similar anthropogenic landscapes.

METHODS

Study Areas

I established five study areas on City and County of Boulder Open Space grasslands in spring, 2000 (Figure 1). Each included 400m of abrupt and unbroken suburban edge and more than 700m of grassland extending away from the edge (Figure 2). Each study area was upland mixed grassland, supporting a variety of native and non-native grasses and herbs, including: yucca (*Yucca glauca*), prickly-pear cactus (*Opuntia* spp.), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloë dactyloides*), needle grasses (*Stipa* spp.), Japanese brome (*Bromus japonicus*), and cheatgrass (*B. tectorum*). The five study areas were chosen adjacent to suburban developments with similar housing densities, because past studies have shown that nest predation rates may vary along an urban gradient and relfect the amount of human development (Blair 1996, Gering and Blair 1999, Fernandez-Juricic 2000, Jokimaki and Huhta 2000). Study areas 1-5 were sampled in summer, 2000, whereas only areas 1-4 were sampled in summer, 2001. Study area 5 was excluded from summer, 2001, due to possible confounding effects of heavy livestock grazing.

At each study area, I placed marker stakes to delineate each hectare throughout the area (400x600m total area). I established two transects within each area parallel to the edge: one at 50m from the edge (transect 1), and one at 450m from the edge (transect 2; Figure 2).

Bird Counts

Fixed-distance line transect counts (e.g., Verner 1985) were conducted at each site between 5:30AM and 10:00AM, four times during May-August 2000 and six times during May-August 2001. Walking a steady pace for 20 minutes along
transects 1 and 2, I recorded the number of birds detected visually or aurally within 50m to each side of a transect. I alternated the order of census between edge and interior transects with each round of census to average possible changes in activity level throughout the morning hours.

Natural Nests

I searched for natural nests of grassland birds within a 400x600m area adjacent to the suburban edge at each study area. I monitored nests of all species, but focused the search effort on western meadowlark, vesper sparrow, and mourning dove (*Zenaida macroura*) because these

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were the most abundant nesting species. Nests were found primarily by dragging a 25m rope systematically through the study areas. Each nest was marked with a white flag five meters to its north, and then monitored every 2-3 days until it successfully fledged or failed. A nest was considered successful if it fledged one young of the parent species. I recorded the fate of the nest, cause of failure (predation, weather, abandonment), distance to the edge, and various vegetation characteristics of the nest site (see Methods - Vegetation Measurements section). Nests that failed due to weather or abandonment were used in the analyses for distributional edge effects, but were removed from the analyses for demographic edge effects because I wanted to limit the demographic study specifically to predation events. In addition, nests from study area 5 were used only in the analyses for distributional edge effects, and were removed from the analyses for demographic edge effects because of possible confounding predation events from livestock.

Artificial Nest Experiment

From May to August 2000 and 2001, I placed and monitored artificial nests along both transects at each study area to determine the relative difference in predation rates between edge and interior. I did not use nests placed at study area 5 during 2000 in the analyses because of suspected livestock predation on the artificial nests.

During the 2000 season, I used three types of artificial nest models: (1) a wicker basket nest (available from Rolf C. Hagen Inc., Montreal, Canada) containing one Japanese quail egg and one clay egg (henceforth called Model A); (2) a wicker basket nest containing two Japanese quail eggs (Model B); and (3) a ground scrape containing two Japanese quail eggs and no wicker nest (Model C). The wicker nests were used to simulate nest builders (e.g., western meadowlark), and the ground scrapes to simulate non-nest builders (e.g., mourning dove). With these three models, I tested whether the presence of an artificial wicker nest structure or the presence of a clay egg influenced predation rates. Past studies suggest that differences in specific characteristics of artificial nests (egg shape and size, nest material) can influence rates of predation (see Major and Kendal 1996 for review). In 2001, I used only Model A because predation rates were equal among nest types in the 2000 season (see Results).

For each experimental round during 2000 and 2001, I placed four nests along both transect 1 and transect 2 (four of each nest type in 2000 for n=12 nests per transect; n=4 nests per

transect in 2001). One nest was placed randomly within every 100m distance interval along a transect. The experiment was repeated four times throughout the season at each study area in 2000, and three times in 2001. In order to decrease possible bias in predation rates associated with microhabitat characteristics at a nest site (see Martin 1993b), I placed each nest within a study area similarly with respect to percent nest cover and visual obstruction. Each nest was monitored for nine days total. If either egg was disturbed (peck hole in quail egg or impression in clay egg), the nest was considered depredated. After the nine days, nests along each transect were randomly relocated and re-supplied with fresh eggs.

I identified predators at artificial nests by comparing beak and tooth impressions in clay eggs obtained in the field to those obtained from specimens in the University of Colorado Museum. This was done to identify the main predators of artificial nests, and to determine if the predator assemblage varied among study areas and between edge and interior settings.

Vegetation Measurements

Because nest predation rates and nest site selection can vary as a function of vegetation structure (Rotenberry and Wiens 1980, Martin 1993a, Winter and Faaborg 1999), I measured vegetation characteristics at each study area and natural nest site. Both study area and nest site vegetation methodologies were adapted from Winter and Faaborg (1999). Study area vegetation characteristics were recorded to detect any possible differences in vegetation structure between edge and interior settings that might cause either distributional edge effects (via possible habitat selection vegetation cues) or demographic edge effects (via possible vegetation impacts on nest fate). Nest site vegetation characteristics were recorded to assess effects of microhabitat on nesting success. By testing for associations between microhabitat vegetation structure and nest fate, I determined if vegetation was a potential influencing force on avian demographics.

I measured vegetation characteristics in July 2000 and 2001 at two randomly chosen points within every hectare at each study area (24 total hectares, n=48 measurements per study area). Measurements taken within the 4 hectares adjacent to the edge at each study area were classified as edge setting measurements, whereas all other measurements were classified as interior measurements. At each vegetation measurement location, I estimated percent cover to the nearest 5% of grass canopy, forb canopy, litter, and bare ground, within a 30x50cm Daubenmire frame (Daubenmire 1959). I measured litter depth and vegetation height at each of

four corners of the Daubenmire frame. Finally, I measured horizontal visual obstruction by placing a Robel pole (Robel et al. 1970) in the center of the Daubenmire frame and recording the highest point that could be seen on the pole from a visual point of 2m away and 1m high in the four cardinal directions.

Five nest site vegetation measurements identical to a single study area vegetation measurement were taken at each natural nest. One measurement was taken with the nest located in the center of the Daubenmire frame, and four additional measurements were taken 75cm away from the nest in the four cardinal directions. In addition, I recorded vegetation nest cover as the percentage of the nest concealed by vegetation from a viewpoint directly overhead. Because vegetation structure may change rapidly throughout the season, I measured nest site vegetation characteristics within a two-week period after the nest successfully fledged young or failed. I did not perform vegetation measurements on artificial nests because artificial nests were placed with similar percent nest cover and visual obstruction.

Data Analyses

I tested for the presence of distributional edge effects by comparing census abundance data and natural nest densities between edge and interior settings. To analyze the abundance data, I conducted a repeated-measures ANOVA (year as the repeat measure, study area as the subject) for each species to test if the average number of birds counted per census differed among three categories of distances from the edge (0-50m, 50-100m, 450-500m). Post-hoc means comparisons with Scheffe p-value adjustments were performed to determine abundance differences between the individual distance categories. Counts of nine species were analyzed: five suburban-nesting species (American robin; common grackle, *Quiscalus quiscula*; European starling, *Sturnus vulgaris*; house finch, *Carpodacus mexicanus*; house sparrow); three grassland nesting species (grasshopper sparrow, vesper sparrow, and western meadowlark); and one suburban / grassland nesting species (mourning dove).

To analyze the distribution of natural nests, I conducted a repeated-measures ANOVA (year as repeat measure, study area as subject) to determine if the number of nests per hectare differed among three categories of distances from the edge (0-50m, 50-100m, 100-600m). Post-hoc means comparisons with Scheffe p-value adjustments were performed to determine nest density differences between the individual distance categories.

