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HOODED WARBLER NESTING SUCCESS ADJACENT TO GROUP-SELECTION AND CLEARCUT EDGES IN A SOUTHEASTERN BOTTOMLAND FOREST

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Abstract. During the 1996, 1997, and 1998 breeding seasons, we located and monitored Hooded Warbler (*Wilsonia citrina*) nests in a bottomland forest and examined the effects of edge proximity, edge type, and nest-site vegetation on nesting success. Successful Hooded Warbler nests were more concealed from below and were located in nest patches with a greater abundance of >0.5-m-tall switchcane (*Arundinaria gigantea*) stems than unsuccessful nests. Daily nest survival rates, clutch size, and number of fledglings per successful nest did not differ between nests near edges of selection-harvest openings within the bottomland and nests near edges of clearcuts adjacent to the bottomland. Daily survival rate, clutch size, and number of fledglings per successful nest did not differ among nests 0–50 m, 51–100 m, and >100 m from the nearest edge, and probability of nest survival was not related to proximity to either edge type. However, probability of parasitism by Brown-headed Cowbirds (*Molothrus ater*) was higher near clearcut edges, and parasitism reduced clutch size and numbers of fledglings per successful nest. The combined effects of edge, especially edge created by the relatively small (≤0.5 ha) group-selection openings, on Hooded Warbler nesting success were minimal. However, our study was conducted in a primarily forested landscape, so cowbird abundance or negative edge effects may have been low relative to agricultural landscapes in the South.

Key words: bottomland, brood parasitism, clearcut, edge effects, group selection, Hooded Warbler, nest success, Wilsonia citrina.

Éxito de Anidación de *Wilsonia citrina* en Sitios Adyacentes a Bordes de Claros Formados por Extracción de Árboles Seleccionados y por Tala Rasa en Bosques Ribereños del Sureste

Resumen. Durante las épocas reproductivas de 1996, 1997 y 1998, ubicamos y monitoreamos nidos de *Wilsonia citrina* en un bosque de ribereño y evaluamos los efectos de la proximidad al borde, el tipo de borde y la vegetación del sitio de anidación sobre el éxito reproductivo. Los nidos exitosos estuvieron más escondidos desde abajo y se ubicaron en parches de bosque con una mayor abundancia de tallos de *Arundinaria gigantea* de más de 0.5 m de alto que los nidos no exitosos. Las tasas de supervivencia diaria de los nidos, el tamaño de la nidada y el número de polluelos emplumados por nido exitoso no difirieron entre nidos ubicados cerca de bordes de aperturas de cosecha selectiva dentro del valle ribereño y nidos cerca de bordes de sitios completamente talados adyacentes al valle. La tasa de supervivencia diaria, el tamaño de la nidada y el número de polluelos emplumados por nido exitoso no difirió entre nidos ubicados a 0–50 m, 51–100 m y >100 m del borde más cercano, y la probabilidad de supervivencia de los nidos no estuvo relacionada con la proximidad a ningún tipo de borde. Sin embargo, la probabilidad de parasitismo por *Molothrus ater* fue mayor cerca de bordes de tala rasa, y el parasitismo redujo el tamaño de la nidada y el número de polluelos emplumados por nido exitoso. Los efectos combinados de borde sobre el éxito de anidación de *W. citrina* fueron mínimos, especialmente aquellos de los bordes creados por los claros relativamente pequeños (≤0.5 ha) formados tras extraer grupos de árboles seleccionados. Sin embargo, nuestro estudio fue realizado en un paisaje principalmente forestal, de modo que la abundancia de *M. ater* o los efectos de borde negativos pueden haber sido menores en relación a paisajes agrícolas del sur.

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INTRODUCTION

Although edges may support increased avian species richness and abundance (Strelke and Dickson 1980), they may also have negative effects. Several studies, especially those in agricultural landscapes, have documented higher nest predation rates near edges (Gates and Gysel 1978, Andren and Angelstam 1988). Yet, other studies failed to document increased predation rates nearer to edges, especially in forested landscapes (Yahner and Wright 1985, Ratti and Reese 1988, Hanski et al. 1996). Vegetation complexity at edges may reduce the efficiency of nest predators (Yahner 1988) and increase concealment from nest parasites (Burhans 1997).

