

PATTERNS OF ARTIFICIAL NEST DEPREDATION IN A LARGE FLOODPLAIN FOREST

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Abstract: We used artificial bird nests to examine the relative effects of local habitat features and the surrounding landscape on the probability of songbird nest depredation in floodplain forests of the Upper Mississippi River. We found that the probability of depredation increased with size of floodplain forest plots. In small plots, the probability of depredation tended to increase away from the forest edge. Small patches of floodplain forest within a large river system can provide valuable nesting habitat for songbirds. We suggest that depredation pressure may be lower due to isolation effects. The probability of nest depredation increased with increasing canopy cover surrounding the nest tree and decreasing cover around the nest. Managers seeking to discourage nest predators in floodplain forests should consider managing for habitats that supply dense cover for nest concealment and an open tree canopy.

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Nest depredation is the largest source of songbird nest failure in many regions of North America, accounting for 55–79% of all nest losses (Ricklefs 1969). Depredation rates on songbird nests depend upon a complex set of processes involving predator–prey dynamics and factors such as predator identity, nest density, prey availability, and prey spatial distribution (Wiens 1976, Donovan et al. 1997). Interactions between predators and their prey can be complex when entire communities of both predators and prey are involved (Oksanen et al. 1992, Schmidt and Whelan 1998). Conservation of songbird populations requires some generalization of this complexity and the linking of general patterns with factors that can be measured and potentially influenced by management.

Several investigators have found that nest placement, such as proximity to an edge, within the focal habitat patch can influence nest depredation in forest songbirds (Paton 1994, Major and Kendal 1996, Donovan et al. 1997). Properties of the surrounding landscape matrix can also influence depredation patterns (Andren 1995, Jokimaki and Huhta 1996). Ornithologists

working in upland forests have found that depredation rates tend to be lower in large forests and away from forest edges (Hartley and Hunter 1998). Unique habitats provide opportunities to test the generality of these ecological patterns.

Large floodplain forests are unique in that they are surrounded by a matrix of water and marsh rather than agricultural land. These forests are exceptionally rich habitats for birds (Knutson et al. 1996) and undergo periodic disturbances due to flooding (Knutson and Klaas 1997). Few studies have examined nest depredation in large floodplain forests (Petit 1989, Knutson et al. 1996). We studied forest songbird nest depredation patterns in floodplain forests of the Upper Mississippi River, a large river ecosystem that still retains much of its natural structure and function, including extensive tracts of floodplain forest (Sparks et al. 1998). Breeding songbird diversity in the study area is high, with about twice as many individual birds per unit area in the floodplain forests as in adjacent upland forests (Knutson et al. 1996). In addition, these forests provide habitat for many neotropical migrant birds that are uncommon or not found in adjacent upland habitats (Knutson and Klaas 1998).

We tested the effects of local habitat features

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and landscape matrix properties on the probability of nest depredation in a large floodplain forest ecosystem where habitat patches are floodplain forests and the matrix is water and marsh. We explored how nest depredation is associated with large-scale landscape factors (plot size and distance from edge) and small-scale, local habitat conditions (nest height, nest tree diameter, cover surrounding the nest, and shrub and tree canopy cover near the nest). We also investigated whether the probability of nest depredation changed over the nesting season. We expected that the probability of nest depredation would be high for nests placed in (1) small plots, (2) near forest edges, (3) close to the ground, (4) in small trees, (5) sparse nest concealment, (6) sparse shrub cover, and (7) sparse tree canopy cover surrounding the nest. We also expected that the probability of nest depredation would be higher early rather than later in the nesting season (Wilson and Cooper 1998).

