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FACTORS AFFECTING SONGBIRD NEST SURVIVAL IN RIPARIAN FORESTS IN A MIDWESTERN AGRICULTURAL LANDSCAPE

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Abstract.—We investigated factors affecting nest success of songbirds in riparian forest and buffers in northeastern Missouri. We used an information-theoretic approach to determine support for hypotheses concerning effects of nest-site, habitat-patch, edge, and temporal factors on nest success of songbirds in three narrow (55–95 m) and three wide (400–530 m) riparian forests with adjacent grassland–shrub buffer strips and in three narrow and three wide riparian forests without adjacent grassland–shrub buffer strips. We predicted that temporal effects would have the most support and that habitat-patch and edge effects would have little support, because nest predation would be great across all sites in the highly fragmented, predominantly agricultural landscape. Interval nest success was 0.404, 0.227, 0.070, and 0.186, respectively, for Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting (*Passerina cyanea)*, and forest interior species pooled (Acadian Flycatcher [*Empidonax virescens*], Wood Thrush [*Hylocichla mustelina*], Ovenbird [*Seiurus aurocapillus*], and Kentucky Warbler [*Oporornis formosus*]). The effect of nest stage on nest success had the most support; daily nest success for Gray Catbird and Indigo Bunting were lowest in the laying stage. We found strong support for greater nest success of Gray Catbird in riparian forests with adjacent buffer strips than in riparian forests without adjacent buffer strips. Patch width also occurred in the most-supported model for Gray Catbird, but with very limited support. The null model received the most support for Northern Cardinal. Riparian forests provided breeding habitat for area-sensitive forest species and grassland–shrub nesting species. Buffer strips provided additional breeding habitat for grassland–shrub nesting species. Interval nest success for Indigo Bunting and area-sensitive forest species pooled, however, fell well below the level that is likely necessary to balance juvenile and adult mortality, which suggests that when riparian forests are located within agricultural landscapes, the potential even for wide riparian forests with adjacent buffer strips to provide high-quality breeding habitat is severely diminished for some species. *Received 24 January 2003, accepted 28 March 2004.*

Resumen.—Investigamos los factores que afectan el éxito de nidificación de aves canoras en bosques riparios y franjas de amortiguamiento en el noreste de Missouri. Usamos un enfoque informativo-teórico para evaluar las hipótesis concernientes a los efectos de la ubicación del nido, el parche de hábitat, el borde y los factores temporales sobre el éxito de nidificación de aves canoras. Evaluamos estos efectos en tres bosques riparios estrechos (55–95 m) y tres bosques riparios anchos (400–530 m) con franjas de amortiguamiento adyacentes de pastizal-matorral, y en tres bosques riparios estrechos y tres anchos sin franjas de amortiguamiento adyacentes de pastizal-matorral. Predijimos que los efectos temporales serían los más respaldados y que los efectos de parche de hábitat y de borde serían los menos respaldos, porque la depredación de nidos sería importante en todos los sitios en un paisaje altamente fragmentado y predominantemente agrícola. El éxito de nidificación en intervalos fue de 0.404, 0.227, 0.070 y 0.186, respectivamente, para *Dumetella carolinensis*, *Cardinalis cardinalis*, *Passerina cyanea* y el conjunto de especies de interior de bosque (*Empidonax virescens*, *Hylocichla mustelina*, *Seiurus aurocapillus* y *Oporornis formosus*). El efecto de la etapa del nido sobre el éxito de nidificación tuvo el mayor respaldo; el éxito de nidificación diario para *D. carolinensis* y *P. cyanea* fue menor en la etapa de puesta de los huevos. Encontramos fuerte respaldo para un éxito de nidificación mayor en *D. carolinensis* en bosques riparios con franjas de amortiguamiento adyacentes que en bosques riparios sin franjas de amortiguamiento adyacentes. El ancho de los parches

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también apareció en el modelo con más respaldo para *D. carolinensis*, pero con un respaldo muy limitado. El modelo nulo recibió el mayor respaldo para *C. cardinalis*. Los bosques riparios proporcionaron hábitat de nidificación para especies sensibles al área remanente de bosque y especies que nidifican en las áreas de pastizal-matorral. Las franjas de amortiguamiento proporcionaron hábitat de nidificación adicional para las especies que nidifican en las áreas de pastizal-arbustal. El éxito de nidificación en intervalos para *P. cyanea* y para el conjunto de especies sensibles al área remanente de bosque, sin embargo, cayó bien por debajo del nivel que es probablemente necesario para balancear la mortalidad de juveniles y adultos. Esto sugiere que cuando los bosques riparios están localizados dentro de paisajes agrícolas, el potencial de proveer hábitat de nidificación de alta calidad, incluso de los bosques riparios anchos con franjas de amortiguamiento adyacentes, disminuye severamente para algunas especies.