Few studies have investigated the effects of edge on natural bird nests in bottomland forests or elsewhere in the southeastern United States. Studies of edge effects using artificial nests have been conducted in the South (Keyser et al. 1998, Sargent et al. 1998, Saracco and Collazo 1999) and throughout the northern hemisphere (Major and Kendall 1996), but the results of this research must be interpreted with caution (Major and Kendall 1996). Lack of parental defense (King et al. 1999), exclusion of certain predators (Haskell 1995, Buler and Hamilton 2000), and lack of parental and nestling activity (Wilson et al. 1998) are reasons artificial nests may not accurately mimic natural nests. Biases also may result when extrapolating findings from other regions of the country to heavily forested portions of the southeastern United States. Inconsistent results among research projects designed to investigate the effects of edge on avian reproductive success may be due to landscape-level or regional variations in vegetation structure, predator communities, and bird communities (Robinson et al. 1993, Donovan et al. 1997), warranting regional and species-specific studies (Hoover and Brittingham 1993, Woodward et al. 2001).

Between 2000 and 2030, timber removals in southern bottomland hardwood forests are projected to increase by 18%, and concurrently, acreage of bottomland forests is expected to decline by 9% (USDA Forest Service 1988). This increased harvesting will increase amounts of edge in bottomland forests. Clearcutting is the most proven and popular method used to regenerate bottomland oaks in the South (Clatterbuck and Meadows 1993). However, complete removal of the forest overstory renders the stand temporarily unsuitable for canopy-dependent bird species (Pashley and Barrow 1993). Group selection is a possible alternative to clearcutting as a way to harvest and regenerate commercially valuable trees in southern bottomland forests. Group selection, in which groups of trees covering no more than 0.5 ha are cleared, retains a portion of the forest canopy and allows sufficient sunlight for some regeneration of shade-intolerant, commercially valuable tree species (Kellison and Young 1997, Meadows and Stanturf 1997). The openings created during group selection may simulate naturally occurring, gap-phase disturbances (Pashley and Barrow 1993), and provide habitat for some early successional birds while retaining most of the overstory for canopy nesting species (Moorman and Guynn 2001). However, the many small openings created during group selection maximize the ratio of edge to opening area and could cause increased levels of nest predation and brood parasitism relative to even-aged forest management practices such as clearcutting (Thompson 1993).

There is a dearth of information on the effects of uneven-aged forest management, like group selection, on Brown-headed Cowbird (*Molothrus ater*) parasitism rates and predation rates of forest-interior bird nests, even though the use of the method is increasing (Thompson 1993). Most studies of the effect of edge on avian reproductive success have focused on edges between different habitat types or between a clearcut and mature forest. Edges created by finer-scale disturbance within discrete habitat units (e.g., natural treefall gaps and selection-harvest openings) have been studied less. Edges of small forest openings may be less visible in the landscape and less likely to serve as visual cues to nest predators and parasites (but see Rich et al. 1994). Therefore, avian reproductive success may be lower along clearcut edges than at the edges of group-selection openings.

Using natural nests, we investigated the effects of group-selection and clearcut edges on the nesting success of the Hooded Warbler (*Wilsonia citrina*) in a southeastern bottomland forest. The Hooded Warbler was chosen as the focal species because (1) it breeds at relatively high densities on the study site (Norris 1963); (2) it nests in the forest understory, making nests relatively easy to locate and monitor; (3) it is an area-sensitive, Neotropical migrant but often forages or nests in small gaps (Evans Odgen and Stutchbury 1994, Bisson and Stutchbury 2000). Although Hooded Warbler densities have been documented to be higher in selection-harvest sites than in other areas (Annand and Thompson 1997, Robinson and Robinson 1999), little is known of the effects selection harvests have on its reproductive success. Our objectives were to (1) determine the effects of group-selection and clearcut edges on Hooded Warbler nest survival and productivity (clutch size, number of fledglings per successful nest) and Brown-headed Cowbird parasitism of Hooded Warbler nests; and (2) quantify relationships between Hooded Warbler nesting success, edge proximity, and vegetation structure.

