

## AVIAN NESTING SUCCESS IN FORESTED LANDSCAPES: INFLUENCE OF LANDSCAPE COMPOSITION, STAND AND NEST-PATCH MICROHABITAT, AND BIOTIC INTERACTIONS

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**ABSTRACT.**—Although area and isolation effects on avian communities in highly fragmented landscapes are well known, importance of landscape composition in more forested landscapes remains poorly understood. We determined if the type (agriculture and silviculture) and extent (percentage within 1 km radius) of disturbance within forested landscapes influenced avian nesting success, and then examined if differences in stand-level habitat structure, nest-patch microhabitat, distance of nests to habitat edges, brood parasitism rates, and nest-predator abundance were potential underlying mechanisms of observed associations between landscape composition and nesting success. We monitored active songbird nests ( $n = 341$ ), surveyed Brown-headed Cowbirds (*Molothrus ater*) and nest predators, and measured stand-level and nest-patch microhabitat from May–July 1998 and 1999. Each of 10 study sites was located within contiguous mature forest in central Pennsylvania and contained either agricultural or silvicultural disturbances ( $n = 5$  each). Sites of the two landscape types had similar ranges of disturbance within 1 km (21–55% for agriculture, 18–51% for silviculture). Daily nest survival for all species combined ( $94.0 \pm 0.55$  in agriculture and  $96.9 \pm 0.87$  in silviculture) and midstory-canopy nesters ( $93.8 \pm 0.97$  in agriculture and  $97.4 \pm 0.75$  in silviculture) were greater within forested landscapes disturbed by silviculture than by agriculture, but rates did not significantly differ between landscapes for ground nesters ( $92.2 \pm 1.32$  in agriculture and  $94.6 \pm 1.63$  in silviculture) or understory nesters ( $95.4 \pm 1.60$  in agriculture and  $95.0 \pm 1.47$  in silviculture). Nest survival was not significantly associated with disturbance extent. Rates of brood parasitism were low, with only 11% of nests containing cowbird eggs or young. Neither nest fate nor differences in daily nest survival between the two landscape types were explained by variation in brood parasitism rates, stand-level or nest-patch habitat characteristics, or distance of nests to edges. Instead, the lower nest success within forested landscapes disturbed by agriculture was best explained by greater abundances of some avian and small mammalian predators (American Crow [*Corvus brachyrhynchos*] and squirrels) in those landscapes in one or both years. Results suggest that landscape composition within forested landscapes significantly influences avian nesting success by altering interactions between nest predators and nesting birds. Received 22 March 2000, accepted 7 June 2001.

NUMEROUS LANDSCAPE-LEVEL studies of avian communities have examined patch area and isolation, finding that diversity, abundance, and nesting success of forest songbirds are reduced in small forest fragments (Lynch and Whigham 1984, Wilcove 1985, Wilcove and Robinson 1990, Donovan et al. 1995, Hoover et al. 1995, Van Horn et al. 1995, Hagan et al. 1996). However, other landscape characteristics can influence avian community structure and organization as well (Andrén 1992, Aberg et al. 1995, Coker and Capen 1995, Friesen et al. 1995,

Robinson et al. 1995, Saab 1999). In particular, both amount of habitat disturbance (Askins and Philbrick 1987, Askins et al. 1987, Donovan et al. 1997, Hartley and Hunter 1998) and types of land uses within landscapes (Andrén 1992, Aberg et al. 1995, Askins 1995, Coker and Capen 1995, Friesen et al. 1995, Kurki and Linden 1995, Huhta et al. 1996, Bayne and Hobson 1997, Saab 1999) can explain variation in avian community structure and nesting success.

Our present understanding of mechanisms behind associations between landscape composition and avian communities is incomplete because multiple underlying factors are seldom examined within single studies. In particular, habitat structure at stand, nest-patch, or both

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scales (Bowman and Harris 1980, Martin and Roper 1988, Holway 1991, Kelly 1993, Martin 1992, Burhans 1997, Johnson 1997), the distribution of bird nests relative to habitat edges (Gates and Gysel 1978, Wilcove 1985, Andr n and Angelstam 1988, Marini et al. 1995), and nest predator communities (Angelstam 1986, Andr n 1992, Nour et al. 1993, Haskell 1995, Bayne and Hobson 1997, Hannon and Cotterill 1998, Sieving and Willson 1998) may strongly affect rates of nest predation or brood parasitism. Thus, any of those factors may be responsible for landscape-level patterns in nesting success.