Riparian forests provide important breeding habitat for songbirds across the United States (Wharton et al. 1981, Knopf 1985, Best et al. 1995). Most research investigating the value of riparian forests for breeding songbirds has examined how riparian forest width affects species richness and abundance in managed coniferous forests (Tassone 1981, Tappe et al. 1994, Darveau et al. 1995, Dickson et al. 1995, Thurmond et al. 1995, Meiklejohn and Hughes 1999) and broadleaf forests (Triquet et al. 1990, Keller et al. 1993, Murray and Stauffer 1995, Hodges and Krementz 1996, Kilgo et al. 1998, Sallabanks et al. 2000). Using richness and abundance alone as indicators of habitat quality can be misleading, and demographic parameters—such as nest success—should be assessed whenever possible (Van Horne 1983, Vickery et al. 1992b).

Habitat features at a variety of spatial scales may influence nest success (Thompson et al. 2002). Many studies have investigated effects of nest-site factors on nest success (reviewed in Martin 1992 and Burhans and Thompson 1998; Burhans et al. 2002); some found relationships, but many have not. Predation and parasitism may be lower (1) at more-concealed nests, because they are more difficult to find (Martin 1992, Burhans and Thompson 1998); (2) in denser nest cover, because predators and cowbirds have to search more cover (Martin and Roper 1988, Filliater et al. 1994, Budnick et al 2002); and (3) at lower nests for aerial predators (or cowbirds) or at higher nests for ground predators (Filliater et al. 1994, Burhans et al. 2002). Results of studies examining the relationship between temporal factors and nest success suggest that variation in predator type, activity, abundance, and prey selection throughout the breeding season may be more important than nest-site factors in explaining nest success (Nolan 1963, Roseberry and Klimstra 1970, Best 1978, Zimmerman 1984, Vickery et al. 1992a, Burhans et al. 2002).

Effects of habitat-patch factors, especially distance to edge, on nest success vary among species, habitats, and regions (Paton 1994, Andrén 1995). Some studies have found a positive relationship between nest success and riparian-forest width or patch size (Chapa 1996, Vander Haegen and DeGraaf 1996; but see Tewksbury et al. 1998 and Knutson et al. 2000) and a negative relationship between nest success and edge type (Chapa 1996, Suarez et al. 1997, Saracco and Collazo 1999; but see Tewksbury et al. 1998). Vander Haegen and DeGraaf (1996) and Knutson et al. (2000) used artificial nests, which may not reflect predation rates of real nests (Martin 1987, Willebrand and Marcström 1988, Roper 1992).

Landscape factors, such as amount of forest cover and level of fragmentation, can be important determinants of nest success (Donovan et al. 1995, Robinson et al. 1995, Tewksbury et al. 1998) and may even dominate habitat-patch factors, such as distance to edge or patch size (Thompson et al. 2002). For example, Donovan et al. (1997) suggested that they did not detect edge effects in highly fragmented landscapes (<15% forest cover) or in unfragmented landscapes (>90% forest cover) because of the effect of landscape factors on abundance and activity patterns of predators.

We used an information-theoretic approach (Burnham and Anderson 2002) to determine support for effects of nest-site, habitat-patch, edge, and temporal factors on nest success of songbirds in riparian forests. We constructed a set of *a priori* candidate models, which represented hypotheses concerning effects on nest success of year, patch width, presence of a grassland–shrub buffer strip, nest stage, julian date, nest height, nest concealment, woody stem density, habitat, distance to forest edge, and distance to stream edge. By comparing support for the models and interpreting parameter estimates for the factors in them, we determined which hypothesized factors had effects on nest success. We predicted that temporal effects would have the most support and that habitat-patch and edge effects would have little support, because nest predation would be great across all sites in the highly fragmented, predominantly agricultural landscape.

Study Area and Methods

We conducted the study on privately owned and state-owned lands in northeastern Missouri during the 2000 and 2001 breeding seasons. We selected 12 study sites along second- and third-order streams of the Fabius and Fox river watersheds in Scotland, Knox, and Clark counties (Peak 2002) and conducted fieldwork on the same sites in both years. Land cover in those counties ranged from 36% to 41% cropland (corn, soybeans, wheat), 30% to 46% nonnative cool-season grasslands, 8% to 13% deciduous upland mixed oak forest (*Quercus* spp.), and 1% to 2% deciduous seasonally flooded mixed bottomland hardwood forest.