METHODS

STUDY AREA

We conducted our research within a 362-ha bottomland forest on the Savannah River Site in Barnwell County, South Carolina (33°09′N, 81°40′W). The forest was composed of 70–100-year-old bottomland hardwoods. Bottomland oaks (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua*) dominated the canopy, which averaged approximately 35 m high (Moorman and Guynn 2001). Loblolly pine (*Pinus taeda*) occurred more commonly on the drier microsites. The midstory was poorly developed, and the understory was patchy with some dense areas of dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). Within the forest, experimental group-selection openings were harvested in December 1994. Four sizes (0.06, 0.13, 0.26, and 0.5 ha) of cuts were replicated six times on 65 ha of the bottomland, with approximately 9% of the 65-ha area harvested. Protocol employed to create the 24 openings followed harvest practices used in commercial group-selection cuts, and skidder trails connected all openings to two upland logging decks. Eight clearcuts were harvested in areas adjacent to the bottomland stand. The clearcuts ranged in size from 25 to 32 ha and ranged in age from 10 to 12 years old at the beginning of the study. The clearcuts either had regenerated naturally ($n = 7$) or had been row-planted to loblolly pine ($n = 1$). Although vegetation in all eight clearcuts was predominantly loblolly pine, hardwoods occurred sporadically throughout each stand. Canopy height in the clearcuts averaged approximately 6 m during the study. All regeneration in the group-selection openings was natural from either seedlings or stump sprouts. Vegetation composition in the group-selection openings varied with soil moisture and possibly harvest disturbance, and canopy height averaged less than 2 m during the study (Moorman and Guynn 2001). Only the group-selection openings on the drier microsites contained significant pine regeneration. Vegetation in most of the openings consisted of blackberry (*Rubus* spp.), grapevines (*Vitis* spp.), and a diversity of hardwoods, including sweetgum, red maple (*Acer rubrum*), American sycamore (*Platanus occidentalis*), and oaks.

NEST SEARCHING AND MONITORING

Hooded Warbler nests were located between 1 May and 15 July in 1996, 1997, and 1998 using systematic foot searches throughout the site and intensive foot searches near singing males. Most nests (78%) were located during the incubation period. We were unable to determine whether nests were first or second attempts because nesting activities of most Hooded Warbler females were not monitored continuously. Once located, the status of each nest was recorded every 2–4 days. The number of young fledged at successful nests was assumed to equal the number of nestlings observed on the last nest visit.

At the end of the breeding season, universal transverse mercator (UTM) coordinates of all Hooded Warbler nests were determined using a global positioning system (GPS). We compiled UTM coordinates for each nest into a coverage of nest locations using the ARC/INFO geographic information system (GIS; Environmental Systems Research Institute 1987). We also created GIS coverages of group-selection and clearcut edges using a GPS in the field and the ARC/INFO software package. The coverages were overlain and distances to the nearest edge of each edge type were calculated for each nest. We grouped all nests into three distance-to-nearest-edge (two types combined) classes (0–50 m, 51–100 m, and >100 m from edge). Although 25-m distance intervals are preferred, especially within 100 m of edge (Paton 1994), we used 50-m increments to maintain adequate sample sizes within groups.

VEGETATION SAMPLING

We measured vegetation at Hooded Warbler nests from early to mid-July in 1996, 1997, and

1998. We made measurements at the nest substrate and in the nest patch, defined as the 5-m-radius circle centered on the nest substrate (Martin and Roper 1988, Kilgo et al. 1996). Measurements taken at the nest included the species used as the substrate, nest height, substrate height, and nest concealment. We calculated an index of concealment by viewing the nest from a distance of 1 m above, below, and at nest level from each of the cardinal directions and estimating percent of the nest obstructed by vegetation (0–4: 0 = 0% concealed, 1 = 1–25% concealed, 2 = 26–50% concealed, etc.) from each of the six angles. We averaged the concealment estimate for the four side measures (Kilgo et al. 1996). When nests were <1 m above ground, concealment from below was estimated from the ground.

At the nest patch, we measured canopy cover, stem density of potential nest substrates (<3 m tall), stem density of dwarf palmetto, stem density of trees (≥3 m tall), percent ground cover, and vegetation profile. Canopy cover was estimated by reading a spherical densiometer 2 m from the nest substrate in each of the four cardinal directions. Potential substrate densities were tallied within five 1-m^2 quadrats located randomly along the four cardinal directions. Potential substrates were classified as switchcane ≤0.5 m tall, switchcane >0.5 m tall, other woody species 0.3–1 m tall, and other woody species 1–3 m tall (Kilgo et al. 1996). We tallied all live trees and snags ≥3 m tall within the 5-m radius patch. Percent ground cover of herbaceous vegetation was estimated (0–5: 0 = 0% concealed, 1 = 1–20% concealed, 2 = 21–40% concealed, etc.) in each of the five 1-m^2 quadrats. We measured understory structure in the nest patch by estimating the percent obstruction (using the same six categories 0–5) for each 0.5-m interval of a 3-m vegetation profile board located 5 m from the nest substrate in each of the cardinal directions (Kilgo et al. 1996). We reduced the number of profile board variables to the percent obstruction of the height interval corresponding to the height of the nest and the average percent obstruction of the six height intervals.

