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COMPARING THE EFFECTS OF LOCAL, LANDSCAPE, AND TEMPORAL FACTORS ON FOREST BIRD NEST SURVIVAL USING LOGISTIC-EXPOSURE MODELS

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Abstract. We studied the bird communities of Mississippi River floodplain and adjacent upland forests to identify factors associated with nest survival. We estimated daily nest survival for forest-nesting birds using competing logistic-exposure models, that will allow a comparison of multiple possible factors associated with nest survival, measured at different spatial or temporal scales. We compared models representing landscape (upland vs. floodplain and forest cover), edge (nest distance to edge and forest edge density), nest-site (nest height, canopy cover, nest concealment, and shrub density), Brown-headed Cowbird (*Molothrus ater*; parasitism rate and cowbird abundance), and temporal effects (year, nest stage, and Julian date of observations). We found that the temporal effects model had the strongest support, followed by the landscape effects model for most species. Nest survival tended to be highest early in the nesting season (May–June) and late in the nest cycle (nestling stage). For Eastern Wood-Pewees (*Contopus virens*) and Prothonotary Warblers (*Protonotaria citrea*), higher nest survival was associated with lower proportions of forest surrounding the plot. Significant effects of nest placement in upland vs. floodplain locations were not observed for any species. Models representing edge, nest-site, and cowbird effects had less statistical support, although higher nest survival was sometimes associated with dense shrubs and more concealment around the nest. Management implications may include timing management disturbances to avoid the early nesting season (May and June). For shrub nesting species, management to open the canopy and allow the shrub layer to develop may be beneficial.

Key Words: Brown-headed Cowbird, demographic monitoring, floodplain forest, information-theoretic, landbird, landscape, logistic-exposure model, Mississippi River, nest-site, nest survival.

COMPARACIÓN DE LOS EFECTOS DE FACTORES LOCALES, DE PAISAJE Y TEMPORALES EN SOBREVIVENCIA DE NIDOS DE AVES FORESTALES UTILIZANDO MODELOS DE EXPOSICIÓN LOGÍSTICA

Resumen. Estudiamos las comunidades de aves de las planicies inundadas del Río Mississippi y los bosques adyacentes de las tierras altas, para identificar factores asociados con la sobrevivencia de nido. Estimamos la sobrevivencia diaria del nido para aves anidadoras de bosque utilizando modelos competentes de exposición logística, que permitirán comparar posibles factores múltiples asociados a la sobrevivencia de nido medidos a distintas escalas espaciales y temporales. Comparamos modelos representando al paisaje (tierras altas vs. planicies inundadas y cobertura forestal), borde (distancia del nido al borde y la densidad del borde de bosque), sitio del nido (altura de nido, cubierta de dosel, ocultación de nido, y densidad de arbustos), el Tordo Cabeza Café (*Molothrus ater*); tasa de parasitismo o abundancia de tordo), y efectos temporales (año, etapa de nido, y fecha Julian de observaciones). Encontramos que el modelo de efectos temporales tiene el soporte más alto para casi todas las especies, seguido del modelo de efectos de paisaje. La sobrevivencia de nido tendía a ser la mayor en la estación temprana de anidación (Mayo–Junio) y tardía en el ciclo de nido (etapa de volantón). Para los Pibí Oriental (*Contopus virens*) y Chipe Dorado (*Protonotaria citrea*), estaba asociada mayor sobrevivencia de nido con menores proporciones de bosque rodeando el sitio. Efectos significativos de colocación de nido en tierras altas vs. localidades de planicies inundadas no fueron observadas por muchas especies. Modelos que representan efectos de borde, sitio de nido y tordo, tienen menor soporte estadístico a pesar de que la sobrevivencia de nido estaba algunas veces asociada con arbustos densos y más ocultación alrededor del nido. Las implicaciones en el manejo quizás incluyan la sincronización de disturbios de manejo para evitar el período de anidación temprana (Mayo y Junio). Para especies de anidación de arbusto quizás sea benéfico el manejo para abrir el dosel y para permitir que se desarrolle la capa arbustiva.

Successful landbird conservation requires that managers have an understanding of the major factors affecting nest survival in a region, while also acknowledging that such factors may not act independently. Survival models, including logistic-exposure models (Shaffer 2004a), permit factors associated with nest survival, possibly measured at different spatial or temporal scales; to be compared in a unified information-theoretic modeling framework (Dinsmore et al. 2002). A variety of factors have been shown to affect nest survival, ranging in scale from landscape variables to factors operating at the scale of a single nest (Faaborg 2002). At large spatial scales, nest survival may be influenced by landscape context, usually represented by the amount of forest in the landscape (Rodewald 2002). Landscapes with fewer edges and less fragmentation are often positively associated with nest survival (Donovan et al. 1997, Stephens et al. 2004). Nests placed near forest edges may have decreased success compared with those placed in the interior of large forests (Batary and Baldi 2004). Factors specific to the nest, such as placement height, canopy cover, vegetation concealment, and shrub density have variable associations with nest survival (Wilson and Cooper 1998, Siepielski et al. 2001). Finally, timing can be important; nest survival often varies annually, by nest-initiation date, or by nest age or stage (laying, incubation, or nestling) (Burhans et al. 2002, Peak et al. 2004, Winter et al. 2004).

We studied the bird community of Mississippi River floodplain and adjacent upland forests to identify factors associated with nest survival for purposes of informing managers of upland and floodplain forests in the region. Our objective was to examine the relative importance of models representing possible major factors affecting nest survival, including landscape, edge, nest-site, Brown-headed Cowbird (*Molothrus ater*), and temporal effects. We expected that temporal, landscape, and edge effects would have a generally stronger association with nest survival than nest-site or cowbird effects for most forest bird species in our study area. However, we also expected that factors affecting nest survival would vary by species or life-history group. Landscape and edge effects were expected to be stronger for area-sensitive species and life history groups. A cowbird-effects model was expected to explain variation in nest success for generalist species, and non-area-sensitive ground species and groups vulnerable to parasitism. Temporal or nest-site effects were expected to better explain variation in nest success for generalist species and non-area-sensitive ground and shrub nesters.

