Nesting Success of Birds in Different Silvicultural Treatments in Southeastern U.S. Pine Forests

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Abstract: *We examined nesting success and levels of nest predation and cowbird parasitism among five different silvicultural treatments: regenerating (3–6 years old), mid-rotation (12–15 years old), and thinned (17–23 years old) pine plantations, single-tree selection, and late-rotation pine-hardwood stands in the Ouachita Mountains of Arkansas from 1993 to 1995. We monitored 1674 nests. Differences in daily mortality and daily predation rate among two or more treatments were found for 4 and 3 of 12 species, respectively. These differences were lost following Bonferroni adjustments, but thinned stands had higher levels of predation than single-tree selection stands when predation levels were averaged across species. Daily predation rates were positively correlated with the relative abundance of birds, suggesting that nest predators respond to prey availability (i.e., nests) in a density-dependent manner. The relative abundance of cowbirds differed among treatments, with the highest densities in regenerating, thinned, and single-tree selection stands. Field Sparrows (Spizella pusilla) and Yellow-breasted Chats (Icteria virens) experienced higher levels of parasitism in thinned than regenerating plantations, whereas White-eyed Vireos (Vireo griseus) experienced higher parasitism in regenerating plantations than in mid-rotation or thinned plantations. Several shrub-nesting and 1 ground-nesting species had lower nesting success in thinned and regenerating plantations than has been reported in previously published studies. Thus, some seral stages of even-aged management may provide low-quality nesting habitat for several early-successional bird species. In contrast, many species nesting in mid-rotation and single-tree selection stands had nesting success similar to or greater than that found in previous studies, suggesting that some silvicultural treatments, when embedded in a largely forested landscape, may provide suitable habitat for forest land birds without affecting their reproductive success.*

Éxito de Nidación de Aves en Diferentes Tratamientos Silviculturales en Bosques de Pinos del Sureste de los Estados Unidos

Resumen: *Examinamos el éxito de nidación, los niveles de depredación de nidos y el parasitismo por tordos en cinco tratamientos silviculturales diferentes: en regeneración (3–6 años de edad), rotación media (12–15 años de edad) y plantaciones raleadas de pinos (17–23 años de edad), selección individual de árboles y rotación tardía en rodales de pino-maderas duras de las montañas Ouachita de Arkansas de 1993 a 1995. Se monitoreó un total de 1,674 nidos. Encontramos diferencias en mortalidad diaria y en tasa de depredación diaria entre dos o más tratamientos para cuatro y tres especies respectivamente de las doce especies observadas. Estas diferencias sin embargo, se perdieron después del ajuste de Bonferroni. Los rodales raleados tuvieron niveles de depredación más altos que los rodales con selección de árboles individuales cuando los niveles de depredación se pro-*

196

scens). Number 87 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, and The American Ornithologist's Union, Washington, D.C.

Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple-brooding, nesting success, and annual productivity of a Neotropical migrant, the Black-throated Blue Warbler (Dendroica caerulescens), in an unfragmented temperate forest. Auk 109:321–333.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (Dendroica caerulescens): implications for population dynamics. Journal of Animal Ecology 65:183–195.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. Biological Conservation 57:239–255.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry. Prentice-Hall, Englewood Cliffs, NJ.

Hutto, R. L., S. J. Hejl, C. R. Preston, and D. M. Finch. 1992. Effects of silvicultural treatments on forest birds in the Rocky Mountains: implications and management recommendations. Pages 386–391 in D. M. Finch and P. W. Stangel, editors. Status and management of Neotropical migratory birds. General technical report RM-229. U.S. Department of Agriculture, Fort Collins, Colorado.

Johnson, D. H. 1990. Statistical comparison of nest success rates. North Dakota Academy of Science Proceedings 44:67.

King, D. I., C. R. Griffin, and R. M. Degraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscape. Conservation Biology 10:1380–1386.

Legendre, L., and P. Legendre. 1984. Écologie numérique I. Le traitement multiple des données écologiques. 2nd edition. Presses de l'Université du Québec, Montréal.

Lorimer, C. G., and L. E. Frelich. 1994. Natural disturbance regimes in old-growth northern hardwoods: implications for restoration efforts. Journal of Forestry 92:33–38.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Medin, D. E., and G. D. Booth. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. Research paper INT-408. U.S. Forest Service, Ogden, Utah.

Nolan, V., Jr. 1961. A method of netting birds at open nests in trees. Auk 78:643–645.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler Dendroica discolor. Ornithological Monographs 26.

Norton, M. R., and S. J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Canadian Journal of Forest Research 27:44–53.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

Porneluzi, P., J. C. Bednarz, L. J. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Conservation Biology 7:618–622.

Probst, J. R., and J. P. Hayes. 1987. Pairing success of Kirtland's Warblers in marginal vs. suitable habitat. Auk 104:234–241.

Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels (Tamiasciurus hudsonicus), and eastern chipmunks (Tamias striatus) on nest predation in northern hardwood forest: an artificial nest experiment. Oikos 57:375–380.

Robinson, W. D., and S. K. Robinson. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conservation Biology 13:58–66.

Rodewald, P. G., and K. G. Smith. 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. Journal of Wildlife Management 62:1411–1417.

Roth, R. R., and R. K. Johnson. 1993. Long-term dynamics of a Wood Thrush population breeding in a forest fragment. Auk 110:37–48.

Sabine, D. L., A. H. Boer, and W. B. Ballard. 1996. Impacts of habitat fragmentation on pairing success of male Ovenbirds, Seiurus aurocapillus, in southern New Brunswick. Canadian Field-Naturalist 110:688–693.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914–1932.

Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance Neotropical migrant: demographic evidence for the importance of breeding season events in the Redstart. Pages 431–442 in J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? Pages 85–120 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Steele, B. B. 1992. Habitat selection by breeding Black-throated Blue Warblers (Dendroica caerulescens) at two spatial scales. Ornis Scandinavica 23:33–42.

Steele, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. Condor 95:568–579.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340–347.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

Thompson, F. R. 1993. Simulated responses of a forest interior migrant bird population to forest management options in central hardwood forests of the United States. Conservation Biology 7:325–333.

Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201–219 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Trine, C. L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology 12:576–585.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (Seiurus aurocapillus). Number 88 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, and The American Ornithologist's Union, Washington, D.C.

Van Horne, D. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Villard, M.-A., P. R. Martin, and D. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (Seiurus aurocapillus). Auk 110:759–768.

Villard, M.-A., G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. Ecology 76:27–40.

Virolainen, M. 1984. Breeding biology of the Pied Flycatcher Ficedula hypoleuca in relation to population density. Annales Zoologici Fennici 21:187–197.

Williams, D. A. 1976. Improved likelihood ratio tests for complete contigency tables. Biometrika 63:33–37.

Ziehmer, R. L. 1993. Uneven-age timber management and forest birds. M.S. thesis. University of Missouri, Columbia.

mediaron entre especies. Las tasas de depredación diarias estuvieron positivamente correlacionadas con la abundancia relativa de aves, sugiriendo que los depredadores de nidos respondían a la disponibilidad de presas (nidos) de una manera densodependiente. La abundancia relativa de tordos varió entre tratamientos con las densidades más altas en rodales en regeneración, raleados, y con selección individual de árboles. Los gorriones (Spizella pusilla) y los chipes pechoamarillos (Icteria virens) experimentaron los niveles más altos de parasitismo en plantaciones raleadas que en las plantaciones en regeneración, mientras que los vireos ojiblanco (Vireo griseus) experimentaron un parasitismo más alto en plantaciones en regeneración que en plantaciones de rotación media o en plantaciones adelgazadas. Diversas especies con nidación en arbustos y una especie con nidación en el suelo tuvieron un menor éxito de nidada en las plantaciones raleadas y en regeneración, al ser comparadas con resultados de éxito de nidada de estudios previos publicados. Por lo tanto, algunos estados serales de manejo de edad uniforme pueden proveer hábitat con baja calidad para la nidación de especies de aves de sucesión temprana. En contraste, muchas especies con nidación en rodales con rotación media y con selección individual de árboles tuvieron un éxito similar o mayor que los reportados en estudios previos, sugiriendo que algunos tratamientos silviculturales incrustados en un paisaje con gran cubierta forestal pueden proveer un hábitat favorable para especies de aves del suelo del bosque, sin afectar su éxito reproductivo.

Introduction

Over 82 million ha of "timberland"—land capable of producing >35 m³/ha/year of timber—are managed in the United States (Powell et al. 1993). Managed forests are commonly harvested through single-tree selection, shelterwood, seed tree, or clearcutting methods (Thompson et al. 1995). These techniques often produce a patchwork of seral stages and differing forest structural types that may affect birds (Thompson et al. 1992, 1995). Indeed, silvicultural practices may affect the abundance and habitat use of a variety of bird species, including some forest species that are showing long-term population changes (Thompson et al. 1992, 1995). Yet studies of the effects of silvicultural practices on breeding birds have been based largely on count data, which may be a misleading indicator of reproductive success (Van Horne 1983; Vickery et al. 1992). Nesting success can provide important information about the quality of managed habitat for the health of bird populations (Martin 1992), but little is known about whether the nesting success of bird species is affected by seral stages of different silvicultural systems.

Artificial nests have been used previously to test for the effects of clearcutting on predation rates. Predation rates for artificial nests placed on the ground and in shrubs were lower in young clearcuts than in unmanipulated stands (Yahner & Wright 1985; Rudnicky & Hunter 1993). These studies tested only young clearcuts and mature forest stands, however, so it is unknown how older clearcuts or other silvicultural treatments affect nest predation rates. Moreover, studies using artificial nests may not be indicative of natural predation rates on real nests (Reitsma 1992; Haskell 1995; Martin et al. 1996), and patterns may depend on the predator regime (Yahner & Cypher 1987; Nour et al. 1993). Artificial nests are probably not an appropriate method for estimating levels of brood parasitism. Thus, the most accu-

rate way to determine whether forestry practices affect nesting birds is to monitor nesting success, predation, and parasitism using real nests (Martin & Geupel 1993).