STATISTICAL ANALYSES

Using the Mayfield method (Mayfield 1975) as modified by Hensler and Nichols (1981), we calculated daily nest survival rates and variances for the incubation, nestling, and entire nesting periods. A survival-rate estimate was calculated for each of the incubation and nestling periods by raising the daily survival rate for that period to the power of the associated number of exposure days (i.e., 12-day incubation period and 8-day nestling period; Evans Ogden and Stutchbury 1994). Survival rate for the entire nesting period was determined by multiplying incubation and nestling period survival rates (Hensler and Nichols 1981).

We compared daily survival rates between nests ≤100 m from group-selection edges and nests ≤100 m from clearcut edges using the program CONTRAST (Sauer and Williams 1989). Five nests were within 100 m of both group-selection and clearcut edges and were excluded from comparisons between the two edge types. We also used CONTRAST to test for differences in daily survival rates among nests in the three distance-to-nearest-edge (two edge types pooled) classes, among nests in each of the three years of the study, and between parasitized and unparasitized nests. Because daily survival rates of nests did not differ ($\chi^2_2 = 0.27$, $P = 0.87$) among the three years of the study (mean ± SE: 0.956 ± 0.012, 0.958 ± 0.010, and 0.964 ± 0.011, respectively), we pooled nests across years. We used ANOVA to test for differences in clutch size and number of fledglings per successful nest among the three distance-to-nearest-edge classes. We compared clutch sizes and numbers of fledglings per successful nest between parasitized and unparasitized nests, and between nests ≤100 m from the nearest group-selection edge and nests ≤100 m from the nearest clearcut edge using Student's *t*-tests.

We tested for correlation between nest-site vegetation variables using Pearson correlation coefficients, and retained only the most easily measured variable of a correlated pair ($r > 0.5$). Three of the nest-site vegetation variables (nest substrate height, number of substrates 1–3 m tall other than switchcane, and mean profile of all 0.5-m profile board intervals between 0 and 3 m) were not included in analyses because they were correlated with other variables. For the remaining nest-site vegetation variables, we used Wilcoxon rank-sum tests to analyze vegetation differences between successful and unsuccessful nests and between parasitized and unparasitized nests (Kilgo et al. 1996). We used Kruskal-Wallis

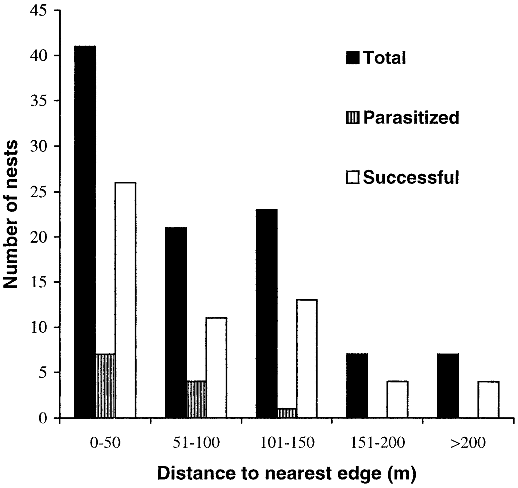

FIGURE 1. Number of total Hooded Warbler nests, number parasitized, and number successful within five distance-to-nearest-edge intervals in a South Carolina bottomland forest, 1996–1998.

tests to analyze vegetation differences among the three distance-to-nearest-edge categories. Nonparametric statistics were used because most vegetation variable data were not normally distributed according to a Shapiro-Wilk test.

We employed multiple logistic regression to determine which factors may be important predictors of nest outcome (success = 1 or failure = 0) and parasitism (parasitized = 1 or unparasitized = 0). For both nest outcome and parasitism, we tested the fit of a model containing distance to group-selection edge, distance to clearcut edge, year, and any habitat variable found to be significant in the univariate analyses. Many warbler nests were located far (>475 m) from the group-selection openings but all nests were within 475 m of a clearcut edge. Therefore, we fit a piecewise linear model with the relationship between probability of nest success and distance to a group-selection opening being linear up to 475 m and beyond 475 having no relationship (Neter et al. 1996). Because all but one of the parasitized nests (92%) were ≤100 m from edge (Fig. 1), we reclassified distance to group-selection and clearcut edge as 0 if ≤100 m and 1 if >100 m for the parasitism model. Because the interaction between distance to a group-selection edge and distance to a clearcut edge was nonsignificant in both models, it was not included in the final models. Values reported are means ± SE. For all analyses, statistical significance was accepted when $P \leq 0.05$ (SAS Institute 1996).