METHODS

The study area was located in the driftless area ecoregion, including portions of the states of Iowa, Minnesota, and Wisconsin (McNab and Avers 1994). Driftless area forests are dominated by oaks (*Quercus* spp.), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*) (Curtis 1959, Cahayla-Wynne and Glenn-Lewin 1978). Forests are confined to steep slopes adjacent to streams and rivers and form a connected, dendritic pattern, while complex topography and erosive soils support a less intensive agriculture than in many parts of the Midwest (McNab and Avers 1994). Forests and agriculture comprise about 12–56% and 2–38% of the landscape, respectively, within 10 km of our study plots (Gustafson et al. 2002, Knutson et al. 2004). The Mississippi River floodplain in this region is unrestricted by levees; forests dominate most islands and main channel borders within the floodplain (Knutson et al. 1996). The floodplain forest-plant community is dominated by silver maple (*Acer saccharinum*), with elm (*Ulmus* spp.), green ash (*Fraxinus pennsylvanica*), swamp white oak (*Quercus bicolor*), cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and river birch (*Betula nigra*) as subdominants (Knutson and Klaas 1997).

We assessed factors affecting the nest survival of six forest bird species—American Redstart (*Setophaga ruticilla*), Prothonotary Warbler (*Protonotaria citrea*), American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Blue-gray Gnatcatcher (*Polioptila caerulea*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). We grouped 21 additional species according to similar life history-strategies; these species had insufficient sample sizes individually (Best et al. 1995). The groups were area-sensitive low nesters—Ovenbird (*Seiurus aurocapilla*) and Wood Thrush (*Hylocichla mustelina*); area-sensitive tree nesters—Acadian Flycatcher (*Empidonax virescens*), Red-eyed Vireo (*Vireo olivaceus*), Scarlet Tanager (*Piranga olivacea*), and Warbling Vireo (*Vireo gilvus*); ground or shrub nesters: Brown Thrasher (*Toxostoma rufum*), Eastern Kingbird (*Tyrannus tyrannus*), Gray Catbird (*Dumetella carolinensis*), Indigo Bunting (*Passerina cyanea*), Northern Cardinal (*Cardinalis cardinalis*), Song Sparrow (*Melospiza melodia*), and Yellow Warbler (*Dendroica petechia*); and cavity nesters—Black-capped Chickadee (*Poecile atricapillus*), Downy Woodpecker (*Picoides pubescens*), Great Crested Flycatcher (*Myiarchus crinitus*), Hairy Woodpecker (*Picoides villosus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), White-breasted Nuthatch (*Sitta carolinensis*), and Yellow-bellied Sapsucker (*Sphyrapicus varius*). Species with fewer than five nests were not modeled.

Nest Searching and Monitoring

We monitored nests from May–August on 10 floodplain and 10 upland plots from 1996–1998. We selected upland plots non-probabilistically from state forests that were not recently logged or grazed. In the floodplain, we randomly selected plots from federal land in the upper Mississippi River, based on forest inventory data (United States Army Corps of Engineers 1990–1997). Study plots were approximately 40 ha in size in the uplands and 20 ha in the floodplain; field effort was similar among all plots.

Nests were located following standard protocols (Martin and Geupel 1993) by following adults and flushing incubating and brooding birds. All active nests were monitored every 2–3 d until the outcome was determined. At each visit, we recorded date, time, parental behavior, nest stage, nest contents, and evidence of cowbird parasitism. Nests were considered successful if they fledged at least one host young. We relied on cues to assess nest success including fledglings seen or heard, adults in the vicinity of the nest with food or scolding, and no evidence of renesting. The location of each nest was defined using a global-positioning system.

We measured nest-site variables immediately after the fate of the nest was determined, including nest height, canopy cover, nest concealment, and shrub density. Nest height was the distance (meters) from the ground to the bottom of the nest cup; canopy cover was the total canopy cover above 5 m from the ground, estimated with a densiometer. Nest concealment was the percent of the nest hidden by vegetation 1 m from the nest in each direction, estimated from the side in four cardinal directions and from the top; the mean of the five estimates was used for analysis. Shrub density was the number of shrub stems <8 cm diameter at breast height (dbh) counted at 10 cm above the ground, within a 5-m circle (0.008 ha) centered on the nest.

We estimated Brown-headed Cowbird abundance from point-count data; cowbirds were counted on each plot between 20 May and 30 June at six points spaced ≥200 m apart. We recorded birds within 50 m of the observer during a 10-min time period (Ralph et al. 1993) and calculated relative abundance as the mean number of cowbirds per survey point, by plot and year.

Landscape Variables

U.S. Geological Survey gap-analysis program classifications were used to represent land cover (Scott et al. 1993). We calculated and summarized landscape metrics for each plot, including the percentage of the landscape in forest cover and forest edge density using a 5-km radius circle (7,854 ha) centered on the plot. The distance (meters) of each nest to the nearest forest edge was measured using land-cover maps of the study plots digitized from 1:15,000 scale aerial photographs taken in 1997 (Owens and Hop 1995). Edge density was defined as the linear distance of forest edge per unit area (meters per hectare) for each plot, represented by the 5-km radius circle (McGarigal and Marks 1995). A 5-km radius was selected because it approximates the home range of cowbirds (Thompson 1994) from breeding to feeding areas.

Statistical Analyses

We used survival analysis (Shaffer 2004a) to model nest survival as a function of nest-specific predictor variables and to estimate daily nest-survival rates. This logistic-exposure approach (Shaffer 2004a) accommodates varying exposure periods, continuous, categorical, and time-specific predictor variables, and random effects. We used a modified logit link function, $(\log_e(\theta^{1/t})/[1 - \theta^{1/t}])$, where θ is the interval survival rate and t is the interval length in days (Peak et al. 2004, Shaffer 2004a), and assumed survival and predictor variables to be constant within a nest-observation interval. Models were fitted using the SAS generalized linear modeling procedure (PROC GENMOD; SAS Institute 2003).

For each species and group we evaluated models representing landscape, edge, nest-site, cowbird, and temporal effects. Specifically, we evaluated a landscape-effects model with forest type (upland or floodplain) and percent forest cover; an edge-effects model with distance to forest edge and forest edge density; a nest-site-effects model with nest height, canopy cover, nest concealment, and shrub density; a cowbird-effects model with parasitism of the nest (parasitized or not parasitized) and cowbird relative abundance; and a temporal-effects model with year, nest stage, and Julian observation date (midpoint between two successive nest visits). We also evaluated a global model with all effects, and an intercept-only (null) model. We dropped the cowbird model for species not vulnerable to cowbird parasitism (American Robins and cavity nesters) and the nest-concealment model for cavity nesters and forest type for species found only in one forest type (Prothonotary Warblers, floodplain; Ovenbird and Wood Thrushs, uplands). For some species and groups, we combined laying and incubation stages because models with too few intervals failed to converge.