Our objective was to determine if nesting success and levels of nest predation and cowbird parasitism in birds differed among silvicultural practices and seral stages. We also compared nesting success in our study to that found in previous studies to determine if populations of species nesting in our managed stands had lower or higher nesting success than populations in other habitats.

Study Area

Our study was conducted on lands of the Ouachita National Forest and Weyerhaeuser Company and Deltic Farm and Timber Company, Inc., in the Ouachita Mountains of westcentral Arkansas. This landscape of over 2 million ha consists of hardwood, second-growth pine, and pine-hardwood forests in various seral stages, interspersed with occasional private residences and farms. Landscape cover in the Ouachita Mountains, based on 100-ha aggregations using a Landsat Thematic Mapper image from 1990, was 66% forest, 24% pasture, 9% agriculture, and 1% urban (Smith et al. 1998). Measurement of forest cover in the Ouachita Mountains was conservative because areas of forest regeneration may have been misclassified as pasture (Smith et al. 1998). Moreover, most of the pasture, agriculture, and urban areas occurred within lower valley sites, leaving the forests largely unfragmented.

We studied five treatments involving 30 stands: three seral stages of pine plantation following clearcutting— (1) regenerating, (2) mid-rotation, and (3) thinned plantations—plus (4) single-tree selection stands and (5) late-rotation pine-hardwood stands. Generally, each treatment contained six replicates, but two mid-rotation plantations were used in 1993 and four were added in

1994. One thinned plantation was dropped after 1993 because of an unplanned herbicide treatment, and another thinned plantation was added in 1994. Silvicultural treatments are applied at the stand level, so stands were our experimental units. A stand is a contiguous group of trees sufficiently uniform in species composition and structure to serve as a management unit (Thompson et al. 1995). Replicate stands within treatments were chosen based on availability and to minimize variation in age (for plantations) and aspect (for single-tree selection stands). Stands ranged in size from 49.4 to 274.9 ha ($\bar{x}$ = 99.8 ha). One study plot was placed in each stand at least 50 m from the edge of the stand. Plots were arranged in stands to maximize the number of census points (up to 12 points) in each stand (see below). Plots were gridded at 25-m intervals with stakes and flagging to facilitate relocation of nests. Study plots ranged in size from 43.8 to 51.2 ha ($\bar{x}$ = 48.0 ha). Landscape cover was calculated for each treatment based on a 5-km-radius circle centered on each plot (Table 1). We divided the landscape into forest, dry crop, pasture, and urban coverages. Urban cover included both residential and commercial coverages.

Regenerating plantations ($\bar{x}$ = 58.4 ha) were 3- to 6-year-old stands that had been replanted following clearcutting. These stands were characterized by an open canopy (11.0% canopy cover), with many small (1–2 m tall) loblolly pines (*Pinus taeda*, $\bar{x}$ = 1319 pines/ha) and a dense shrub layer of oak (*Quercus* spp.), hickory (*Carya* spp.), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), winged elm (*Ulmus alata*), red maple (*Acer rubrum*), and blackberry (*Rubus* spp.). Ground cover also was dense and was composed predominantly of forbs, grasses, and shrubs. Not all trees were removed during harvesting; mature hardwoods (>8 cm diameter at breast height [dbh]) and snags (>15 cm dbh) were retained at densities of $\bar{x}$ = 57.4/ha and $\bar{x}$ = 13.7/ha, respectively. The majority of hardwoods were 8–23 cm dbh.

Mid-rotation plantations ($\bar{x}$ = 87.1 ha) were 12- to 15-year-old stands characterized by a dense canopy (69.5% canopy cover) of loblolly pine, small hardwoods ($\bar{x}$ = 50.6/ha), and snags ($\bar{x}$ = 1.5/ha). Mid-rotation plantations were dominated by loblolly pine ($\bar{x}$ = 828 pines/ha, pine basal area $\bar{x}$ = 12.2 m²/ha), with an understory (vegetation height 0.5–5.0 m) composed of shrubs and saplings of oak, hickory, dogwood (*Cornus* spp.), elm,

blueberry (*Vaccinium* spp.), and dense tangles of greenbriar (*Smilax* spp.) and blackberry. Ground cover was composed primarily of leaf litter and forbs.