To analyze the natural nest fate data, I performed a multiple logistic regression to determine if nest fate (successful versus failure) differed as a function of vegetation nest cover, study area, and two categories of distance from the edge (0-100m, 100-600m). Nest cover was included in this model as a general test for vegetation associations with nest fate. I performed a second logistic regression to determine if nest fate (successful versus failure) differed among species.

To assess habitat quality differences between edge and interior, I computed the number of fledglings per hectare at each of the study areas. I then conducted a repeated-measures ANOVA (year as repeat measure, study area as subject) to determine if the number of fledglings per hectare differed among three categories of distances from the edge (0-50m, 50-100m, 100-600m). Post-hoc means comparisons with Scheffe p-value adjustments were performed to determine differences in the number of fledglings per hectare between the individual distance categories.

Artificial nest predation rate was calculated for each transect at a study area as the percentage of the number of failed nests per total number of nests along a transect. I then averaged the predation rates from the individual repeated experiments (four experiments in 2000 and three experiments in 2001) to produce a single predation rate for each transect at a study area within a season. A standard arcsine transformation was performed to normalize the data (Zar 1996). To analyze the effects of nest characteristics on predation, I performed a one-way ANOVA to test if the transect predation rate differed among the three nest models in 2000. To test for demographic edge effects, I performed a two-way repeated-measures ANOVA (year as the repeat measure, study area as the subject) to determine if the predation rate differed as a function of landscape setting (edge transect versus interior transect), study area, and a transect-by-study area interaction (i.e., to determine if the magnitude of edge effects differed among study areas).

To assess if vegetation structure was a driving force for both distributional and demographic edge effects, I tested for vegetation differences among study areas and between landscape settings, using three vegetation measurements (bare ground cover, vegetation height, and vegetation visual obstruction; see Methods - Vegetation Measurements for description of measurements). Using the study area vegetation data, I performed a two-way repeated-measures

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ANOVA for each vegetation metric to determine if the metric varied as a function of study area, landscape setting (edge versus interior), and a study area-by-landscape setting interaction.

To determine if nest site selection was affected by the vegetation structure within a study area, I compared nest site vegetation to the study area vegetation. My specific aim was to determine if birds nesting in study areas with low vegetation cover were able to locate optimal nest sites within these areas.

To address this aim, I first determined if birds nesting within low cover study areas chose nest sites with less vegetation structure compared to nest sites within high cover areas. For each of four nest site vegetation measurements (bare ground cover, vegetation height, vegetation visual obstruction, and nest cover), I conducted a one-way repeated-measures ANOVA for each of three species (western meadowlark, vesper sparrow, mourning dove) to determine if the vegetation measurement differed among study areas for a given species.

Because differences in nest site vegetation among study areas could be a random reflection of the study area vegetation structure, I secondly determined if nest site selection occurred within an area. I did this by comparing the vegetation structure between nest sites and the average study area vegetation measurements, using three vegetation measurements (bare ground cover, vegetation height, and vegetation visual obstruction). I conducted a one-way repeated-measures ANOVA for each of three species (western meadowlark, vesper sparrow, mourning dove) to determine if the vegetation measurement differed between nest sites and the average study area measurements.

Assuming birds chose the best nest sites within an area, nest site selection should be minimal or absent within areas where the average study area vegetation structure closely reflects optimal nesting conditions. Conversely, nest site selection should be high within areas where the average study area vegetation structure differs greatly from optimal nesting conditions. To examine this degree of nest site selection among study areas, I compared the difference in vegetation structure between nest sites and the average study area structure among the different study areas. For each species (western meadowlark, vesper sparrow, and mourning dove), I computed a metric to reflect the difference in vegetation structure between nest sites and the average study area structure within an area, hereafter termed the "selectivity" for nest sites. Using three vegetation measurements (bare ground cover, vegetation height, and vegetation

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visual obstruction), the selectivity for nest sites for each vegetation measurement was calculated as:

$$\text{Selectivity} = (V_{NS} - V_{SA}) / V_{SA}$$

where V_{NS} is the average nest site vegetation measurement for a species within a study area, and V_{SA} is the average study area vegetation measurement.

Grouping the three species, I performed a separate correlation analysis for each vegetation measurement to determine if the selectivity for nest sites was correlated to the average study area vegetation measurement, V_{SA}. All statistical tests were performed using SAS statistical software version 8.02 (SAS 2001).

RESULTS

The abundances of suburban and grassland birds differed between edge and interior settings for all species except western meadowlark and mourning dove (Table 1). All suburban nesting birds had higher densities in 0-50m from the edge than 450-500m; grasshopper sparrow had higher densities in 450-500m than 0-50m; and vesper sparrow had higher densities in 450-500m than 50-100m (Scheffe-adjusted $p < 0.05$; Table1).

Averaged across all species and study areas, the number of nests per hectare differed among distance categories from the edge (F=5.49, $p < 0.05$; Figure 3). The number of nests per hectare was significantly less in 0-50m than both 50-100m and 100-600m (Scheffe-adjusted $p < 0.05$), but did not differ between 50-100m versus 100-600m (Scheffe adjusted $p > 0.05$).

A total of 137 natural nests of all species were monitored (common nighthawk, *Chordeiles minor*, n=2; lark sparrow, n=11; grasshopper sparrow, n=8; mourning dove, n=22; vesper sparrow, n=39; western meadowlark, n=55). Mean predation rate was 20% greater on nests <100m from an edge compared to 100-600m, suggesting a demographic edge effect; however, this result was not statistically significant at the _=0.05 level (Wald $\chi^2 = 2.56$, p=0.1095; Figure 4). Mean predation rate did not differ among study areas (Wald $\chi^2 = 0.51$, $p > 0.05$; Figure 5) or among species (Wald $\chi^2 = 5.63$, $p > 0.05$; Figure 6), but did vary as a function of vegetation nest cover (Wald $\chi^2 = 4.35$, $p < 0.05$; Figure 7).

The number of fledglings per hectare differed among distance categories from the edge (F=4.94, p<0.05; Figure 8). The number of fledglings per hectare was significantly less in 0-50m than 100-600m (Scheffe-adjusted p<0.05), but did not differ between 0-50m versus 50-100m or 50-100m versus 100-600m (Scheffe-adjusted p>0.05).

A total of 384 artificial nests were used in 2000, and 96 nests were used in 2001. Predation rates did not differ between nest models in 2000 (F=0.24, p>0.05; Figure 9). There was a significant plot-by-transect interaction (F=4.25, p<0.05), revealing that the magnitude of demographic edge effects on artificial nests differed among study areas. Averaged across both transects, study areas 1 and 2 had lower predation rates than areas 3 and 4 (Scheffe-adjusted p<0.05). Only study area 3 had a significantly higher mean predation rate along the edge transect compared to the interior transect (Scheffe-adjusted p<0.05; Figure 10). A total of 57 depredated clay eggs were successfully identified to the predator guild (bird versus mammal predator; Table 2).

All three study area vegetation measurements differed among study areas (vegetation height: F=34.36, p<0.0001, Figure 11; bare ground cover: F=7.80, p<0.0001, Figure 12; visual obstruction: F=15.63, p<0.0001, Figure 13), but did not differ between landscape settings (vegetation height: F=1.81, p>0.05; bare ground cover: F=0.17, p>0.05; visual obstruction: F=0.37, p>0.05) or a study area-by-landscape setting interaction (vegetation height: F=0.57, p>0.05; bare ground: F=1.41, p>0.05; visual obstruction: F=0.19, p>0.05). In general, study areas 1 and 2 had taller vegetation (Figure 11), less bare ground (Figure 12), and more visual obstruction (Figure 13) than areas 3-5, although not all means comparisons were significant. Henceforth, study areas 1 and 2 are referred to as high-cover study areas, and areas 3-5 are referred to as low-cover study areas.