We evaluated the candidate models using a small sample variant of the Akaike information criterion (AIC_c) and the associated Akaike weight, w_i (Burnham and Anderson 2002). Akaike information criterion for small sample sizes is defined as –2 log likelihood + 2 × K (the number of estimated parameters) × (small sample correction factor), where the correction factor = N/(N – K – 1) and N = number of observation intervals (Hurvich and Tsai 1989). Differences between the AIC_c values for the i^{th} model and that of the model with the smallest AIC_c value were denoted ΔAIC_{ci}; a ΔAIC_{ci} of 2–5 units was considered evidence of stronger support (Burnham and Anderson 2002). A given w_i indicates the weight of evidence in favor of model *i* being the best supported model (among those considered), and was defined as $e^{-\Delta AICci/2}$. For convenience, ΔAIC_{ci} is hereafter denoted ΔAIC_c.

We presented odds ratios for predictor variables with confidence intervals that excluded 1 from the model with the smallest AICc value. To clarify the interpretation, an odds ratio of 1.5 for year 1996 vs. 1998 indicates that the odds of daily nest survival were 50% higher in 1996 than in 1998. A predictor was included in only one model per species or species group.

Daily nest survival for each species was estimated using the model with the smallest AICc value. The predicted probabilities represent the probability of a nest surviving 1 d, are comparable to Mayfield daily nest survival estimates (Mayfield 1961, Johnson 1979), and are conditional on median (continuous) or mean (categorical) covariate values. Conditional interval nest survival was estimated using the model with the smallest AICc value and the literature-based mean number of laying, incubation, and nestling days (Ehrlich et al. 1988). For the life history groups of species, we used a weighted average of the appropriate number of laying, incubation, and nestling days (Baicich and Harrison 1997). Nest survival was estimated for all species in the study. For species in the life-history groups, nest-survival estimates were conditional on temporal effects (day, stage, and year) only.

RESULTS

We monitored 1,142 nests among all the species. Nests tended to be located in areas with relatively high canopy cover (79%), high stem counts of shrubs, and 50–110 m from an edge (Table 1). Predictor means often varied substantially by species (Table 2). For example, Prothonotary Warbler nests were found closer to the forest edge (24 m) than other species; in contrast, area-sensitive low nesters placed their nests in forest interiors (263 m from an edge; Table 2).

As expected, the models with strongest support varied among the species and life history groups (Table 3). The temporal model had the most general support in explaining nest survival across species; it was the best supporting model for American Redstarts, Rose-breasted Grosbeaks, and cavity nesters and had moderate support (ΔAIC_c < 10) for all other species and groups (Table 3). The landscape model was the best supporting model for Eastern Wood-Pewees and had moderate support for American Robins, Blue-gray Gnatcatchers, area-sensitive low nesters, area-sensitive tree nesters, and ground and shrub nesters.

The edge-, nest-site-, and cowbird-effects models received less support among the species and groups we studied (Table 3). The global model was the best model for Prothonotary Warblers and ground and shrub nesters and had moderate support for American Redstarts, Eastern Wood-Pewees, and Rose-breasted Grosbeaks (Table 3). American Robins, Blue-gray Gnatcatchers, area-sensitive low nesters, and area-sensitive tree nesters had the null model as their best model. In each case, a second

TABLE 1. PREDICTOR VARIABLES USED TO EVALUATE NEST SURVIVAL OF BIRDS BREEDING IN FLOODPLAIN AND UPLAND FORESTS OF THE DRIFTLESS AREA, 1996–1998.

Variable [a]	Scale	N	Mean	SD	Median	Min	Max
Day	day	5,507	169.5[b]	15.3	169.5[b]	130.0[c]	223.8[d]
Edge (meters)	nest	1,142	109.1	132.0	50.2	0.2	794.5
Nest height (meters)	nest	1,142	7.2	5.6	5.7	0.0	31.5
Canopy cover (percent)	nest	1,142	78.6	22.1	86.0	0.0	100.0
Concealment	nest	1,142	66.3	28.4	70.0	0.0	100.0
Shrub	nest	1,142	76.1	105.9	41.0	0.0	914.0
Forest (percent)	plot	20	41.0	11.9	45.0	12.0	56.1
Edge density (meters/hectare)	plot	20	56.2	15.2	54.3	19.7	75.2
Cowbird abundance	plot	20	0.5	0.3	0.3	0.0	1.0

[a] Day = Julian day midpoint between two successive nest visits; Edge = distance in meters from nest to forest edge; Nest height = nest height in meters; Canopy cover = percent total canopy cover >5m in height; Concealment = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Edge density = forest-edge density measured in meters/hectare within a 5-km radius circle centered on the plot; Cowbird abundance = mean relative abundance of cowbirds per survey point, across all plots.

[b] Corresponds to approximately June 18.

[c] Corresponds to approximately May 10.

[d] Corresponds to approximately August 11.

TABLE 2. Predictor variables (mean ± SE) and counts of categorical variables used to evaluate nest survival, by species and life-history groupings of birds nesting in floodplain and uplands forest of the Driftless Area, 1996–1998.