Thinned plantations ($\bar{x}$ = 100.8 ha) were 17- to 23-year-old plantations that had been commercially thinned 3–5 years prior to our study (62.2% canopy cover). During commercial thinning, every other row and selected trees within remaining rows were removed, and lower branches on the remaining trees were pruned. Thinning facilitates tree growth, creates a more open canopy, and promotes growth of a dense shrub layer. Thinned stands were composed predominantly of loblolly pines ($\bar{x}$ = 241 pines/ha, pine basal area $\bar{x}$ = 8.5 m²/ha), small hardwoods ($\bar{x}$ = 46.4/ha) and snags ($\bar{x}$ = 5.5/ha). The shrub layer and remaining understory were composed of shrubs and saplings of oak, hickory, dogwood, elm, blackgum, winged sumac (*Rhus copallina*), and tangles of greenbrier, honeysuckle (*Lonicera japonica*), blackberry, and poison ivy (*Toxicodendron radicans*). Ground cover was composed primarily of leaf litter, forbs, grasses, and shrubs.

Single-tree selection is a form of uneven-aged management in which single trees of a certain age, diameter, or species are harvested periodically. Single-tree selection stands ($\bar{x}$ = 108.8 ha) were characterized by a dense canopy (67.1% canopy cover) composed of a mixture of shortleaf pine (*Pinus echinata*; $\bar{x}$ = 450 pines/ha, pine basal area $\bar{x}$ = 12.3 m²/ha) and oaks ($\bar{x}$ = 222 hardwoods/ha). Single-tree selection stands averaged 201.9, 17.4, and 1.2 hardwoods/ha and 363.0, 81.5, and 6.2 pines/ha in 8.0–22.9, 23.0–37.9 and ≥38 cm dbh size classes, respectively. The understory was composed of oak, elm, and hickory shrubs and saplings, pine seedlings, poison ivy, and blueberry. Ground cover consisted primarily of leaf litter and grass.

Late-rotation stands were mixed pine-hardwood forests that had not been harvested or had been only lightly harvested during the past 50 years. Late-rotation stands ($\bar{x}$ = 155.1 ha) were characterized by a dense overstory (78.1% canopy cover) of shortleaf pine ($\bar{x}$ = 314 pines/ha, pine basal area $\bar{x}$ = 14.0 m²/ha) and a mid-story of oak, blackgum, red maple, and hickory ($\bar{x}$ = 327 hardwoods/ha, hardwood basal area $\bar{x}$ = 6.8 m²/ha). The understory consisted of oak, dogwood, and hickory saplings, and a mix of shrubs, blueberry, and poison ivy. Ground cover was composed primarily of leaf litter.

Table 1.   Percent landscape cover (standard error) within 5 km of plots among five silvicultural treatments in the Ouachita Mountains of westcentral Arkansas.

Landscape cover	Treatment				
	regenerating	mid-rotation	thinned	single-tree selection	late-rotation
Forest	81.37 (1.70)	74.03 (3.20)	76.94 (2.83)	66.24 (1.42)	82.36 (1.58)
Dry crops	1.67 (0.46)	7.54 (0.86)	3.80 (0.83)	8.86 (1.37)	2.60 (1.01)
Pasture	15.79 (0.70)	17.52 (2.98)	14.93 (1.20)	23.39 (0.73)	14.64 (1.80)
Urban	0.64 (0.59)	0.24 (0.12)	3.60 (2.77)	0.24 (0.11)	0.04 (0.04)

Methods

Bird Censusing

Census points were chosen so that they were located at least 200 m from other census points and 100 m from the edge of the plot. We estimated the relative abundance of all breeding bird species using 8–12 ($\bar{x}$ = 10.6) fixed-radius (50 m) point counts per plot.

Prior to beginning censusing, experienced bird watchers spent 1–2 weeks practicing bird identification and distance estimation so that their skills would be similar. All plots were censused three times between 1 May and 30 June each year from 1993 to 1995. We counted only species that were known to breed in westcentral Arkansas (James & Neal 1986). A few migrants may have been counted during the first replicate; estimates of abundance were averaged over three replicates, however, so the influence of migrants on estimates of abundance was minimal. Censuses were not conducted during high winds (wind speed >5.4 m/second [19 km/hour]), rain, or fog. At each point, the species and sex (if known) of each bird seen or heard within 50 m were recorded for 10 minutes. Time of day, wind speed, temperature, and sky condition were also recorded at each census point. The order of points censused was changed with each census, and most replicates per plot were censused by different observers.

Nest Searching and Monitoring

Plots were searched for nests every 2 days from 1 April to 15 July each year. Nests were found by following adults carrying nesting material or by following adults back to the nest during incubation or feeding of young (Martin & Geupel 1993). Nests were monitored every 2–4 days to determine outcome and to check for Brown-headed Cowbird (*Molothrus ater*) parasitism. When possible, nests were checked with binoculars from a distance and high nests were checked with a pole and mirror. Nests that were too high to check directly were considered successful if adults were seen feeding fledglings or if the nests were observed long enough to include the incubation and nestling periods for the species.