Nest site vegetation structure was typically less within the low-cover study areas than within high-cover areas for each species (Table 3). Mourning dove nest site vegetation differed among study areas in percent nest cover (F=4.19, p=<0.05), vegetation height (F=5.79, p<0.05), and bare ground (F=6.50, p<0.01), but not visual obstruction although marginal (F=3.28, p=0.0599). Vesper sparrow nest site vegetation differed among study areas in percent nest cover (F=16.11, p<0.0001), vegetation height (F=12.74, p<0.0001), bare ground (F=2.99, p<0.05), and visual obstruction (F=7.82, p=0.001). Western meadowlark nest site vegetation differed among

study areas in nest cover (F=3.14, p=0.05), marginally differed in height (F=2.37, p=0.0650) and visual obstruction (F=2.24, p=0.0782), but did not differ in bare ground (F=0.58, p>0.05).

Nest site selection occurred with each species for most vegetation measurements (vegetation height, Figure 14; bare ground cover, Figure 15; visual obstruction, Figure 16). Mourning doves selected nest sites with taller vegetation height (F=194.05, p<0.0001) and more visual obstruction (F=41.21, p<0.0001), but did not select for bare ground (F=0.94, p>0.05). Vesper sparrows selected nest sites with less bare ground (F=20.94, p<0.0001) and more visual obstruction (F=31.62, p<0.0001), but did not select for vegetation height (F=0.00, p>0.05). Western

meadowlarks selected nest sites for taller vegetation height (F=11.38, p<0.001), less bare ground (F=106.85, p<0.0001), and more visual obstruction (F=54.01, p<0.0001).

Among three species on four study areas, selectivity for nest sites was negatively related to plot vegetation height (r = -0.8383, p=0.001; Figure 17) and visual obstruction (r = -0.5934, p<0.05; Figure 18), but unrelated to bare ground (r = 0.1466, p>0.05; Figure 19).

DISCUSSION

General Patterns of Edge Effects

Grassland birds experienced distributional edge effects on a species-specific level. Some species utilized grassland habitat within 50m of the edge very rarely (e.g., grasshopper sparrow), whereas other species were more willing to utilize these landscape settings (e.g., western meadowlark, mourning dove). In addition, nest densities were greater within interior settings across all species and study areas. Vegetation patterns did not differ between edge and interior settings within any of the study areas, suggesting that birds were choosing to avoid edges based on other environmental cues.

Demographic edge effects were present on both artificial nests and natural nests. Overall, predation rates on artificial nests were higher within edge settings and on low-cover study areas. However, only study area 3 -- a low-cover area -- had significantly higher predation rates within edge compared to interior settings (Figure 10). Although nests were scarce in edge settings, predation rates on natural nests were nearly 20% greater in edge settings than in interior settings across all species and study areas. In addition, the number of fledglings per hectare was

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significantly less in edge settings, suggesting that interior areas may be higher in habitat quality than edges.

Birds selected nest sites with relatively tall and dense vegetation at each study area; however, they apparently were unable to locate nest sites on low-cover areas with as much vegetation as on high-cover areas. Therefore, low-cover study areas may not have provided optimal nest sites for some grassland species. Results from artificial and natural nests suggest that less vegetation structure, both within a study area and at a nest site, may lower nesting success within these landscapes. In general, a lack of optimal nest sites may render some avian species susceptible to increased predation rates if the predators are able to locate nests more readily within low-cover areas.

Distributional Edge Effects on Grassland Nesting Species

Grassland nesting species differed in their degree of edge avoidance, ranging from mourning doves with no edge avoidance behavior, to the high degree of avoidance demonstrated by grasshopper sparrows. Mourning doves did not avoid edges (Table 1); on the contrary, they were approximately two times more abundant in edge settings than in interior settings. This pattern is likely due to mourning doves' behavioral capacity to nest both within suburbia and grassland settings, and may be a result of suburban-nesting individuals leaving suburbia to forage in nearby grassland habitat.

Of species nesting exclusively in grassland habitat, western meadowlarks avoided edges less than other species. Their mean abundance within interior settings was approximately one and a half times greater than within 0-100m from the edge. However, western meadowlarks were more abundant within 0-50m compared to 50-100m from the edge (Table 1). This increased abundance within the first 50m of the edge may have been due to perch sites provided by fences at the suburban-grassland edge at each study area. In addition, some male birds were observed singing from perches in the tops of trees within suburbia, suggesting that western meadowlarks were relatively insensitive to distributional edge effects on abundance compared to other grassland species.

Vesper sparrows and grasshopper sparrows both avoided edge settings, and their abundances differed significantly between these settings. The abundance of vesper sparrows in interior was approximately two times greater than 0-100m from the edge (Table 1). Similar to

western meadowlarks, vesper sparrows were more abundant within 0-50m than 50-100m from the edge, possibly due to perch sites on the edge fencelines. Grasshopper sparrows demonstrated the highest degree of edge avoidance, and were over four times more abundant in interior settings than in edge settings. In addition, they were rarely seen within 0-50m from the edge in the two years of the study (Table 1).

Nest densities of all species combined were approximately three times greater within interior settings than within the first 50m of the edge (Figure 3). However, due to low sample size of natural nests within edge settings, I did not test for a species-specific and study area-specific response on the distribution of nest site edge effects. Therefore, I am unable to ascertain if study area-specific conditions or species-specific behaviors may have affected a bird's choice to nest within edge settings.

Grassland birds may use multiple cues that lead to their avoidance of edge settings in both a species-specific and study area-specific manner. Because vegetation structure did not differ between edge and interior settings within any study areas, birds appeared to be choosing to avoid edges based on other environmental selection cues. Other researchers have proposed a multitude of mechanisms that may cause changes in avian distributions in relation to habitat alterations, including food availability, spatial configuration of habitat patches, predator abundance and behavior, interspecific competition, human disturbance, and nest parasitism (Marzluff 2002).

Because food availability is a strong selective force on avian fecundity (Martin 1995), bird species have evolved habitat selection cues based on food resources. For example, Zanette et al. (2000) compared food abundance between large and small forest fragments, concluding that food abundance was a factor influencing distributional area sensitivity of Eastern yellow robin (*Eopsaltria australis*). Differences in food availability between edge and interior settings may be an environmental cue leading to distributional edge effects. All three of the major grassland species in this study rely primarily on insects, grass seeds, and forb seeds as food sources (Ehrlich et al. 1988); in addition, the suburban-nesting birds rely on similar food sources and foraged in high densities within edge settings. Therefore, suburban-nesting birds may have reduced these food sources within edges compared to interior. This spatial reduction in food resources may have led to interspecific competition for food resources between the bird guilds and subsequent avoidance of edge settings by grassland-nesting species.

These interspecific competitive interactions are known to affect avian choice of territories and nest sites (Whitcomb et al 1981, Ambuel and Temple 1983), and may have been a factor driving the species-specific avoidance of edge settings. Although western meadowlark seemed to utilize edge areas and thus be affected less by possible competitive interactions, vesper sparrow and grasshopper sparrow may have been susceptible to competition from the suburban birds, thereby leading to their avoidance of these areas.

Although these multiple mechanisms (i.e., food abundance, interspecific competition, predator assemblage) can affect distributional edge effects, species-specific edge avoidance is a conserved behavioral trait across multiple studies. For example, grasshopper sparrows have been shown to have a high degree of edge avoidance across study sites (Bock et al. 1999), although local mechanisms (e.g., food availability, interspecific competition) undoubtedly varied among the sites. Bock et al. (1999) found similar degrees of species-specific edge avoidance for western meadowlark, vesper sparrow, and grasshopper sparrow as found in this study. Because a common factor among these study sites is the presence of an edge structure, birds may be responding to this structure as an additional environmental cue. One explanation for the evolution of edge avoidance is that birds have evolved a negative stimulus to the presence of an edge, due to experiencing increased predation rates at natural edges throughout their evolutionary history (Winter et al. 2000). Although increased predation pressures may not be present at all natural edges or artificial edges, and may vary temporally, certain species may retain this behavioral avoidance to edge structures due to lower fitness throughout their evolutionary history. However, the extent to which birds are making choices on landscape features for territory and nest site selection is largely unknown (Rolstad et al. 2000).

