

AVIAN NEST SUCCESS IN MIDWESTERN FORESTS FRAGMENTED BY AGRICULTURE

MELINDA G. KNUTSON^{1,5}, GERALD J. NIEMI², WESLEY E. NEWTON³ AND
MARY A. FRIBERG^{4,6}

¹U.S. Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road,
La Crosse, WI 54603

²Natural Resources Research Institute and Department of Biology, University of Minnesota,
Duluth, MN 55811

³U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street SE,
Jamestown, ND 58401

⁴University of Minnesota, Graduate Program in Conservation Biology, 1518 North Cleveland Ave.,
St. Paul, MN 55108

Abstract. We studied how forest-bird nest success varied by landscape context from 1996 to 1998 in an agricultural region of southeastern Minnesota, southwestern Wisconsin, and northeastern Iowa. Nest success was 48% for all nests, 82% for cavity-nesting species, and 42% for cup-nesting species. Mayfield-adjusted nest success for five common species ranged from 23% for the American Redstart (*Setophaga ruticilla*) to 43% for the Eastern Wood-Pewee (*Contopus virens*). Nest success was lowest for open-cup nesters, species that reject Brown-headed Cowbird (*Molothrus ater*) eggs, species that nest near forest edges, and Neotropical migrants. The proportion of forest core area in a 5-km radius around the plot had a weakly negative relationship with daily survival rate of nests for all species pooled and for medium or high canopy nesters, species associated with interior and edge habitats, open-cup nesters, and nests located between 75 and 199 m from an edge. The proportion of forest core area was positively related to daily survival rate only for ground and low nesters. Our findings are in contrast to a number of studies from the eastern United States reporting strong positive associations between forest area and nesting success. Supported models of habitat associations changed with the spatial scale of analysis and included variables not often considered in studies of forest birds, including the proportion of water, shrubs, and grasslands in the landscape. Forest area may not be a strong indicator of nest success in landscapes where all the available forests are fragmented.

Key words: agriculture, Driftless Area, forest fragmentation, functional group, landscape, midwestern United States, nest success.

Éxito de Nidificación de Aves en Bosques del Medio-Oeste Fragmentados por Agricultura

Resumen. Entre 1996 y 1998 comparamos el éxito de nidificación en diferentes especies y paisajes en 18 parcelas ubicadas en una región agrícola del sudeste de Minnesota, sudoeste de Wisconsin y noreste de Iowa. El éxito de nidificación fue del 48% para todas especies, del 82% para las especies que nidifican en cavidades y del 42% para las especies con nidos en forma de taza. El porcentaje del éxito de nidificación ajustado según el criterio Mayfield para cinco especies comunes varió entre el 23% para *Setophaga ruticilla* y el 43% para *Contopus virens*. El éxito de nidificación fue menor para aves con nidos en forma de taza, para especies que rechazan los huevos de *Molothrus ater*, para especies que nidifican cerca del borde del bosque y para migrantes neotropicales. Al considerar áreas circulares de 5 km de radio, detectamos una correlación negativa débil entre la proporción de área de bosque y el índice de supervivencia diario de nidos para todas especies estudiadas, para las que nidifican en alturas medianas y altas del dosel, para especies asociadas con hábitats del interior o del borde del bosque, para especies de nidos en forma de taza y para nidos ubicados entre 75 y 199 m del borde. Sólo las especies que nidifican sobre el suelo o a baja altura presentaron una correlación positiva entre la proporción de área de bosque y el índice de supervivencia diario. Nuestros resultados contrastan con varios estudios del este de los Estados Unidos que muestran fuertes asociaciones positivas entre el área de bosque y el éxito de nidificación. Los modelos de asociación de hábitat empleados cambiaron con la

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⁵ E-mail: melinda_knutson@usgs.gov

⁶ Present address: USDA Forest Service, Alaska Region, Juneau, AK 99802.

escala espacial de análisis e incluyeron variables usualmente no consideradas por otros estudios, como la proporción de agua, arbustos o pastizales en el paisaje. Es posible que el área de bosque no sea un factor importante en el éxito de nidificación en paisajes donde todo el bosque disponible está fragmentado.

INTRODUCTION

Theoretical models predict that forest fragmentation should negatively affect forest-nesting bird populations when forests occupy <30% of the landscape and a number of other species-specific conditions are met (With et al. 1997, Fahrig 1998). Andren (1994) suggests that for birds, at least 30% of the landscape should be occupied by suitable habitat, a figure that is consistent with modeling results (Donovan and Thompson 2001). Some models also predict a threshold effect: populations change rapidly when the proportion of forest falls below a critical level (With and King 1999, Hanski and Ovaskainen 2000).