We located potential study sites by examining digital orthophoto quarter-quadrangles and conducting site visits. Study sites were in a 400-m-long segment of a forested riparian area. We selected sites ≥4 km apart to increase independence of bird and predator communities. We minimized differences in the landscape surrounding sites by selecting sites with similar percentages of forest and agricultural cover within a 10-km radius.

Width of the forested portion of the study area included river and forest on both sides of it. We calculated width of the forested riparian area as the mean of 9 width measurements (1 every 50 m) made on digital orthophoto quarter-quadrangles. Narrow riparian forests were 55–95 m and wide riparian forests were 400–530 m. Primary tree species in the riparian forests were cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), oak (*Quercus* spp.), maple (*Acer* spp.), river birch (*Betula nigra*), and honey locust (*Gleditsia triacanthus*). Primary shrub species were Missouri gooseberry (*Ribes missouriense*), buckbrush (*Symphoricarpos orbiculatus*), multiflora rose (*Rosa multiflora*), black raspberry (*Rubus occidentalis*), and silver maple (*Acer saccharinum*). The primary forb in the riparian forests was stinging nettle (*Urtica* spp.) (Peak 2002).

Three narrow and three wide riparian-forest study sites had adjacent grassland–shrub buffer strips along one edge, which resulted in a gradual transition from forest to row crop (a "soft" edge). The other three narrow and three wide riparian forest sites did not, which resulted in an abrupt ("hard") edge between forest and row crop. Buffer strips were planted 3–7 years prior to the study, under the Conservation Reserve Program, the Environmental Quality Incentives Program, or the Wildlife Habitat Incentives Program authorized by the 1996 Farm Bill (Federal Agricultural Improvement and Reform Act of 1996, PL 104-127). Buffer strips were 30–45 m wide and consisted of mixed grasses, shrubs, forbs, and saplings. Primary tree species in the buffer strips included black walnut (*Juglans nigra*), oak, hickory (*Carya* spp.), cottonwood, ash (*Fraxinus* spp.), and maple. Primary shrub species were black raspberry, multiflora rose, and buckbrush. The primary forb was goldenrod (*Solidago* spp.). The primary grass species was big bluestem (*Andropogon gerardi*) (Peak 2002).

Avian monitoring.—We conducted nest searches on entire study sites, including both sides of the river and the adjacent buffer strip, from 1 May to mid-August (Ralph et al. 1993). We focused searches on territories of focal species for which we had not yet found a nest or where we suspected a renesting attempt. Nest locations were marked with plastic flagging at distances ≥5 m from the nest. We monitored nests every three or four days during the beginning of the nesting cycle and daily as fledging dates approached. For each visit, we recorded date, time of visit, nesting stage (laying, incubation, nestling), description of nest contents, parental activity, and occurrences of parasitism and predation. We determined Universal Transverse Mercator coordinates for each nest after the breeding season, using a Pathfinder Pro XR (realtime mode) global positioning system unit (GPS; Trimble, Sunnyvale, California) with an accuracy level of ~1 m.

We considered a nesting attempt complete when all nestlings fledged, all contents of the nest disappeared, or the adults abandoned the nest. We confirmed fledging by sighting fledglings, listening for fledgling begging calls, or sighting parents carrying food or scolding near the nest. A nest was considered successful if it fledged ≥1 conspecific young. If no fledglings were located, adults did not scold when we were close to the nest site, or a renesting attempt was located within the territory shortly after completion of the nesting attempt, we considered the nest to have failed.

We considered nests to have failed because of predation if they were empty before the expected fledge date and we observed no signs of fledging, failure caused by weather or other natural events, abandonment, or Brown-headed Cowbird (*Molothrus ater*) parasitism. We attributed nest failure to weather or other natural events when nests were destroyed in floods or when all contents were present and the nest was holding water or the contents were on the ground below a tilted nest after a severe storm. Nests were considered to have failed for unknown reasons when nest contents remained unchanged and adults were not present during subsequent visits. Nest were considered to have failed because of Brown-headed Cowbird parasitism after a cowbird egg was deposited in the nest and adults were not present during subsequent visits.

Nest-site measurements.—We measured nest-site characteristics within 10 days after fledging or nest failure. We measured nest height from ground to bottom of nest cup; estimated percentage of the nest cup concealed by vegetation at nest height, 1 m from the nest in each cardinal direction; calculated the mean of those four percentages to obtain one estimate for analysis; and counted the number of woody stems (≥50 cm in height and with a diameter at breast height [DBH] of <0.5 cm) in a 0.001-ha circle centered on the nest.