RESULTS

We located 33, 35, and 31 Hooded Warbler nests in 1996, 1997, and 1998, respectively. Of the 99 nests, 13 were parasitized and 58 fledged Hooded Warblers. Of the 41 failed nests, 4 were abandoned, 3 were lost because of severe weather, and 34 were depredated. Of the 34 depredated nests, 5 were destroyed or displaced from their substrate, 1 contained eggshell fragments and a partially eaten acorn, and the remaining 28 were undisturbed but empty. Mayfield survival rates of all nests located during the study were 0.63 during the incubation period, 0.70 during the nestling period, and 0.44 during the entire nesting period. For unparasitized nests, the average clutch size was 3.2 ± 0.1 and the average number of young fledged per successful nest was 2.9 ± 0.1.

Hooded Warbler nests were clumped near edges of both types with approximately twice as many nests 0–50 m from edge than in any of the other intervals and very few nests >200 m from edge (Fig. 1). Number of tall switchcane stems, the most common nest substrate used by Hooded Warblers, was greatest within 50 m of edge (Table 1).

NEST SURVIVAL AND PRODUCTIVITY

Concealment rankings from below were higher at successful nests (0.9 ± 0.1) than at unsuccessful nests (0.7 ± 0.1; $Z = -1.96$, $P = 0.05$), and successful nests (10.0 ± 0.8) were surrounded by a greater number of tall (>0.5 m) switchcane stems than unsuccessful nests (7.6 ± 0.8; $Z = -2.05$, $P = 0.04$). No other vegetation variables differed significantly between successful and unsuccessful nests. Daily survival rates, clutch sizes, and number of fledglings per successful nest did not differ between nests ≤100 m from the nearest group-selection edge and nests ≤100 m from the nearest clearcut edge (Table 2). Daily nest survival rates, clutch sizes and number of fledglings per successful nest did not differ among the three distance-to-nearest-edge classes (Table 3). In the multiple logistic regression model, probability of nest success was not significantly associated with proximity to group-selection edges (Wald $\chi^2_2 = 1.42$, $P =$

TABLE 1. Mean ± SE nest-site and nest-patch vegetation characteristics for Hooded Warbler nests in three distance-to-nearest-edge classes in a South Carolina bottomland forest, 1996–1998.

Vegetation variable	Distance from edge (m)			P[a]
	0–50 (n = 41)	51–100 (n = 21)	>100 (n = 37)	
Nest height (m)	0.9 ± 0.0	0.9 ± 0.0	0.8 ± 0.0	0.15
Concealment				
Below (0–4)[b]	0.9 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.57
Above (0–4)	3.0 ± 0.2	3.4 ± 0.2	2.8 ± 0.2	0.08
Side (0–4)	1.8 ± 0.1	1.8 ± 0.2	1.7 ± 0.1	0.77
Canopy cover (%)	94.0 ± 0.0	94.0 ± 0.0	94.0 ± 0.0	0.63
Number cane stems (≤0.5 m)	4.8 ± 0.5	5.7 ± 1.0	5.6 ± 0.7	0.65
Number cane stems (>0.5 m)	10.7 ± 1.0	8.7 ± 1.4	7.2 ± 0.7	0.05
Number other substrates	0.3 ± 0.1	0.2 ± 0.0	0.7 ± 0.2	0.76
Ground cover (0–5)[c]	1.2 ± 0.1	1.1 ± 0.1	1.2 ± 0.1	0.57
Number palmetto stems	15.4 ± 2.1	16.2 ± 3.4	11.4 ± 1.4	0.56
Number trees (≥3.0 m)	15.7 ± 2.7	10.0 ± 0.9	10.2 ± 0.7	0.13
Number snags (≥3.0 m)	0.5 ± 0.1	0.6 ± 0.2	0.5 ± 0.1	0.76
Profile at nest level (0–5)[c]	3.5 ± 0.2	3.6 ± 0.2	3.5 ± 0.2	0.73

[a] Kruskall-Wallis test.

[b] Index of the percent of the nest concealed when viewed from 1 m: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%.

[c] Index of percent obstruction: 0 = 0%, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%.

0.49), proximity to clearcut edges (Wald $\chi^2_1 = 0.66$, $P = 0.42$), or number of tall switchcane stems (Wald $\chi^2_1 = 2.86$, $P = 0.09$). Probability of nest success increased as nest concealment from below increased (Wald $\chi^2_1 = 3.83$, $P = 0.05$).