Demographic Edge Effects on Grassland Nesting Species

Predation rates on both natural and artificial nests were greater within edge settings compared to interior settings (Figures 4 and 10). Patton (1994) reviewed studies on avian demographic edge effects and found that they usually occurred within 50m from the edge, although this can be highly variable (e.g., Wilcove 1985, Winter et al. 2000). Results from my study support Patton's findings, where highest rates of predation on natural nests were within 0-100m of the edge. In addition, the number of fledglings per hectare were lowest within these edge settings. Averaged across all study areas, natural nest predation rates were 100% within the

first 50m from the edge, approximately 75% within 50-100m from the edge, and below 65% in each 100m-distance interval out to 600m from the edge (Figure 4). However, a test for predation rate differences among these two distance intervals was insignificant, possibly due to a low sample size within the first 100m of the edge, where birds generally avoided nesting. Averaged across all study areas, artificial nest predation rates were 46% along edge transects and 24% along interior transects.

Edge effects on demography are study area- and species-specific phenomena (Marzluff and Restini 1999, Lahti 2001). A number of mechanisms may explain this study area- and species-specific nature of demographic edge effects: (1) the most abundant nesting species among study areas differ in their degree of susceptibility to predation pressures; (2) the predator assemblage differs among the study areas; or (3) characteristics of a study area that influence the efficiency of predator foraging (e.g., vegetation structure) differ among areas. Although these three factors are distinct mechanisms, they can act in concert to affect the specific nature of demographic edge effects.

Species may vary in their susceptibility to demographic edge effects based on nest concealment, nest defense, and/or movement to and from a nest. With and King (2001) modeled avian population persistence as a function of habitat loss and species-specific edge effects on demography, and found that species-specific edge effects were the major determinant of population persistence. In general, species differ markedly in their choice of nest sites across ecosystems and within the same ecosystem. As an example from my study, mourning dove nests typically had double the bare ground cover and half the vegetation nest cover of vesper sparrow and western meadowlark nests (Table 3). If predators were more efficient at locating nests based on nest site vegetation characteristics, certain species may have been more susceptible to predation. Although a test for species-specific differences on natural nest predation was not significant, the mean predation rate ranged from nearly 77% for mourning doves to 45% for lark sparrows (Figure 6). In addition, species and individuals within a species vary in their degree of nest defense and movement to and from a nest, which could have an effect on predation susceptibility.

Predation rates on artificial nests did not differ among the different nest models, suggesting that predators could detect these nests equally well and did not preferentially depredate a nest based on its characteristics. The major differences among the individual nest

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models were both olfactory (e.g., clay versus no clay) and visual cues (e.g., wicker versus no wicker); therefore, both aerial predators and ground-foraging predators, which rely on these different cues in foraging, could theoretically respond differently to the nest models. The results of my study support work by Bayne and Hobson (1999), who found that clay eggs did not bias predation rates on artificial nests. Use of the wicker nest, clay, and quail eggs undoubtedly introduced non-grassland scents into the experiment. Although some authors have proposed the avoidance of artificial nests by some predators due to human scent (Willebrand and Marcstrom 1988), others have found that human scent does not influence predation rates (Skagan et al. 1999).

Artificial nests appeared to be more susceptible to predation by bird species than mammal predators (Table 2). Where only mammal predators were present (e.g., plot 1), predation rates were lower than areas with primarily avian predators (e.g., plot 3). These results support work by Willebrand and Marcstrom (1988), who concluded that artificial nests are primarily susceptible to avian predators. In addition, they suggest that natural nests are primarily susceptible to predation from mammalian predators. The fundamental assumption underlying the efficacy of artificial nest experiments is that the predator community on artificial nests is identical to the predator assemblage on natural nests. If the assemblage does not differ, relative predation rate differences among areas within similar habitat types should be similar for artificial nests and natural nests. However, if the predator assemblage between artificial and natural nests does indeed differ, then artificial nests are useful only as a method to identify and quantify the predator assemblage on artificial nests. Because I did not identify predators on natural nests, I was unable to test this assumption. This assumption -- that the predator assemblages of artificial and natural nests are identical -- needs to be addressed appropriately in future studies to determine the usefulness of artificial nest experiments.

My study areas differed markedly in vegetation structure, which may have influenced the efficiency of predator foraging among areas. Soderstrom et al. (1998) concluded that the risk of predation on grassland ground nesters in Sweden was a function of the vegetation structure within an area, along with the composition of the predator community. Study areas 3 and 4 had less vegetation structure than areas 1 and 2 in all vegetation measurements analyzed (Figures 11, 12, 13), and experienced nearly double the predation rates on artificial nests, where the edge predation rates were 25-50% greater in edge than interior (Figure 10).

One explanation consistent with this pattern is that the predator assemblage among study areas consisted primarily of suburban predators, such as striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), coyote (*Canis latrans*), house cat (*Felis catus*), black-billed magpie (*Pica pica*), blue jay (*Cyanocitta cristata*), and *Buteo* species. Abundances of these predators are often high within suburban settings because they can readily adapt to live within these areas. In addition, abundances of top-trophic level predators are often reduced within anthropogenic landscapes, which may result in abundance increases of mesopredators (Crooks and Soulé 1999). In this study, suburban predators may have been more adept at foraging for nests within low-cover study areas, and typically only foraged within 100m of the edge. Within the low-cover areas, they were consequently able to locate nests readily, causing a measurable demographic edge effect on artificial nests. Within the high-cover areas, they were less likely to locate nests, leading to low predation rates overall and no measurable demographic effects.

Although natural nests were scarce in edge settings due to distributional edge effects across all study areas, predation rates were nearly 20% greater in these areas compared to interior settings, and the number of fledglings per area was less within edges. Increases in predation rates within edge settings could be due to mechanisms similar to those driving artificial nest predation rates as discussed above. Specifically, these increases in predation rates on natural nests could be due to either changes in the predator assemblages between landscape settings, or changes in the vegetation structure, consequently affecting the efficiency of predator foraging between these settings.

Nest cover was the only significant variable predicting natural nest fate, where increases in nest cover led to a higher probability of nest success (Figure 7). Multiple studies have shown that vegetation structure, and nest cover in particular, is a major factor influencing predation rates (Martin 1992). Although the selectivity for nest sites was greater on my low-cover study areas, each species (western meadowlark, vesper sparrow, and mourning dove) still was unable to locate nest sites in low-cover areas with as much vegetation structure as nest sites in high-cover areas (Table 3). These results suggest that birds were unable to locate optimal nest sites within areas of less vegetation structure.

Because nest predation is the major factor causing nesting failure, and therefore in determining avian fecundity (Martin 1993b), decreasing vegetation structure may have strong effects on the source-sink dynamics within an area (Pulliman 1988). Although certain species

may be able to compensate for increased predation rates by re-nesting within a season (Morrison and Bolger 2002), chronic low vegetation cover may lead to negative population growth rates. Avian species have experienced changes in vegetation structure throughout their evolutionary history. For example, vegetation patterns may change through temporally variable weather patterns such as El Niño - La Niña cycles, and temporally variable natural grazing regimes caused by population-level oscillations. However, birds have not evolved with the chronic livestock grazing now present throughout many of the grassland ecosystems worldwide. Because livestock grazing often leads to reduced vegetation cover and density (Saab et al. 1995), avian fecundity across many of these areas may be decreasing as a result of sub-optimal nest site conditions.

