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Influence of grassland type, nest type, and shrub encroachment on predation of artificial nests in Chihuahuan Desert grasslands

Lisa C. Mason  
New Mexico State University, Las Cruces

Martha J. Desmond  
New Mexico State University, Las Cruces

M. Sofia Agudelo  
New Mexico State University, Las Cruces

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Nest predation on eggs and nestlings profoundly affects reproductive success of birds and is considered the primary cause of nest failure in most land birds (Ricklefs 1969, Rotenberry and Wiens 1989, Major et al. 1994, Martin 1995). Birds have evolved numerous defenses to reduce predation risk, and studies have shown increased rates of nest predation to be associated with habitat fragmentation, nest location within a patch, and nest type (Donovan et al. 1995, Robinson et al. 1995, Dion et al. 2000, Flaspohler et al. 2001, Manolis et al. 2002). In the desert Southwest nest construction of most passerine nests can be divided into 3 categories: open-cup ground nests such as Horned Larks (Eremophila alpestris) and Eastern Meadowlarks (Sturnella magna), open-cup shrub nests within 3 m of the ground such as Black-throated Sparrows (Amphispiza bilineata), and Cactus Wrens (Campylorhynchus brunneicapillus), were placed in 10 grasslands of tobosa (Pleuraphis mutica) and black grama (Bouteloua erioides) with low and heavy levels of mesquite encroachment. Nest predation varied among nest types, grassland types, and shrub encroachment, with highest levels of predation occurring on open-cup shrub nests in tobosa grasslands with heavy shrub encroachment. We detected a significant interaction between nest type and shrub encroachment, but not between grassland type and nest type or grassland type and shrub encroachment. Combined predation rates from the 3 nest types were positively associated with shrub density. The encroachment of shrubs into desert grasslands may act as a corridor for a diversity of species historically not associated with desert grasslands to occupy or move through a patch, increasing vulnerability to nest predation.

The transformation of desert grasslands to a shrub-dominated system in the Chihuahuan Desert has been an ongoing process over the past 150 years. This desertification of the landscape has been primarily attributed to the introduction of domestic livestock to the region in the late 1800s combined with periodic drought (Buffington and Herbel 1965, Fredrickson et al. 1998, Kerley and Whitford 2000). Former open grasslands dominated by black grama (Bouteloua erioides) and tobosa (Pleuraphis mutica), the 2 grassland types diagnostic of Chihuahuan Desert grasslands, are being replaced by shrubs, primarily honey mesquite (Prosopis glandulosa) and creosote bush (Larrea tridentata). For example, on the USDA Jornada Long Term Experimental Range (LTER) in southern New Mexico, plots with >90% grass cover in the 1950s had <25% grass cover by 1963 (Buffington and Herbel 1965).

The system-level response to these landscape-scale changes has not been thoroughly investigated. Whitford (1997) found that species richness, diversity, and abundance of birds and small mammals were higher in desertified sites. He attributed this to grassland species persisting while shrub-adapted species colonized these sites. Pidgeon et al. (2001) found avian diversity was highest in mesquite-dominated plots compared to black grama grasslands and...
2 other shrub community types. While similarities were apparent among communities, they found that 30% of the avifauna was unique to each of the 4 vegetation communities. They suggest shrub encroachment has resulted in a major turnover in the avifauna of the region. In addition to these observed shifts in avian and mammalian species composition, Kerley and Whitford (2000) report that rodents have replaced ants as the primary granivore in the Chihuahuan Desert.

Shifts in ecosystem structure and function will have long-term consequences on survival and reproduction of associated fauna. We were particularly interested in the effects of this shift on nest predation in birds. Many species of small mammals and birds are nest predators, and the higher diversity and abundance of these taxa in desertified sites in the southwestern United States may contribute to a shift in the role of predation on avian nests in this system. We hypothesized nest predation in tobosa and black grama grassland patches would not differ between patch type but would differ between high and low levels of shrub encroachment, with higher rates of predation in shrub-encroached sites. We hypothesized that predation rates and types of predators would differ among the 3 nest types due to variability in detection. We predicted that predation rates would be highest for open-cup ground nests and lowest for spherical shrub nests due to differences in accessibility and concealment from predators. Spherical shrub nests have greater concealment of nest contents than open-cup nests, and others have suggested open-cup ground nests experience higher rates of predation in grassland systems (Martin 1993a). We predicted small mammals would be the primary predator on ground nests, whereas avian predators would be the primary predator for both types of shrub nests.