Habitat-patch measurements.—We mapped forest edges, stream edges, and buffer strips with a Trimble Pathfinder Pro XR (realtime mode) GPS unit. Using ARC/INFO (Environmental Systems Research Institute, Redlands, California), we calculated distance to forest edge and distance to stream edge and classified nests into a habitat category, either forest or buffer strip.

Landscape metrics.—We calculated mean patch size and landscape metrics for narrow and wide riparian forests with and without adjacent buffer strips. We obtained habitat and land-use data from Missouri Resources Assessment Partnership Landcover Project (MORAP; see Acknowledgments; data were interpreted from circa-1990 TM satellite data and have a 30-m pixel size). We condensed the original 16 MORAP classes into the following land-cover categories using ARC/INFO: (1) forestland (Eastern red cedar [*Juniperus virginiana*]–deciduous forest and woodland, eastern red cedar forest and woodland, mixed deciduous forest and woodland, shortleaf pine–oak [*Pinus echinata–Quercus* spp.] forest and woodland, shortleaf pine forest and woodland, and bottomland hardwood forest and woodland); (2) grassland (cool-season grasslands, warm-season grasslands, and glade complex); (3) water (swamp, marsh and wet herbaceous vegetation, and open water); (4) row-crop land (corn, soybeans, wheat); and (5) urban land (urban impervious, urban vegetated, and barren or sparsely vegetated).

We used FRAGSTATS (McGarigal and Marks 1994) to calculate landscape metrics within a 5-km radius of the center of each study site. We selected a 5-km radius because it was a compromise between larger radii used in landscape-scale nesting studies (Donovan et al. 1995, Robinson et al. 1995) and the smaller radii (4 km) needed to eliminate overlap of landscapes around our study sites. We calculated percentage of landscape in urban land, row crops, grassland, and forestland; size of patch the study site was located in (patch area), and mean patch size and percentage of land-cover core area for grassland and forestland. Core was defined as the habitat interior >60 m from the habitat edge, on the basis of Paton's (1994) observation that edge effects occurred more often at distances ≤50 m and our use of a land-cover map with 30-m resolution.

Data analyses.—We examined factors affecting nest success of the three most common species: Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), and Indigo Bunting (*Passerina cyanea*). Acadian Flycatcher (*Empidonax virescens*), Kentucky Warbler (*Oporonis formosus*), Ovenbird (*Seiurus aurocapilla*), and Wood Thrush (*Hylocichla mustelina*) were uncommon and occurred only in wide riparian forests, so we pooled observations of those species (hereafter "area-sensitive forest species") for analysis. We used a general-linear-model approach (McCullagh and Nelder 1989) based on a binomial distribution (interval nest fate = 0 if failed and 1 if successful) and a logit link function (logistic regression) to estimate daily nest-success and evaluate factors potentially affecting nest survival (Dinsmore et al. 2002, Shaffer 2004). Because nest-observation intervals were often >1 day and varied in length (mean = 3.02 days), we used the following modified logit link function: $g(\theta) = \log_e(\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the interval survival rate and t is the interval length in days (Shaffer 2004). That approach differed from Dinsmore et al.'s (2002) in that we assumed survival and explanatory variables to be constant within a nest-observation interval; however, it did not require nest age to be known. It allowed modeling of time-dependent explanatory variables, such as nest stage, by allowing their values to change among nest-observation intervals, but assumed that they were constant within an interval (Shaffer 2004). We fitted models with PROC GENMOD (SAS Institute, Cary, North Carolina) by selecting a binomial response distribution and supplying the user-defined link function described above. Preliminary analyses indicated that including site as a random effect in the models to acknowledge possible covariance among nests from the same site did not improve the models; therefore, we present the models without site.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for alternative *a priori* models, and hence for our hypotheses concerning effects of nest-site, habitat-patch, edge, and temporal factors on nest success of songbirds in riparian forests. Our set of *a priori* candidate models included a habitat-effects model with buffer (no buffer, buffer) and width (narrow, wide); a temporal-effects model with year, nest stage (for each nest observation interval), and julian date; an edge-effects model with distance to forest edge, distance to stream edge, and habitat (buffer, forest); a nest-site-effects model with nest height, nest concealment, and stem total; models consisting of all two-way combinations of nest-site, habitat, edge, and temporal effects; a global model with all effects; and a null model with only an intercept (Table 1). By comparing support for

Table 1. *A priori* candidate models explaining nest success of songbirds in northeastern Missouri, 2000–2001. Number of parameters (K) in each model included the intercept and each explanatory variable. Models with a lower ΔAIC and a greater Akaike weight (w_i) have more support. Values for the model with the most support are in bold; n = total number of nest-observation intervals for a species.