We calculated nesting success and levels of predation by the Mayfield method (Mayfield 1961, 1975; Hensler & Nichols 1981), using daily mortality rates and daily predation rates, respectively. A nest was considered successful if it fledged at least one young, excluding cowbirds. Thus, daily mortality rates were influenced by both predation and parasitism, whereas daily predation rates reflect mortality due to predation alone. Observation of fledglings near the nest was considered evidence of fledging. A nest was assumed successful if nestlings were observed in the nest 2 days prior to the expected fledging date. A nest was considered to have suffered predation when eggs or nestlings that were too young to fledge disappeared between nest visits. A nest was considered parasitized if a cowbird egg or cowbird nestling was found in the nest. Only nests found during nest building, egg laying, or incubation were used to calculate parasitism rates. Because several species nesting on our plots are considered cowbird rejectors (Rothstein 1975), levels of cowbird parasitism may have been underestimated for some species.

Statistical Analyses

We tested for differences among treatments in daily nest mortality and nest predation rates for each species using the computer program CONTRAST (Hines & Sauer 1989) and procedures described by Sauer and Williams (1989), which use a modified chi-square distribution. We calculated levels of cowbird parasitism using percentages and tested for differences among treatments using log-likelihood G tests. All post-hoc tests were corrected for multiple comparisons with Bonferroni adjustments (i.e., by multiplying the number of comparisons by the p value calculated for each comparison). If the product was <0.10, the test was considered significant. We used a Type I error rate of 0.10 to reduce the probability of committing a Type II error (i.e., concluding that effects are not different when they actually are).

The relative abundance of birds was calculated for each plot as the total number of individuals detected at a census point, averaged across census replicates and years. Species abundance was affected by census date and wind speed. We used analysis of covariance, with census date and wind speed as covariates, to compare densities of Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), and Brown-headed Cowbirds among treatments. Because nest predators and cowbirds may show a functional response to bird abundance (Lowther & Johnston 1977; Gates & Gysel 1978; Martin 1988, 1996; Barber & Martin 1997), we used Pearson product-moment correlation analyses to test for relationships between (1) daily predation rates and the relative abundance of all birds and (2) levels of cowbird parasitism and host abundance for each plot. Host abundance was calculated for each plot as the total number of potential cowbird hosts detected at a census point, averaged across census replicates and years. We considered a species a potential cowbird host if that species had been documented previously as such (Friedmann & Kiff 1985).

Results

During 1993–1995, we found 1674 nests of 55 species (26 resident species, 3 short-distance migrants, 26 long-

distance [Neotropical] migrants). Numbers of nests varied among treatments: 631 in regenerating, 213 in mid-rotation, 401 in thinned, 341 in single-tree selection, and 88 in late-rotation stands.

Nesting Success

For 12 species, we had sufficient sample sizes (≥ 7 nests/treatment) to compare daily mortality rates among treatments (Table 2). We pooled nest mortality data across years for each of the 12 species. Differences in daily mortality rate among treatments were found for White-eyed Vireo (*Vireo griseus*), Pine Warbler (*Dendroica pinus*), Yellow-breasted Chat (*Icteria virens*), and Northern Cardinal (*Cardinalis cardinalis*). These differences, however, were lost for all species following Bonferroni adjustments (Table 2). Daily mortality rates did not differ among two or more treatments following Bonferroni adjustments for Carolina Chickadee (*Poecile carolinensis*), Carolina Wren (*Thryothorus ludovicianus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), White-eyed Vireo, Black-and-white Warbler (*Mniotilta varia*), Prairie Warbler (*Dendroica discolor*), Pine Warbler, Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat, Northern Cardinal, Indigo Bunting (*Passerina cyanea*), and Field Sparrow (*Spizella pusilla*) (Table 2).

Nest Predation

Predation accounted for failure in 80% of failed nests. Both Pine Warblers and Yellow-breasted Chats had greater daily nest predation rates in thinned stands ($\chi^2 = 3.22$, df $= 1$, $p = 0.07$, and $\chi^2 = 2.66$, df $= 1$, $p = 0.10$, respectively). Cardinals also differed in their daily nest predation rates among treatments ($\chi^2 = 7.86$, df $= 3$, $p = 0.05$), but these differences were lost for all species following Bonferroni adjustments.

We calculated Mayfield estimates of predation across species based on species means (to weight species equally) and found that predation rates differed among treatments (analysis of variance, $F_{4,40} = 3.26$, $p = 0.021$). Thinned plantations had higher predation levels than single-tree selection stands (Table 3). In addition, predation rates were lower in single-tree selection than other treatments when considered collectively across individual bird species ($p < 0.05$, sign test). Predation levels in other treatments were similar and intermediate between those of thinned and single-tree selection stands.

Predators may show a density-dependent response to their prey. We calculated daily predation rates per plot based on species means (to weight species equally). Only species with at least four nests in a plot were included. We compared daily predation rates with the relative abundance of all birds detected during point counts in each plot. The relative abundance of individu-

als was positively correlated with daily predation rates ($r = 0.629$, df $= 28$, $p < 0.001$; Fig. 1).