**Study Area**

Research was conducted during summer 2003 on the USDA Jornada LTER, located 30 miles north of Las Cruces, New Mexico. This area is primarily a mosaic of black grama, tobosa, and dropseed (*Sporobolus* spp.) grasslands in various stages of desertification, including heavy mesquite encroachment and coppice dune formation. Other dominant vegetation includes three-awns (*Aristida* spp.), burrograss (*Scleropogon brevifolius*), fluffgrass (*Dasyochloa pulchela*), snakeweed (*Gutierrezia* spp.), creosote bush (*Larrea tridentata*), tarbush (*Flourensia cernua*), soaptree and torrey yucca (*Yucca elata and Y. torreyi*), and cane cholla (*Opuntia imbricata*). Annual precipitation averages 23 cm but can be variable, and most rainfall comes in the form of monsoonal summer rains between July and September (Brown 1982).

**Methods**

We selected 10 grassland patches from the Jornada LTER’s GIS database of cover types based on 3 criteria: dominant grassland type (black grama or tobosa), size of the grassland patch, and level of shrub encroachment. We attempted to select an even number of open and shrub-encroached tobosa and black grama grasslands and to avoid complications due to grassland patch size. With one exception (19 ha) all grassland patches were >40 ha (19–522 ha), and all transects were located centrally within each patch to avoid edge effects. The center of each grassland patch was selected from the GIS database, its coordinates determined, and a 1050-m transect was established using the center of the plot as the transect center.

Artificial nests were placed in patches beginning 28 June and monitored every 4 days over a 12-day period, mimicking the incubation period of most passerines (Davison and Bollinger 2000, Dion et al. 2000). Data collection was completed by 13 July. In the desert Southwest peak nesting is timed with the monsoonal rains (Mendez 2000, Agudelo and Desmond unpublished data), which typically arrive in mid-July. Three types of artificial nests were used in this study: open-cup ground nests, open-cup shrub nests, and spherical (enclosed) shrub nests. We constructed open-cup ground nests by creating a small scrape within a grass clump and lining the scrape with live and dead grass to mimic the natural nest of an Eastern Meadowlark. Open-cup shrub nests were constructed with wicker and hemp, respectively. Open-cup shrub nests were lined with dead grass to mimic the natural nest of a Black-throated Sparrow, and spherical shrub nests were commercial finch and canary nests constructed of wicker and hemp, respectively. Open-cup shrub nests were lined with dead grass and covered with natural vegetation, small sticks, and forbs to mimic the natural nest of a Cactus Wren. These
nests were placed in shrubs 1–2 m from the ground. Commercial canary nests, constructed of hemp, were stained to achieve a more natural color and along with finch nests were left outside for a week prior to use in this study to take on a natural odor. Attempts were made to mimic the design and placement of natural nests such that artificial nests would not be more conspicuous to a visual predator (Martin 1987, 1995).

Twenty-one nests, spaced 50 m apart, were placed within each grassland patch at alternating distances of 18 m from the transect line or to the nearest appropriate shrub or grass patch. We alternated nest types and recorded their coordinates with a GPS unit. Two eggs were placed within each nest, a Japanese Quail (Coturnix coturnix) egg and an artificial egg. Artificial eggs were constructed from a non-hardening modeling clay, permoplast, and were modeled to mimic quail eggs. Nests were considered predated if the quail egg was missing or damaged or the nest destroyed (Dion et al. 2000). Clay eggs were used to determine predator type and not rates of predation (Davison and Bollinger 2000, Part and Wretenberg 2002).

To determine predator type when a quail egg was damaged or destroyed, we analyzed the clay eggs. Marks left on clay eggs were compared to the dentition of native species, and these nest predators were divided into broad categories, including small mammals, larger mammals, avian, and snakes. Avian predators are typically thought to leave a single narrow hole in the egg or an obvious beak mark. A destroyed nest site or teeth and claw marks in the clay eggs are generally considered mammalian predation. Snakes leave the nest site undisturbed or may create a hole in the nest bottom, removing the quail egg but leaving no marks on clay eggs (Davison and Bollinger 2000, Dion et al. 2000, Pietz and Granfors 2000). We handled all nests, nest material, and eggs using latex gloves, and our boots were washed upon arrival at each study site.