STUDY AREA

Our study area included floodplain forests of the Upper Mississippi River from Winona, Minnesota to Lansing, Iowa (river navigation pools 6 through 9), a distance of about 110 km. The width of the river ranges from 2–3 km in the study area. This section of the Mississippi River is unleveed, with 4 locks and dams and an engineered 2.7-m navigation channel flanked by backwater pools, marshes, and floodplain forests. The study area is located in the Driftless Area Ecoregion (Bailey et al. 1994) and is part of the Upper Mississippi River National Wildlife and Fish Refuge, designated a globally important bird area by the American Bird Conservancy (U.S. Department of the Interior 1998) because of exceptionally high bird use during migration and during the breeding season. Floodplain forests in the study area range from large (>200 ha) contiguous forests to small (<20 ha) forested islands (Knutson and Klaas 1998). Silver maple (*Acer saccharinum*) was the dominant tree species in the study area, along with green ash (*Fraxinus pennsylvanica*) and elm (*Ulmus* spp.). Shrubs were sparse, but thick patches of poison ivy (*Toxicodendron radicans*) and prickly ash (*Zanthoxylum americanum*) were present in some locations. The understory of the closed canopy forest was dominated by nettles (*Urtica* spp.) and canopy gaps were

dominated by reed canary grass (*Phalaris arundinaceae*).

METHODS

Nest Construction, Placement, and Plot Selection

Nests were constructed of 2.5-cm wire mesh, with finished dimensions approximately 10 × 7 cm and lined with leaves or grass from the site. Two fresh northern bobwhite (*Colinus virginianus*) eggs were placed in each nest. The eggs were dulled with mud from the site to simulate natural egg speckling. Field workers handled the eggs and nests with rubber gloves and wore rubber waders to minimize human scent. Nests were checked on the sixth day after placement.

Artificial nests were placed from late May through early July in 1993 and 1994. A trial consisted of placing equal numbers of artificial nests with 2 eggs in large and small forest plots over a 2-day period. Three trials were conducted in 1993 and 4 trials in 1994. Nests were placed along transects that were 100 m apart and oriented perpendicular to the forest–water edge. In large plots, nests were placed at 25, 50, 100, and 200 m from the forest–water edge. In small plots, nests were placed at 25 and 50 m from the edge. Nests were placed 2–3 m above the ground to simulate understory nesting birds, such as the American redstart (*Setophaga ruticilla*), a common nester in these forests (Knutson and Klaas 1997). Ground nests were not used because there are very few ground-nesting forest songbirds in this habitat.

Large and small plots were randomly selected using land cover maps of the study area. Study plots were a minimum of 100 m (small plots) to 400 m (large plots) wide to accommodate the experimental transects. We calculated forest area and proportion of forest within 800 m of plot perimeters to verify assignment to the large and small size classes.

Depredation Rate and Habitat Measurements

Disturbances to the artificial nest were recorded as (1) weather damage with no depredation, (2) 1 or 2 eggs missing without nest damage, (3) eggs pecked or broken without nest damage, (4) eggs missing or broken with damage to the nest, and (5) all other disturbances. For the purposes of model testing described below, weather-damaged nests were eliminated

and all other disturbed nests were considered depredated.

Nest-specific habitat covariates were recorded, including nest height, measured with a clinometer, and a visual estimate of nest (leaf) cover within 0.5 m of the nest. We recorded the nest tree diameter (dbh) at 1.3 m above the ground in 4 size classes: 8–15, 16–30, 31–50, and >50 cm. Tree canopy cover within an 11.3-m (0.04 ha) radius surrounding the nest was visually estimated in 3 classes: 0–50, 51–75, and 76–99%. Shrub cover (woody plants 0.5–4 m tall) was visually estimated in 3 classes: 0–5, 6–30, and >30%, within an 11.3-m radius circle surrounding the nest.

Data Analysis

We examined spatial patterns of depredation on artificial nests and potential effects of nest-specific covariates using a generalized linear mixed model (Karim and Zeger 1992, Breslow and Clayton 1993, Wolfinger and O'Connell 1993). The generalized linear mixed model is an extension of a generalized linear model (McCullagh and Nelder 1989) that includes both fixed and random effects. Our model is a generalization of logistic regression (Hosmer and Lemeshow 1989) that includes categorical design points and random subject effects. Prominent model features include: (1) an assumption that the number of depredation events in a fixed number of nests follows a binomial distribution; (2) the existence of multiple nest-specific covariates; and (3) a random effect for transects nested within the unique combinations of forest fragments (sites), years, and trials that serves as the error term for tests of site, year, and trial effects. This modeling approach allows us to use the natural probability distribution for nest depredation and to construct appropriate tests of design effects and the covariates.

