The Condor 104:496–506

PREDATION ON REAL AND ARTIFICIAL NESTS IN SHRUBSTEPPE LANDSCAPES FRAGMENTED BY AGRICULTURE

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Abstract. Clearing of shrubsteppe communities for agriculture has created a highly fragmented landscape in eastern Washington, a condition that has been shown to adversely affect nesting success of birds in some forest and grassland communities. We used artificial nests monitored by cameras to examine relative effects of fragmentation, distance to edge, and vegetation cover on nest predation rates and to identify predators of shrubsteppe-nesting passerines and grouse. Predation rate for artificial nests was 26% (n = 118). Fragmentation had a strong influence on predation rates for artificial nests, with nests in fragmented landscapes about 9 times more likely to be depredated as those in continuous landscapes. Daily survival rate (± SE) for 207 real nests of 4 passerine species also was greater in continuous (0.978 ± 0.004) than in fragmented (0.962 ± 0.006) landscapes, although pattern of predation between real and artificial nests was not consistent among sites. Artificial nests were depredated by Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica hudsonia*), Sage Thrashers (*Oreoscoptes montanus*), least chipmunks (*Tamias minimus*), and mice. Most nests in fragments were depredated by corvids (58%), whereas only Sage Thrashers and small mammals depredated nests in continuous landscapes. Increased predation by corvids and lower nest success in fragmented landscapes may have played a part in recent declines of some shrubsteppe birds. Future research should measure annual reproductive success of individual females and survival rates of juveniles and adults.

Key words: *artificial nests, cameras, grouse, nest predators, nest success, passerines, shrubsteppe.*

Depredación de Nidos Naturales y Artificiales en Paisajes de Estepa Arbustiva Fragmentados por Agricultura

Resumen. El reemplazo de estepa arbustiva por campos de cultivo ha creado un paisaje altamente fragmentado en el este de Washington, afectando adversamente el éxito de nidificación de aves en algunas comunidades de bosque y pastizal. Usamos nidos artificiales monitoreados por cámaras para examinar los efectos relativos de la fragmentación, la distancia al borde y la cobertura de la vegetación sobre las tasas de depredación de nidos, y para identificar los depredadores de paserinos y gallinas silvestres (Phasianidae) que nidifican en la estepa arbustiva. La tasa de depredación de los nidos artificiales fue del 26% (n = 118). La fragmentación tuvo una fuerte influencia en las tasas de depredación de nidos artificiales, ya que los nidos en paisajes fragmentados tuvieron una probabilidad de ser depredados 9 veces mayor que aquellos en paisajes continuos. La tasa de supervivencia diaria (± EE) de 207 nidos naturales pertenecientes a 4 especies de paserinos también fue mayor en paisajes continuos (0.978 ± 0.004) que fragmentados (0.962 ± 0.006), aunque el patrón de depredación entre nidos naturales y artificiales no fue consistente entre sitios. Los nidos artificiales fueron depredados por *Corvus corax*, *Pica hudsonia*, *Oreoscoptes montanus*, *Tamias minimus* y ratones. La mayoría de los nidos en fragmentos fueron depredados por *C. corax* (58%), mientras que sólo *O. montanus* y pequeños mamíferos depredaron nidos en paisajes continuos. Un incremento en la depredación por parte de *C. corax* y un menor éxito de los nidos en paisajes fragmentados puede haber jugado un rol en la disminución de algunas aves de la estepa arbustiva. Futuras investigaciones deberían medir el éxito reproductivo anual de hembras individuales y las tasas de supervivencia de juveniles y adultos.

Manuscript received 13 August 2001; accepted 26 March 2002.

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INTRODUCTION

Rates of nest predation can vary with landscape characteristics such as fragmentation (Wilcove 1985, Johnson and Temple 1990, Burger et al. 1994) and distance to habitat edge (Gates and Gysel 1978, Niemuth and Boyce 1997), and differences in predator communities among landscapes may play a large part in observed patterns of predation (Donovan et al. 1997, Marzluff and Restani 1999). Greater rates of nest predation have been reported for grassland (Johnson and Temple 1990, Burger et al. 1994, Winter and Faaborg 1999) and forest birds in fragments surrounded by agricultural fields and urban development (Robinson et al. 1995, Donovan et al. 1997). In contrast, forest fragments in extensive, forested landscapes fragmented by timber harvest generally have been found to have predation rates similar to or lower than those in continuous mature forests (Rudnicky and Hunter 1993, Vander Haegen and DeGraaf 1996, Hanski et al. 1996). Predator communities associated with farmed or otherwise developed lands often are implicated in higher predation rates in adjacent remnants of native habitat (Andren et al. 1985, Wilcove 1985, Andren 1992).