Variable[a]	American Redstart (*Setophaga ruticilla*)	American Robin (*Turdus migratorius*)	Blue-gray Gnatcatcher (*Polioptila caerulea*)	Eastern Wood-Pewee (*Contopus virens*)	Prothonotary Warbler (*Protonotaria citrea*)	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	Area-sensitive tree nesters	Area-sensitive low nesters	Cavity nesters	Ground/shrub nesters
Day	167.8 (0.5)	168.1 (0.8)	163.2 (0.8)	184.8 (0.5)	168.3 (0.5)	164.2 (0.6)	171.6 (0.6)	169.7 (1.1)	165.5 (0.6)	168.4 (0.6)
Edge (meters)	121.0 (7.7)	81.6 (10.4)	82.7 (12.9)	168.3 (14.0)	23.5 (2.2)	164.3 (20.5)	146.0 (13.7)	263.0 (33.7)	109.2 (12.2)	73.4 (7.2)
Nest height (meters)	6.0 (0.2)	6.3 (0.5)	13.5 (0.6)	14.7 (0.4)	2.9 (0.2)	8.3 (0.7)	9.4 (0.4)	2.2 (0.5)	8.3 (0.4)	3.2 (0.3)
Canopy cover (percent)	85.3 (1.1)	82.4 (1.7)	79.9 (2.0)	87.5 (1.0)	71.7 (2.3)	72.2 (3.2)	83.7 (1.3)	88.4 (1.7)	79.6 (1.7)	63.5 (2.4)
Concealment	56.6 (1.4)	58.7 (2.1)	50.8 (2.6)	25.8 (2.3)	96.5 (0.6)	67.2 (2.1)	59.8 (2.1)	51.4 (4.8)	97.2 (0.8)	69.1 (1.9)
Shrub	64.9 (6.0)	59.0 (6.1)	62.2 (13.9)	62.2 (6.6)	19.1 (4.2)	111.8 (13.4)	73.1 (9.5)	87.4 (11.8)	69.7 (9.0)	152.6 (11.9)
Forest (percent)	39.1 (0.7)	34.5 (1.2)	43.2 (1.0)	42.2 (1.0)	42.1 (0.6)	39.0 (1.4)	43.3 (1.0)	46.6 (1.0)	38.4 (0.9)	31.7 (1.2)
Edge density (meters/hectare)	59.1 (0.8)	53.9 (1.7)	61.3 (1.3)	57.7 (1.3)	64.2 (0.8)	53.6 (1.8)	59.9 (1.4)	53.6 (1.7)	54.7 (1.1)	47.7 (1.5)
Cowbird abundance	0.8 (0.1)	1.0 (0.1)	1.1 (0.1)	1.2 (0.1)	0.9 (0.1)	1.2 (0.1)	1.1 (0.1)	1.2 (0.1)	0.9 (0.1)	1.0 (0.1)
Floodplain/upland	164/32	91/18	32/34	37/63	134/0	20/53	39/82	0/34	89/59	116/45
1996/1997/1998	31/79/86	22/35/52	7/32/27	11/39/50	39/44/51	9/39/25	16/54/51	9/19/6	25/50/73	21/62/78

[a] Day = Julian day midpoint between two successive nest visits; Edge = distance in m from nest to forest edge; Nest height = nest height in m; Canopy cover = percent total canopy cover >5 m in height; Concealment = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Edge density = forest edge density measured in meters/hectare within a 5-km radius circle centered on the plot; Cowbird abundance = relative abundance of cowbirds on plot within a year; numbers of nests by treatment (floodplain and upland) and year (1997, 1997, 1998).

TABLE 3. CANDIDATE MODELS EXPLAINING NEST SURVIVAL IN FLOODPLAIN AND UPLAND FORESTS OF THE DRIFTLESS AREA, 1996–1998, BY SPECIES AND LIFE-HISTORY GROUP.

Species	Model	K	ΔAIC_c	w_i
American Redstart	Temporal effects	6	0.0	0.98
(*Setophaga ruticilla*) (N = 825)	Global	16	9.3	0.01
American Robin	Null	1	0.0	0.66
(*Turdus migratorius*) (N = 512)	Landscape effects	3	3.1	0.14
	Edge effects	3	3.4	0.12
	Nest-site effects	5	5.3	0.05
	Temporal effects	6	7.2	0.02
	Global	14	7.5	0.02
Prothonotary Warbler	Global	14	0.0	0.79
(*Protonotaria citrea*) (N = 629)	Temporal effects	5	2.8	0.20
	Nest-site effects	5	8.8	0.01
Eastern Wood-Pewee	Landscape effects	3	0.0	0.90
(*Contopus virens*) (N = 622)	Temporal effects	6	6.8	0.03
	Null	1	7.1	0.03
	Edge effects	3	7.6	0.02
	Global	16	9.1	0.01
	Nest-site effects	5	9.4	0.01
Blue-gray Gnatcatcher	Null	1	0.0	0.38
(*Polioptila caerulea*) (N = 354)	Temporal effects	5	0.4	0.31
	Cowbird effects	3	2.3	0.12
	Edge effects	3	2.4	0.12
	Landscape effects	3	3.7	0.06
	Nest-site effects	5	6.5	0.02
Rose-breasted Grosbeak	Temporal effects	6	0.0	0.96
(*Pheucticus ludovicianus*) (N = 318)	Null	1	8.5	0.01
	Edge effects	3	9.0	0.01
	Global	16	9.0	0.01
Area-sensitive low nesters (N = 146)	Null	1	0.0	0.44
	Landscape effects	2	0.8	0.30
	Edge effects	3	2.7	0.11
	Cowbird effects	3	2.8	0.11
	Temporal effects	5	5.2	0.03
	Nest-site effects	5	7.9	0.01
Area-sensitive tree nesters (N = 565)	Null	1	0.0	0.33
	Temporal effects	6	0.1	0.32
	Landscape effects	3	1.5	0.16
	Nest-site effects	5	2.5	0.09
	Cowbird effects	3	3.7	0.05
	Edge effects	3	3.8	0.05
Ground and shrub nesters (N = 714)	Global	16	0.0	0.45
	Nest-site effects	5	0.9	0.29
	Edge effects	3	2.8	0.11
	Temporal effects	6	3.8	0.07
	Landscape effects	3	4.8	0.04
	Null	1	5.7	0.03
	Cowbird effects	3	7.2	0.01
Cavity nesters (N = 702)	Temporal effects	5	0.0	0.99

Notes: Models are ranked by ΔAIC_c; K = number of parameters including the intercept, N = number of observation intervals. For the sake of brevity, models with $\Delta AIC_c > 10$ are not shown.

model was a close competitor (within 1 ΔAICc unit and model weight >30%), with the exception of American Robins, a generalist species.

Among the predictor variables associated with nest survival, those representing temporal, landscape, and nest-site effects had the most support (Table 4; Fig. 1a–s). Nest concealment and shrub density were supported for Prothonotary Warblers and nest height and concealment were supported for ground and shrub nesters (Table 4; Fig. 1a–s). Nest stage, year, or Julian day were supported for seven species and groups. Daily nest-survival estimates from the best model for each species ranged from a low of 0.938 for Song Sparrows to a high of 0.994 for Red-headed Woodpeckers (Table 5).

DISCUSSION

The logistic-exposure modeling approach allowed us to evaluate a variety of factors that could influence nest survival in the driftless area

TABLE 4. CONDITIONAL ODDS RATIOS AND 95% CONFIDENCE INTERVALS (CI) FOR SELECTED PREDICTOR VARIABLES FROM MODELS WITH SMALLEST AIC_C VALUES FOR INDIVIDUAL SPECIES AND LIFE HISTORY GROUPINGS FOR BIRDS NESTING IN FLOODPLAIN AND UPLAND FORESTS OF THE DRIFTLESS AREA, 1996–1998.