In our model, y_{ijklm} denotes nest depredation status in the i th trial (T_i), during the j th year (Y_j), in the k th size of forest fragment (S_k), along the l th transect ($\tau_{ijk(l)}$) nested within year, size, and trial, and at the m th distance ($D_{k(m)}$) from the edge of the k th-sized fragment. The value $y_{ijklm} = 1$ indicates nest depredation occurred and $y_{ijklm} = 0$ indicates otherwise. We assume that y_{ijklm} followed a Bernoulli distribution (binomial distribution for $n_{ijklm} = 1$) given by $f(y_{ijklm} | \pi_{ijklm}) = \pi_{ijklm}^{y_{ijklm}} (1 - \pi_{ijklm})^{(1-y_{ijklm})}$. We

modeled the Bernoulli parameters π_{ijklm} by using

$$\begin{aligned} \log\left(\frac{\pi_{ijklm}}{1 - \pi_{ijklm}}\right) &= \mu + T_i + Y_j + TY_{ij} + S_k + TS_{ik} + YS_{jk} \\ &+ TYS_{ijk} + \tau_{ijk(l)} + D_{k(m)} + YD_{jk(m)} \\ &+ \beta_1 H_{ijklm} + \beta_2 N_{ijklm} + \beta_3 U_{ijklm} + \beta_4 C_{ijklm} \\ &+ \beta_5 X_{ijklm} + \epsilon_{ijklm}, \end{aligned}$$

where the term on the left-hand side is the logit of depredation probability π_{ijklm} , μ is the overall mean, TY_{ij} is the interaction between trial and year (other interactions have a similar form), the $\beta_1 \dots \beta_5$ are parameters for the linear effects of nest height (H), nest cover (N), understory density (U), canopy cover (C), and tree dbh (X), and ϵ_{ijklm} is residual error. For our nest depredation events, the conditional variance of ϵ_{ijkl} has the form $\phi \pi_{ijkl} (1 - \pi_{ijkl})$, where ϕ is an extra-binomial dispersion or scale parameter that is estimated by maximum likelihood. For the binomial distribution, $\phi = 1$; values of ϕ that are substantially less than or greater than one indicate under- or over-dispersion relative to the binomial distribution. We treated transects as random-effect subjects from which multiple measurements of nest depredation were made, and we assumed that the $\tau_{ijk(l)}$ were normally distributed with mean zero and variance σ_τ^2 . Although an examination of spatial covariance patterns among nests might have been interesting, it was not permitted by our sampling design.

Like simpler logistic regression models, the parameters in our model have natural interpretations. The quantity π_{ijklm} is the probability of nest depredation in the i th trial during the j th year in the size of forest fragment, and at the m th distance from the edge. We used graphs of the predicted probabilities of nest depredation ($\hat{\pi}_{ijklm}$) to demonstrate apparent patterns in nest depredation.

We fitted this model using the SAS-based Glimmix software (<http://www.sas.com/techsup/download/stat/glmm612.sas>) that produces restricted pseudo-likelihood estimates (Wolfinger and O'Connell 1993) of model parameters. We used Satterthwaite approximations (Griesbrecht and Burns 1985) to estimate degrees of freedom for the fixed-effects tests. We began our