We counted all shrubs along a 1000 × 3-m transect in the center of each plot. These shrub counts were used as a relative index of shrub encroachment within each patch and were used to classify sites as relatively open or shrub encroached.

We tested whether predation rates differed as a function of grassland type (black grama vs. tobosa), shrub encroachment (high vs. low), and nest type (open-cup ground, open-cup shrub, or spherical shrub) using a 3-way analysis of variance. Rates of predation among nests placed in cholla, mesquite, and yucca shrubs were examined using a 1-way analysis of variance for spherical and open-cup shrub nests combined. Simple linear regression was used to examine the association between predation rate and shrub density.

**RESULTS**

Of 210 nests placed in Chihuahuan Desert grasslands, 89 (39%) were lost to predation. Rates of predation varied among nest types ($F_{2,18} = 4.77, P = 0.022$), with significantly higher predation on open-cup shrub nests; 60% of open-cup shrub nests, 41% of spherical shrub nests, and 16% of open-cup ground nests were lost to predators throughout the study (Table 1). Predation also varied between grassland types ($F_{1,18} = 7.94, P = 0.011$; Table 1) with significantly higher rates of predation on tobosa grasslands. Grassland patches were divided into 4 open and 6 shrub-encroached sites based on shrub counts within 3000-m² transects; sites with low shrub encroachment had 26–94 shrubs per transect ($\leq 313$ shrubs · ha$^{-1}$) compared to 156–282 shrubs per transect (520–940 shrubs · ha$^{-1}$) at high encroached sites. A detectable difference was found in nest predation between grassland patches with high and low shrub encroachment ($F_{1,18} = 8.63, P = 0.009$; Table 1), with significantly higher predation on the high shrub-encroached sites. A significant interaction was detected between nest type and shrub encroachment ($F_{2,18} = 3.65, P = 0.047$). No interactions were detected between nest type and grassland type, shrub encroachment and grassland type, or among all 3 variables ($P > 0.05$). Rates of predation did not differ among nests located in cholla, mesquite, and yucca shrubs ($P > 0.05$; Table 2). Overall, predation was found to increase linearly with the number of shrubs ($R^2 = 0.47, df = 9, P = 0.028$).

Determination of nest predators using permoplast eggs was difficult to confirm, and no strong quantitative determination could be made. Avian predators appeared to be the most common predator, followed by mammals and possibly snakes. However, 28% of the permoplast eggs analyzed could not be grouped into a predator category.
DISCUSSION

Predation rates did vary between the 2 grassland types, with higher predation in tobosa-dominated grasslands. This is contrary to our prediction and was likely related to several factors that could not be controlled in our site selection. Although no differences were detected in rates of predation among shrub types, rates of predation were lower for yuccas compared with mesquite and cholla, and this shrub type occurred almost exclusively in black grama grasslands. The predominance of cholla and mesquite in tobosa grasslands and mesquite and yucca in black grama grasslands may have contributed to a cumulative difference in predation rates among grassland types. Although we attempted to control for grassland size, 2 of our tobosa grassland patches were <50 ha (19 and 42), and all shrub nests within each of these 2 patches were destroyed by predators, suggesting patch size may influence predation rates within desert grasslands. However, the limited number of plots and the distribution of shrub types among plots prevented a thorough investigation of the interaction of shrub and grassland type and the effect of patch size.

Contrary to our prediction, nests in shrubs were more vulnerable to predation than open-cup ground nests. This was particularly true for open-cup shrub nests, which appeared more vulnerable to visual predators. Visual cues for locating nests seemed important; most predators leaving marks on permoplast eggs left marks consistent with avian predators. However, recent studies using video cameras have concluded that identification of specific predators based on sign left at the nest can be misleading (Pietz and Granfors 2000, Thompson and Burhans 2003). Specifically, snakes will sometimes leave a hole in the bottom of the nest, and contrary to common belief, large mammals will often leave the nest site undisturbed (Pietz and Granfors 2000, Thompson and Burhans 2003). Open-cup ground nests appeared to be better concealed and more difficult for predators to locate regardless of the level of shrub encroachment. This agrees with Vander Haegen et al. (2000), who found a positive relationship between patch size and predation rates for shrub-nesting species such as Sage Thrashers and Brewer’s Sparrows but no relationship for the ground-nesting Vesper Sparrow. However, Davison and Bollinger (2000) found no difference in predation rates between ground and elevated nests in Conservation Reserve Program grasslands in Illinois.