Field studies confirm that many forest-nesting bird species achieve their highest reproductive potential in the interiors of large, unfragmented forests (Robinson, Thompson et al. 1995). The incidence of Brown-headed Cowbird (*Molothrus ater*) parasitism and predation is generally lowest in regions with a high proportion of forest in the eastern and midwestern United States (Robinson, Thompson et al. 1995, Donovan et al. 1997, Hochachka et al. 1999). Positive associations between forest area and bird reproductive success, along with plausible ecological explanations for the underlying functional predator-prey and parasite-host dynamics (Chalfoun, Ratnaswamy, and Thompson 2002), have prompted managers to recommend increasing the size of forest patches and reducing the amount of forest edge (Faaborg et al. 1995). However, the relations between forest area, nest distance from edge, and nest success can vary (Hahn and Hatfield 1995, Hanski et al. 1996, Bielefeldt and Rosenfield 1997, Tewksbury et al. 1998). Also, cowbird effects on bird reproduction can vary with the regional context of the study and with the spatial scale of inquiry (Tewksbury et al. 1998, Hochachka et al. 1999, Fauth 2001, Gustafson et al. 2002).

Wildlife managers engaged in ecosystem management are interested in how shared life-history characteristics of multiple species (functional groups) are related to habitat quality (Verner 1984, Poiani et al. 2000). Multiple-species groupings can be guilds or management assem-

blages (Verner 1984, Block et al. 1995, Blondel 2003). Ecologists are now investigating functional groups as a metric for comparing ecosystem-level properties of taxonomically distinct faunas (Bellwood et al. 2002, French and Picozzi 2002, Rosenfeld 2002). Functional groups have been used to examine patterns of bird abundance in relation to habitat features (Freemark and Merriam 1986, Best et al. 1996, Miller et al. 1997, Jones et al. 2000), evaluate effects of habitat management or cumulative habitat changes (Croonquist and Brooks 1991, Whitaker and Montevecchi 1999), develop biotic indicators of habitat quality (O'Connell et al. 1998, Martin and Eadie 1999, Canterbury et al. 2000), and examine competitive interactions among species (Schmidt and Whelan 1998). If life-history characteristics are consistent indicators of reproductive vulnerability, membership in a functional group could be one factor in identifying species of conservation concern (Thompson et al. 1993, Freemark et al. 1995, Carter et al. 2000).

We assessed the variation in nest success of birds breeding in forests fragmented by agriculture for five species and several functional groups commonly considered in a management context. We also examined relationships between the nest success of these functional groups and landscape context (the proportion of different land cover types and edge) using three landscape scales.

METHODS

Our study plots were located in the Driftless Area Ecoregion of North America, including portions of the states of Illinois, Iowa, Minnesota, and Wisconsin (McNab and Avers 1994; Fig. 1). The landforms are dissected, upland plateaus with steep bedrock ridges descending to river drainages that ultimately flow to the Mississippi River. Forests of the Driftless Area were historically a transition zone between forest and grassland. Before European settlement, the ecoregion was covered by an oak (*Quercus* spp.) savanna complex of mixed grasslands with upland forests of sugar maple (*Acer saccharum*) and basswood (*Tilia americana*) and riverine

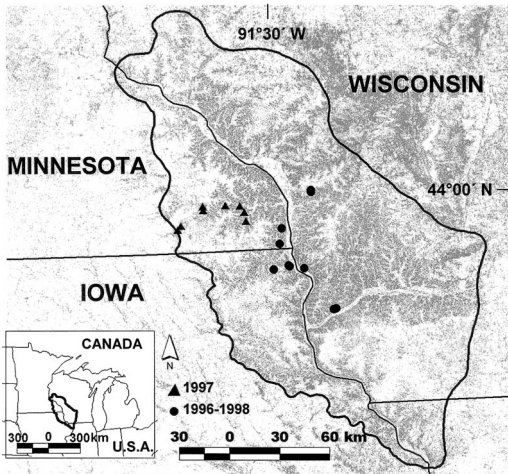


FIGURE 1. Location of upland forest study plots in the Driftless Area Ecoregion, 1996–1998. Gray areas indicate forest cover. Triangles indicate plots monitored in 1997 in addition to the eight plots monitored in all other years (circles).

forests of elm (*Ulmus* spp.), ash (*Fraxinus* spp.) and cottonwood (*Populus deltoides*; Cahayla-Wynne and Glenn-Lewin 1978, Curtis 1959). These oak savannas, under fire suppression and modern agricultural practices, have succeeded to closed-canopy oak-hickory (*Carya* spp.) woodlands within a matrix of row and forage crops (Glenn-Lewin et al. 1984, Leach and Givnish 1999). Forests are confined to steep slopes adjacent to streams and form a connected, dendritic pattern. Complex topography and erosive soils support less intensive agriculture than in many parts of the Midwest, with agriculture replacing the grasslands and occupying 30–40% of the landscape (McNab and Avers 1994).