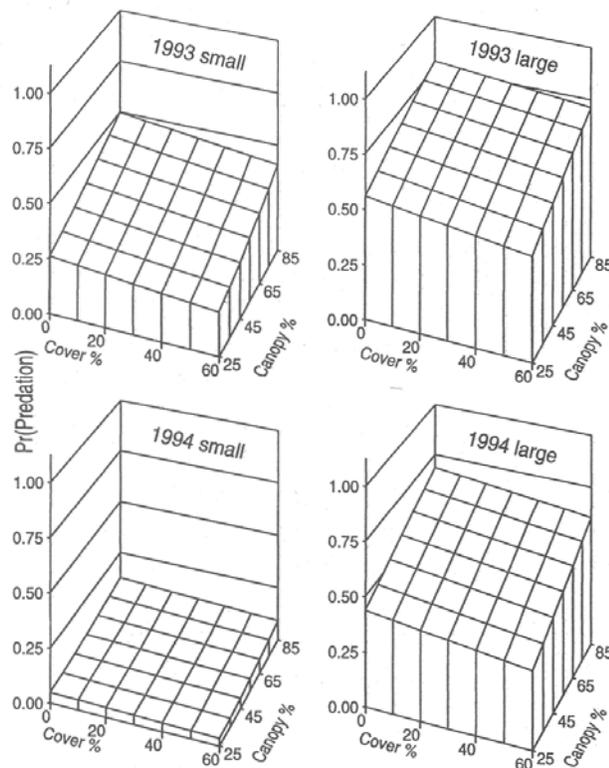


Fig. 1. Probability of predation for artificial nests placed in the floodplain of the Upper Mississippi River, 1993–94, predicted from the fit to a mixed-effects logistic model. Plots are for the second trials in each year and show effects of year, plot size, percent nest cover (cover %) and percent canopy cover (canopy %).

analysis by fitting this full model and, in subsequent steps, deleted nonsignificant effects one-by-one until we identified the simplest model that adequately fitted the data. However, nonsignificant main effects were retained whenever any main-effects terms were involved in a statistically significant interaction. We assessed overall model fit by using the scaled deviance (McCullagh and Nelder 1989) and used *F* tests based on Wald statistics (Wolfinger and

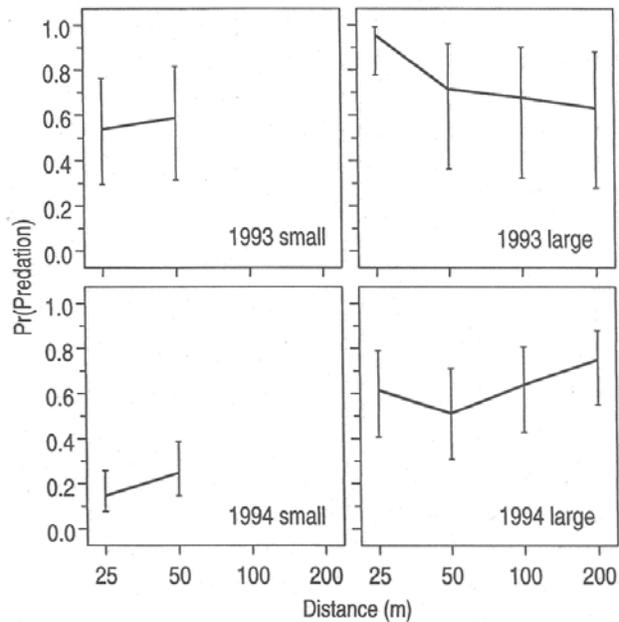


Fig. 2. Predicted probabilities of predation for artificial nests placed in the floodplain of the Upper Mississippi River, 1993–94, as functions of the interaction between year and distance nested within plot size. Vertical bars are 95% CI.

O’Connell 1993) for this model simplification. The deviance is twice the difference between the log likelihoods for the data and the model and provides a measure of goodness of fit. The scaled deviance is the deviance divided by the scale parameter.

RESULTS

Forest Composition and Sample Size

We confirmed our assignment of plots to size classes by observing that the amount of forested land within 800 m of our large plot perimeters averaged 214 ha (range: 196–226 ha); for small plots it averaged 104 ha (range: 70–159 ha). Forested habitat comprised about 62% of the

Table 1. Tests of significance of fixed and random effects in the final generalized logistic model of artificial nest depredation in forest fragments in the floodplain of the Upper Mississippi River, 1993–94. The test for the random effect of transect within site (combinations of year, size, and trial) is an approximate normal-theory Wald test. Tests of the fixed effects are described in the text. Denominator degrees of freedom were computed by Satterthwaite approximation (Griesbrecht and Burns 1985).