		Gray Catbird (n = 892)		Northern Cardinal (n = 239)		Indigo Bunting (n = 790)	
Model	K	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i
Habitat effects	4	8.03	0.015	2.76	0.106	23.75	0.000
Temporal effects	5	7.53	0.019	4.43	0.046	**0.00**	**0.717**
Edge effects	4	25.43	0.000	4.36	0.048	23.73	0.000
Nest-site effects	4	24.97	0.000	3.24	0.083	22.78	0.000
Habitat and temporal effects	7	**0.00**	**0.817**	7.38	0.011	4.02	0.096
Habitat and edge effects	7	5.72	0.047	1.18	0.233	26.86	0.000
Habitat and nest-site effects	7	9.95	0.005	5.47	0.027	26.60	0.000
Temporal and edge effects	8	11.37	0.003	8.90	0.005	12.32	0.001
Temporal and nest-site effects	8	11.15	0.003	8.81	0.005	3.55	0.121
Edge and nest-site effects	7	27.34	0.000	7.14	0.012	27.34	0.000
Global	13	4.40	0.090	8.71	0.005	12.32	0.002
Null	1	21.70	0.000	**0.00**	**0.420**	19.94	0.000

each of the models, we were able to draw conclusions concerning our hypotheses about the importance of each effect and each combination of effects on nest success of songbirds in riparian forests.

We evaluated goodness-of-fit of the global model for each species with Hosmer and Lemeshow (2000) goodness-of-fit tests. We visually inspected plots of standardized deviance residuals for the global model plotted against the explanatory values but found no large values (≥3) that suggested outliers or patterns indicative of the need for transformations. We used PROC REG (SAS Institute, Cary, North Carolina) to estimate tolerance for variables in the global model to diagnose multi-collinearity (Allison 1999); there were no signs of multi-collinearity (tolerance ≥0.64 for all variables in all models). We then used Akaike's Information Criterion (AIC) to rank models for each species from most- to least-supported given the data (Burnham and Anderson 2002). We calculated ΔAIC (difference between lowest observed AIC value and value for the current model) and Akaike weights (w_i, a measure of model support based on ΔAIC that sums to 1 across all candidate models) as measures of model support. We considered model-selection uncertainty by using the entire set of candidate models to calculate odds ratios based on model-averaged coefficients and 95% confidence intervals (CI) based on unconditional standard errors (Burnham and Anderson 2002). We calculated model-averaged coefficients as the sum of coefficients multiplied by AIC weights (w_i) from Burnham and Anderson's (2002) model. We used 0 for a coefficient when a model did not contain the explanatory variable, so that the model-averaged coefficients represented the contribution of the explanatory variable across the entire set of candidate models (Burnham and Anderson 2002). We converted model-averaged coefficients to odds ratios because of their more intuitive interpretation. For example, an odds ratio of 1.5 for laying stage would indicate that the odds of nest success was 50% greater during laying stage than during nestling stage, the reference category. The percentage of change in the odds ratio for each 1-unit change in a continuous variable is interpreted by subtracting 1 and multiplying the odds ratio by 100 (Allison 1999). Except where otherwise noted, we interpret only odds ratios with CIs that do not include 1.

We estimated daily nest success for each species with the most-supported model. Because we modified the link function for logistic regression to account for the length of each nest interval, the predicted probabilities represent probability of a nest surviving 1 day and are comparable to daily survival estimated by other methods (Mayfield 1961, Johnson 1979). We present estimates for each level of the explanatory factors whose CIs surrounding their model-averaged odds ratios did not include 1, assuming a balanced population across all levels of the remaining factors (lsmeans statement, PROC GENMOD). We also estimated interval nest success (percentage surviving the entire nest cycle) using the most-supported model and assuming a balanced population across all factors except nest stage, for which we used the appropriate number of laying, incubation, and nestling days (Ehrlich et al. 1988, Payne 1992, Van Horn and Donovan 1994, Cimprich and Moore 1995, Roth et al. 1996, McDonald 1998, Halkin and Linville 1999).

Results

We monitored 484 nests of the three most common species (Gray Catbird, Northern

Cardinal, and Indigo Bunting) and area-sensitive forest species pooled. Two-hundred and sixty-three nests were monitored in 2000, and 221 were monitored in 2001. The major cause of nest failure was predation; 295 of 484 nests (61%) were depredated. One-hundred and thirty-four nests (28%) were parasitized by Brown-headed Cowbirds.