We collected nesting data from 18 mature forest plots dominated by oak, elm, and maple. All plots were located on state forests free from grazing by domestic livestock. The proportion of total forest cover within landscape circles centering on the plots ranged from 5–100% (1-km circle), 12–56% (5 km), and 13–53% (10 km).

NEST SEARCHING AND MONITORING

We measured nest survival rates from May to July on 10 plots each year from 1996 to 1998, and eight additional plots in 1997 (Fig. 1). We located nests following standard protocols (Martin and Geupel 1993, Martin et al. 1997) by following adults and flushing incubating and

brooding birds. All active nests were monitored every 2–3 days until fledging or failure. The sum of the laying, incubation, and nestling periods was used as the observation period for each nest. Observation days began with the first day a nest was observed and ended with the last observed active date for successful nests and nests with uncertain fate; observation days ended with the midpoint between the last active visit and the first inactive visit for failed nests (Manolis et al. 2000). Nests were considered successful if they fledged at least one host young. We recorded the location of each nest using a PLGR+96 (Rockwell International Corporation, Cedar Rapids, Iowa) global positioning system. We used the Mayfield method (Mayfield 1961, Johnson 1979) to estimate daily survival rate (DSR) of nests for each combination of plot, year, and nest classification, with plot as the experimental unit.

FUNCTIONAL GROUPS

We assigned nests to functional groups by species life-history and habitat associations commonly used in management contexts (Ehrlich et al. 1988, Best et al. 1996, Sauer et al. 2003). The functional groups we considered included nest type (open cup, cavity), vulnerability to cowbird parasitism (cowbird egg acceptors, rejectors, inappropriate hosts), typical nest height (ground or low canopy [≤ 2 m], medium or high canopy [> 2 m]), habitat preference (interior forest, interior-edge and edge) and migration distance (resident, short-distance migrant, Neotropical migrant; Appendix). We also classified nests by the distance from each nest to the nearest forest edge, measured from geographic information system landcover maps. We divided the nests into three distance-to-edge classes (0–74, 75–199, ≥ 200 m); each of the three classes was represented by nearly equal numbers of nests, irrespective of species.

LANDSCAPE VARIABLES

We calculated landscape metrics using U.S. Geological Survey Gap Analysis Program classifications (Scott et al. 1993). Landscape metrics were derived from 1, 5, and 10-km-radius circles centered on the plot (314, 7854, and 31 426 ha, respectively), using the program FRAGSTATS (McGarigal and Marks 1995). Metrics used included the proportion of each circle represented by forest core area, shrub area, water, urban land use, the ratio of grass to agriculture, and the

edge density of forests. We defined the proportion of forest core area as the area of forest located at least 100 m from a forest edge, expressed as a proportion of total area within the landscape circle. Forest core area was used rather than forest area because it better represents the area of forest suitable for interior forest birds (Temple 1986). Edge density was the linear distance of forest edge per unit area (m ha^{-1}). To reduce model parameters and retain one variable representing row crops and grasslands, we used the ratio of the proportion of grassland and forage crops to the proportion of row crops (grass to agriculture ratio) in the multivariate landscape analysis. We screened the landscape metrics to reduce multicollinearity; our final set of variables had bivariate Pearson $r < 0.7$.

STATISTICAL ANALYSES

We assessed the effects of year, functional group, and the interaction of year and functional group using a repeated measures ANOVA in an incomplete block design. Each plot served as the block for the functional group, with year as the repeated measures factor (Littell et al. 1996), resulting in 38 plot-by-year combinations. We conducted separate ANOVAs for each functional group and we included year in each ANOVA to measure year-to-year variation. We used PROC MIXED, the mixed linear model procedure of SAS (SAS Institute 1997) and weighted DSR by observation days. Fisher's protected LSD procedure was used to evaluate significant differences ($\alpha = 0.05$) among least-squares means in the ANOVAs; we report SE rather than P -values adjusted for multiple tests (Milliken and Johnson 1984, Johnson 1999).

We used multiple regression procedures with Mallows's C_p selection (PROC REG, SAS Institute 1990) to derive landscape habitat models for DSR using landscape habitat metrics as explanatory variables, weighting by observation days. The experimental unit was the plot-year. Regression analyses were conducted for each of three landscape scales (1, 5, and 10-km circles) for all species and each functional group. We report adjusted R^2 as a measure of how well the model explains variation in DSR (Neter et al. 1990). For the landscape models, we assumed that DSR on a plot was a relatively unbiased estimate of the true DSR for the species or group of species, and we treated each plot-year as an independent observation.