Shrubsteppe communities once dominated the nonforested regions of the Columbia River Basin (Daubenmire 1970), although much of these former shrublands and grasslands have been converted to agricultural fields (Quigley and Arbelbide 1997). In Washington, most of the historic steppe and shrubsteppe communities have been cleared for agricultural or urban development, creating a highly fragmented landscape (Dobler et al. 1996). Several species of birds occur only in shrubsteppe communities and several of these are classified as state-threatened species in Washington or are candidates for listing. Data from the Breeding Bird Survey indicate that several shrubsteppe-associated birds, such as the Brewer's Sparrow (*Spizella breweri*) and Loggerhead Shrike (*Lanius ludovicianus*), are declining in the West (Saab and Rich 1997), and both Greater Sage-Grouse (*Centrocercus urophasianus*) and Sharp-tailed Grouse (*Tympanuchus phasianellus*) have declined dramatically in Washington over the last 40 years (Schroeder, Hays, Livingston et al. 2000, Schroeder, Hays, Murphy, and Pierce 2000). We know little about the effects of habitat fragmentation on productivity of shrubsteppe birds, although other landscape effects such as area sensitivity have been documented (Knick and Rotenberry 1995, Vander Haegen et al. 2000).

Artificial nests have been used to explore patterns of nest predation and to identify potential predators of bird nests (reviews in Paton 1994, Marzluff and Restani 1999). Rationale for this technique is grounded in the belief that relative rates of nest predation between treatments (e.g., habitat types) are similar for real and artificial nests (Wilcove 1985), although until recently this assumption had been little tested (King et al. 1999, Dion et al. 2000). In their study of the effects of grazing on nest predation in montane riparian systems, Ammon and Stacey (1997) reported greater predation associated with grazing for both real and artificial nests. Similarly, Wilson et al. (1998) reported that predation on artificial nests followed a pattern comparable to that of real Wood Thrush (*Hylocichla mustelina*) nests, declining with increasing size of the forest patch. In contrast, Davison and Bollinger (2000) found a different pattern for artificial vs. real nests among their different grassland study sites.

We used artificial nests monitored by cameras to explore patterns of predation for shrub and ground nesting passerines and ground nesting prairie grouse. Our objectives were (1) to examine the effects of habitat fragmentation and site-specific variables on survival of artificial nests, (2) to compare predation rates of artificial nests with that of real nests, and (3) to identify predators of nests in shrubsteppe communities.

METHODS

STUDY AREA

The study took place in eastern Washington, within the geographic region known as the Columbia Basin. The region is characterized by hot, dry summers and cold winters. Precipitation falls mainly during winter with annual totals ranging from 15 to 55 cm, decreasing from north to south across the study area (Daubenmire 1970). A considerable portion of the study area is farmed, with dryland wheat the main crop in higher-rainfall zones, whereas irrigated orchards, vineyards, and row crops prevail in lower-rainfall zones.

Predation rates were measured in study sites located in large, continuous stands of shrubsteppe and in shrubsteppe fragments in an agricultural matrix (Fig. 1). We selected 6 large stands (median 115 368 ha), each separated by

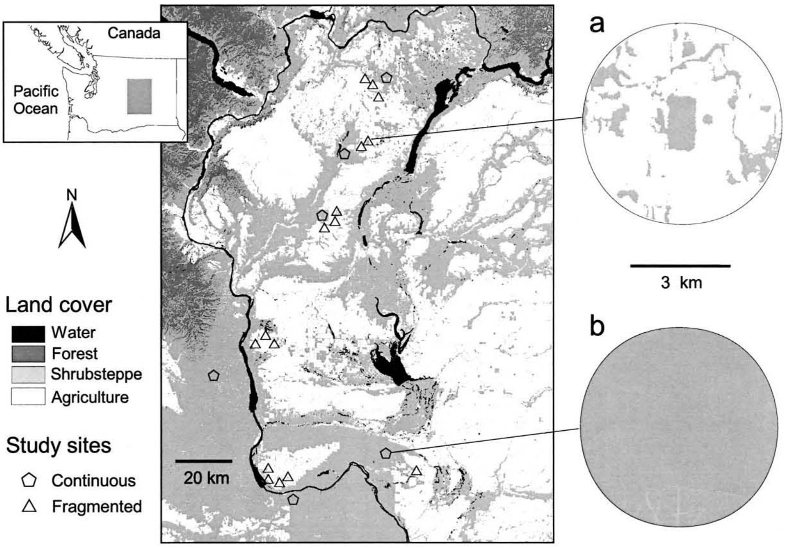

FIGURE 1. Location of study sites within the main study area in eastern Washington. Enlargements show representative (a) fragmented and (b) continuous landscapes surrounding study sites.