Effect	Model parameters	Degrees of freedom		<i>F</i>	<i>P</i> -value
		Numerator	Denominator		
Trial	T_i	3	106	1.3	0.26
Year	Y_j	1	90	5.0	0.03
Size	S_k	1	117	12.0	<0.01
Trial × size	TS_{ik}	3	107	4.6	<0.01
Distance within size	$D_{l(k)}$	4	230	1.9	0.10
Year × distance within size	$YD_{jl(k)}$	5	243	2.2	0.05
Transect within site	σ_τ^2	—	—	—	<0.01
Nest cover	β_2	1	314	3.6	0.06
Canopy cover	β_4	1	314	5.4	0.02

area surrounding large plots and 35% of the area surrounding the small plots. We conducted 3 trials in 1993 (trial 1: $N_{28-29 \text{ May}} = 56$, trial 2: $N_{9-10 \text{ June}} = 56$, trial 3: $N_{2 \text{ July}} = 63$) and 4 trials in 1994 (trial 1: $N_{24-25 \text{ May}} = 64$, trial 2: $N_{8-9 \text{ June}} = 64$, trial 3: $N_{21-22 \text{ June}} = 64$, trial 4: $N_{5-6 \text{ July}} = 64$). Trial 3 in 1993 was dropped from the analysis because it was conducted under flooded conditions. Nearly the entire floodplain was under water due to unusually high rainfall.

Habitat Variables and Evidence of Nest Depredation

Nest height was $2.5 \pm 0.5\text{m}$ ($\bar{x} \pm \text{SD}$); dbh of the nest tree averaged 21.7 ± 14.7 cm, leaf cover within 0.5 m of the nest averaged $32.3 \pm 42.4\%$, tree canopy cover averaged $78.1 \pm 18.5\%$, and shrub cover averaged $21.2 \pm 18.0\%$. In 74.4% ($N = 142$) of depredated nests the eggs were missing with the nest itself left undisturbed; 16.2% ($N = 31$) of nests were damaged in addition to the loss of eggs; 8 nests had eggs that were pecked or broken; 2 nests were lost to weather-related causes.

Depredation Rates at Artificial Nests

Large forest plots generally had a higher probability of nest depredation than small forest plots (Fig. 1). The only exception to this pattern was trial 1 in 1993, where the pattern was reversed, and trial 1 of 1994 where the probability of nest depredation was similar between large and small plots. These 2 exceptions created the statistically significant interaction between size and trial (Table 1). The probability of nest depredation increased with the increasing density of canopy cover surrounding the nest tree and decreasing nest cover around the nest (Table 1, Fig. 1). In small plots, the probability of nest depredation tended to increase away from the forest edge (Fig. 2). The opposite pattern held for large plots between 25 and 50 m from the forest edge. Opposite patterns were observed between the 2 years at the 100- and 200-m distances. Although this complex pattern of nest predation over distance from edge was only marginally significant ($P = 0.10$ for distance within site and $P = 0.06$ for the interaction of year and distance within site; Table 1), deletion of both terms involving distance significantly reduced overall model fit. Therefore, we conclude that this complex effect of distance from edge is likely real. Nest height, understory density, and tree dbh were not statistically significant (P

> 0.05) in predicting the probability of a depredation event and were omitted from the final model. Our estimate of the extra-dispersion parameter $\hat{\Phi}$ was 0.7 indicating slight underdispersion relative to the binomial distribution. The scaled deviance was 377 with 348 df and indicated an adequate fit to the data (McCullagh and Nelder 1989). Our estimate of the transect variance component $\hat{\sigma}_\tau^2$ (1.94, SE = 0.53) was significantly different from 0 (Table 1).