We explored the effects of temporal correlation because bird responses were measured on 10 plots in sequential years (Oksanen 2001). We assessed the possibility of temporal correlation by incorporating temporal covariance structures into the above-mentioned models using PROC MIXED. Models were compared using likelihood-ratio tests. Models were not improved by incorporating a temporal covariance structure in the model. Temporal correlation, if present, was expected to be positive. Therefore, the presence of temporal correlation would lead to underestimated variances and P -values in models that did not explicitly accommodate that correlation. While the addition of temporal covariance to selected models did not improve models, we recognize that this could be a function of small sample sizes. We addressed the possibility of weak temporal correlation by using a relatively conservative alpha level of 0.025.

RESULTS

NEST SUCCESS

We monitored 905 nests among 49 bird species (Appendix). Nest success was 48% for all nests, 82% for cavity nesting species ($n = 129$), and 42% for cup-nesting species ($n = 776$). Thirty percent of all nests were depredated, 5% failed because of weather, 2% failed because of cowbird parasitism, 6% had unknown fates, and 9% were abandoned. Among those species that accept cowbird eggs ($n = 599$, Friedmann and Kiff 1985), 16% of nests were parasitized, but only 3% failed to raise their own young because of cowbird parasitism.

Species with the highest nest counts were the American Redstart, Blue-gray Gnatcatcher, Eastern Wood-Pewee, Rose-breasted Grosbeak, and Scarlet Tanager (Table 1; scientific names in Appendix). Mayfield-adjusted nest success for the five species ranged from 23% for the American Redstart to 43% for the Eastern Wood-Pewee. There were no significant differences in DSR among these five species ($P = 0.50$), and no differences were observed within species among years ($P = 0.75$). These species are all open-cup nesters, medium or high nesters, and they all accept cowbird eggs. Therefore, they do not represent all functional groups.

There were no differences in DSR among years when all species were pooled ($P = 0.16$; Table 2). Cavity nesters had higher DSR than

TABLE 1. Least-squares mean \pm SE daily survival rates (DSR) of nests for the five species with the highest number of nests monitored (n) in upland forests of the Driftless Area Ecoregion of the midwestern United States, 1996–1998.

Species	n	No. of observation days	DSR \pm SE	Nest success (%) ^a
Eastern Wood-Pewee	90	1695	0.974 \pm 0.006	43
Blue-gray Gnatcatcher	72	1180	0.963 \pm 0.009	34
American Redstart	62	727	0.944 \pm 0.018	23
Scarlet Tanager	70	1003	0.963 \pm 0.009	35
Rose-breasted Grosbeak	72	969	0.964 \pm 0.012	36

^a Nest success = (DSR ^{x}) \times 100, where x is the expected length in days of the total nesting period (includes laying, incubation and nestling periods; Mayfield 1961). See Appendix for the expected length of the nesting period for each species.

did open-cup nesters ($F_{1,16} = 19.3$; $P < 0.01$), and this was consistent among years ($P = 0.36$). No differences were observed in DSR between ground or low nesting species and those that nest in the medium or high canopy ($P = 0.39$), nor

did they vary among years ($P = 0.17$). Bird species that reject Brown-headed Cowbird eggs had lower DSR in comparison with species that accept cowbird eggs. However, both had lower DSR in comparison with those species that are

TABLE 2. Least-squares mean \pm SE daily nest survival rates (DSR) by year and functional group in upland forests of the Driftless Area Ecoregion of the midwestern United States, 1996–1998. Means with the same letters are not statistically different among years or functional groups ($P < 0.05$).

Year and functional group	n (nests)	No. of observation days	DSR \pm SE
Year (all species, pooled)			
1996	82	1104	0.976 \pm 0.005 A
1997	629	9675	0.970 \pm 0.002 A
1998	194	2830	0.964 \pm 0.003 A
Nest type			
Open	776	11 254	0.966 \pm 0.002 A
Cavity	129	2356	0.991 \pm 0.005 B
Nest height			
Ground or low	186	2217	0.963 \pm 0.005 A
Medium or high	719	11 393	0.971 \pm 0.003 A
Vulnerability to cowbird parasitism			
Acceptor	599	8457	0.964 \pm 0.003 B
Rejector	109	1577	0.930 \pm 0.013 A
Inappropriate host	197	3576	0.989 \pm 0.005 C
Habitat association			
Edge	176	2337	0.958 \pm 0.006 A
Interior-edge	538	8781	0.974 \pm 0.003 B
Interior forest	191	2492	0.966 \pm 0.005 AB
Nest distance to forest edge			
Near (0–74 m)	296	4429	0.971 \pm 0.004 AB
Medium (75–199 m)	269	4367	0.979 \pm 0.004 B
Far (\geq 200 m)	305	4355	0.962 \pm 0.004 A
Migration strategy			
Neotropical	637	9588	0.967 \pm 0.003 A
Short distance	137	2042	0.976 \pm 0.008 AB
Resident	131	1979	0.988 \pm 0.009 B