≥22 km, to represent continuous landscapes, and we selected 2–3 shrubsteppe fragments (median 146 ha) in the agricultural landscape surrounding each continuous stand (for a total of 16 fragments) to represent fragmented landscapes. Fragment sizes ranged from 8–968 ha. The 6 continuous study sites were located in stands of 7278, 56 380 (2 sites), 174 355 (2 sites), and 202 495 ha. All sites were characterized by a shrub layer dominated by big sagebrush (*Artemisia tridentata*) and an herbaceous layer dominated by native bunchgrasses. Ground-nesting passerines that breed on the study area include Vesper Sparrow (*Pooecetes gramineus*), Horned Lark (*Eremophila alpestris*), and Western Meadowlark (*Sturnella neglecta*), whereas shrub-nesting passerines include Sage (*Amphispiza belli*) and Brewer's Sparrows, Sage Thrasher (*Oreoscoptes montanus*), and Loggerhead Shrike (Vander Haegen et al. 2000). Greater Sage-Grouse and Sharp-tailed Grouse also nest on the study area along with several introduced gallinaceous birds.

ARTIFICIAL NESTS

We placed artificial nests along transects in continuous stands of shrubsteppe and in fragments of shrubsteppe in an agricultural matrix. In continuous stands, nests were placed at points 200 m apart along an 800-m transect. At each point, one shrub nest and one ground nest were placed on opposite sides of the transect and >20 m apart. Ground nests were generally placed at the base of a bunchgrass plant or near the base of a shrub to facilitate relocation. Nest baskets were buried in the soil such that the rim was level with the ground. Shrub nests were wired to branches of a shrub (almost exclusively big sage) at 0.5–1 m above the ground. Four nests were placed in each fragment stand, with 1 pair <20 m from the nearest edge and a second pair 60–80 m from the nearest edge. Nests were wicker baskets (10-cm diameter, 4 cm deep) and were baited with 2 quail eggs (*Coturnix coturnix*) at the beginning of each trial. Rubber gloves were used when handling eggs and nests.

We set out nests and eggs on 15 and 16 May 1996 and checked them for signs of predation 7 and 14 days later. The 14-day exposure period simulated the 12–14 day incubation period typical of local passerines (Ehrlich et al. 1988) and approximately one half of the typical incubation period for Greater Sage-Grouse and Sharp-tailed Grouse. May is the peak of nesting for local passerines (Vander Haegen and Walker 1999) and is the typical renesting period for Greater Sage-Grouse (Schroeder 1997) on the study area. A nest was considered depredated if ≥1 egg was missing, broken, or out of the nest.

CAMERA NESTS

One nest at each point was monitored by an automatic-focusing 35-mm camera (Olympus Corp., Woodbury, New York) for the duration of the experiment (alternating ground and shrub nests at successive points). Cameras had automatic film advance allowing identification of subsequent predators, and automatic flash allowing identification of nocturnal as well as diurnal predators. An electrical microswitch placed beneath one egg in the nest activated the camera when the egg was disturbed (Danielson et al. 1996). Photographs recorded the date and time of exposure. Cameras were held in camouflaged, waterproof housings secured to 40-cm-high wooden stakes driven into the soil 2 m from the nest. Telephone wire connected the camera to the switch in the nest, and wires were buried beneath plant litter or soil where they crossed the ground. To make cameras less conspicuous to corvids, we positioned cameras beneath the shrub canopy, mounted on stakes immediately next to a shrub.

We continued to monitor camera nests for 14 days past the end of the predation experiment to obtain additional predator photographs. Camera nests were checked every 7 days and if depredated, the film was replaced, any egg fragments were removed, and two new eggs were placed in the nest. The fate of camera nests over the first 14 days was recorded identically to that of noncamera nests and included in calculations of predation rates. The first visitor photographed at a depredated nest was assumed to be the initial predator; only the first visit to each nest was used to calculate number of nests depredated by different predator species. Instances where subsequent predators were photographed at a nest were termed "subsequent visits."