MANAGEMENT RECOMMENDATIONS

The interface of grassland habitat with suburban developments has the potential to support grassland bird diversity to some degree; however, this degree is dependent on both the species present and multiple characteristics of an area. Some species (e.g., western meadowlark) will utilize edge settings readily, but other species (e.g., grasshopper sparrow) will not use these settings. Increases in nest predation may also be present in edge settings, but the degree of these effects may be limited because some bird species typically avoid nesting within these areas. The scale of both distributional and demographic edge effects is typically between 50-100m from the edge, suggesting that a 50-100m habitat buffer is sufficient for landscape planning focused on conserving avian diversity. Although distributional edge effects may be less than 100m, certain species will still avoid habitat patches that are below a certain size. Therefore, successful conservation strategies within these landscapes must maintain habitat patches of appropriate size, taking into account a 50-100m buffer of unused or less-used edge settings. Because of the species-specific nature of both area and edge effects, management strategies designed to protect the total diversity within a landscape should focus on the most edge- and area-sensitive species, such as the grasshopper sparrow (With and King 2001).

Because the degree of fragmentation in many areas is already set, scientists and managers must develop methods of compensating for additional habitat loss and degradation by improving the quality of habitat within anthropogenic landscapes. Although some species may avoid edges

regardless of local mechanisms occurring within these settings, other species may respond favorably to management and manipulation of local factors affecting distribution. Avian demographic rates within edge landscapes can be improved either by controlling the predator assemblage (see Heske et al. 2001 for predator control methods) or by manipulating site characteristics that affect the foraging efficiency of the predator guild. In the case of Boulder Open Space grasslands, reductions in livestock grazing at suburban edges could improve grassland bird nesting success by increasing vegetation cover.

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BIBLIOGRAPHY

Ambuel, B and SA Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Bayne, EM and KA Hobson. 1999. Do clay eggs attract predators to artificial nests? Journal of Field Ornithology 70:1-7.

Blair, RB. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506-519.

Bock, CE. 1997. The role of ornithology in conservation of the American West. Condor 99: 1-6.

Bock, CE, JH Bock, and BC Bennett. 1999. Songbird abundance in grasslands at a suburban interface on the Colorado High Plains. Studies in Avian Biology 19:131-136.

Daily, GC. 1997. Countryside biogeography and the provision of ecosystem services. Pp. 104-113 in (PH Raven, editor) Nature and human society: the quest for a sustainable world. National Academy Press, Washington, D.C.

Daily, GC, PR Ehrlich, et al. 2001. Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11: 1-13.

Dale, VH, S Brown, et al. 2000. Ecological principles and guidelines for managing the use of land. Ecological Applications 10:639-670.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-64.

Donovan, TM, PW Jones, et al. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. Ecology 78:2064-2075.

Ehrlich, PR, DS Dobkin, and D Wheye. 1988. A birder's handbook. Simon and Schuster, Inc., New York.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation 100:65-74.

Fernandez-Juricic, E. 2000. Avifaunal use of wooded streets in an urban landscape. Conservation Biology 14:513-521.

Gates, JE and LW Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Gering, JC and RB Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532-541.

Grimm, NB, JM Grove, et al. 2000. Integrated approaches to long-term studies of urban ecological systems. Bioscience 50:571-584.

Herkert, JK. 1995. Analysis of Midwestern breeding bird population trends - 1966- 1993. American Midland Naturalist 134:41-50.

Herkert, JK. 1997. Population trends of the Henslow's sparrow in relation to the conservation reserve program in Illinois, 1975-1995. Journal of Field Ornithology 68:235-244.

Heske, EJ, SK Robinson, et al. 2001. Nest predation and neotropical migrant songbirds: piecing together the fragments. Wildlife Society Bulletin 29:52-61.

Jokimaki, J and E Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838-847.

Knight, RL. 1998. Ecosystem management and conservation biology. Landscape and Urban Planning 40:41-45.

Knopf, FL. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247-257.

Lahti, DC. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365-374.

Lawton, JH, and KJ Gaston. 2001. Indicator Species. Pp. 437-450 *in* (SA Levin, editor-in-chief) Encyclopedia of Biodiversity, Volume 3. Academic Press, San Diego.

Major, RE, GH Pyke, et al. 1994. Can nest predation explain the timing of breeding season and the pattern of nest dispersion of New Holland Honeyeaters? Oikos 69:364-372.

Major, RE and CE Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. Ibis 138:298-307.

Martin, TE. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pp. 455-473 in (JM Hagan III and DW Johnson, editors) Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution, Washington, D.C.

Martin, TE. 1993a. Nest predation among vegetation layers and habitat types - revising the dogmas. American Naturalist 141:897-913.

Martin, TE. 1993b. Nest predation and nest sites - new perspectives on old patterns. Bioscience 43:523-532.

Martin, TE. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

Marzluff, JM. 2002. Worldwide urbanization and its effects on birds. Pp. 19-48 *in* (JM Marluff, R Bowman, and R Donnelly, editors) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, Massachusetts.

Marzluff, JM and M Restani. 1999. The effects of forest fragmentation on avian nest predation. Pp. 155-169 *in* (JA Rochelle et al., editors) Forest fragmentation: wildlife and management implications. Brill, Leiden, The Netherlands.

Misenhelter, MD and JT Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. Ecology 81:2892-2901.

Nias, RC. 2001. Endangered Ecosystems. Pp. 407-424 *in* (SA Levin, editor-in-chief) Encyclopedia of Biodiversity, Volume 2. Academic Press, San Diego.

Paton, PWC. 1994. The effect of edge on avian nest success - how strong is the evidence. Conservation Biology 8:17-26.

Peterjohn, BG, and JR Sauer. 1993. North American Breeding Bird Survey annual summary 1990-1991. Bird Populations 1:52-67.

Peterjohn, BG, and JR Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey. Studies in Avian Biology 19:27-44.

Pulliam, HR. 1988. Sources, Sinks, and Population Regulation. American Naturalist 132:652-661.

Ricklefs, RE. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology, No. 9.

Robinson, SK, FR Thompson, et al. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rolstad, J, B Loken, et al. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. Oecologia 124:116-129.

Rosenzweig, ML. 2001. Loss of speciation rate will impoverish future diversity. Proceedings of the National Academy of Sciences of the United States of America 98:5404-5410.

Rotenberry, JT and JA Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation - a multivariate-analysis. Ecology 61:1228-1250.

Saab, VA, CE Bock, et al. 1995. Livestock grazing effects in western North America. Pp. 311-353 *in* (TE Martin and DM Finch, editors) Ecology and management of neotropical migratory birds. Oxford University Press, New York.

Sala, OE, FS Chapin, et al. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

SAS Institute. 2001. SAS System for Windows, v.8.02. Cary, North Carolina, USA.

Skagen, SK, TR Stanley, et al. 1999. Do mammalian nest predators follow human scent trails in the shortgrass prairie? Wilson Bulletin 111:415-420.

Verner, J. 1985. Assessment of counting techniques. Pp. 247-302 *in* (RF Johnston, editor) Current Ornithology, volume 2. Plenum Press, New York.

Vickery, PD, ML Hunter, JV Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281-288.

Vickery, PD, PL Tubaro, et al. 1999. Conservation of grassland birds in the Western Hemisphere. Studies in Avian Biology 19:2-26.

Whitcomb, RF, JF Lynch, et al. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-205 *in* (RL Burgess and DM Sharpe, editors). Forest island dynamics in man-dominated landscapes. Springer Verlag, New York.

Wilcove, DS. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Winter, M and J Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13:1424-1436.

Winter, M, DH Johnson, et al. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256-266.

With, KA and AW King. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biological Conservation 100:75-88.

Zanette, L and B Jenkins. 2000. Nesting success and nest predators in forest fragments: A study using real and artificial nests. Auk 117:445-454.

Zanette, L, P Doyle, et al. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81:1654-1666.

Zar, JH. 1996. Biostatistical analysis. Prentice Hall, NJ.

Table 1. Summary of means and tests comparing bird abundance as a function of distance from the edge (means with SE bars). F and p values are from overall repeat-measures ANOVA. For each species, mean values marked with different letters significantly differ using post-hoc means comparisons (Scheffe-adjusted p<0.05).