inappropriate cowbird hosts ($F_{2,32} = 16.1$; $P < 0.01$); there was a weak tendency for these differences to vary among years ($F_{4,41} = 2.4$; $P = 0.06$).

When the nests were grouped by species' habitat associations, nests of species associated with interior-edge habitats had higher DSR compared with nests of edge species ($F_{2,34} = 3.3$; $P = 0.05$; Table 2). This pattern was also consistent among years ($P = 0.92$). When nests were grouped by the measured distance of nests to a forest edge, nests located intermediate distances from the edge had higher DSR compared with nests in forest interiors ($F_{2,29} = 4.0$; $P = 0.03$; Table 2). This pattern was consistent among years ($P = 0.44$). Nest success was similar between edges and forest interiors, whether nests were grouped by species associations or by the measured distance of nests to a forest edge (Table 2). Neotropical migrants tended toward lower DSR than resident species but were not significantly different from short-distance migrants, which were intermediate ($F_{2,33} = 3.1$; $P = 0.06$; Table 2). This pattern was consistent among years ($P = 0.83$).

LANDSCAPE ASSOCIATIONS

We obtained eight significant multiple regression models across all functional groups for the 5- and 10-km-radius circles, and three models for the 1-km-radius circles (Table 3). In most instances, the 5- and 10-km models were similar and had similar explanatory power (R^2). Our landscape models explained 18–36% of the variability in DSR. In general, the intercepts in the regression models approximated the DSR, and regression coefficients were small, indicating that large changes in the explanatory variables were associated with small changes in DSR (Fig. 2). However, small changes in DSR may be biologically meaningful because the interval estimate for nest success (Mayfield 1975) is a power function of DSR and the number of days in the nesting cycle.

Forest core area and the proportion of water were negatively associated with DSR for all species and several functional groups (Table 3, Fig. 2). Water was always negatively associated with DSR when it appeared in a model. Forest core area was positively associated with DSR only for ground and low nesting species (5 and 10 km). The proportion of shrubs was positively related to DSR for nests found intermediate dis-

tances (75–199 m) from the edge (5 and 10 km models). Forest edge density was negatively associated with nests of interior-edge species (1 km) and for nests near a forest edge (5 km). As grassland increased relative to row crops, DSR tended to be lower in a number of functional groups.

DISCUSSION

Life-history functional groupings are useful when applied in a management context; identifying at-risk functional groups helps managers focus their efforts on multispecies habitat management (Best et al. 1996, Canterbury et al. 2000, O'Connell et al. 2000). We found that patterns of daily nest survival among functional groups were stable over the three years of our study, indicating that the patterns we observed were not random. We found that open-cup nesters, species that reject cowbird eggs, Neotropical migrants, nests of edge and interior forest species, and nests located both near the edge and far from an edge experienced the lowest nest success. These patterns of nest success are consistent with other information about population status and reproductive threats to forest birds. Habitat edges are generally considered at high risk for nest predation but predation patterns can be complex and landscape specific (Chalfoun, Thompson, and Ratnaswamy 2002). Breeding Bird Survey data for the Eastern Region of North America for 1980–1991 (Peterjohn et al. 1995) and 1980–2000 (Sauer et al. 2003) indicate that open-cup nesters, shrub breeders (including edge species) and Neotropical migrants have low proportions of species with increasing population trends. Flather and Sauer (1996) found Neotropical migrants were more sensitive to landscape structure than resident species or short-distance migrants; Neotropical migrant abundance was related to attributes such as proportion of forest and wetland habitats, amount of edge habitat, and the size of forest patches.