PARASITISM

Rankings of ground cover were lower at parasitized nests (0.9 ± 0.1) than at unparasitized nests (1.2 ± 0.0; $Z = -2.38$, $P = 0.02$). Daily survival rates during the incubation period, nestling period, and nesting period did not differ between parasitized and unparasitized nests (Table 4). Clutch size of parasitized nests was lower than clutch size of unparasitized nests by 0.8 eggs, and parasitism reduced the number of fledglings per successful nest by 0.9 young (Table 4). Of the 120 Hooded Warbler eggs laid in nondepredated, unparasitized nests, 11 (9%) did not hatch. Of the 11 Hooded Warbler eggs laid in parasitized nests that were not depredated, four (36%) failed to hatch. In nondepredated, parasitized nests, all cowbird eggs hatched, and all warbler eggs that did hatch yielded fledglings. In the multiple logistic regression model,

TABLE 2. Survival rates and productivity of Hooded Warbler nests within 100 m of group-selection edges and clearcut edges in a South Carolina bottomland hardwood forest, 1996–1998.

	Group-selection edge		Clearcut edge		P[a]
	mean ± SE	n	mean ± SE	n	
Daily survival rate					
Incubation period	0.958 ± 0.019	17	0.973 ± 0.012	26	0.50
Nestling period	0.969 ± 0.018	15	0.939 ± 0.018	31	0.24
Nesting period	0.963 ± 0.013	20	0.956 ± 0.011	37	0.68
Clutch size[b]	3.1 ± 0.1	14	3.3 ± 0.1	23	0.48
Productivity[b,c]	2.8 ± 0.3	10	3.0 ± 0.2	17	0.50

[a] P-values for survival rate comparisons are from the program CONTRAST. P-values for other comparisons are from Student's t-tests.

[b] Parasitized nests not included in analyses.

[c] Number of fledglings per successful nest.

TABLE 3. Survival rates and productivity of Hooded Warbler nests in three distance-to-nearest-edge classes in a South Carolina bottomland forest, 1996–1998.

	Distance to nearest edge (m)						
	0–50		51–100		>100		
	mean ± SE	*n*	mean ± SE	*n*	mean ± SE	*n*	P^a
Daily survival rate							
Incubation period	0.971 ± 0.012	32	0.957 ± 0.019	16	0.957 ± 0.014	29	0.70
Nestling period	0.957 ± 0.014	34	0.949 ± 0.022	16	0.958 ± 0.015	28	0.93
Nesting period	0.964 ± 0.009	41	0.953 ± 0.014	21	0.958 ± 0.010	37	0.79
Clutch size[b]	3.2 ± 0.1	28	3.3 ± 0.2	13	3.1 ± 0.1	27	0.43
Productivity[b,c]	2.8 ± 0.2	20	2.9 ± 0.3	11	2.9 ± 0.2	20	0.91

[a] *P*-values for survival rate comparisons are from the program CONTRAST. *P*-values for other comparisons are from ANOVA.

[b] Parasitized nests not included in analyses.

[c] Number of fledglings per successful nest.

probability of parasitism was greater nearer to clearcut edges (Wald $\chi^2_1 = 4.13$, $P = 0.04$) and at nest sites with less ground cover (Wald $\chi^2_1 = 4.43$, $P = 0.04$). The proximity of nests to group-selection edges was not significantly related to parasitism probability (Wald $\chi^2_1 = 0.24$, $P = 0.63$).

DISCUSSION

NEST SURVIVAL AND PRODUCTIVITY

We failed to document any effect of edge on the nest survival or productivity of Hooded Warblers. Most Hooded Warbler nests were located 0–50 m from an edge, where dense patches of tall switchcane were most common. Despite the apparent crowding of nests near edges, these areas did not act as ecological traps (Gates and Gysel 1978). Survival rates and productivity estimates were similar for nests near group-selection and clearcut edges and for nests located at varying distances from the nearest edge of either type. Other studies have documented either lower nesting success along external, abrupt edges than along edges of group-selection cuts (Suarez et al. 1997), or reduced nesting success along edges of both group-selection cuts and clearcuts when compared to the adjacent, interior forest (King et al. 1998). Differences among these studies most likely are the result of variations in landscape, habitat, and species-level factors (Donovan et al. 1997, Woodward et al. 2001).