DISCUSSION

Our finding of a higher probability of nest depredation in large tracts of forest is the reverse of patterns usually observed in upland forests. Many studies of upland forests, including tropical forests, have documented lower nest depredation in large than small forests (Wilcove 1985, Andren and Angelstam 1988, Small and Hunter 1988, Yahner and Scott 1988, Donovan et al. 1997, Cooper and Francis 1998), but some have not (Yahner and Voytko 1989, Nour et al. 1993, Leimgruber et al. 1994, Huhta et al. 1998). Andren (1995) reviewed 40 studies that examined the effect of habitat edge and patch size on nest depredation. The review showed that higher nest depredation near edges and in small patches is common in landscapes where farmland predominates, but it is often not observed in forest mosaics, open habitats, or on islands. Our landscape fits the island category and our results agree with the findings of Andren (1995). Small and Hunter (1988) also found a lower probability of depredation on artificial nests near a forest-water edge. The contradicting patterns of trial 1 in both years may indicate that either the predators or how they use the landscape are different early in the nesting season (May).

Our finding that nest depredation tends to increase away from forest-water edges in fragmented plots was consistent across years, but edge depredation patterns in large plots varied from year to year (Fig. 2). The pattern observed in 1993 on large plots is similar to patterns observed in upland forests within an agricultural matrix (Andren 1995), where nest depredation rates decline as distance from edge increases. Many nesting studies in upland habitat also report higher nest depredation near forest edges (Paton 1994, Fenske-Crawford and Niemi 1997). In contrast, our 1994 data indicated that

predators use both edges and interiors equally well in floodplain forests.

Large forest patches may be primary habitats for floodplain predators. Small forest patches are likely too small to support a resident predator population (other than small mammals), thus explaining why we observed lower depredation rates in small patches. Water covers 27–44% of the total floodplain area in the pools we studied (Lastrup and Lowenberg 1994), potentially limiting predator movement and isolating small forest patches. Theoretical models describing predator–prey dynamics in patchy habitat predict that depredation results from “spill over” of predators from high-quality habitats into low-quality habitats (Angelstam 1986, Morris 1988, Oksanen 1990, Oksanen et al. 1992). Small forest patches in a floodplain matrix may experience “spill over” effects of predators visiting from larger patches. Andren (1992) found that the behavior of bird predators may also be influenced by landscape features; corvid depredation on nests was lower in smaller forest fragments.

Our failure to find a significant trial (i.e., time) effect is consistent with other studies (Best and Stauffer 1980, Yahner et al. 1989, Nour et al. 1993, Leimgruber et al. 1994, Sloan et al. 1998). Songbird nest depredation may be density-dependent, where higher nest density is associated with higher depredation rates (Gates and Gysel 1978, Martin 1988, Schmidt and Whelan 1998). High depredation pressure should correspond to the time when predators can most efficiently obtain rewards for raiding nests (Wiens 1976), such as early in the nesting season, when most nests contain eggs or young. This hypothesis is consistent with a few studies observing declines in depredation rates over the nesting season (Howell 1942, Nice 1957). However, floodplain forest predators are primarily dependent upon more dependable food sources and only opportunistically depredate bird eggs, which may explain our relatively even distribution of predation pressure over the nesting season.

Our findings support the hypothesis that nest concealment reduces depredation events. Other studies have found similar relationships (Angelstam 1986, Leimgruber et al. 1994, Cooper and Francis 1998, Huhta et al. 1998), but others have not (Best and Stauffer 1980, Yahner and Voytko 1989, Reitsma et al. 1990, Donovan et al. 1997, Jobin and Picman 1997). Nest con-

cealment is effective in deterring bird predators but not mammalian predators on duck nests (Clark and Nudds 1991). Understory density was not a significant factor in our study, even though we expected a thick understory to decrease efficiency of predators.

The primary predators in our study occupied mature closed-canopy floodplain forests with sparse understory vegetation. The predators were more active in large than in small forest plots, were deterred by cover concealing the nest and sparse canopy cover, and were negatively affected by flooding (M. Knutson, this study, unpublished data). Depredation on natural nests by mink (*Mustela vison*) and common grackles (*Quiscalus quiscula*) was observed in the study area. Field observations indicate that grackles play a significant role in nest depredation in these forests.