Nest predation, followed by nest abandonment and weather were the most important causes of nest failure in our study. Predation is recognized as the dominant cause of nest failure for most songbird populations (Ricklefs 1969, Powell and Steidl 2000), including those occupying agricultural landscapes (Best and Stauffer 1980, Donovan et al. 1995). Many common nest predators found in our study area, such as the red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*),

TABLE 3. Multiple linear regression models explaining daily survival rate (DSR) of nests for all species and species grouped by functional groups in upland forests of the Driftless Area Ecoregion of the midwestern United States, 1996–1998. Models include the following variables: the proportions of each circle represented by forest core area, shrub area, water, urban land use, the ratio of grass to agriculture, and the edge density of forests. The proportion of forest core area is the area of forest located at least 100 m from a forest edge, expressed as a proportion of total area within the landscape circle. Edge density is the linear distance of forest edge per unit area (m ha⁻¹). The grass to agriculture ratio is the ratio of the proportion of grassland and forage crops to the proportion of row crops. All variables were calculated for three landscape scales: 1, 5, and 10-km circles centered on each study plot. All significant models are reported ($\alpha < 0.025$).

Functional group	Landscape scale (radius of circle, km)	Multiple regression model	Adjusted R ²	P <
All species	5	0.98 – (0.0004 forest core area) – (0.0005 water)	0.31	0.01
	10	0.98 – (0.0005 forest core area) – (0.0005 water)	0.27	0.01
Vulnerability to cowbird parasitism				
Inappropriate host	1	0.99 – (0.0004 grass to agriculture ratio)	0.21	0.01
Nest distance to forest edge				
Near (0–74 m)	1	0.97 – (0.001 grass to agriculture ratio)	0.34	0.001
	5	0.99 – (0.0004 forest edge density) – (0.0007 water)	0.32	0.01
	10	0.97 – (0.001 water)	0.24	0.01
Medium (75–199 m)	5	0.99 – (0.001 forest core area) – (0.008 urban) + (0.009 shrub)	0.35	0.01
	10	0.99 – (0.001 forest core area) – (0.009 urban) + (0.01 shrub)	0.36	0.01
Habitat association				
Interior-edge	1	1.0 – (0.0004 forest core area) – (0.0003 forest edge density)	0.25	0.02
	5	0.98 – (0.0006 forest core area) – (0.0005 water)	0.25	0.01
	10	0.98 – (0.0007 forest core area) – (0.0005 water)	0.24	0.01
Migration strategy				
Neotropical	5	0.97 – (0.0005 water)	0.19	0.01
	10	0.97 – (0.0008 water)	0.18	0.02
Nest height				
Medium or high	5	0.98 – (0.0006 forest core area) – (0.0005 water)	0.26	0.01
	10	0.98 – (0.0009 forest core area)	0.19	0.01
Ground or low	5	0.92 + (0.002 forest core area)	0.21	0.01
	10	0.92 + (0.002 forest core area)	0.19	0.02
Nest type				
Open	5	0.97 – (0.0004 forest core area) – (0.0004 water)	0.23	0.02
	10	0.98 – (0.006 grass to agriculture ratio) – (0.005 urban)	0.22	0.02