Species	Predictor variable[a]	Odds ratio	CI
American Redstart[b]	Laying + incubation vs. nestling	0.477	0.309, 0.734
(*Setophaga ruticilla*)	1996 vs. 1998	1.871	1.003, 3.492
	1997 vs. 1998	1.518	1.014, 2.271
Prothonotary Warbler[b]	Day	0.955	0.929, 0.982
(*Protonotaria citrea*)	Laying + incubation vs. nestling	0.401	0.209, 0.769
	Concealment	1.059	1.016, 1.104
	Shrub	1.015	1.001, 1.029
	Forest	0.828	0.712, 0.962
Eastern Wood-Pewee[b]	Forest	0.940	0.901, 0.980
(*Contopus virens*)			
Blue-gray Gnatcatcher	Day	0.970	0.944, 0.996
(*Polioptila caerulea*)	1996 vs. 1998	5.478	1.049, 28.606
Rose-breasted Grosbeak[b]	Day	0.939	0.906, 0.974
(*Pheucticus ludovicianus*)	Laying + incubation vs. nestling	0.380	0.179, 0.805
	Shrub	1.004	1.000, 1.008
Area-sensitive tree nesters	Day	0.969	0.944, 0.994
	Incubation vs. nestling	0.489	0.270, 0.886
Cavity nesters[b]	Day	0.972	0.946, 0.999
	1997 vs. 1998	0.345	0.156, 0.765
Ground-shrub nesters	1996 vs. 1998	2.714	1.092, 6.744
	Concealment	1.015	1.006, 1.024
	Nest height	1.103	1.022, 1.191

Note: for the sake of brevity, values are shown only for species and variables with CI's that exclude 1, the null value.
[a] Day = Julian day midpoint between two successive nest visits; Nest height = nest height in meters; Concealment = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot.
[b] For these species, intervals for the nesting stage of laying were included with incubation intervals for analysis.

ecoregion. Many a priori expectations were supported by the data. For example, temporal and, to a lesser extent, landscape factors were confirmed as having strong support across species, but edge effects appeared less important than expected. We also confirmed that factors affecting nest survival varied by species or life history group and that none of the models were supported for a generalist species like American Robins.

The strong support for the temporal-effects model across species suggests that nest survival in general varies more by year, nest stage, and timing during the nesting season than by any of the other modeled sets of factors. Our observation that nest survival tended to be higher early in the nesting season and late in incubation is in agreement with other studies of temporal effects on nest survival (Pescador and Peris 2001, Dinsmore et al. 2002, Peak et al. 2004, Winter et al. 2004). The strong annual variation in nest survival that we observed is commonly identified in nesting studies (Fauth 2000, Sillett et al. 2000, Winter et al. 2005a).

Species with the strongest support for landscape effects had higher nest survival with less forest cover in the landscape, not more, contrary to our expectations (Hartley and Hunter 1998). Our finding that Eastern Wood-Pewees had higher nest survival in plots with less landscape forest cover fits with general habitat associations for the species; it is not known to be sensitive to forest fragmentation (Rodewald and Smith 1998). Our finding that Prothonotary Warblers also benefited from less landscape forest cover was unexpected; this species is heavily dependent upon large floodplain and wetland forests (Hoover 2006). This apparent contradiction remains unexplained. We found only weak support for our expectation that landscape effects would be important for area-sensitive species like Blue-gray Gnatcatchers and Rose-breasted Grosbeaks (Best et al. 1996, Burke and Nol 2000), as well as area-sensitive low nesters and tree nesters. Others have also observed Blue-gray Gnatcatchers breeding in narrow floodplains (Kilgo et al. 1998). We were surprised to find little support for differences in nest survival between floodplain and upland plots for species that nested in both habitats. Tree species composition, humidity, and other environmental factors are quite different between these two habitat types; bird relative abundances are twice as high in the floodplain as in the uplands (Knutson et al. 1996, Knutson et al. 2006).

The nest-site-effects model had more support than we expected for most species, although it failed to rank as the best model for any species or group. Eastern Wood-Pewees tend to respond positively to management that opens the canopy