Predation accounted for a large percentage (83%) of nest failures, which is common for species of relatively small body size (Ricklefs 1969). Evidence suggests the primary nest predators on the bottomland site likely were snakes. Corvids, such as Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*), were present at low densities in the bottomland (Moorman 1999). Gray rat snakes (*Elaphe ob-*

TABLE 4. Survival rates and productivity of parasitized and unparasitized Hooded Warbler nests in a South Carolina bottomland forest, 1996–1998.

	Parasitized		Unparasitized		
	mean ± SE	*n*	mean ± SE	*n*	P^a
Daily survival rate					
Incubation period	0.987 ± 0.013	9	0.958 ± 0.009	69	0.07
Nestling period	0.921 ± 0.034	11	0.961 ± 0.010	67	0.26
Nesting period	0.958 ± 0.017	13	0.960 ± 0.007	86	0.91
Clutch size	2.4 ± 0.2	9	3.2 ± 0.1	68	<0.001
Productivity[b]	2.0 ± 0.3	6	2.9 ± 0.1	51	0.01

[a] *P*-values for survival rate comparisons are from the program CONTRAST. *P*-values for other comparisons are from Student's *t*-tests.

[b] Number of host fledglings per successful nest.

soleta spiloides) were observed moving along the tops of switchcane stems, apparently in search of nests, on two occasions (CEM, pers. obs.). Gray rat snakes and black racers (*Coluber constrictor*) were present at relatively high densities (Gibbons and Semlitsch 1991), and the two snake species did not occur more frequently near group-selection edges than in the interior of the bottomland stand (Cromer 1999). Because snakes were not more common along edges, nest success would not be expected to vary with edge proximity. Uniform distribution of nest predation by snakes previously has been reported (Best 1978), but nest predation by mammals, especially medium-sized mammals, is more likely to be concentrated at edges (Best 1978, Keyser et al. 1998).

Successful nests were located in denser patches of tall cane (>0.5 m) and were more concealed from below than unsuccessful nests. Other studies of Hooded Warblers have documented few or no relationships between nest-site characteristics and nest success (Howlett and Stutchbury 1996, Kilgo et al. 1996, Bisson and Stutchbury 2000). In a sample smaller than used in this study, Kilgo et al. (1996) detected no effect of the number of potential substrates in the nest patch or of nest concealment on Hooded Warbler nest predation. Howlett and Stutchbury (1996) experimentally manipulated nest concealment and recorded no differences in success between 15 nests with surrounding vegetation removed and 15 control nests. However, Howlett and Stutchbury (1996) did not manipulate the number of substrate stems surrounding the nest, which may be an equally important predictor of nest success according to our research. In environments with many predator species, the high incidence of nest predation and the diversity of nest-searching tactics used by those predators may preclude the existence of predictably safe nest sites (Filliater et al. 1994). However, on our study site, snakes appeared to be the predominant nest predator. Snakes, specifically gray rat snakes, may be less successful in locating a bird's nest in structurally complex habitats (Mullin et al. 1998). By placing nests in switchcane, a common substrate, and particularly in a switchcane stem closely surrounded by high densities of switchcane, Hooded Warblers may have reduced the likelihood of nest predation (Martin and Roper 1988).

PARASITISM

The probability of parasitism of Hooded Warbler nests increased nearer to clearcut edges. The Savannah River Site is a forested area of about 78 000 ha, but our bottomland study site was within 3.5 km of the Savannah River Site boundary, where agricultural fields and pastures are common. Brown-headed Cowbirds travel up to 7 km between foraging and roosting or breeding locations (Thompson 1994, Coker and Capen 1995), so our study site was well within the range of individual cowbirds foraging outside of the Savannah River Site. Parasitism rates are higher in heavily fragmented landscapes (Robinson et al. 1995), and landscapes with high numbers of cowbird foraging sites contain higher densities of cowbirds, which also may lead to higher rates of parasitism (Hoover and Brittingham 1993, Robinson et al. 1993, Stutchbury 1997). However, most of the area within a 7-km radius around our research site was forested, so cowbird numbers may be low relative to other more fragmented landscapes in the region, and our estimates of cowbird parasitism may not be representative of agricultural landscapes in the South.

Relationships between Brown-headed Cowbird parasitism and edge proximity vary regionally and with landscape context within a region (Rothstein and Robinson 1994, Hahn and Hatfield 1995, Donovan et al. 1997). In the Northeast, Hahn and Hatfield (1995) found no effect of edge proximity on rates of parasitism, and they documented higher nest parasitism rates for birds nesting in the forest interior than for field or edge-nesting species. Donovan et al. (1997) determined that cowbird abundance was highest in the most fragmented habitats but did not vary between core and edge habitat in highly fragmented, moderately fragmented, or unfragmented landscapes in the midwestern United States. However, on our study site cowbirds apparently concentrated their nest-searching efforts near edges of harvest openings >0.26 ha. During 1997, Brown-headed Cowbirds were detected more frequently in and adjacent to 0.5-ha gaps than in unharvested areas, 0.06-ha gaps, 0.13-ha gaps, or 0.26-ha gaps (Moorman and Guynn 2001). The low rates of parasitism (2.7%) for all nests >100 m from edge suggest the effects of edge did not extend beyond 100 m on our study site.