We used a multiscale approach to investigate how landscape composition affected nesting success and examined three spatial scales: landscape (314 ha), local (25 ha), and nest-patch (0.04 ha). Because territories of most Neotropical migratory songbirds are smaller than 2 ha in size, a 314 ha area was expected to be sufficiently large to be perceived as a landscape by most forest birds. The local scale was chosen because it generally included at least several territories per species and represented a relatively homogeneous forest stand in terms of floristics and structure. The nest-patch scale was selected according to guidelines established by BBIRD (Martin et al. 1996). First, at the landscape scale, we determined if the primary type (agriculture and silviculture) and extent (percentage within 1 km radius) of disturbance within forested landscapes influenced nesting success of birds in contiguous forest stands. Next we explored if greater nest failure in certain landscapes could be explained by (1) vulnerability to predation due to habitat characteristics at stand or nest-patch scales (e.g. nests were less concealed in certain landscapes and were, therefore, more vulnerable to predation), (2) nest placement relative to habitat edges (e.g. nests were closer to edges in certain landscapes), (3) brood parasitism, and (4) predator abundance (e.g. there were more predators in certain landscapes).

#### METHODS

*Study-site selection.*—Ten, 25 ha sites within contiguous mature forest (approximately 80–110 years old) were selected in the Ridge and Valley province of central Pennsylvania. Five sites each occurred within forested landscapes disturbed by agriculture and those disturbed by silviculture. Those pairs of sites

were selected from a larger group of 34 randomly chosen study sites for another study (Rodewald 2000, Rodewald and Yahner 2001), and the criteria were that they be publicly owned and that pairs have similar amounts of disturbance within the surrounding landscape. Agricultural disturbances consisted primarily of row crops with scattered pastures and hayfields, whereas silvicultural disturbances were clearcuts ( $\leq 15$  years old) with or without scattered residual trees. Sites within the two landscape types had similar amounts of forest cover within 1 km of the site center (agriculture mean = 39%, range = 21–55%; silviculture mean = 35%, range = 18–51%) and occurred interspersed throughout the study area. Forest cover was determined using LANDSAT thematic mapper imagery and ARC/INFO software (Environmental Systems Research Institute 1997). At each site, at least 80% of the nonforest cover within 1 km of the study site consisted of only one disturbance type. Both disturbance types occurred as perforations or patches within the forest matrix. Topographic relief and other minor disturbances within the surrounding landscape were similar among sites. All sites had little or no slope, similar vegetative structure and composition, were 250–500 m in elevation, and did not occur along ridgetops. Sites were separated by at least 3 km for independence. Common tree species in the study area included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and hickory (*Carya* spp.). Common understory species were vaccinium (*Vaccinium* spp.), mountain-laurel (*Kalmia latifolia*), witch-hazel (*Hamamelis virginiana*), and the saplings of dominant tree species, especially red maple.

*Nest searching and monitoring.*—Active nests (at least one egg or nestling) were monitored, and nests of common forest species were emphasized, especially Eastern Wood-Pewee, Ovenbird, Red-eyed Vireo, Scarlet Tanager, and Wood Thrush. From mid-May until late-July 1998 and 1999, each site was visited every three to five days. Although nest-searching efforts were concentrated in areas at least 100 m from habitat edges, nests were sometimes found closer to edges. Located nests were marked with numbered flags placed at least 10 m from the nest. Nests were checked at least every three to five days, more often if near fledging time. During a nest check, number of eggs (host and cowbird), number of nestlings, activity of parent (if seen), and any disturbance to the nest were noted. The nest was approached via different routes upon every nest check to prevent leaving a scent trail directly to the nest. If a potential nest predator was seen within  $\sim 50$  m of the nest, the nest was checked at a later time. Each nest was determined to be successful (at least one young fledged) or failed on the basis of length of nes-

tling stage, destruction of nest, or detection of the fledglings.

Each species was classified into one of three guilds: ground nester, understory nester (generally nesting <5 m), or midstory-canopy nester (generally nesting >5 m). Mayfield estimates of daily nest survival ( $1 - [\text{number of nests failed}/\text{total nest exposure days on a site}]$ ) (Mayfield 1961, 1975) were calculated for each site for all species combined and for each guild. Although nesting success was greater in 1998 than in 1999, pattern of differentiation between landscape types was similar in each year. Thus, nest data were pooled over the two years to increase number of nests per site and accuracy of nesting success estimates. Rates of brood parasitism were low across our sites, and differences between the two landscapes were tested with chi-square approximation. Because nest survival data were normally distributed and had homogeneous variance, differences in daily nest survival of all species combined and each guild were analyzed separately using one-way analyses-of-variance for disturbance type and correlation analyses for disturbance extent (SAS Institute 1990).