The relative abundance of two avian predators, American Crows ($F_{4,2538} = 8.58$, $p < 0.001$) and Blue Jays ($F_{4,2538} = 11.62$, $p < 0.001$), differed among treatments (Fig. 2). Crows were most abundant in mid-rotation and thinned stands and least abundant in single-tree selection and late-rotation stands. Regenerating stands had intermediate numbers of crows. Blue Jays reached their highest densities in mid-rotation and single-tree selection stands and lowest densities in regenerating stands. Thinned and late-rotation stands had Blue Jay densities intermediate between those of regenerating and mid-rotation stands (Fig. 2).

Cowbird Parasitism

Sample sizes were large enough to allow comparison of cowbird parasitism levels among two or more treatments for seven species (Table 4). Parasitism levels did not differ among treatments for Common Yellowthroats, Indigo Buntings, Prairie Warblers, or Northern Cardinals (all $p > 0.10$). White-eyed Vireos ($G = 14.86$, df $= 2$, $p < 0.001$) experienced higher parasitism in regenerating than in mid-rotation or thinned stands. Yellow-breasted Chats ($G = 8.16$, df $= 2$, $p = 0.017$) and Field Sparrows ($G = 6.98$, df $= 1$, $p = 0.008$) showed the opposite pattern, with higher parasitism levels in thinned than in regenerating stands (Table 4). When we examined means across species, mid-rotation stands tended to show lower parasitism than other treatments, but small sample sizes precluded statistical testing (Table 4). This trend seems real, given that White-eyed Vireo, with the largest sample size, showed an absence of parasitism in mid-rotation stands, in contrast to other treatments (Table 4) and other studies (Barber & Martin 1997).

The relative abundance of cowbirds differed among treatments ($F_{4,2538} = 17.49$, $p < 0.001$): regenerating, thinned, and single-tree selection stands were similar and had more cowbirds than mid-rotation and late-rotation stands (Fig. 3a). Cowbird abundance was positively associated with host abundance ($r = 0.418$, df $= 31$, $p = 0.019$; Fig. 3b) and negatively associated with percent canopy cover ($r = -0.394$, df $= 30$, $p = 0.031$; Fig. 4a), but host abundance and canopy cover each explained <18% of the variation in cowbird abundance. In addition, these significant associations were likely driven or confounded by the highly significant relationship between host abundance and percent canopy cover ($r = -0.676$, df $= 30$, $p < 0.001$; Fig. 4b). Cowbird abundance was not correlated with host abundance after canopy cover was controlled for ($r_p = 0.216$, df $= 27$, $p = 0.261$), nor was cowbird abundance correlated with canopy cover after host abundance was controlled for ($r_p = -0.172$, df $= 28$, $p = 0.373$). Thus the effects of host abundance and canopy cover cannot be separated.

Table 2.   Number of successful and total nests, number of observation days, daily mortality rate (standard error), and nesting success of bird species found among different silvicultural treatments in the Ouachita Mountains of westcentral Arkansas, 1993–1995.