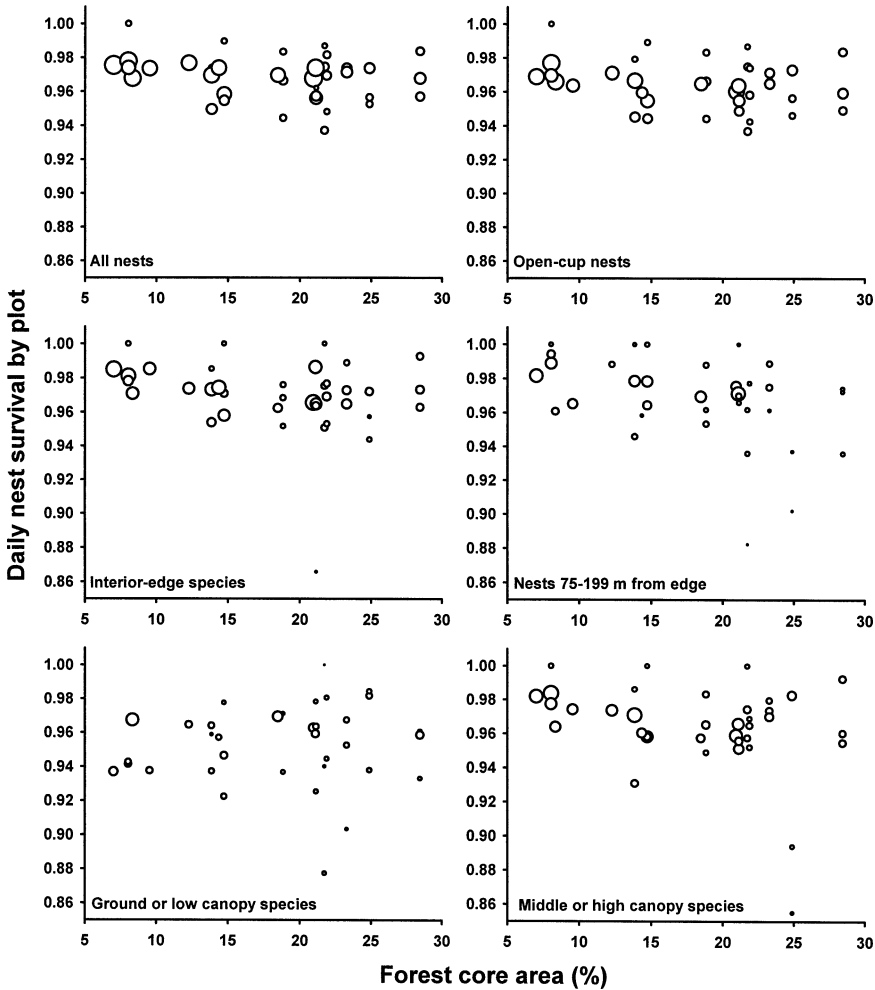


FIGURE 2. The relationship between daily survival rate (DSR) of nests by plot and the proportion of forest core area within a 5-km-radius centered on the plot. Forest core area was a significant variable in the final multivariate regression model for the functional groups shown. The size of the circles corresponds to the number of observation days (weighting) in the regression model. Two outliers with low weights for ground or low and medium or high canopy species are not shown.

Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), American Crow (*Corvus brachyrhynchos*), Common Grackle (*Quiscalus quiscula*), and Blue Jay use agriculture, grasslands, and woodlands, and their behavior is influenced by the composition of the landscape matrix (Dijak and Thompson 2000, Chalfoun, Ratnaswamy, and Thompson 2002). The variety and abundance of nest predators and their behavior patterns form a complex phenomenon that results in spatial patterns of nest success that may vary over time or space.

We did not observe the high rates of cowbird parasitism reported by other studies in the agricultural Midwest (Robinson, Rothstein et al. 1995), and we observed that cowbird parasitism was highest in the forest interiors (Gustafson et al. 2002). We attribute both the patterns of nest failure and cowbird parasitism to the fragmented nature of all the forests in our study area, where even the interiors of large forests are vulnerable. Hahn and Hatfield (1995), working in New York, obtained a similar result. At the landscape scale, our study area retains a higher proportion

of forest than central Iowa or Illinois, where cowbirds and predators have been shown to depress nest success, possibly explaining our relatively low rates of parasitism (Brawn and Robinson 1996, Stallman and Best 1996, Hultquist and Best 2001).

Evidence is mounting that the expected positive association between avian nest success and forest area is not universally observed in all landscapes, indicating that the ecological processes that underlie this association are complex. Along with us, others have also failed to find strong negative effects of forest fragmentation on breeding success (Fauth 2001, Hersek et al. 2002, Morrison and Bolger 2002) or have found poor reproduction in large forests (Hanski et al. 1996, Wilson and Cooper 1998, Farnsworth and Simons 1999). The patterns of cowbird parasitism and nest predation are not the same in the eastern and western United States, possibly because the western United States has less row-crop agriculture and less urban development than the east, and was historically a more fragmented landscape (Cavitt and Martin 2002, Morrison and Hahn 2002). Tewksbury et al. (1998) cited the naturally fragmented nature of their Montana study area as one reason they failed to find fragmentation effects on nest success. Friesen et al. (1999) observed that forest size and nest distance to edge were not closely associated with nest success or productivity in a highly fragmented agricultural landscape with 14% forest cover in southwestern Ontario, Canada. Empirical studies exploring the effects of habitat fragmentation “demonstrate a wide variety of direct and indirect effects, sometimes with mutually opposing implications” (Haila 2002:321). Another review of ecological experiments testing the effects of terrestrial habitat fragmentation found that highly mobile taxa, such as birds and mammals, do not generally respond to habitat fragmentation according to theoretical expectations (Debinski and Holt 2000).

We attribute the differences in our findings from those of other Midwestern studies (Robinson, Thompson et al. 1995, Donovan et al. 1997) to the high level of forest fragmentation in our study area, which makes virtually all forest areas accessible to nest predators and cowbirds. Our study included a narrower range of forest area than other regional Midwestern studies, occupying the lower half of the range ex-

amined by Robinson, Thompson et al. (1995). However, weather conditions, food resources, availability of mates, or other factors may periodically influence nest success enough to mask habitat fragmentation effects. The one indication that larger forests in our study area may buffer predator effects is the positive association between forest core area and DSR for ground and low nesters. Ground and low nesters may benefit from a lower abundance of nest predators in larger forests (Chalfoun, Ratnaswamy and Thompson 2002).