Gray Catbird.—We monitored 175 Gray Catbird nests for 892 intervals; 76 nests were successful. Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global model fit the observed values ($\chi^2 = 7.01$, df = 8, $P < 0.54$). Examining the results of model selection, we found the most support for our hypothesis concerning effects of habitat-patch and temporal factors on nest success, but there was also some support for our global model with all effects (Table 1). Laying stage was the most important factor explaining daily nest success of Gray Catbird. Odds of nest success were 65% lower during the laying stage than during the nestling stage (Table 2 and Fig. 1). Nest success was also lower during incubation than during nestling stage and in riparian forests with no adjacent buffer strip than in riparian forests with an adjacent buffer strip (Table 2 and Fig. 1). Width also occurred in the most-supported model, and the odds of nest success were 63% greater in narrow than in wide riparian forests, but the CI barely overlapped 1 (Table 2). Interval nest success—assuming 3-, 11-, and 10-day laying, incubation, and nestling period, respectively, and a balanced population across other factors—was 0.404 in the most-supported model.

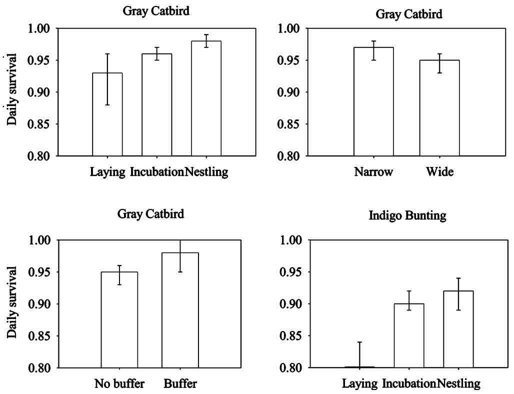

Fig. 1. Effects of nest stage, riparian forest width, and presence of a buffer strip on daily survival rates (mean ± 95% confidence intervals) of Gray Catbird ($n = 892$ intervals) and effects of nest stage on Indigo Bunting ($n = 790$ intervals) in northeastern Missouri, 2000–2001.

Northern Cardinal.—We monitored 55 Northern Cardinal nests for 239 intervals; 22 nests were successful. Hosmer and Lemeshow (2000) goodness-of-fit test indicated problems with model fit ($\chi^2 = 16.18$, df = 8, $P = 0.039$). Model selection indicated that the null model received the most support; the habitat-patch and edge-effects model and the habitat-effects model received some support (Table 1). Daily nest success estimated with the null model was 0.940 (0.920–0.955); interval nest success, assuming a 24-day nest cycle, was 0.227.

Indigo Bunting.—We monitored 223 Indigo Bunting nests for 790 intervals; 42 nests were successful. Hosmer and Lemeshow (2000)

Table 2. Odds ratios and 95% confidence intervals (CI) for explanatory variables based on model-averaged results from 11 *a priori* candidate models predicting nest success of songbirds in northeastern Missouri, 2000–2001.

	Gray Catbird		Northern Cardinal		Indigo Bunting	
Variable	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
Concealment	0.999	0.998, 1.001	1.003	0.991, 1.014	1.000	0.999, 1.001
Nest height	1.000	1.000, 1.000	1.002	0.998, 1.006	1.000	0.999, 1.002
Incubation versus nestling	0.627	0.397, 0.989	0.803	0.527, 1.220	0.855	0.601, 1.216
Laying versus nestling	0.351	0.177, 0.695	0.755	0.353, 1.613	0.368	0.240, 0.563
Buffer (no buffer vs. buffer)	0.581	0.357, 0.946	0.970	0.492, 1.912	1.008	0.941, 1.080
Distance to edge	1.000	0.999, 1.002	1.006	0.999, 1.014	1.000	0.999, 1.000
Habitat (buffer vs. forest)	0.977	0.865, 1.103	1.253	0.482, 3.274	1.039	0.922, 1.172
Date	1.000	0.991. 1.010	1.003	0.994, 1.011	1.002	0.996, 1.001
Distance to stream	1.001	0.999, 1.003	1.007	0.998, 1.016	1.000	0.999, 1.001
Stem total	0.999	0.998, 1.001	0.996	0.987, 1.005	1.000	0.999, 1.002
Width (narrow vs. wide)	1.630	0.980, 2.711	2.921	0.922, 9.252	0.981	0.891, 1.080
Year (2000 vs. 2001)	1.451	0.987, 2.134	1.010	0.692, 1.484	0.954	0.711, 1.280

goodness-of-fit test indicated that the global model fit the observed values ($\chi^2 = 6.50$, df = 8, $P = 0.59$). We found the most support for our hypothesis concerning effects of temporal factors on nest success, but there was also some support for our hypothesis concerning temporal and habitat-patch effects (Table 1). Laying stage was the most important factor explaining daily nest success for Indigo Bunting; odds of nest success were 63% lower during laying stage than during nestling stage (Table 2 and Fig. 1). Confidence intervals for all other odds ratios overlapped 1 (Table 2). Interval nest success in the most-supported model—assuming 3-, 12-, and 9-day laying, incubation, and nestling period, respectively, and a balanced population across other factors—was 0.070.