To examine the time to nest discovery among predator groups we calculated the time in days between setting out eggs and occurrence of the first visitor to each camera nest. Because nests were not moved following depredation and predators may remember locations of nests, each nest was used only once in this analysis. To examine the potential effects of our visitation to nests on timing of nest predation, we calculated the time in hours between setting out eggs and occurrence of the first visitor to each nest.

At the conclusion of the experiment we measured vegetation cover at each nest site with a 0.5 × 1.5 m density board held upright at the nest and viewed from the four cardinal directions at a distance of 3 m. Vegetation was well developed by the start of the first trial so it is unlikely that cover at the nest sites changed appreciably during the experiment. An observer estimated the proportion of the board obscured by vegetation in two height classes (0–0.5 m and 0.5–1 m). We used the mean of the eight values (four from 0–0.5 m and four from 0.5–1.0 m) to represent vegetation cover at each nest site. Distance to edge for each nest was measured in the field or from a geographic information system for the study area. Edges were defined by agricultural fields (including Conservation Reserve Program fields planted with exotic bunchgrasses) or by roads that separated the stand from agricultural fields.

REAL NESTS

We measured survival rates for real nests on a subset of sites used for the artificial nest experiment (4 continuous stands and 4 sets of fragments) during April–July 1996. We located nests by following adults and by flushing incubating and brooding birds. All active nests were marked with flagging at a distance of ≥ 8 m and monitored every 2–3 days until fledging or failure. Fates were determined using standard protocol (Ralph et al. 1993). We calculated nest survival rates using the Mayfield (1975) method, and compared daily survival rates of nests between treatments using χ^2 analysis in program CONTRAST (Sauer and Williams 1989). Nests categorized as abandoned were excluded from this analysis. We combined nests of the four most common species (comprising 94% of all nests found) to derive a measure of nesting success for each site.

STATISTICAL ANALYSES

We used logistic regression (PROC LOGISTIC; SAS Institute 1990) to examine the effects of variables associated with each artificial nest on predation rates. To test for effect of landscape we developed a model using all nests and the following variables: landscape (continuous or fragmented), height (ground or shrub), and vegetation cover. To examine the influence of distance from edge on predation rates we developed a second model using only nests in fragmented landscapes (most nests in continuous landscapes were >600 m from the nearest edge). Presence of a camera at the nest was included as a variable in both models to test for its effect on predation. Suitability of each model was determined by using the likelihood-ratio test and associated chi-square statistic with a significance

TABLE 1. Logistic regression analyses of predation on artificial nests in fragmented and continuous shrubsteppe landscapes, eastern Washington.

Variable	Parameter estimate ± SE	Wald χ^2	P
Model 1: Fragmented and continuous landscapes			
Intercept	−0.28 ± 1.06	0.1	0.79
Landscape class	2.18 ± 0.58	14.2	0.001
Nest height	0.23 ± 0.47	1.2	0.63
Camera	0.56 ± 0.46	1.5	0.23
Vegetation cover	−3.07 ± 1.26	6.0	0.02
Model 2: Fragmented landscapes only			
Intercept	2.57 ± 1.41	3.4	0.07
Distance to edge	−0.001 ± 0.008	0.01	0.91
Nest height	0.69 ± 0.55	1.5	0.22
Camera	0.33 ± 0.54	0.4	0.55
Vegetation cover	−3.91 ± 1.48	7.0	0.008

TABLE 2. Visitors to artificial nests in continuous and fragmented shrubsteppe landscapes, eastern Washington. Numbers in parentheses indicate visits subsequent to the initial visit.

	Ground nests		Shrub nests	
Species	Continuous (n = 12)	Fragmented (n = 16)	Continuous (n = 13)	Fragmented (n = 16)
Common Raven	0	3 (8)	0	3 (10)
Black-billed Magpie	0 (1)	3 (6)	0	5 (15)
Sage Thrasher	0	0 (4)	2 (6)	2 (1)
Least chipmunk	3 (2)	2 (5)	4 (6)	1 (1)
Mice	2 (3)	5 (8)	1	0 (2)
Totals	5 (6)	13 (31)	7 (12)	11 (29)

level of $P < 0.05$. Significance of individual variables within the model was tested with the Wald statistic and its associated chi-square. Odds ratios (Hosmer and Lemeshow 1989) were calculated for significant main effects. We used log-linear analysis to test for different patterns in nest survival between real and artificial nests among sites after first calculating nest survival for artificial nests using Mayfield analysis. We used the Pearson correlation coefficient to examine the relationship between patch size and success rate of artificial nests. Means are reported ± SE.