Evidence from our depredated nests (eggs missing without other disturbance) implicates birds or snakes as primary predators (Best 1974, Best and Stauffer 1980, Hensley and Smith 1986). House wrens (*Troglodytes aedon*) were common in our forests; pecked eggs without loss were attributed to house wrens (Belles-Isles and Picman 1986a,b). Unfortunately, identifying nest predators by evidence left at the nest is not always a reliable method (Bayne et al. 1997, Marini and Melo 1998).

MANAGEMENT IMPLICATIONS

Nesting studies in Midwestern landscapes suggest that characteristics of the landscape matrix can drive processes at smaller scales and should be the first predictor of nest depredation risk for forest songbirds (Donovan et al. 1997). We derived similar conclusions in a landscape where water is the primary component of the matrix. In very large floodplain systems like the Upper Mississippi River, the large forest patches are probably the primary habitats for nest predators. Small patches of floodplain forest within a large river system can provide valuable nesting habitat for songbirds. We suggest that depredation pressure may be lower due to isolation effects. However, in smaller riparian systems, where floodplain forests are connected to adjacent upland habitats, isolation and its benefits are lost. In smaller riparian systems, there are clear advantages to managing for large contiguous forests (Stauffer and Best 1980, Knutson et al. 1996). In addition to considerations of the matrix surrounding habitat patches, man-

agers seeking to discourage nest predators in floodplain forests should consider managing for habitats that supply dense cover for nest concealment and an open tree canopy.

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LITERATURE CITED

- ANDREN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794–804.
- . 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225–255 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, New York, New York, USA.
- , AND P. ANGELSTAM. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544–547.
- ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365–373.
- BAILEY, R. G., P. E. AVERS, T. KING, AND W. H. MCNAB. 1994. Ecoregions and subregions of the United States. U.S. Forest Service, ECOMAP Team, Washington, D.C., USA.
- BAYNE, E. M., K. A. HOBSON, AND P. FARGEY. 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. *Ecography* 20:233–239.
- BELLES-ISLES, J. C., AND J. PICMAN. 1986a. Destruction of heterospecific eggs by the gray catbird. *Wilson Bulletin* 98:603–605.
- , AND ———. 1986b. House wren nest-destroying behavior. *Condor* 88:190–193.
- BEST, L. B. 1974. Blue racers prey on field sparrow nests. *Auk* 91:168–169.
- , AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82:149–158.
- BRESLOW, N. E., AND D. G. CLAYTON. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.
- CLARK, R. G., AND T. D. NUDDS. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. *Wildlife Society Bulletin* 19:534–543.
- COOPER, D. S., AND C. M. FRANCIS. 1998. Nest predation in a Malaysian lowland rain forest. *Biological Conservation* 85:199–202.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- FENSKE-CRAWFORD, T. J., AND G. J. NIEMI. 1997. Predation of artificial ground nests at two types of edges in a forest-dominated landscape. *Condor* 99:14–24.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledgling outcome in field-forest edges. *Ecology* 59:871–883.
- GRIESBRECHT, F. G., AND J. C. BURNS. 1985. Two-stage analysis based on a mixed model: large-sample theory and small-sample simulation results. *Biometrics* 41:477–486.
- HARTLEY, M. J., AND M. L. HUNTER, JR. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conservation Biology* 12:465–469.
- HENSLEY, R. C., AND K. G. SMITH. 1986. Eastern bluebird responses to nocturnal black rat snake nest predation. *Wilson Bulletin* 98:602–603.
- HOSMER, D. W., JR., AND S. LEMESHOW. 1989. *Applied logistic regression*. John Wiley & Sons, New York, New York, USA.
- HOWELL, J. C. 1942. Notes on the nesting habits of the American robin (*Turdus migratorius* L.). *American Midland Naturalist* 29:529–603.
- HUHTA, E., J. JOKIMAKI, AND P. HELLE. 1998. Predation on artificial nests in a forest dominated landscape—the effects of nest type, patch size and edge structure. *Ecography* 21:464–471.
- JOBIN, B., AND J. PICMAN. 1997. The effect of egg coloration on predation of artificial ground nests. *Canadian Field Naturalist* 111:591–594.
- JOKIMAKI, J., AND E. HUHTA. 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. *Ornis Fennica* 73:97–113.
- KARIM, M. R., AND S. L. ZEGER. 1992. Generalized linear models with random effects: salamander mating revisited. *Biometrics* 48:631–644.
- KNUTSON, M. G., J. P. HOOVER, AND E. E. KLAAS. 1996. The importance of floodplain forests in the conservation and management of neotropical migratory birds in the midwest. Pages 168–188 in F. R. Thompson, editor. *Management of midwestern landscapes for the conservation of neotropical migratory birds*. U.S. Forest Service General Technical Report NC-187.
- , AND E. E. KLAAS. 1997. Declines in abundance and species richness of birds following a major flood on the Upper Mississippi River. *Auk* 114:367–380.
- , AND ———. 1998. Floodplain forest loss and changes in forest community composition and