Area-sensitive forest species pooled.—We found 31 nests of area-sensitive forest species: 4 Acadian Flycatcher nests, 6 Ovenbird nests, 10 Wood Thrush nests, and 11 Kentucky Warbler nests. Of those, one Acadian Flycatcher nest, three Ovenbird nests, three Wood Thrush nests, and five Kentucky Warbler nests were successful. Daily nest success estimated with the null model for those species pooled was 0.935 (0.900–0.958); interval nest success, assuming a 25-day nest cycle, was 0.186.

Landscape metrics.—Patch area varied considerably between narrow and wide riparian forests. Percentage of row crop located in the local landscape surrounding each width-buffer level was similar. The landscape was predominantly agricultural, 71.56–82.15% row crops and grasses. Forest was a minor part of the landscape (4.73–7.89%), and the small mean patch size indicated that forest occurred in numerous small fragments (Table 3).

Discussion

Our estimates of interval nest success (Gray Catbird, 0.404; Northern Cardinal, 0.227; Indigo Bunting, 0.070; area-sensitive forest species pooled, 0.186) were within the range of nest success estimates reported for the same species in other highly fragmented forests across the Midwest (Robinson 1992, Robinson et al. 1995, Fessler 2001). Nest success, however, was much less than that reported for the same species in less fragmented forests across the Midwest (Robinson et al. 1995). Donovan et al. (1995) reported a nest success estimate of 0.520 for Wood Thrush and 0.400 for Ovenbird in contiguous forests located in Missouri, Wisconsin, and Minnesota. Woodward et al. (2001) reported a nest success estimate of 0.410 for Indigo Bunting and 0.405 for Northern Cardinal in regenerating forest and glades located within more-forested landscapes in southern Missouri. We believe that our nest success was much lower than those because of the highly fragmented, linear nature of the riparian forest and surrounding agricultural landscape.

We found only limited support for our hypotheses concerning habitat-patch and edge effects on nest success—which is consistent with our predictions. We believe that the limited support for those effects is attributable to low nest success across all riparian forests, resulting from the overwhelming effect of the surrounding agricultural landscape. Local-scale processes, such as edge and habitat-patch effects, may be constrained by habitat characteristics at the landscape scale (Donovan et al. 1997, Hartley and Hunter 1998, Tewksbury et al. 1998). Donovan et al. (1997) found strong evidence that, in the Midwest, edge effects are dependent on landscape context and that nest success was low in fragmented landscapes similar to those in the present study. Landscape effects are also more common than local or edge effects on distribution of predators (Chalfoun et al. 2002). Furthermore, distributions of raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) are positively associated with forest fragments dispersed throughout developed and agricultural habitats (Noren 1941, Reynolds 1945, Pedlar et al. 1997, Dijak and Thompson 2000). Even though patch size varied considerably among wide and narrow riparian forests, mean patch size of the surrounding landscape was small for all riparian forests (Table 3), which demonstrates the high level of fragmentation of all riparian forests.

Other studies have reported a positive relationship between patch size and nest success (reviewed in Paton 1994). Results of studies examining the relationship between width of riparian forest and nest success, however, vary among regions, species, and habitats (Chapa 1996, Vander Haegen and DeGraaf 1996, Tewksbury et al. 1998, Knutson et al. 2000). It appears that even the wide riparian forests in the present study were not wide enough to affect nest success of some species in highly fragmented riparian

Table 3. Landscape metrics (mean and 95% confidence intervals) within a 5-km radius of narrow and wide riparian forests, with and without adjacent buffer strips, in northeastern Missouri, 2000–2001 ($n = 12$).