RESULTS

ARTIFICIAL NESTS

Photographs from cameras at one continuous site (Reeves Butte) revealed that Common Ravens "trap-lined" the nests on this site shortly after they were checked at 7 days. Four of five camera nests were depredated by ravens within 44 min of each other and <2 hr after being checked. Previous to this nest check no nests had been depredated on the site. Nests from this site were eliminated from the logistic regression and correlation analyses, and photographs from the Reeves Butte site were not included in the assessment of nest predators. Counting only first visitors to nests, only two other visits occurred on the day the nests and eggs were set out: one by a magpie after 10 hr, and one by a raven after 1 hr. These two visits seemed to be isolated events and we included them in analyses.

Predation rate for artificial nests was 26% ($n = 118$). In the main logistic regression model, landscape had a strong influence on risk of predation (Table 1), with nests in fragmented landscapes about nine times more likely to be depredated as those in continuous landscapes (odds ratio = 8.8, 95% CI = 2.8–27.7). Vegetation cover at the nest site also affected risk of predation (Table 1), with nests surrounded by more vegetation less likely to be depredated (odds ratio = 0.05, 95% CI = 0.01–0.54). Nest height and presence of a camera did not influence predation rate. There were no significant second or third order interactions in the model.

In the second model, distance to edge had no effect on predation rate (Table 1). Vegetation cover was the only significant variable in the model and both the direction and magnitude of its effect on predation rate was similar to that in the full model. There were no significant second or third order interactions in the model. Predation rate of artificial nests was not correlated with patch size either among all sites ($r = 0.28$, $P = 0.25$, $n = 21$) or when fragment sites alone were used in the analysis ($r = 0.11$, $P = 0.68$, $n = 16$).

Potential nest predators were photographed at 36 of 57 camera nests. In addition to the 36 initial visitors photographed at each nest, 78 subsequent visits were recorded for a total of 104 photographed visits (Table 2). Camera nests in fragments were visited by Common Ravens, Black-billed Magpies, Sage Thrashers, least chipmunks (*Tamias minimus*), and deer mice (*Peromyscus maniculatus*). In several photographs it was impossible to differentiate deer mice from northern grasshopper mice (*Onychomys leucogaster*), so hereafter they are referred to as "mice." Most (58%) nests in fragments were visited by corvids, whereas 33% were visited by small mammals and 8% by Sage Thrashers. In contrast, only Sage Thrashers and small mammals visited nests in continuous stands, with seven nests visited by least chipmunks, three by mice, and two by Sage Thrashers. These patterns were supported by the breakdown of species visiting nests subsequent to the initial visit (Table 2).

Sage thrashers were photographed at nine different nests across seven sites. One photograph showed a thrasher lifting an intact egg from the nest with its beak; however, neither egg in the nest was damaged. In seven cases, Sage Thrashers were photographed at nests that were not subsequently depredated (thrashers were the first visitor in three of these cases). Only one nest appeared to have been depredated by Sage Thrashers. On three separate visits one egg had been removed from the nest and a thrasher was the only visitor photographed. The first egg removed was lying intact beneath the nest, the second egg removed was missing, and the third egg removed was lying beneath the nest and had small holes penetrating the shell.

Our camera data revealed that small mammals were frequent visitors to nests; however, only 17% of these nests showed evidence of predation. To further consider the potential role of small mammals in this system, we ran the logistic regression models again after first designating as depredated all camera nests that were visited by mammalian predators. This modification had little effect on either model, the most substantive change being a reduction in the odds ratio for landscape to 5.3 (95% CI = 2.0–14.1). Small mammals visited about twice the proportion of camera nests (including subsequent visits) in fragmented landscapes (63%) than continuous landscapes (31%), suggesting that they might be a greater predation threat in fragments.

Date and time stamps on predator photographs revealed different visitation patterns for bird and mammal predators. Corvids tended to depredate nests sooner than small mammals (Fig. 2), although time elapsed between nest placement and predation was highly variable for each group. Further, of 14 nests visited first by corvids, four were subsequently visited by small mammals, whereas none of 18 nests first visited by small mammals were subsequently visited by corvids. Magpies, ravens, thrashers, and chipmunks visited nests only during daylight, whereas visits by mice were almost exclusively nocturnal.