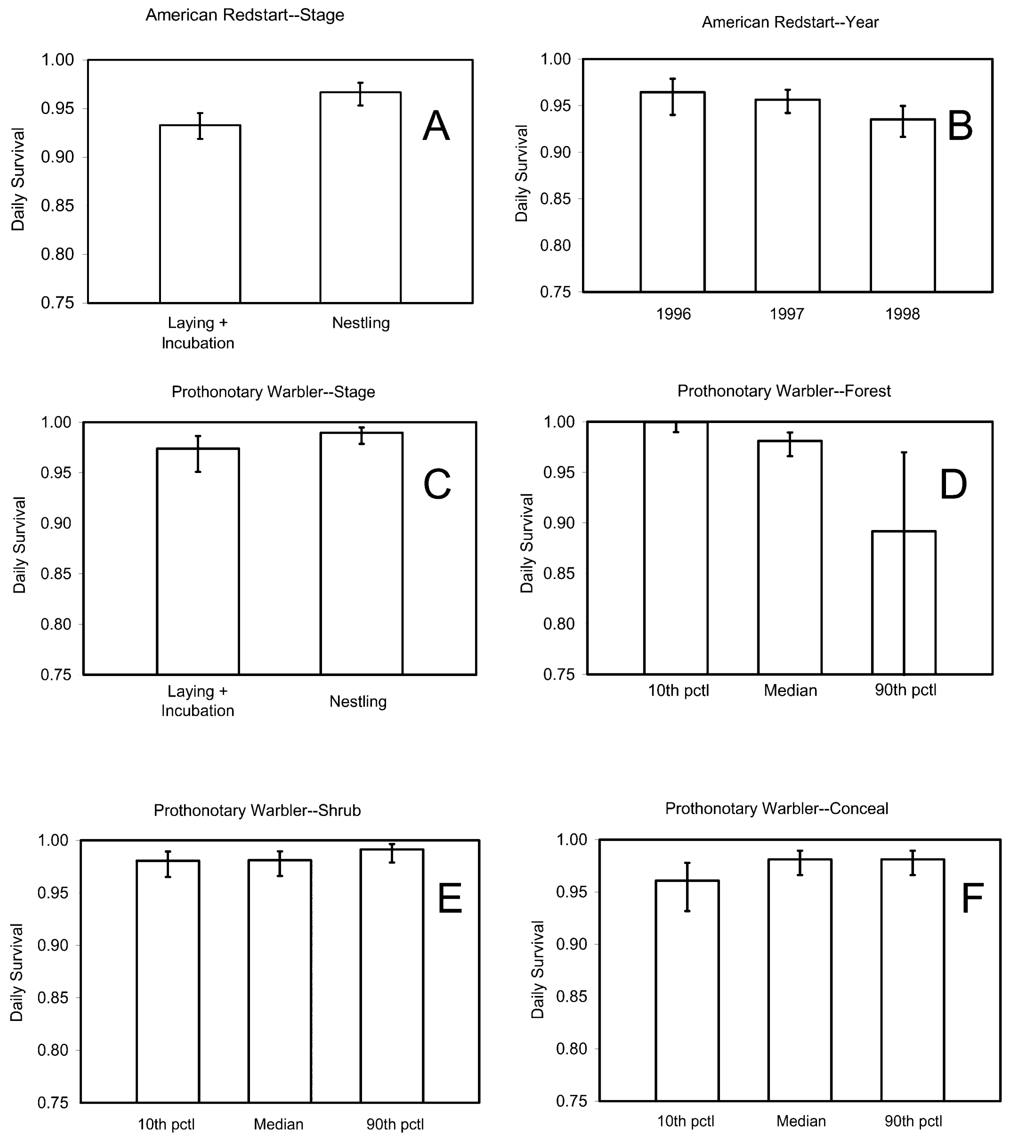

FIGURE 1A–F. Effects of predictor variables on daily survival rates of individual species and groups of birds nesting in floodplain and upland forests of the driftless area, 1996–1998. Day = Julian day midpoint between two successive nest visits; Nest height = nest height in m; Conceal = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Year = 1996, 1997, 1998; Stage = laying, incubation, nestling. For continuous variables, survival rates are estimated at their 10th, 50th (median) and 90th percentiles. *Figure 1 is continued on the next page.*

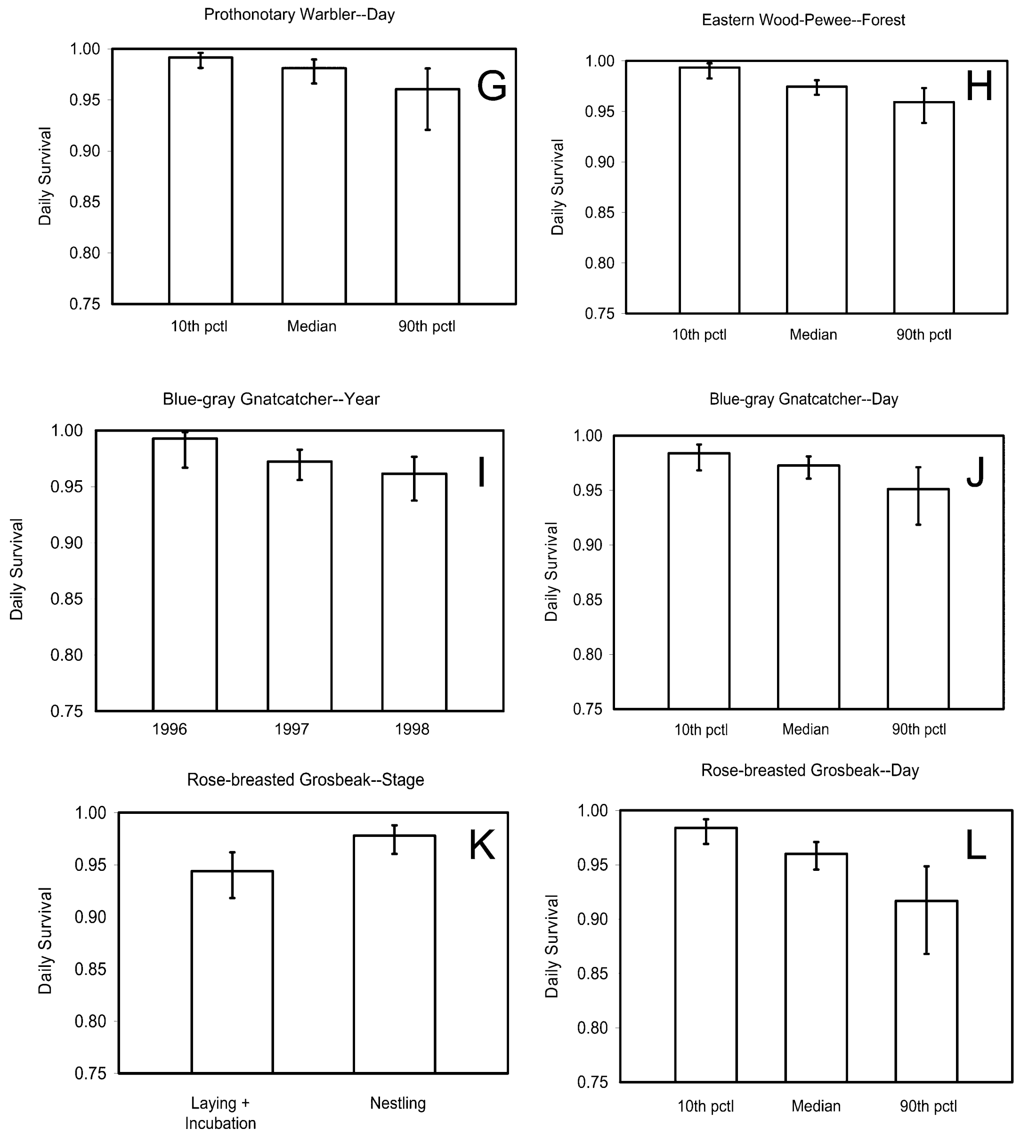

FIGURE 1G–L. *Continued.* Effects of predictor variables on daily survival rates of individual species and groups of birds nesting in floodplain and upland forests of the driftless area, 1996–1998. Day = Julian day midpoint between two successive nest visits; Nest height = nest height in m; Conceal = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Year = 1996, 1997, 1998; Stage = laying, incubation, nestling. For continuous variables, survival rates are estimated at their 10th, 50th (median) and 90th percentiles. *Figure 1 is continued on the next page.*