*Stand-level habitat characteristics.*—To describe habitat characteristics, we established three habitat sampling points at least 150 m from habitat edges and spaced at 150 m intervals along a transect bisecting the site. Because habitat structure within sites was relatively homogeneous on the basis of a visual assessment, that sampling effort seemed to reasonably characterize the habitat of each site. Twenty-two habitat characteristics were measured at a 0.04 ha circular plot centered on the point (modified from James and Shugart 1970) including numbers of trees by species in three diameter breast height (DBH) classes (8–23, 23–38, and >38 cm DBH); standing dead trees in two DBH classes (15–30 and >30 cm); numbers of fallen logs ( $\geq 7.5$  cm in diameter,  $\geq 1.0$  m long) and stumps ( $\geq 7.5$  cm diameter,  $\geq 0.25$  m tall; hereafter logs and stumps are collectively referred to as woody debris); soil temperature ( $^{\circ}\text{C}$  at 10 cm below ground); soil pH; and soil moisture (percentage). Soil characteristics were measured at three locations per circular plot (5 m and 0, 120, and 240 $^{\circ}$  from plot center). Soil pH and moisture were measured using a Kelway soil tester at least two to three days following precipitation. Within a 5 m radius of each sampling point, numbers of small woody stems (>0.5 m tall, <8.0 cm DBH) in size classes 0–2.5 cm and >2.5 cm (measured 10 cm above ground) were recorded by species, and percentages of ground cover (<0.5 m in height) of shrub, grass, forb, fern, moss, litter, log, rock, and bare ground were recorded to the nearest 5%. Two, 20 m perpendicular transects also were established through the center of each sampling point in north–south and east–west directions. Percentage canopy cover (using ocular tube sightings) and litter depth (cm) were measured at 2 m intervals along those transects.

Measurements for each habitat characteristic were averaged over the three points within a site. For three variables, the less meaningful variable of highly correlated pairs ( $r > 0.7$ ,  $P < 0.001$ ) were excluded from analyses. Differences in 19 microhabitat and microclimate characteristics between forested landscapes disturbed by agriculture or silviculture were tested by using Kruskal-Wallis (chi-square) tests with the Bonferroni method of controlling the effective alpha level at (0.05/number of tests performed) (Sokal and Rohlf 1995). The small number of sites ( $n = 10$ ) did not provide enough degrees of freedom to perform multivariate procedures.

*Nest-patch microhabitat and distance to edge.*—Because of time limitations, nest-patch microhabitat characteristics were measured only for the four most common species: Ovenbird, Red-eyed Vireo, Scarlet Tanager, and Wood Thrush. In July 1998 and 1999, the following nest characteristics were recorded (Martin et al. 1996): nest height (meters), distance to edge (meters), DBH of plant with nest (centimeters), number of support branches, mean diameter of support branches (centimeters), distance from central axis (meters), and percentage of nest concealed by vegetation from overhead and four cardinal directions (for ground nesters only).

Within an 0.04 ha plot around the nest, the following habitat characteristics were recorded using the same protocol as for stand-level habitat measurements: canopy height, trees and snags by species and three size classes, and amount of woody debris. At 20 locations along two perpendicular transects running north–south and east–west through the plot, percentage canopy (>5 m) and ground cover (<0.5 m) were estimated using an ocular tube. Ground cover was categorized as live vegetation, moss, bare soil, leaf litter, log, or rock. At those same points, litter depth (centimeters) was measured with a ruler, and woody stems were counted in 0.5 m height interval classes ranging from 0.5–3.0 m using a 3 m tall PVC pole.

Several highly correlated ( $P \leq 0.001$ ) or collinear habitat variables were either dropped or combined into the following new variables: total number of trees ( $\geq 8.0$  cm DBH), total number of stems (0.5–3.0 m in height), and concealment (mean percentage lateral concealment of nest from the four cardinal directions), percentage unvegetated ground cover (cover by litter, rock, and bare soil). Percentage overhead concealment, numbers of snags, canopy height, ground cover (<0.5 m) by vegetation, moss, and log were dropped from analysis because of strong correlations with other variables. Total number of trees and stems, woody debris, leaf litter depth, nest height, nest plant DBH, diameter of support branches, and distance from central axis were log-transformed to meet assumptions of normality. For ground nesters and all species combined, the following nest-patch and placement characteristics were

analyzed: distance from habitat edge (meters), percentage canopy cover, percentage unvegetated ground cover, amount of woody debris, total number of trees, total number of stems, and leaf litter depth. For understory and midstory canopy nesters, an additional four variables were included in analyses: nest height, nest plant DBH, diameter of support branches, and distance from central axis.