Several studies (Major and Kendal 1996, Part and Wretenberg 2002) using artificial nests to measure vulnerability of nest predation have cautioned that rates of predation differ between

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### Table 1

<table>
<thead>
<tr>
<th>Nest type</th>
<th>Grassland type</th>
<th>Shrub encroachment</th>
<th>Predation rate</th>
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</thead>
<tbody>
<tr>
<td>O.C. ground (7)</td>
<td>Black grama</td>
<td>Low</td>
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<tr>
<td>O.C. ground (21)</td>
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<td>Tobosa</td>
<td>High</td>
<td>0.14</td>
</tr>
<tr>
<td>O.C. shrub (7)</td>
<td>Black grama</td>
<td>Low</td>
<td>0.14</td>
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<tr>
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<td>0.48</td>
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<tr>
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<td>Tobosa</td>
<td>High</td>
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### Table 2

<table>
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<th>Nest substrate</th>
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<tr>
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<tr>
<td>Cholla</td>
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<td>0.50</td>
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<tr>
<td>Yucca</td>
<td>26</td>
<td>0.37</td>
</tr>
<tr>
<td>Ground</td>
<td>70</td>
<td>0.14</td>
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</table>
real and artificial nests because they are perceived differently by predators. Activity of adult birds at the nest site may attract predators (Roper and Goldstein 1997), or differential search modes among predator types such as olfactory versus visual cues may result in differential rates of predation (Major and Kendal 1995, Martin 1993b). Relative rates of predation on artificial nests can, however, be compared among patch types and nest types and are useful for identifying vulnerability to predation and potential predators (Sieving et al. 1998, Dion et al. 2000). Davison and Bollinger (2000) found similar rates of predation between real and artificial nests in grasslands in Illinois when artificial nests more closely mimicked natural nests. In this study it appears that the combination of shrub encroachment and search behavior likely interacted to increase rates of nest predation. However, the significant interaction detected between shrub encroachment and nest type and the positive association of predation with shrub density indicate that shrub encroachment may be a major factor affecting predation on nests in this habitat.

More traditional studies of fragmentation, with clearly defined edges, have demonstrated that forest or grassland fragmentation contributes to increased rates of predation and brood parasitism (Flaspholer et al. 2001, Manolis et al. 2002). In this study the encroachment of shrubs into grassland patches is a form of fragmentation, but the ecotone between the 2 habitat types is less clearly defined. The increased presence of shrubs throughout grassland patches in the desert Southwest may act as a corridor for a diversity of species historically not associated with desert grasslands to occupy or move through the patch. Other studies have reported higher abundance and diversity of small mammals and birds in desertified sites (Whitford 1997, Pidgeon et al. 2001). Many birds and small mammals are recognized egg predators and likely contributed to higher rates of predation in mesquite-encroached grasslands.

Several factors may account for the higher rates of nest predation observed in desertified sites. As part of the desertification process, there has been a decline in the cover of perennial grasslands and a change in the spatial distribution of vegetative cover from a homogeneous distribution to a temporally or spatially clumped or heterogeneous distribution (Buffington and Herbel 1965, Neilson 1986, Schlesinger et al. 1990). Desertified sites may be easier for predators to search because of the clumped distribution of resource patches. The higher avian and mammalian diversity observed in desertified sites (Whitford 1997, Kerley and Whitford 2000, Pidgeon et al. 2001) may support a higher abundance of predators as well as a spatially clumped distribution of potential prey sources. Predators may concentrate in desertified areas because they are easier to search and have a higher density of prey including nesting birds. To confirm these results, we recommend that this experiment be repeated on natural nests within open and shrub-encroached Chihuahuan Desert grasslands.

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LITERATURE CITED