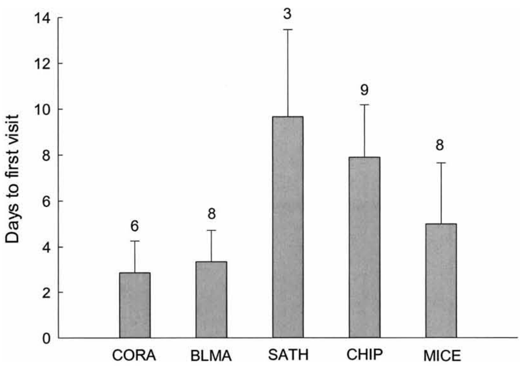

FIGURE 2. Number of days (mean ± SE) between placement of artificial nests and visits by Common Ravens (CORA), Black-billed Magpies (BLMA), Sage Thrashers (SATH), least chipmunks (CHIP), and mice (MICE) in shrubsteppe communities in eastern Washington. Data include only first visitor to each nest. Sample size shown above bars.

REAL VERSUS ARTIFICIAL NESTS

Nest success of the four most common species found on our plots averaged 46% ($n = 207$). All failed nests were depredated, although two had first been parasitized by Brown-headed Cowbirds (*Molothrus ater*). Daily survival rate for real nests for all species combined was greater in continuous than in fragmented landscapes (Table 3); this pattern was also present for Brewer's Sparrow. Sage Thrasher nest success tended to be higher in continuous landscapes, whereas the Vesper Sparrow exhibited a weak trend in the opposite direction (Table 3). Daily survival rate for artificial nests, calculated using Mayfield analysis, also was greater ($\chi^2_1 = 13.5$, $P = 0.001$) in continuous (0.992 ± 0.003) than in fragmented (0.964 ± 0.007) landscapes, reflecting the results of the logistic regression analysis. At the scale of individual sites, however, the pattern of predation differed for real and artificial nests (Fig. 3); log-linear analysis of survival rates as a function of site and nest type (real vs. artificial) revealed a significant interaction ($F_{3,8} = 5.7$, $P = 0.05$). Number of real nests located at two sets of fragment sites were insufficient to calculate daily survival rates.

TABLE 3. Daily survival rate (± SE) for real nests in continuous and fragmented shrubsteppe landscapes, eastern Washington, 1996. Sample size (nests) in parentheses.

Species	Daily survival rate		χ^2	*P*
	Continuous	Fragmented		
Sage Thrasher	0.984 ± 0.006 (34)	0.961 ± 0.014 (19)	2.5	0.11
Brewer's Sparrow	0.989 ± 0.004 (50)	0.964 ± 0.009 (45)	7.1	0.008
Vesper Sparrow	0.934 ± 0.021 (14)	0.957 ± 0.016 (15)	0.1	0.39
Sage Sparrow	0.964 ± 0.011 (28)	—[a]	—	—
Overall	0.978 ± 0.004 (126)	0.962 ± 0.006 (81)	4.7	0.03

[a] Sample size ($n = 2$) was insufficient to calculate daily survival rate.

DISCUSSION

PREDATORS

Predation rate for artificial nests was greater in fragmented than continuous shrubsteppe landscapes, a result likely attributable to increased predation by Black-billed Magpies and Common Ravens. Corvids have been identified as important nest predators in several systems (Yahner and Wright 1985, Sullivan and Dinsmore 1990, Andren 1992), particularly in fragmented landscapes. In our study, small mammals were photographed at nests in both fragmented and continuous landscapes, whereas corvids were photographed depredating nests almost exclusively in fragments. As in other systems, corvids in shrubsteppe often are associated with agricultural and other human-modified habitats; this is particularly true of Black-billed Magpies that depend largely on trees for nesting. Point-count surveys of continuous and fragmented shrubsteppe that included many of the sites used in this study revealed significantly greater abundance of magpies in fragmented landscapes (WMV, unpubl. data). Ravens were common in both landscapes and they depredated nests in continuous shrubsteppe, as evidenced by photographs at our Reeves Butte site; however, nests may be more difficult to locate in extensive stands of shrubsteppe.