Species (scientific name)	Treatment	No. successful/total	Observation days	Daily mortality rate (SE)	Nesting success[a,b]
Yellow-billed Cuckoo (*Coccyzus americanus*)	mid-rotation	5/13	135.5	0.0590 (0.0202)	24.7
Red-bellied Woodpecker (*Melanerpes carolinus*)	regenerating	8/10	317.5	0.0063 (0.0044)	78.2
Hairy Woodpecker (*Picoides villosus*)	regenerating	4/7	69.5	0.0432 (0.0244)	13.7
Eastern Kingbird (*Tyrannus tyrannus*)	regenerating	12/19	442.5	0.0158 (0.0059)	58.2
Eastern Wood-Pewee (*Contopus virens*)	regenerating	6/12	183.0	0.0328 (0.0132)	38.0
Carolina Chickadee (*Poecile carolinensis*)	regenerating	4/9	135.5	0.0369 (0.0162)	33.6
	single-tree selection	5/7	121.0	0.0165 (0.0116)	61.7
Carolina Wren (*Thryothorus ludovicianus*)	regenerating	6/8	53.5	0.0374 (0.0259)	30.7
	single-tree selection	10/10	97.0	0.000 (0.000)	100.0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	regenerating	15/36	548.0	0.0383 (0.0082)	34.8
	thinned	5/10	126.5	0.0395 (0.0173)	33.7
Eastern Bluebird (*Sialia sialis*)	regenerating	16/29	460.0	0.0283 (0.0077)	38.8
White-eyed Vireo (*Vireo griseus*)	regenerating	7/13	84.0	0.0714 (0.0281)	13.5**
	mid-rotation	21/33	462.5	0.0259 (0.0074)	49.2
	thinned	9/21	160.5	0.0748 (0.0208)	12.3
Red-eyed Vireo (*Vireo olivaceus*)	late-rotation	3/7	87.0	0.0460 (0.0225)	32.3
Black-and-white Warbler (*Mniotilta varia*)	mid-rotation	7/9	104.0	0.0192 (0.0135)	62.7
	thinned	3/7	44.0	0.0909 (0.0433)	10.2
	single-tree selection	14/17	150.0	0.0200 (0.0114)	61.6
Prairie Warbler (*Dendroica discolor*)	regenerating	23/70	635.0	0.0740 (0.0104)	16.5
	thinned	10/22	188.0	0.0638 (0.0178)	20.5
Pine Warbler (*Dendroica pinus*)	thinned	7/17	111.5	0.0897 (0.0271)	10.5**
	single-tree selection	24/29	208.0	0.0240 (0.0106)	55.8
	late-rotation	8/11	30.0	0.1000 (0.0548)	8.0
Kentucky Warbler (*Oporornis formosus*)	mid-rotation	11/14	113.5	0.0264 (0.0151)	52.6
Worm-eating Warbler (*Helmitheros vermivorus*)	mid-rotation	13/20	188.5	0.0371 (0.0183)	40.3
Common Yellowthroat (*Geothlypis trichas*)	regenerating	11/16	70.5	0.0719 (0.0306)	17.1
	thinned	6/19	189.5	0.0686 (0.0184)	18.2
Yellow-breasted Chat (*Icteria virens*)	regenerating	46/90	972.5	0.0432 (0.0065)	36.2*
	mid-rotation	4/8	66.5	0.0602 (0.0292)	24.0
	thinned	28/84	833.0	0.0600 (0.0082)	24.1
Northern Cardinal (*Cardinalis cardinalis*)	regenerating	4/18	184.0	0.0761 (0.0195)	16.2*
	mid-rotation	10/27	254.0	0.0669 (0.0157)	20.3
	thinned	15/32	409.0	0.0416 (0.0099)	37.7
	single-tree selection	7/10	129.0	0.0233 (0.0133)	58.2
Indigo Bunting (*Passerina cyanea*)	regenerating	30/62	567.0	0.0564 (0.0097)	27.9
	mid-rotation	8/21	239.5	0.0543 (0.0146)	29.3
	thinned	32/74	658.5	0.0638 (0.0095)	23.5
	single-tree selection	73/135	1151.0	0.0532 (0.0067)	29.6
	late-rotation	6/11	90.0	0.0556 (0.0241)	28.4
Field Sparrow (*Spizella pusilla*)	regenerating	21/40	290.0	0.0655 (0.0145)	22.5
	thinned	9/23	205.0	0.0683 (0.0176)	21.1
Chipping Sparrow (*Spizella passerina*)	single-tree selection	8/11	108.0	0.0278 (0.0158)	48.1
Orchard Oriole (*Icterus spurius*)	regenerating	8/17	210.0	0.0286 (0.0115)	48.5
Summer Tanager (*Piranga rubra*)	single-tree selection	5/14	119.5	0.0753 (0.0241)	17.9

[a] *Nesting success calculated by Mayfield method.*
[b] *p < 0.10, **p < 0.05 significance values prior to Bonferroni adjustments.*

Discussion

We found no differences in daily predation or daily mortality rates among treatments for individual bird species after Bonferroni adjustments, but significant differences before Bonferroni adjustments suggest that increased sample sizes would yield differences. When compared across species, predation rates were greater in thinned

Table 3.   Mayfield estimates of nest predation for bird species and mean nest predation rates among five silvicultural treatments in the Ouachita Mountains of westcentral Arkansas, 1993–1995.*

Species	Treatment				
	regenerating	mid-rotation	thinned	single-tree selection	late-rotation
Yellow-billed Cuckoo		64.7 (13)			
Red-bellied Woodpecker	11.6 (10)				
Hairy Woodpecker	86.3 (7)				
Eastern Kingbird	32.1 (19)				
Eastern Wood-Pewee	55.2 (12)				
Carolina Chickadee	58.1 (9)			38.3 (7)	
Carolina Wren	69.3 (8)			0.0 (10)	
Blue-gray Gnatcatcher	55.1 (36)		47.7 (10)		
Eastern Bluebird	61.2 (29)				
White-eyed Vireo	47.8 (13)	44.6 (33)	79.0 (21)		
Red-eyed Vireo					56.9 (7)
Black-and-white Warbler		37.3 (9)	90.0 (7)	27.5 (17)	
Prairie Warbler	77.3 (70)		64.8 (22)		
Pine Warbler			83.3 (17)	44.2 (29)	55.7 (10)
Kentucky Warbler		47.4 (14)			
Worm-eating Warbler		47.5 (20)			
Common Yellowthroat	64.8 (16)		79.2 (19)		
Yellow-breasted Chat	60.2 (90)	65.4 (8)	73.2 (84)		
Northern Cardinal	75.8 (18)	75.3 (27)	60.1 (32)	30.2 (10)	
Indigo Bunting	62.9 (62)	60.9 (21)	62.9 (74)	58.4 (133)	63.2 (11)
Field Sparrow	71.3 (40)		66.7 (23)		
Chipping Sparrow				51.9 (11)	
Orchard Oriole	54.9 (17)				
Summer Tanager				82.1 (14)	
Mean (SE)	59.0 (4.5)	55.4 (4.6)	70.7 (4.0)	41.6 (8.6)	58.6 (2.3)