- structure in the Upper Mississippi River: a wildlife habitat at risk. *Natural Areas Journal* 18:138–150.
- LAUSTRUP, M. S., AND C. D. LOWENBERG. 1994. Development of a systematic land cover/land use database for the Upper Mississippi River System derived from Landsat thematic mapper satellite data. National Biological Survey, Environmental Management Technical Center, Onalaska, Wisconsin, USA.
- LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58:254–260.
- MAJOR, R. E., AND C. E. KENDAL. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298–307.
- MARINI, M. A., AND C. MELO. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* 100:395–399.
- MARTIN, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Sciences* 85:2196–2199.
- MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. Second edition. Chapman and Hall, New York, New York, USA.
- MORRIS, D. W. 1988. Habitat-dependent population dynamics and community structure. *Evolutionary Ecology* 2:253–269.
- NICE, M. M. 1957. Nesting success in altricial birds. *Auk* 74:305–321.
- NOUR, N., E. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography* 16:111–116.
- OKSANEN, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. *Evolutionary Ecology* 4:220–234.
- , L. OKSANEN, AND M. GYLLENBERG. 1992. Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator-prey dynamics. *Evolutionary Ecology* 6:383–398.
- PATON, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17–26.
- PETIT, L. J. 1989. Breeding biology of prothonotary warblers in riverine habitat in Tennessee. *Wilson Bulletin* 101:51–61.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375–380.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.
- SCHMIDT, K. A., AND C. J. WHELAN. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *American Naturalist* 152:393–402.
- SLOAN, S. S., R. T. HOLMES, AND T. W. SHERRY. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* 62:529–539.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62–64.
- SPARKS, R. E., J. C. NELSON, AND Y. YIN. 1998. Naturalization of the flood regime in regulated rivers: the case of the Upper Mississippi River. *BioScience* 48:706–720.
- STAUFFER, D. F., AND L. B. BEST. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alteration. *Journal of Wildlife Management* 44:1–15.
- U.S. DEPARTMENT OF THE INTERIOR. 1998. Upper Mississippi wildlife refuges are globally important to migratory birds. *People, Land, and Water* 5:22.
- WIENS, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81–120.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–1214.
- WILSON, R. R., AND R. J. COOPER. 1998. Breeding biology of Acadian flycatchers in a bottomland hardwood forest. *Wilson Bulletin* 110:226–232.
- WOLFINGER, R., AND M. O'CONNELL. 1993. Generalized linear mixed models: a pseudo-likelihood approach. *Journal of Statistical Computation and Simulation* 48:233–243.
- YAHNER, R. H., T. E. MORRELL, AND J. S. RACHAEL. 1989. Effects of edge contrast on depredation of artificial avian nests. *Journal of Wildlife Management* 53:1135–1138.
- , AND D. P. SCOTT. 1988. Effects of forest fragmentation on depredation of artificial nests. *Journal of Wildlife Management* 52:158–161.
- , AND R. A. VOYTKO. 1989. Effects of nest-site selection on depredation of artificial nests. *Journal of Wildlife Management* 53:21–25.

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