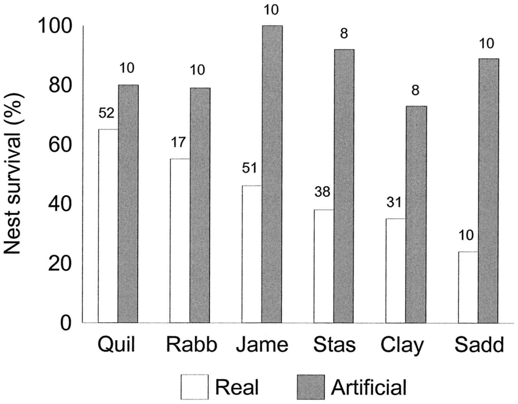

FIGURE 3. Survival of real vs. artificial nests followed dissimilar patterns among sites in shrubsteppe communities in eastern Washington. Sites are on *x*-axis, in order of decreasing survival of real nests ("Stas" and "Clay" are fragments; the others are continuous sites). Sample size shown above bars.

Small mammals may be important nest predators for birds nesting in shrubsteppe, as has been suggested for some other communities (Reitsma et al. 1990, Hannon and Cotterill 1998). Chipmunks visited ground and shrub nests in about equal numbers, whereas mice visited primarily ground nests and thus would likely have less effect on shrub-nesting birds. Small mammals have difficulty opening quail-sized eggs (Haskell 1995, DeGraaf and Maier 1996) and therefore are unlikely predators for eggs of larger shrubsteppe birds such as grouse. Eggs of small passerines are readily opened by small mammals (DeGraaf and Maier 1996) and mice have been implicated as significant predators of ground-nesting birds (Maxon and Oring 1978). It is unclear what part adults may play in defending their nests against these small predators, although continued research using videocameras (e.g., Thompson et al. 1999) may be revealing.

Sage Thrashers are not known to eat bird eggs (Reynolds et al. 1999), and we suspect that thrashers photographed at our nests were more curious than predatory. Although thrashers could have been responsible for three depredations, in most cases they visited nests without causing damage, despite evidence that they are capable of both handling and puncturing quail eggs. Sage Thrashers are common in both continuous and fragmented shrubsteppe in Washington and seem to show an affinity for fragmented landscapes (Vander Haegen et al. 2000). If Sage Thrashers do depredate nests our visitation rates suggest that their influence on nesting success would be similar in continuous and fragmented landscapes.

PATTERNS OF NEST PREDATION

Predation rate for real nests on our study area was greater in fragments, supporting the results of the artificial nest experiment. When species were considered separately, Sage Thrashers and Brewer's Sparrows, both predominantly shrub-nesters, followed this pattern whereas the ground-nesting Vesper Sparrow did not. Vesper Sparrow nests were generally well concealed in bunchgrasses, making them more difficult to locate than shrub nests for human nest-searchers, and perhaps also for visually oriented predators like corvids. These relative trends in predation among species are consistent with increased predation by corvids in fragmented landscapes, suggested by our camera data.

The character of habitat edge in shrubsteppe often differs from that associated with other communities where nest predation has been studied (Rotenberry 1998). Edge is typically defined by the presence of trees, such as the boundaries of clearcuts (Yahner and Wright 1985, Rudnicky and Hunter 1993, King et al. 1998) or the ecotone of remnant prairie and surrounding woodland (Johnson and Temple 1990, Burger et al. 1994). Trees are uncommon in many shrubsteppe communities, and on our study sites edge was associated with agricultural fields. Lack of an edge effect on nest predation in our study was likely a result of a predator community that either lived in the shrubsteppe (chipmunks and mice; "the enemy from within," Hannon and Cotterill 1998) or that gained no advantage for finding nests along the habitat edge due to lack of trees to act as observation posts (corvids). Edge effects >80 m would not have been documented by our study; however, edge effects on nest predation have most commonly been documented within 50 m of stand boundaries (Paton 1994, Donovan et al. 1997, Winter et al. 2000).

Lack of an association between patch size and predation rate among our fragment sites may be related to the different character of edge in shrubsteppe landscapes and the degree of fragmentation in our study area. Predators associated with agricultural lands may move easily through adjacent shrubsteppe (Rotenberry 1998), and the mere presence of agricultural fields or developed lands in the landscape may play a larger part than the size of the fragment in determining activity of magpies and other generalist predators. The shrubsteppe landscape in eastern Washington has a fine-grained fragmentation relative to some other regions; shrubsteppe landscapes with a coarser grain may experience different edge and patch-size effects on nest predation. The interaction of landscape and local variables on factors affecting avian productivity has been elucidated for midwestern forests (Robinson et al. 1995, Donovan et al. 1997), but this remains a pressing need for grassland and shrubland communities.