Differences in nest-patch microhabitat characteristics between successful and failed nests were transformed when necessary and tested using multivariate analysis-of-variance (MANOVA) for all species combined, ground nesters, understory nesters, and midstory canopy nesters. Because several estimates of concealment were missing and would have caused the deletion of those observations from analysis, differences in nest concealment for ground nests between nest fate or landscape types were not analyzed in the MANOVA, but were tested using a Kruskal-Wallis (chi-square) test.

To examine differences in nest-patch microhabitat between the two landscape types, each nest-patch characteristic was averaged over nests within a site. Because of insufficient degrees-of-freedom for MANOVA ( $n = 10$ ), differences in nest-patch microhabitat were tested using univariate analyses-of-variance with Bonferroni corrections for all species combined, ground, understory and midstory canopy nesters. All statistical analyses were conducted using SAS statistical software (SAS Institute Inc. 1990).

*Brown-headed cowbirds and avian nest predators.*—Relative abundances of Brown-headed Cowbirds, American Crows, and Blue Jays (*Cyanocitta cristata*) were assessed at the three stand-level habitat sampling points. Upon arrival at each point, the surveyor (A.D.R.) allowed a 1 min period to elapse before recording all birds seen or heard for a 10 min period within 50 m radius of the sampling point. Sites were visited twice each June in 1998 and 1999. Surveys were conducted between 0545–1045 on mornings without strong wind ( $>20 \text{ mi h}^{-1}$ ) or rain. Abundance data for each species were summed over the three point counts per site and averaged over the four visits to produce one measure of abundance per site. Because the data met assumptions of normality and equal variance, differences in abundance between the two landscape types were tested using analyses-of-variance for each species (SAS Institute 1990).

*Mammalian and reptilian nest predators.*—From late-May until early July 1998 and 1999, surveys of potential nest predators were conducted on the 10 sites. Four surveys were conducted each year along a  $200 \times 100 \text{ m}$  strip transect bisecting each site (Wilson et al. 1996). All mammalian and reptilian potential predators seen or heard during the  $\sim 15 \text{ min}$  survey were recorded. Surveys were conducted between 0700–1000 on days without strong wind ( $>20 \text{ mi h}^{-1}$ ) or rain. Numbers of individuals for each species

were averaged over the four visits each year. Abundance data from transects were not normally distributed and, thus, were analyzed separately for each species using Kruskal-Wallis (chi-square) tests (SAS Institute 1990).

## RESULTS

*Nesting success and landscape composition.*—Of 341 nests monitored over the two-year period (4,216.5 exposure days), 82% were those of Eastern Wood-Pewee, Ovenbird, Red-eyed Vireo, Wood Thrush, and Scarlet Tanager (Table 1). Estimates of daily nest survival were lower within forested landscapes disturbed by agriculture than by silviculture for all species combined ( $F = 6.377$ ,  $df = 1$  and  $8$ ,  $P = 0.036$ ) and midstory-canopy nesters ( $F = 8.640$ ,  $df = 1$  and  $8$ ,  $P = 0.019$ ), but not for ground nesters ( $F = 1.309$ ,  $df = 1$  and  $8$ ,  $P = 0.24$ ) nor understory nesters ( $F = 0.032$ ,  $df = 1$  and  $7$ ,  $P = 0.86$ ) (Fig. 1). Although the incidence of brood parasitism by Brown-headed Cowbirds tended to be greater in forested landscapes disturbed by agriculture than by silviculture (13.4 vs. 8.3% of nests, respectively), the difference was not significant ( $\chi^2 = 1.278$ ,  $df = 1$ ,  $P = 0.26$ ). Daily nest survival was unrelated to extent of disturbance within forested landscapes for all species combined ( $r = -0.314$ ,  $n = 10$ ,  $P = 0.38$ ), ground nesters ( $r = 0.028$ ,  $n = 10$ ,  $P = 0.94$ ), understory nesters ( $r = 0.089$ ,  $n = 10$ ,  $P = 0.82$ ), and midstory canopy nesters ( $r = -0.419$ ,  $n = 10$ ,  $P = 0.23$ ).

*Stand-level habitat characteristics.*—No habitat characteristics differed between stands in forested landscapes disturbed by agriculture or silviculture on the basis of a Bonferroni-corrected  $\alpha = 0.05$  for all univariate tests.