SPECIES	ANOVA		MEAN (± SE) ABUNDANCE		
	F VALUE	Pr > F	0-50m	50-100m	450-500m
Western meadowlark	1.76	>0.05	1.88 ± 0.39 [a]	1.36 ± 0.34 [a]	2.27 ± 0.34 [a]
Vesper sparrow	3.78	<0.05	0.61 ± 0.22 [a,b]	0.33 ± 0.12 [a]	0.91 ± 0.28 [b]
Grasshopper sparrow	9.29	<0.05	0.04 ± 0.04 [a]	0.79 ± 0.37 [a,b]	1.63 ± 0.57 [b]
Mourning dove	0.51	>0.05	0.31 ± 0.16 [a]	0.26 ± 0.15 [a]	0.15 ± 0.08 [a]
European starling	4.25	<0.05	1.69 ± 0.67 [a]	1.09 ± 0.37 [a,b]	0.19 ± 0.10 [b]
Common grackle	3.08	<0.05	1.96 ± 0.65 [a]	1.07 ± 0.35 [a,b]	0.43 ± 0.19 [b]
Ameican robin	6.44	<0.01	1.46 ± 0.42 [a]	0.72 ± 0.25 [a,b]	0.00 ± 0.00 [b]
House finch	3.77	<0.05	1.96 ± 0.71 [a]	1.40 ± 0.46 [a,b]	0.11 ± 0.11 [b]
House sparrow	4.02	<0.05	1.19 ± 0.41 [a]	0.97 ± 0.44 [a,b]	0.00 ± 0.00 [b]

Table 2. Summary of artificial nest predator identities from tooth and beak impressions on clay eggs, among study areas, between transects, and between the predator guild (no impressions were recorded on plot 2).

STUDY AREA	TRANSECT	BIRD	MAMMAL
1	Edge	0	3
1	Interior	0	2
3	Edge	15	1
3	Interior	6	2
4	Edge	9	5
4	Interior	3	4

Table 3. Summary of nest site vegetation measurements among species and study areas (means ± SE).

| SPECIES	STUDY AREA	NEST COVER (%)	BARE GROUND COVER (%)	VISUAL OBSTRUCTION (cm)	VEGETATION HEIGHT (cm)	N
western meadowlark	1	86.4 ± 3.2	8.6 ± 1.8	12.9 ± 1.1	24.0 ± 2.1	7
	2	85.0 ± 5.0	7.5 ± 2.5	13.1 ± 0.6	22.5 ± 0.5	2
	3	78.9 ± 4.1	11.3 ± 1.7	12.8 ± 0.1	19.8 ± 1.5	19
	4	70.2 ± 5.2	8.4 ± 1.9	10.7 ± 0.5	19.7 ± 1.2	22
	5	49.0 ± 10.3	13.0 ± 5.6	8.0 ± 0.6	13.4 ± 2.5	5
vesper sparrow	1	94.7 ± 1.6	14.3 ± 3.2	15.6 ± 1.1	25.1 ± 2.0	15
	3	82.5 ± 7.8	31.9 ± 6.6	10.9 ± 1.0	18.5 ± 2.2	8
	4	50.8 ± 6.2	26.2 ± 3.8	9.0 ± 1.0	12.4 ± 1.0	13
	5	81.7 ± 4.4	18.3 ± 10.9	9.2 ± 2.2	9.4 ± 2.1	3
mourning dove	1	43.8 ± 8.4	25.0 ± 3.4	15.9 ± 1.3	30.8 ± 2.4	12
	2	35.0 ± 14.6	28.8 ± 5.2	21.9 ± 5.7	34.6 ± 4.4	4
	3	7.5 ± 2.8	46.7 ± 5.7	11.5 ± 2.2	19.4 ± 2.5	6
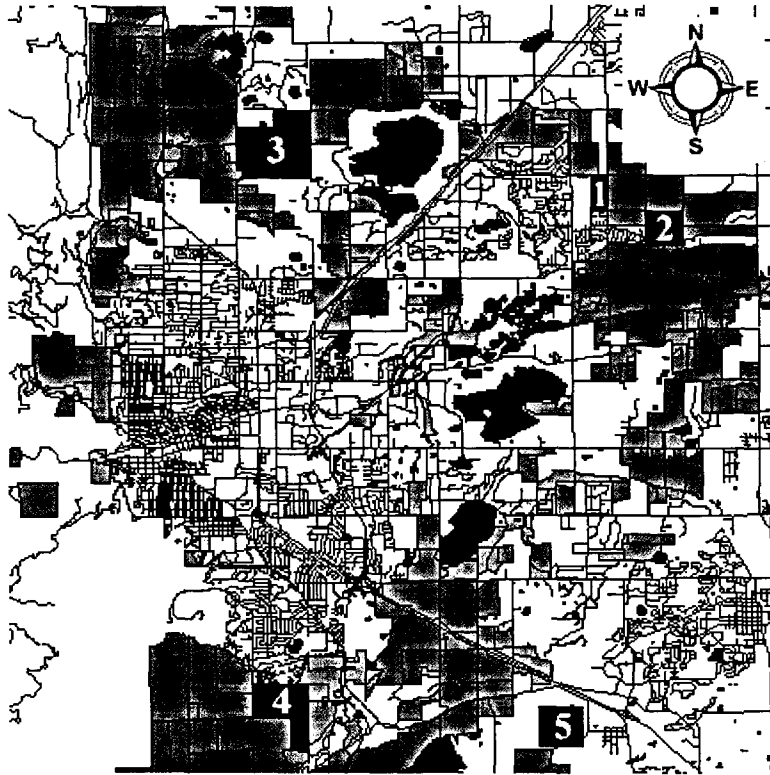
Figure 1. Map of study area locations within City of Boulder Open Space and Boulder County Open Space lands.
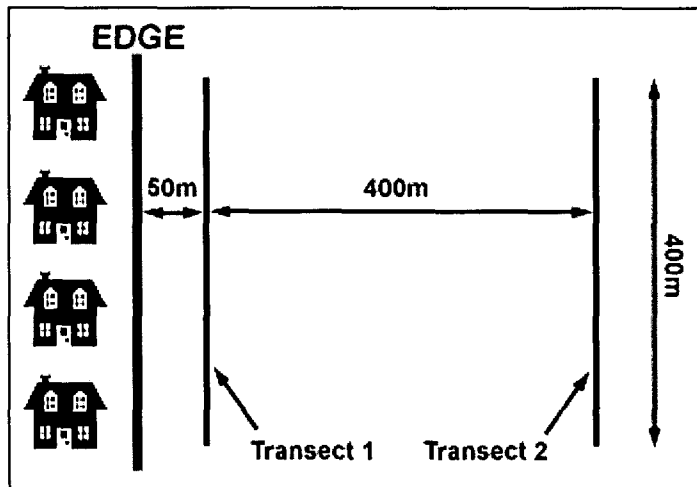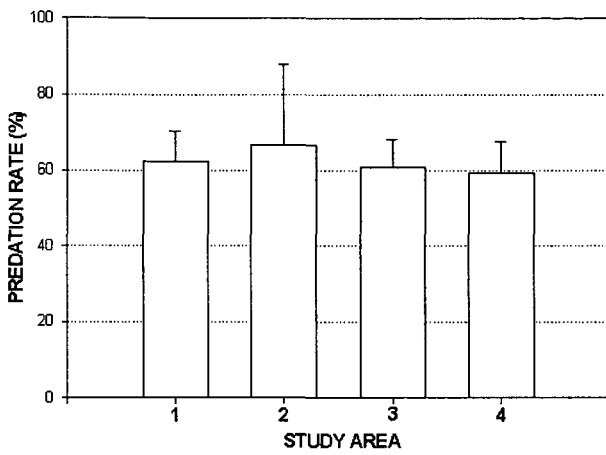