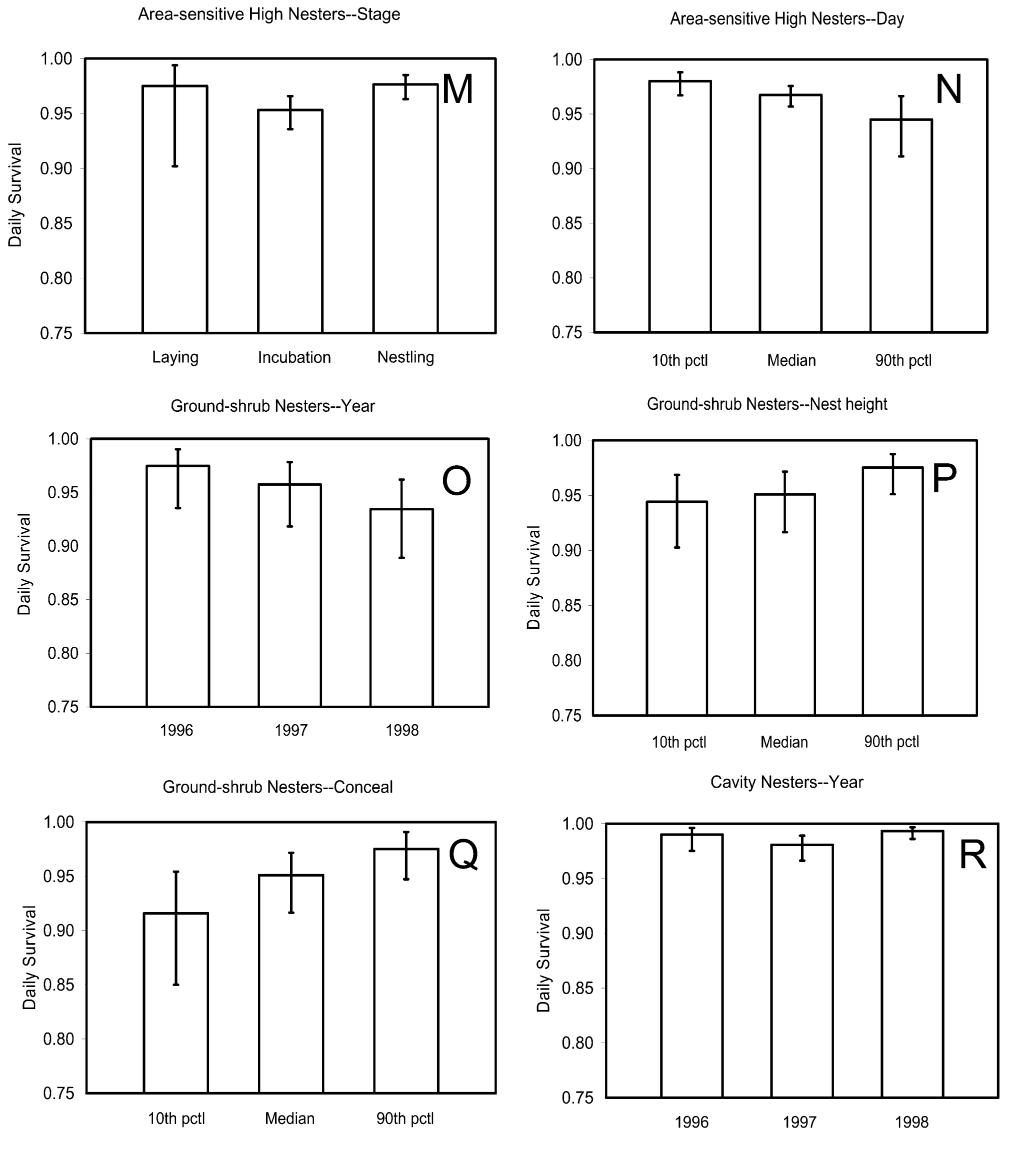

FIGURE 1M–R. *Continued.* Effects of predictor variables on daily survival rates of individual species and groups of birds nesting in floodplain and upland forests of the driftless area, 1996–1998. Day = Julian day midpoint between two successive nest visits; Nest height = nest height in m; Conceal = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Year = 1996, 1997, 1998; Stage = laying, incubation, nestling. For continuous variables, survival rates are estimated at their 10th, 50th (median) and 90th percentiles. *Figure 1 is continued on the next page.*

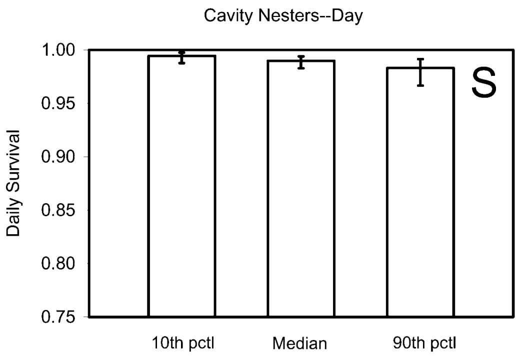

FIGURE 1S. *Continued.* Effects of predictor variables on daily survival rates of individual species and groups of birds nesting in floodplain and upland forests of the driftless area, 1996–1998. Day = Julian day midpoint between two successive nest visits; Nest height = nest height in m; Conceal = nest concealment calculated as the mean of side cover and overhead cover values; Shrub = number of shrub stems >10 cm above the ground and <8 cm dbh within a 5-m radius circle centered on the nest; Forest = percentage of landscape made up of forest within a 5-km radius circle centered on the plot; Year = 1996, 1997, 1998; Stage = laying, incubation, nestling. For continuous variables, survival rates are estimated at their 10th, 50th (median) and 90th percentiles.

and understory (Rodewald and Smith 1998, Artman et al. 2001), but we found only weak support for nest-site effects for this species. Ground and shrub nesters showed moderate support for nest-site effects, as expected, but the global model was their best model, indicating that this group of birds is responding to multiple factors across all the models. Our finding that concealment was supported for ground and shrub nesters is in agreement with previous studies of shrub-nesting species (Murphy 1983, Weidinger 2002, Albrecht 2004), while nest height for ground-shrub nesters has also been observed as a factor in nest survival of roadside bird communities (Shochat et al. 2005b) and Bell's Vireos (*Vireo bellii*) (Budnik et al. 2002). To our knowledge, concealment and shrub density has not been previously reported in association with nest survival for Prothonotary Warblers.

The two models with relatively weak support in our study (cowbird and edge effects) have been intensively studied in dozens of other research studies with mixed results. Comprehensive reviews indicate that cowbirds and landscape edges are factors that can affect nest survival in biologically important ways; however, negative effects are not observed in every study (Thompson et al. 2000, Batary and Baldi 2004, Lloyd et al. 2005). The relatively weak support we observed for the cowbird-effects model suggests that parasitism was not a major factor affecting nest survival in our study. Low rates of parasitism are unusual for the midwestern US, although the heaviest cowbird effects typically come from landscapes with even lower forest cover than our study area (Fauth 2000). Species-specific comparative data on edge effects is difficult to find because much of the literature is based on artificial nest studies or focuses on general effects on the bird community rather than species-specific vulnerability (Batary and Baldi 2004, Moore and Robinson 2004). However, other studies in the midwestern U.S. have identified negative effects of fragmented (high-edge) landscapes on landbird nest survival (Donovan et al. 1997).