*Nest-patch microhabitat and distance to edge.*—Nest-patch microhabitat and distance of nest to edge (Table 2) were not associated with nest fate for all species combined ( $F = 1.451$ ,  $df = 7$  and  $248$ ,  $P = 0.19$ ), ground nesters ( $F = 0.862$ ,  $df = 7$  and  $82$ ,  $P = 0.54$ ), understory nesters ( $F = 1.640$ ,  $df = 11$  and  $44$ ,  $P = 0.12$ ), and midstory canopy nesters ( $F = 1.074$ ,  $df = 11$  and  $81$ ,  $P = 0.39$ ). However, nest concealment of successful ground nests was marginally greater than failed ground nests ( $59.07 \pm 4.18$  vs.  $49.18 \pm 4.07$ ,  $F = 2.853$ ,  $df = 1$  and  $74$ ,  $P = 0.095$ ). Forested landscapes disturbed by agriculture and silviculture did not differ in nest-patch characteristics nor distance to edge for all spe-

TABLE 1. Number of nests found for each species at the 10 nest study sites in central Pennsylvania, 1998–1999.

Species	Number of nests
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	1
Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	2
Eastern Wood-Pewee ( <i>Contopus virens</i> )	22
Acadian Flycatcher ( <i>Empidonax virescens</i> )	7
Eastern Phoebe ( <i>Sayornis phoebe</i> )	1
Blue-headed Vireo ( <i>Vireo solitarius</i> )	6
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	66
Blue-gray gnatcatcher ( <i>Poliophtila caerulea</i> )	3
Wood Thrush ( <i>Hylocichla mustelina</i> )	65
Hermit Thrush ( <i>Catharus guttatus</i> )	4
American Robin ( <i>Turdus migratorius</i> )	6
Gray Catbird ( <i>Dumetella carolinensis</i> )	2
Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )	2
Black-throated Green Warbler ( <i>Dendroica virens</i> )	3
Hooded Warbler ( <i>Wilsonia citrina</i> )	4
Worm-eating Warbler ( <i>Helminthos vermivorus</i> )	4
Ovenbird ( <i>Seiurus aurocapillus</i> )	90
Louisiana Waterthrush ( <i>Seiurus motacilla</i> )	2
Common Yellowthroat ( <i>Geothlypis trichas</i> )	1
American Redstart ( <i>Setophaga ruticilla</i> )	1
Scarlet Tanager ( <i>Piranga olivacea</i> )	35
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	5
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	3
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	1
Indigo Bunting ( <i>Passerina cyanea</i> )	5

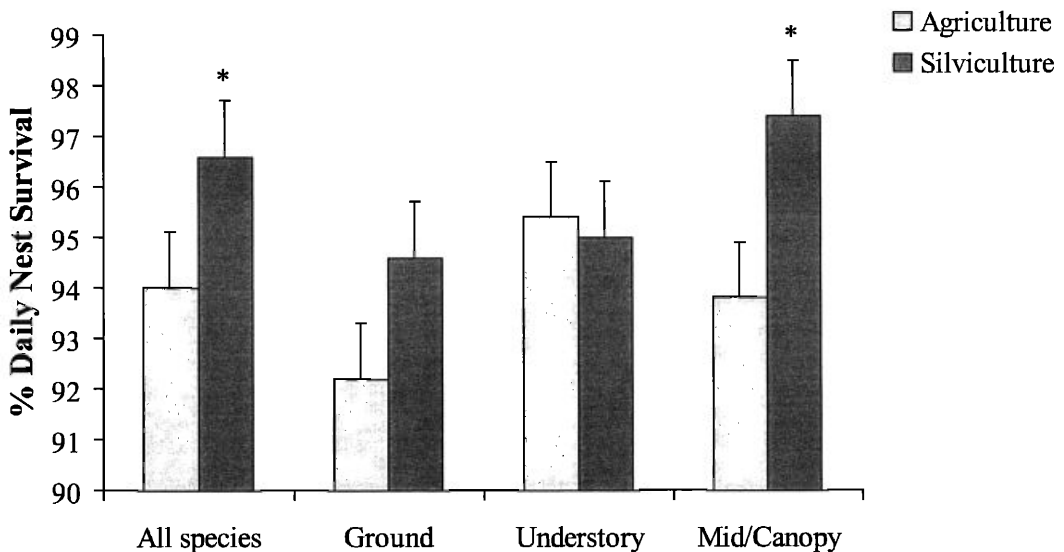
FIG. 1. Differences in daily nest survival of all species combined, ground nesters, understory nesters, and midstory-canopy nesters in 10 forest sites within landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998–1999. \* indicates  $P < 0.05$ .

TABLE 2. Mean ( $\pm$  SE) and associated P-values of 11 nest-patch characteristics (untransformed) of successful and failed nests in 10 forested landscapes disturbed either by agriculture or silviculture in the Ridge and Valley Province of central Pennsylvania, 1998–1999. P-values from a *posteriori* univariate analyses.