Figure 2. A generic study area overview of the transect layout, where transect 1 is 50m from the edge and transect 2 is 450m from the edge.
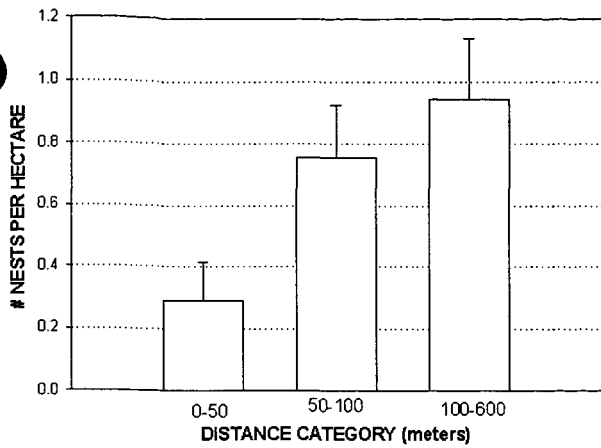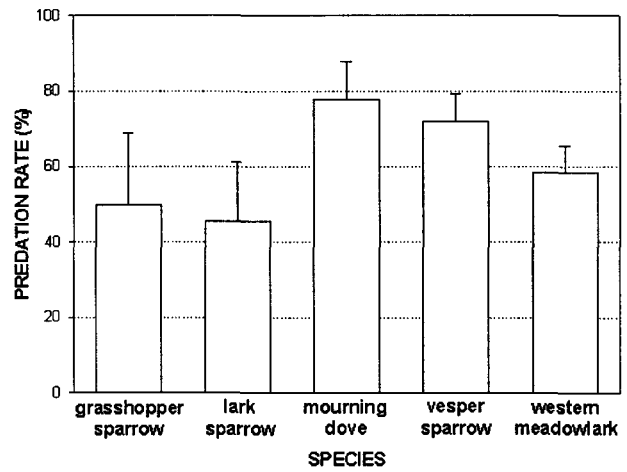
Figure 3. Mean (± SE) number of nests per hectare among three categories of distance from the edge, for all species combined.
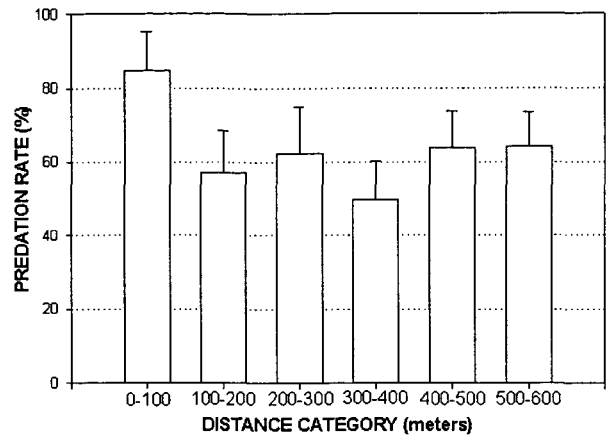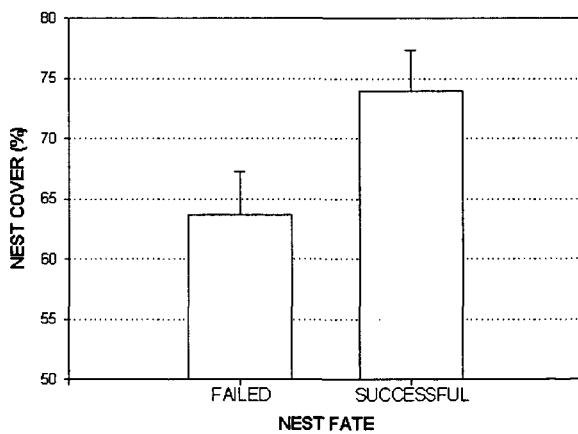

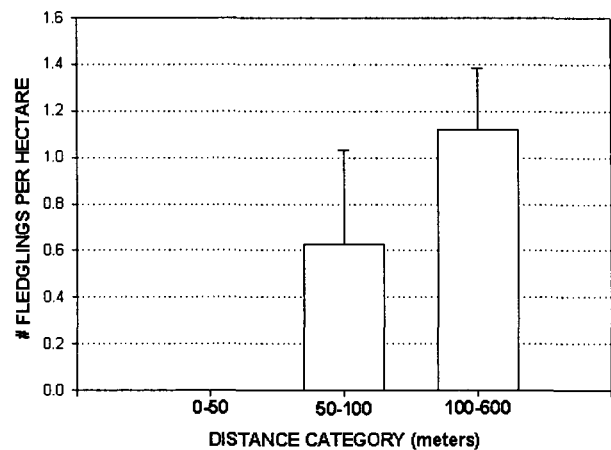**Figure 4.** Mean (± SE) predation rate on natural nests among six categories of distance from the edge.

Figure 5. Mean (± SE) predation rate on natural nests among the four study areas.

Figure 6. Mean (± SE) predation rate on natural nests among species.

Figure 7. Mean (± SE) nest cover of natural nests for failed and successful nests.

Figure 5. Mean (± SE) number of fledglings per hectare among three categories of distance from the edge, for all species combined.

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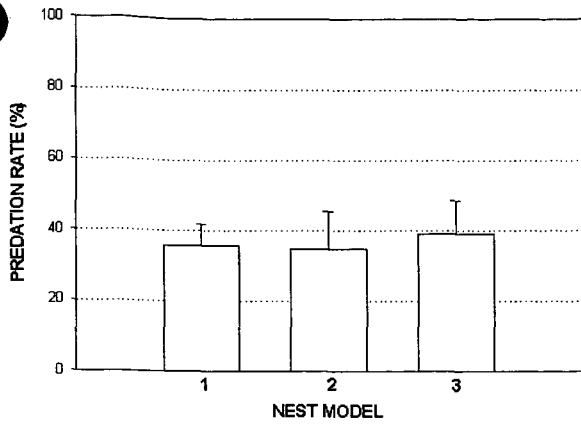
Figure 9. Mean (± SE) predation rate on artificial nests among the three nest models. Model 1 was 1 clay and 1 quail egg in wicker nest; model 2 was 2 quail eggs in wicker nest; model 3 was 2 quail eggs without wicker nest.
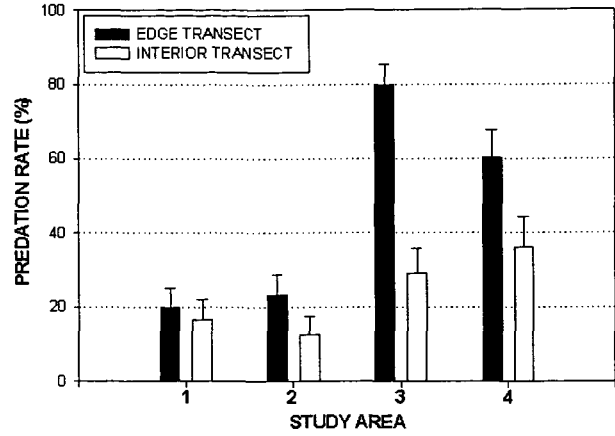
Figure 10. Mean (± SE) predation rate on artificial nests among study areas and landscape setting transects.
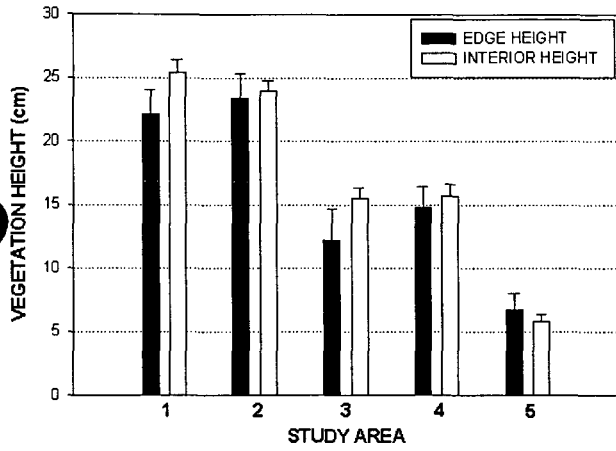
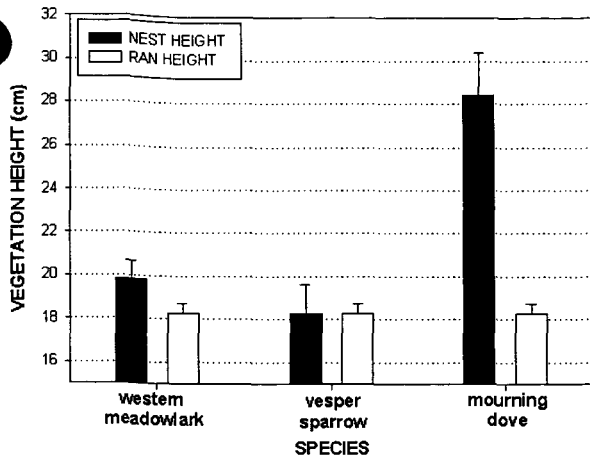**Figure 11.** Mean (± SE) study area vegetation height (cm) among study areas and landscape setting transects.
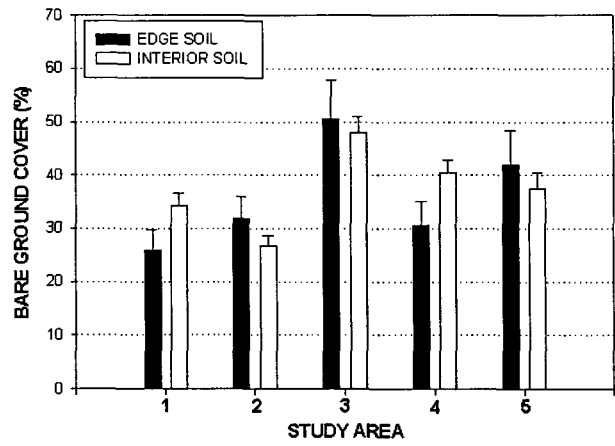
Figure 12. Mean (± SE) study area bare ground cover (%) among study areas and landscape settings.
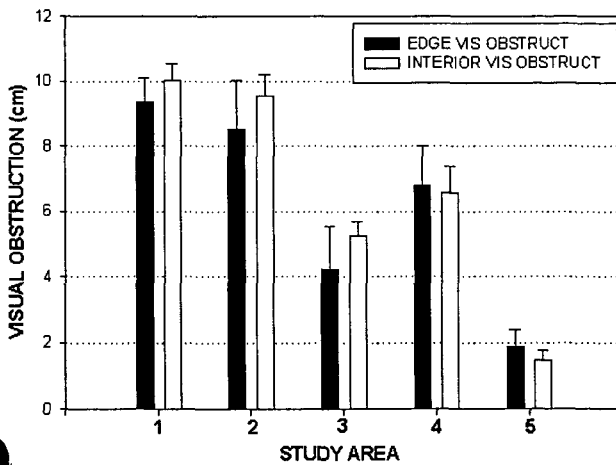
Figure 13. Mean (± SE) study area visual obstruction (cm) among study areas and landscape settings.