We located 60 nests built by species other than the Hooded Warbler and none were parasitized (Moorman 1999). Hooded Warblers may have been parasitized preferentially because they bred at high densities on the site or because they built relatively conspicuous nests. Most vegetation characteristics of parasitized and unparasitized Hooded Warbler nest sites, however, were similar on our study site with the exception that patches around unparasitized nests had greater ground cover. Because female cowbirds often search for nests from the ground (Lowther 1993), less ground cover potentially made the nests more visible.

Contrary to other studies (Martin 1992), parasitism by cowbirds did not reduce the survival rate of Hooded Warbler nests. Nest predators on the study site may not have cued on the presence of cowbird nestlings. Only one Hooded Warbler pair deserted a parasitized nest and that was late in the nestling period and in a nest in which no Hooded Warbler eggs hatched. The presence of warbler nestlings in parasitized nests may have prevented abandonment by the adults. Clutches of Hooded Warbler eggs were smaller in parasitized nests because female Brown-headed Cowbirds removed eggs (Ortega 1998). Additionally, evidence of a single incident of egg removal by a cowbird nestling was observed (CEM, pers. obs.). Although Brown-headed Cowbird parasitism reduced the productivity of individual warbler nests, all but one nondepredated parasitized nest fledged Hooded Warbler chicks. Even though nests located nearer to clearcut edges were more likely to be parasitized, the productivity of these nests was not depressed because overall parasitism rates were relatively low. Therefore, the overall effects of Brown-headed Cowbird parasitism on Hooded Warbler nesting success were minimal relative to other regions within the bird's range (Evans Ogden and Stutchbury 1994).

MANAGEMENT IMPLICATIONS

Conservation of forest-interior species, such as the Hooded Warbler, partially depends on identifying and preserving the habitat features that affect breeding productivity (Martin 1992). Clearcutting may reduce the success of nests in the adjacent forest interior (Rudnicky and Hunter 1993, King et al. 1996, Flaspohler et al. 2001), so selection harvesting has been cited as a possible management alternative. However, group selection creates more edge per unit area of forest harvested (Franklin and Forman 1987), and negative edge effects in selection-harvest stands may be equal to or greater than in edges adjacent to clearcuts (Thompson 1993, King et al. 1998). However, we failed to document reduced nest survival or productivity at the edges of clearcuts or group cuts. The proportion of Hooded Warbler nests depredated during this study was similar to rates reported in other regions (Evans Ogden and Stutchbury 1994), and slightly lower than documented by Sargent et al. (1996) in a study conducted on the Savannah River Site in bottomland hardwood forests. Agricultural landscapes of the southeastern United States likely contain a more diverse guild of nest predators than was present on our study site, which may result in edge effects different than those documented in this study. Management for dense patches of switchcane along silvicultural edges may help prevent high predation rates of Hooded Warbler nests in fragmented landscapes, while concurrently benefiting other species, such as Swainson's Warbler (*Limnothlypis swainsonii*), that nest or forage in canebrakes. Although parasitism rates were much lower than reported for Hooded Warblers in other regions (Evans Ogden and Stutchbury 1994), 11 of the 13 parasitized nests were $<$100 m from edges of openings $\geq$0.26 ha (Moorman 1999). Because Hooded Warblers are a common host species of Brown-headed Cowbirds, they should receive special concern in areas with high cowbird densities.

Full assessment of management implications would require evaluating the impacts of group-selection and clearcut harvesting on the reproduction, survival, and abundance of Hooded Warblers as well as other species in the breeding bird community. Hooded Warbler abundance in and around the group-selection openings was similar to abundance in the uncut portions of the bottomland stand (Moorman and Guynn 2001), and warbler abundance along clearcut edges was relatively high, as indicated by the number of nests placed within 50 m of edge. However, pre- and post-harvest density estimates may be necessary to accurately determine the effects of cutting on the Hooded Warbler population. Because edge effects may vary with species, habitat, landscape context, and region, further research in the southeastern United States is warranted.

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