Nest-patch characteristic	All species combined				Ground nesters				Understory nesters				Midstory-canopy nesters			
	Success	Failure	P-value		Success	Failure	P-value		Success	Failure	P-value		Success	Failure	P-value	
Nest height (m)									4.17 (0.61)	3.20 (0.39)	0.123		10.07 (0.86)	8.80 (0.90)	0.355	
Nest plant DBH (cm)									10.74 (1.74)	13.67 (2.34)	0.481		23.74 (1.95)	21.46 (2.38)	0.207	
Support branch diameter (cm)									1.57 (0.17)	1.97 (0.20)	0.137		1.83 (0.33)	1.39 (0.17)	0.395	
Distance from central axis (cm)									1.51 (0.29)	1.37 (0.32)	0.983		2.57 (0.28)	2.38 (0.28)	0.544	
Distance to edge (m)	116.52 (6.18)	127.16 (5.91)	0.214		136.49 (10.68)	138.11 (9.58)	0.911		101.03 (13.06)	106.21 (11.70)	0.869		112.09 (8.94)	129.57 (9.44)	0.110	
Number of trees	21.26 (0.73)	19.41 (0.66)	0.086		22.86 (1.42)	19.08 (0.90)	0.039		20.97 (1.73)	17.06 (1.15)	0.136		20.35 (0.91)	21.48 (1.29)	0.523	
Number of stems	16.40 (1.27)	15.61 (1.25)	0.416		12.41 (1.94)	12.47 (1.25)	0.389		29.31 (2.86)	25.88 (3.43)	0.075		11.56 (1.20)	11.87 (1.64)	0.273	
Canopy cover (%)	71.13 (1.31)	70.98 (1.60)	0.945		71.08 (2.28)	68.11 (2.74)	0.437		68.44 (2.95)	71.97 (2.91)	0.301		72.73 (1.87)	73.59 (2.59)	0.389	
Amount of woody debris	10.84 (0.47)	10.17 (0.54)	0.145		10.43 (0.90)	8.98 (0.77)	0.155		9.75 (1.01)	12.27 (1.48)	0.363		11.75 (0.62)	10.04 (0.64)	0.092	
Unvegetated ground cover (%)	65.89 (1.79)	61.52 (1.78)	0.086		56.49 (2.90)	54.91 (2.11)	0.652		69.69 (3.47)	73.03 (3.70)	0.792		70.00 (2.65)	60.87 (3.22)	0.021	
Litter depth (cm)	1.84 (0.10)	1.70 (0.10)	0.137		1.83 (0.17)	1.65 (0.19)	0.194		1.75 (0.21)	1.62 (0.17)	0.341		1.89 (0.14)	1.81 (0.17)	0.624	

cies combined and the three nesting guilds (Table 3).

*Nest predators and Brown-headed Cowbirds.*—Only Blue Jays, American Crows, squirrels (*Sciurus* spp. and *Tamiasciurus hudsonicus*), and eastern chipmunks (*Tamias striatus*) were encountered frequently enough to permit analysis. Squirrels ( $\chi^2 = 4.452$ ,  $df = 1$ ,  $P = 0.035$ ) and chipmunks ( $\chi^2 = 13.14$ ,  $df = 1$ ,  $P < 0.001$ ) were significantly more abundant in 1999 than in 1998. When analyzed separately by year, squirrels were more abundant within forested landscapes disturbed by agriculture than by silviculture in 1998 ( $\chi^2 = 3.75$ ,  $df = 1$ ,  $P = 0.053$ ), but not in 1999 (Table 4,  $\chi^2 = 0.18$ ,  $df = 1$ ,  $P = 0.67$ ). No significant difference between the two landscape types was detected for eastern chipmunks in either 1998 ( $\chi^2 = 0.012$ ,  $df = 1$ ,  $P = 0.91$ ) or 1999 ( $\chi^2 = 0.548$ ,  $df = 1$ ,  $P = 0.46$ ). American Crows ( $F = 24.50$ ,  $df = 1$  and  $8$ ,  $P = 0.001$ ) and Brown-headed Cowbirds ( $F = 22.05$ ,  $df = 1$  and  $8$ ,  $P = 0.002$ ) were significantly more abundant within forested landscapes disturbed by agriculture than by silviculture (Table 4), but there was no difference for Blue Jays ( $F = 2.62$ ,  $df = 1$  and  $8$ ,  $P = 0.14$ ).