We also found that landscape factors not reported in some studies (the proportions of water, shrubs and grass in the landscape, and forest edge density) also contributed to habitat models of nest success. Raccoons (*Procyon lotor*) are commonly identified as one of the major nest predators in Midwestern forests (Donovan et al. 1997). Our own work with cameras and artificial nests (MAF, unpubl. data) indicates that raccoons are a common nest predator of ground nests in our study area. Ideal raccoon habitat is found within our study area; woodlands are adjacent to rivers and streams in a matrix of row-crop agriculture (Oehler and Litvaitis 1996, Pedlar et al. 1997, Gehrt and Fritzell 1998, Dijak and Thompson 2000). The positive association between raccoons and water may partially explain the consistent negative associations between DSR and the proportion of water in our study.

Our landscape habitat models explained a surprising proportion of variation in DSR (18–36%), given the strong influence that factors not included in the models (nest concealment, predator activity, climate, weather, etc.) could exert on DSR. Also notable was the large number of functional groups that had no significant habitat association with DSR at the 1-km-radius scale (Table 3). Although the 1-km-scale habitat models performed as well as or better than the 5- and 10-km scales for three functional groups, this was the exception, not the rule. Also, the habitat factors represented in the models at different spatial scales were not always the same, suggesting that changing the spatial scale can also change the habitat associations observed (Gustafson et al. 2002). Thompson et al. (2002) proposed a multiscale conceptual model of the effects of fragmentation on birds, with processes at larger scales providing a context for processes operating at smaller scales. Our finding that

landscape metrics from the 5- and 10-km spatial scales were more frequently represented in our final models than 1-km metrics is consistent with a multiscale model. The ecological processes underlying the habitat associations we observed tend to operate at these larger spatial scales: the home ranges of both cowbirds and large mammal nest predators approximate the 5- and 10-km spatial scales (Oehler and Litvaitis 1996, Pedlar et al. 1997, Thompson et al. 2000).

We recognize that nest success is not an analog of annual productivity because productivity is also influenced by breeding strategies such as multibrooding (Thompson et al. 2001). Population models that incorporate breeding strategies and adult and juvenile survival are required to compare population rates of change among habitats or populations (Powell et al. 1999). However, forest-dependent populations are predicted to decline when forest cover falls below a threshold, estimated at 20–30% forest (Andren 1994, Fahrig 1998, Donovan and Thompson 2001). From a conservation perspective, forests in our study area are predicted to be at or just below the threshold level of forest composition needed to sustain forest bird populations. Conservation strategies for forest-nesting birds would seek to increase the proportion of forest cover in the ecoregion. The dendritic landscape pattern of the forests increases contiguity via corridors, but also increases edge habitat; contiguity may buffer some fragmentation effects on populations (With et al. 1997, Hersek et al. 2002). The interaction between habitat area and contiguity may be biologically important for birds, although the independent influences of these factors will be a challenge to measure in real landscapes.

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APPENDIX. Continued.

Species	Functional groups ^a	No. of nests	No. of observation days	Daily survival rate		Expected nest period (days) ^c	Nest success (%) ^d	
				Mean ± SE ^b	95% CI		Mean ± SE	95% CI
Field Sparrow								
<i>Spizella pusilla</i>	O,L,A,E,S	10	88	0.943 ± 0.025	0.895–0.992	23.5	25 ± 19	7–82
Northern Cardinal								
<i>Cardinalis cardinalis</i>	O,H,A,IE,RS	19	205	0.941 ± 0.016	0.909–0.974	25.5	21 ± 11	9–51
Rose-breasted Grosbeak								
<i>Pheucticus ludovicianus</i>	O,H,A,IE,N	72	969	0.960 ± 0.006	0.947–0.972	28.0	32 ± 6	22–45
Indigo Bunting								
<i>Passerina cyanea</i>	O,L,A,E,N	30	350	0.948 ± 0.012	0.925–0.972	25.5	26 ± 9	14–48

^a Functional groups: Nest type: O = open, C = cavity; nest canopy location: L = ground or low, H = medium or high; vulnerability to cowbird parasitism: A = acceptor, R = rejector, I = inappropriate host; habitat association: IF = interior forest, IE = interior or edge, E = edge; migration strategy: N = Neotropical, S = short distance, RS = resident.

^b DSR is based on total observation days for the laying, incubation, and nestling periods. Some values differ slightly from Table 1. In Table 1, DSR was calculated using least-squares means of 38 plot-by-year combinations in order to test for differences among species; however, for the Appendix nests were pooled across all plots.

^c From Ehrlich et al. (1988).

^d Nest success = $(DSR^x) \times 100$, where x is the expected length in days of the total nesting period (includes laying, incubation and nestling periods; Mayfield 1961).