Landscape metric	Narrow, no buffer	Narrow, buffer	Wide, no buffer	Wide, buffer
Patch area (ha)	257.28	61.77	509.40	528.72
	(–294.08, 808.64)	(–107.86, 231.40)	(–836.44, 1855.24)	(–744.37, 1801.81)
Urban land (%)	0.00	0.81	0.18	0.04
	–	(–2.28, 3.90)	(–0.35, 0.72)	(–0.13, 0.21)
Row-crop land (%)	32.08	43.06	31.75	22.29
	(6.86, 57.31)	(15.07, 71.05)	(22.57, 40.93)	(8.41, 36.17)
Grassland (%)	50.07	43.35	47.84	54.20
	(30.52, 69.63)	(24.87, 641.83)	(37.17, 58.51)	(28.14, 80.25)
Forestland (%)	17.58	11.99	19.40	22.64
	(12.03, 23.13)	(1.71, 22.26)	(5.27, 33.54)	(7.11, 38.16)
Mean grassland patch size (ha)	40.86	27.73	30.13	53.24
	(–7.05, 88.76)	(11.22, 44.24)	(8.95, 51.31)	(–46.67, 153.15)
Mean forest patch size (ha)	6.75	4.73	6.9	7.89
	(4.86, 8.65)	(3.54, 5.93)	(3.81, 10.17)	(2.02, 13.76)
Grassland in core area (%)	20.76	15.45	18.29	24.26
	(6.58, 34.95)	(3.56, 27.34)	(9.66, 26.91)	(1.30, 47.21)
Forestland in core area (%)	5.09	2.93	7.29	8.37
	(3.44, 6.74)	–0.21, 6.07)	(–3.32, 17.90)	(–3.19, 19.93)

forests located within agricultural landscapes where predators are likely abundant.

We found strong support for greater nest success of Gray Catbird in forests with adjacent buffer strips. Some studies have found nest success to be lower in abrupt (hard) edges and greater in more gradual (soft) edges, such as those created when grassland–shrub buffer strips are planted between forest and crop-field (reviewed in Paton 1994, Suarez et al. 1997, Saracco and Collazo 1999) but others have not (Fenske–Crawford and Niemi 1997, Tewksbury et al. 1998). Buffer strips could yield lower predation rates by decreasing visibility of nests along edges, decreasing density of potential prey, or decreasing use of the edge as a natural travel corridor (Johnston and Odum 1956, Bider 1968, Dunn 1977, Chasko and Gates 1982, Harris 1984). Presence of a buffer strip was not important in explaining nest success of Indigo Bunting or Northen Cardinal. That a relationship between nest success and presence of a buffer strip was found for one bird species and not the others may be attributable to factors inherently different among the species. For example, studies have found that differences in the behaviors birds use to deter nest predation help explain why nest success is not always related to nest-site factors (Gochfeld 1984, Marzluff 1985, Martin 1992).

We found the most support for our hypothesis concerning temporal effects on nest success, which is consistent with our predictions. Daily nest success for Gray Catbird and Indigo Bunting was negatively affected by laying stage and, to a lesser extent, incubation stage. Some previous studies have found a decline in nest success during the incubation stage (Holcomb 1972, reviewed in Martin 1992, Sockman 1997), whereas others have found a decline in nest success during the nestling stage (Young 1963, Robertson 1972, Schaub et al. 1992, Burhans et al. 2002). Variation in predation rates during the nesting cycle may reflect temporal patterns in the predator community or availability of alternative prey (Thompson and Nolan 1973), or may reflect cues used by dominant predators to locate nests (MacDonald 1973, Herzog and Burghardt 1974, Eichholz and Koenig 1992).

Results of model simulations using demographic parameters based on the generalized population ecology of a Neotropical migratory songbird (juvenile survival rate = 0.30, adult survival rate = 0.60, nest attempts = 3 per season, female young fledged per successful nest = 2) suggest that a nest success rate of 0.250 to 0.300 is required to balance juvenile and adult mortality (Donovan and Thompson 2001). In northeastern Missouri, interval nest success for Indigo Bunting and for area-sensitive forest species pooled (0.070 and 0.186, respectively) fell well below that level. On the basis of the low nest success we observed for some species, we suggest that narrow, forested riparian corridors in agricultural landscapes may function as population sinks (Pulliam 1988) for some species in some years.

Our study illustrates (1) the importance of assessing avian demographic parameters, such as nest success, and (2) how land-management practices may affect breeding songbird populations. Riparian forests provided breeding habitat for area-sensitive forest species and for grassland–shrub nesting species, such as Gray Catbird, Northern Cardinal, and Indigo Bunting. Buffer strips provided additional breeding habitat for grassland–shrub nesting species. When riparian forests are located within agricultural landscapes, however, nest success may be marginal, and the potential even for wide riparian forests with adjacent buffer strips to provide high-quality breeding habitat may be severely diminished for some species. Nevertheless, as long as sink habitat is balanced by an appropriate amount of source habitat, and sink habitat is not preferred over available source habitat, sink habitat should be maintained, because it provides additional breeding habitat and may contribute to long-term population viability of these species in some years (Pulliam 1988, Donovan and Thompson 2001).

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