#### DISCUSSION

Although previous studies conducted in fragmented areas have demonstrated reduced nesting success in small patches (Wilcove 1985, Wilcove and Robinson 1990, Hoover et al. 1995) or agricultural landscapes (Andr n 1992, Askins 1995, Kurki and Linden 1995, Robinson et al. 1995), effects of landscape composition on nesting success within forested landscapes have been less examined, especially away from forest edges. Therefore, our results are important because they have shown that daily nest survival of all species combined and midstory-canopy nesters were lower within forested landscapes disturbed by agriculture than by silviculture, irrespective of amount of disturbance within forested landscapes (<55% disturbance within 1 km). Because disturbance type and extent within landscapes were not confounded in our experimental design, this study provides evidence that type of land use occurring within forested landscapes can influence avian nesting success independently of extent of disturbance.

Associations between nest fate and habitat structure at stand or nest-patch scales have been detected in numerous studies (Bowman and Harris 1980, Conner et al. 1986, Martin and Roper 1988, Martin 1992, Mitchell et al. 1996, Johnson 1997, but see Filliater et al. 1994). However, at our sites neither nest fate nor differences in nesting success between the two landscape types were explained by stand-level habitat characteristics, nest-patch microhabitat, or distance of nests to edges. Instead, the lower nest survival within forested landscapes disturbed by agriculture was best explained by greater abundances of some avian and small mammalian predators in those landscapes in one or both years. In particular, annual variation in nesting success paralleled squirrel numbers, suggesting that those small mammals may have influenced nest predation at our sites. Although other studies indicate that squirrels are important nest predators in forest ecosystems (Darveau et al. 1997, Song and Hannon 1999, Bayne and Hobson 1997, Boulet et al. 2000), our sampling methods do not allow us to assess relative importance of predation by squirrels versus by other nocturnal predators, such as raccoons (*Procyon lotor*), which are often more abundant within agricultural landscapes (Pedlar et al. 1997, Heske et al. 1999, Dijak and Thompson 2000).

Nest-predator distribution and abundance may have been influenced by structural or temporal differences between the two disturbance types within landscapes. For example, agricultural disturbances may have provided seasonal habitat or food resources to nest predators, especially if an area was known to be a reliable resource over many years. Fragmented agricultural landscapes are known to have greater abundances of generalist predators (e.g. corvids) than silvicultural landscapes (Andr n 1992, Haskell 1995, Bayne and Hobson 1997), and agricultural edges can exert stronger adverse effects on nesting success of birds than silvicultural edges (Angelstam 1986, Hanski et al. 1996, Suarez et al. 1997). The findings of our study are novel because differences in both predator communities and nesting success were detected away from habitat edges within primarily forested landscapes.

Lack of an association between nest fate and nest-patch microhabitat may have been related to types of nest predators. For example, nest

TABLE 3. Mean ( $\pm$  SE) and associated *P*-values of 11 nest-patch characteristics (untransformed) for forested landscapes disturbed either by agriculture (Agric) or silviculture (Silvic) in the Ridge and Valley Province of central Pennsylvania, 1998–1999. Each transformed characteristic was tested using analyses-of-variance with the Bonferroni method for controlling effective alpha level (corrected critical  $\alpha = 0.007$ ).

Nest-patch characteristic	All species combined			Ground nesters			Understory nesters			Midstory-canopy nesters		
	Agric	Silvic	<i>P</i> -value	Agric	Silvic	<i>P</i> -value	Agric	Silvic	<i>P</i> -value	Agric	Silvic	<i>P</i> -value
Nest height (m)							3.34 (0.21)	3.31 (0.58)	0.678	10.69 (1.50)	8.78 (1.15)	0.542
Nest plant DBH (cm)							12.68 (3.62)	10.74 (3.27)	0.742	23.69 (1.87)	20.72 (3.35)	0.949
Support branch diameter (cm)							1.68 (0.28)	1.67 (0.24)	0.898	1.68 (0.32)	1.58 (0.18)	0.644
Distance from central axis (cm)							1.69 (0.48)	1.21 (0.42)	0.488	2.37 (0.31)	2.55 (0.44)	0.367
Distance to edge (m)	131.68 (7.92)	115.52 (7.31)	0.172	136.36 (8.14)	137.73 (8.27)	0.909	132.78 (18.42)	72.46 (16.91)	0.063	137.90 (10.37)	115.62 (8.00)	0.128
Number of trees	22.69 (1.79)	19.13 (0.97)	0.138	23.61 (1.41)	18.79 (1.31)	0.026	18.89 (1.49)	15.46 (2.79)	0.595	22.28 (2.56)	20.54 (0.61)	0.570
Number of stems	15.58 (3.68)	15.83 (3.11)	0.681	10.43 (2.43)	10.75 (3.74)	0.846	29.76 (5.95)	31.93 (9.03)	0.854	14.56 (3.15)	13.31 (3.21)	0.795
Canopy cover (%)	72.80 (3.74)	70.60 (1.70)	0.607	71.52 (4.37)	70.43 (1.96)	0.825	67.87 (0.91)	66.09 (6.25)	0.820	74.02 (3.14)	72.50 (1.44)	0.672
Amount of woody debris	8.76 (1.13)	11.79 (0.91)	0.077	9.06 (2.15)	11.81 (0.79)	0.164	8.33 (0.19)	12.27 (1.94)	0.239	8.86 (0.89)	11.52 (0.84)	0.065
Unvegetated ground cover (%)	56.61 (5.72)	68.07 (2.83)	0.110	53.25 (3.77)	59.02 (3.46)	0.292	68.70 (3.16)	71.84 (5.87)	0.690	60.74 (8.35)	70.26 (3.63)	0.326
Litter depth (cm)	1.85 (0.29)	1.89 (0.15)	0.709	1.60 (0.34)	1.94 (0.22)	0.374	1.44 (0.27)	1.66 (0.11)	0.156	2.01 (0.29)	1.88 (0.14)	0.839