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Figure 14. Mean (± SE) vegetation height (cm) for nest sites versus average study area for three species.
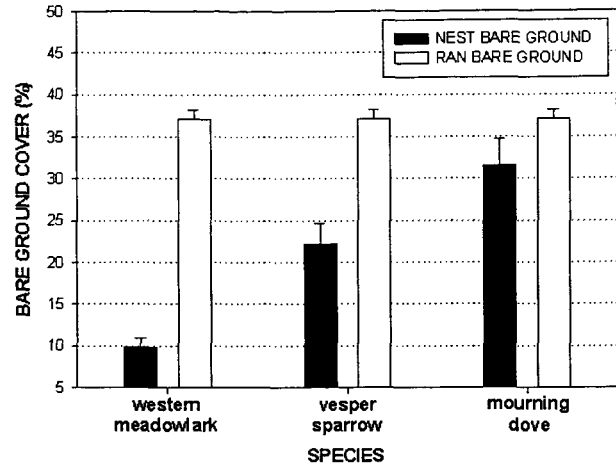

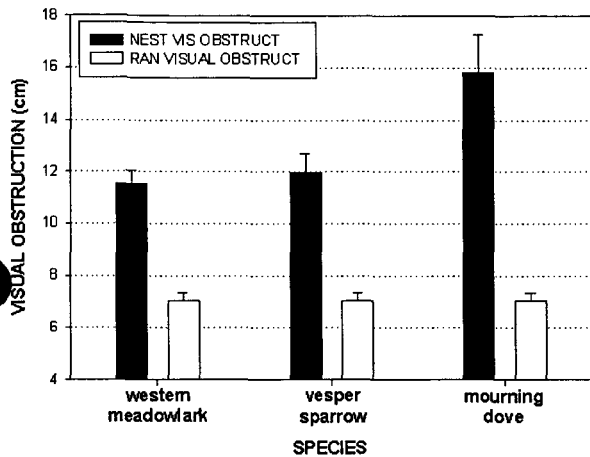**Figure 15.** Mean (± SE) bare ground cover (%) for nest sites versus average study area for three species.

Figure 16. Mean (± SE) visual obstruction (cm) for nest sites versus average study area for three species.
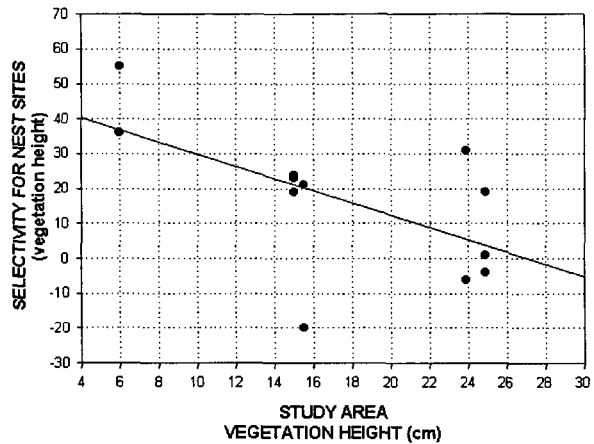

Figure 17. Correlation between the magnitude of nest site selection and the study areas vegetation height (cm). Each point represents one of three species on one of four study areas.
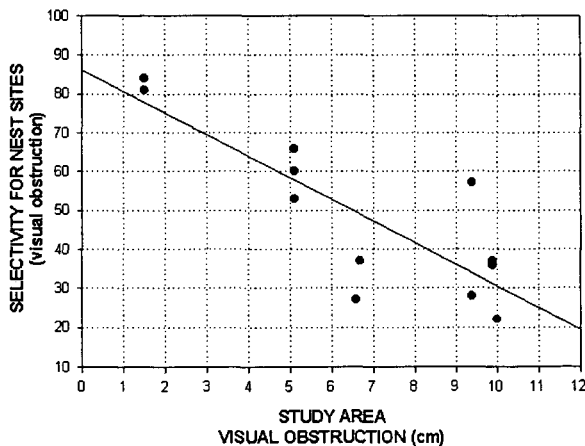

Figure 18. Correlation between the magnitude of nest site selection and the study area visual obstruction (cm). Each point represents one of three species on one of four study areas.
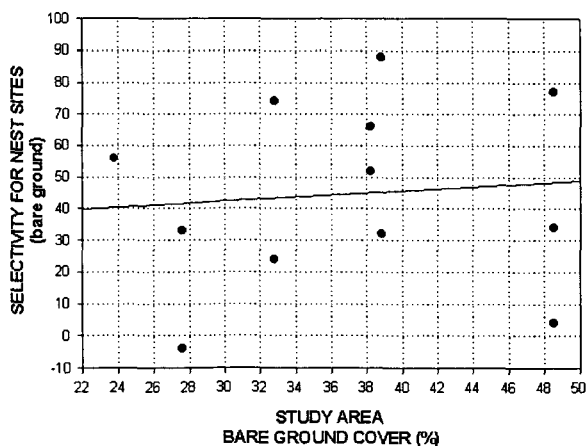

Figure 19. Correlation between the magnitude of nest site selection and the study area bare ground cover (%). Each point represents one of three species on one of four study areas.