While we believe that our artificial nest experiment provided a measure of relative activity of several potential nest predators in different landscapes, we also recognize inherent biases in the use of artificial nests (with or without cameras) that may attract or deter potential nest predators (Martin 1987). Coyotes are common on our study areas, but may have avoided our camera nests because of human scent (Macivor et al. 1990) or reluctance to approach novel items in their environment (Hernandez et al. 1997). In contrast, corvids are attracted to novel items in their environment and may have been attracted to the cameras, despite our best attempts at camouflage. Snakes can be important nest predators (Savidge 1987) but are unlikely to recognize unattended eggs in artificial nests as food (Marini and Melo 1998). In our study, predators not represented adequately by experiments using quail eggs (e.g., small mammals, snakes) may have been driving predation of passerine nests on some sites. Small mammals were the dominant predator visiting artificial nests in continuous sites, and their limited capacity to open quail-size eggs is well known (Haskell 1995, DeGraaf and Maier 1996). In contrast, corvids may have driven predation in fragments, where they were both more abundant and more frequent visitors to camera nests.

As with virtually all studies of this type, our artificial nests included only eggs and thus may only represent predation during the incubation phase of nesting. The added scent and activity associated with the nestling phase adds elements not replicated in egg-only studies, and some potential predators may not be represented. For example, snakes can be important nest predators in grasslands (Davison and Bollinger 2000) and predation of nests by snakes is greater during the nestling stage (James et al. 1983, Thompson et al. 1999). Gopher snakes (*Pituophis catenifer*) depredated nestling Sage Sparrows on our study area (WMV, unpubl. data) and may have been attracted by increased activity of adults at the nest or by scent of young. Snakes and other predators that use chemical cues to find prey may be more important in the later days of nesting and their effects likely were under-represented in our study.

We conclude that while artificial nests baited with quail eggs paralleled the general pattern of predation on real nests between landscapes, this technique was incapable of detecting the finer-scale pattern among study sites that likely reflected local variation in predator communities. Using smaller eggs (Maier and DeGraaf 2000) and more realistic nests (Davison and Bollinger 2000) might increase the utility of this technique for shrubsteppe passerines, but predation by snakes would remain an unknown source of variation.

Findings from our artificial nest study may be more representative of species like Greater Sage-Grouse and Sharp-tailed Grouse, where egg size is more appropriate and the nestling stage is sharply abbreviated. Ours is the first study to report predation rates as a function of fragmentation in shrubsteppe, and our findings indicate a benefit to nesting in continuous habitat. Clawson and Rotella (1998) reported no effect of patch size on predation of artificial nests in remnant shrubsteppe among agricultural fields and planted grassland, but their shrubsteppe patches were generally small (<16 ha) and their sampling design included no unfragmented habitat. Ravens can be significant predators of Sage Grouse nests (Batterson and Morse 1948) and our camera data implicate corvids as major predators in fragmented shrubsteppe. Greater vegetation cover at successful nests has been reported both for artificial (DeLong et al. 1995, Clawson and Rotella 1998, this study) and real (Wallestad and Pyrah 1974, Gregg et al. 1994) Sage Grouse nests, also implicating visual predators like corvids.

Our results identify one component of productivity (nest predation) that may play a part in the reported declines of some shrubsteppe birds. Lower rates of nest success in fragmented landscapes may drive local populations to act as sinks (Pulliam 1988), requiring periodic immigration of individuals from source populations (presumably large, continuous sites) to avoid extirpation. In landscapes like eastern Washington, where fragmentation of shrubsteppe is a continuing phenomenon, conversion of source habitats into sinks could drive populations gradually downward. Clearly, lower nesting success implied by our findings does not necessarily equate to reduced annual productivity, as females could make up the difference by persistent renesting, by double brooding, or through greater juvenile survival rates (Powell et al. 1999, Murray 2000). Assessing the full effects of habitat fragmentation on the productivity of shrubsteppe birds will require measuring annual reproductive success of individual females or pairs, along with adult and juvenile survival rates.

ACKNOWLEDGMENTS

Support for this project was provided by the National Fish and Wildlife Foundation, Washington Department of Fish and Wildlife, Washington Department of Natural Resources, U.S. Forest Service, U.S. Department of Energy, and Battelle-Pacific Northwest Laboratory. Reviews by D. Dobkin, T. Maier, J. Marzluff, and K. Nelson improved the manuscript. K. Riding provided statistical support, and P. Doran, L. Fitzner, D. Friesz, R. Handler, L. Lipinski, L. Marsh, S. Negri, M. Nelson, D. Peterson, and J. Slotterback assisted with fieldwork. Mention of trade names does not constitute endorsement by the U.S. Government.

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