TABLE 4. Mean ( $\pm$  SE) abundance of potential nest predators in forested landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998–1999.

Species or group	Agricul- ture		Silvicult- ure		P-val- ue
	Mean	SE	Mean	SE	
Both years <sup>a</sup>					
American Crow	1.15	0.19	0.10	0.10	0.001
Blue Jay	0.95	0.35	0.35	0.13	0.144
1998 only <sup>b</sup>					
Squirrels	0.20	0.09	0.00	0.00	0.053
Eastern chip- munks	0.70	0.30	0.75	0.51	0.911
1999 only <sup>b</sup>					
Squirrels	0.60	0.24	0.60	0.18	0.671
Eastern chip- munks	4.25	0.87	4.85	0.68	0.459

<sup>a</sup> Surveyed using 10-minute, 50 m radius point counts.

<sup>b</sup> Surveyed using 200  $\times$  100 m strip transects.

concealment should be more important when predation is caused by visually oriented birds than by mammals or other predators (Clark and Nudds 1991, Colwell 1992, Yahner and Scott 1988). Species richness of predator communities may also be important. In areas with many different species of predators, nest-searching techniques are expected to be diverse and, as a result, no nest-patch features are predictably safe (Filliater et al. 1994). For the four common forest bird species at our sites, nest-site selection at the landscape scale seemed more important than at the nest-patch or stand level.

If landscape composition within forested landscapes influences nest-predator abundance, as suggested by our data, then nesting success is not necessarily the only component of avian communities that will be affected. Nest predation events can affect site fidelity and re-nesting location (Sieving and Willson 1998, Haas 1998). Thus, nest predation may represent a proximate mechanism that governs habitat selection by a bird and, in this way, can mediate avian community structure (Martin 1988a, b; Sieving and Willson 1998, Rodewald and Yahner 2001). For instance, lower species richness and abundances of certain species of Nearctic-Neotropical migratory songbirds in small forest fragments (e.g. Forman et al. 1976, Ambuel and Temple 1983, Lynch and Whigham 1984, Blake and Karr 1984, 1987; Robbins et al. 1989) are generally attributed to more intense nest

predation than in larger forested stands. Similarly, in our study area, forest bird species richness and abundance were lower on sites with greater levels of nest predation as compared to sites with lower levels of nest predation (Rodewald 2000, Rodewald and Yahner 2001). Such potentially significant effects of nest predation on avian community structure and nesting success suggest that landscape composition should be considered in forest-management and conservation plans, especially given that most public and private reserves either include or are surrounded by multiple land uses.

#### ACKNOWLEDGMENTS

We are especially grateful to J. Avery, W. Cooper, R. Cronauer, J. Frank, J. Giocomo, A. Harpster, R. Kossoff, A. Lyter, P. Rodewald, A. Siepielski, M. Stitzer, and J. Urbanic for field and technical assistance. M. C. Brittingham, W. L. Myers, P. G. Rodewald, and K. C. Steiner provided valuable comments on earlier drafts of this manuscript. Research funds were generously provided by the Wild Resource Conservation Fund of the Pennsylvania Game Commission, SDE/Graduate Women in Science Inc., and the Wilson Ornithological Society (Paul A. Stewart Award). We also thank the Henry Luce Foundation for the Penn State Women in Science and Engineering Clare Boothe Luce Fellowship to A. D. Rodewald from 1997–1999.

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Associate Editor: J. Brawn