The ability to directly assess the relative importance of a wide variety of factors that may affect nest survival, measured at multiple-spatial scales, has major implications for the management of bird populations. With this information, managers will be able to allocate resources more efficiently and identify when the major factors associated with nest survival are beyond their control. For example, landscape-scale factors respond to changes in public policy and economics, whereas local-scale variables associated with the nest site itself are modified by silvicultural methods and other site-scale habitat management (Duguay et al. 2000, Bettinger et al. 2005).

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TABLE 5. CONDITIONAL MEDIAN DAILY NEST-SURVIVAL ESTIMATES AND INTERVAL-SURVIVAL ESTIMATES WITH ASSOCIATED 95% CONFIDENCE INTERVALS (CI) FROM BEST MODELS FOR SPECIES AND LIFE-HISTORY GROUPINGS OF BIRDS NESTING IN FLOODPLAIN AND UPLAND FORESTS OF THE DRIFTLESS AREA, 1996–1998.

Species	Nests found	Nests successful	Exposure days	Nesting cycle (N of days)	Daily survival estimate (CI)	Interval survival estimate (CI)
American Redstart (*Setophaga ruticilla*)	196	66	2,488.5	24	0.949 (0.940, 0.958)	0.262 (0.182, 0.348)[a]
American Robin (*Turdus migratorius*)	109	68	1,785.5	30	0.974 (0.966, 0.981)	0.458 (0.352, 0.559)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	66	26	1,315.0	28	0.973 (0.961, 0.981)	0.460 (0.326, 0.585)
Eastern Wood-Pewee (*Contopus virens*)	100	50	2,131.5	33	0.975 (0.966, 0.981)	0.428 (0.323, 0.528)
Prothonotary Warbler (*Protonotaria citrea*)	134	82	2,095.0	28	0.981 (0.966, 0.990)	0.558 (0.325, 0.740)[b]
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	73	33	1,063.0	27	0.960 (0.946, 0.971)	0.300 (0.157, 0.458)[c]
Area-sensitive low nesters	34	18	474.0	29	0.968 (0.947, 0.981)	0.388 (0.208, 0.565)
Ovenbird (*Seiurus aurocapilla*)	12	7	174.5	26	0.971 (0.932, 0.988)	0.463 (0.160, 0.727)
Wood Thrush (*Hylocichla mustelina*)	22	11	299.5	30	0.966 (0.938, 0.982)	0.356 (0.147, 0.574)
Area-sensitive tree nesters	121	58	1,890.5	29	0.968 (0.957, 0.976)	0.446 (0.128, 0.672)[d]
Acadian Flycatcher (*Empidonax virescens*)	15	11	225.5	32	0.982 (0.953, 0.993)	0.559 (0.214, 0.804)
Red-eyed Vireo (*Vireo olivaceus*)	24	10	339.5	28	0.957 (0.929, 0.975)	0.294 (0.127, 0.485)
Scarlet Tanager (*Piranga olivacea*)	43	21	676.0	28	0.967 (0.950, 0.978)	0.391 (0.240, 0.539)
Warbling Vireo (*Vireo gilvus*)	39	16	649.5	29	0.961 (0.942, 0.973)	0.312 (0.179, 0.456)
Cavity nesters	148	132	2,453.5	40	0.990 (0.983, 0.994)	0.661 (0.500, 0.782)
Black-capped Chickadee (*Poecile atricapillus*)	27	23	341.5	35	0.982 (0.961, 0.992)	0.531 (0.246, 0.753)
Downy Woodpecker (*Picoides pubescens*)	20	18	270.0	37	0.989 (0.966, 0.996)	0.658 (0.275, 0.874)
Great Crested Flycatcher (*Myiarchus crinitus*)	20	15	461.5	33	0.985 (0.968, 0.993)	0.601 (0.345, 0.785)
Hairy Woodpecker (*Picoides villosus*)	21	21	231.0	46	0.969 (0.936, 0.985)	0.232 (0.048, 0.500)
Red-bellied Woodpecker (*Melanerpes carolinus*)	14	12	332.5	42	0.988 (0.968, 0.995)	0.599 (0.257, 0.825)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	6	5	170.5	44	0.994 (0.956, 0.999)	0.772 (0.162, 0.964)
White-breasted Nuthatch (*Sitta carolinensis*)	5	4	90.5	46	0.989 (0.925, 0.998)	0.597 (0.028, 0.930)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	35	34	556.0	44	0.989 (0.976, 0.995)	0.619 (0.344, 0.806)
Ground-shrub nesters	161	66	2338.5	26	0.951 (0.917, 0.972)	0.271 (0.104, 0.474)
Brown Thrasher (*Toxostoma rufum*)	9	5	167.0	28	0.976 (0.937, 0.991)	0.504 (0.163, 0.774)
Eastern Kingbird (*Tyrannus tyrannus*)	6	4	178.5	37	0.983 (0.948, 0.995)	0.528 (0.140, 0.815)
Gray Catbird (*Dumetella carolinensis*)	53	21	797.5	27	0.962 (0.946, 0.973)	0.347 (0.221, 0.478)
Indigo Bunting (*Passerina cyanea*)	17	7	217.0	27	0.953 (0.914, 0.974)	0.271 (0.089, 0.496)
Northern Cardinal (*Cardinalis cardinalis*)	22	7	283.5	25	0.945 (0.912, 0.967)	0.246 (0.099, 0.431)
Song Sparrow (*Melospiza melodia*)	7	3	67.5	27	0.938 (0.846, 0.977)	0.178 (0.011, 0.528)
Yellow Warbler (*Dendroica petechia*)	47	19	627.5	24	0.954 (0.935, 0.968)	0.325 (0.197, 0.461)

[a] Assuming 4-, 11-, and 9-d laying, incubation, and nestling period, respectively.
[b] Assuming 5-, 13-, and 10-d laying, incubation, and nestling period, respectively.
[c] Assuming 4-, 13-, and 10-d laying, incubation, and nestling period, respectively.
[d] Assuming 4-, 13-, and 12-d weighted average laying, incubation, and nestling period, respectively.