*Numbers in parentheses are sample sizes of nests.

plantations than in single-tree selection stands. Predation is often the major cause of nest mortality among birds (Ricklefs 1969; Martin 1992, 1993). The greater predation rates in thinned plantations may partially re-

flect the fact that these treatments included a higher proportion of shrub-nesting species, which generally experience higher nest predation than other nest types (Martin 1993). But this cannot fully explain the higher
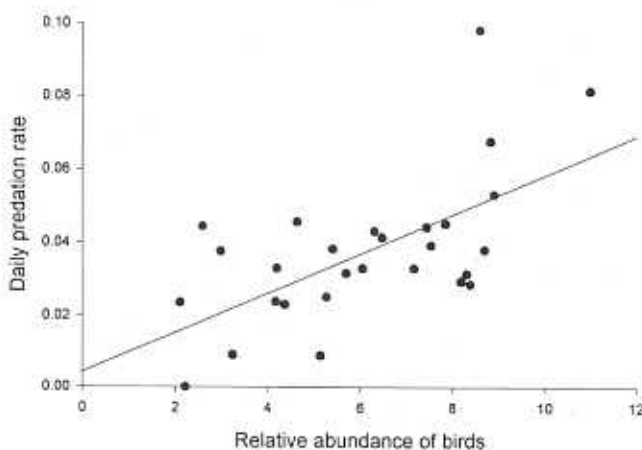

Figure 1. Relationship between daily predation rate and relative abundance of birds. Relative abundance is measured as the number of individuals detected per census point. Daily predation rate is the mean predation rate of species with at least four nests in a plot. Each point represents the mean daily predation rate and relative abundance of birds found in a single plot (48 ha average size) from 1993 to 1995.
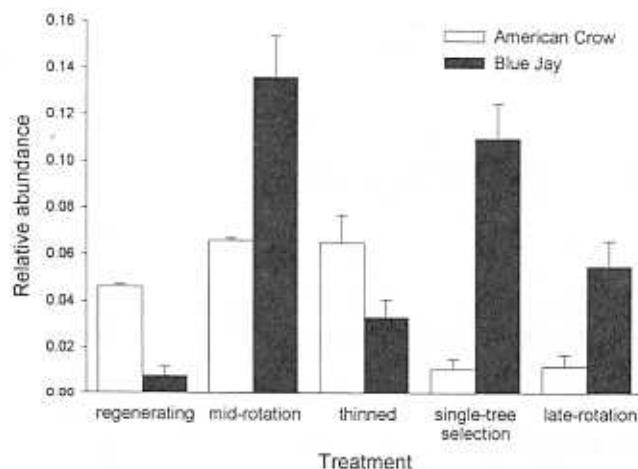

Figure 2. Relative abundance of American Crows and Blue Jays among five different silvicultural treatments in the Ouachita Mountains of westcentral Arkansas, 1993–1995: regenerating, mid-rotation, and thinned plantations and single-tree selection and late-rotation pine-hardwood stands. Relative abundance is measured as the mean number of individuals detected per point, and bars represent 1 standard error.

Table 4.   Percentage of nests parasitized by Brown-headed Cowbirds of host species among five different silvicultural treatments in the Ouachita Mountains of westcentral Arkansas, 1993–1995.[a]

Species[b]	Treatment				
	regenerating	mid-rotation	thinned	single-tree selection	late-rotation
White-eyed Vireo***	57.1 (7)	0.0 (21)	30.8 (13)	—	—
Prairie Warbler	11.7 (60)	—	10.0 (10)	—	—
Common Yellowthroat	14.3 (7)	—	13.3 (15)	—	—
Yellow-breasted Chat*	0.0 (74)	0.0 (6)	7.6 (66)	—	—
Field Sparrow**	3.3 (30)	—	31.3 (16)	—	—
Northern Cardinal	7.7 (13)	7.7 (13)	11.1 (27)	0.0 (7)	—
Indigo Bunting	16.3 (43)	7.1 (14)	20.4 (54)	28.6 (91)	0.0 (4)
Mean (SE), 4 spp.	20.3 (12.7)	3.7 (2.1)	17.5 (5.2)		
Mean (SE), all 7 spp.	15.8 (7.2)	3.7 (2.1)	17.8 (3.7)	14.3 (14.3)	0.0 (0.0)

[a] Numbers in parentheses are sample sizes of nests. To weight species equally, means are based on species means. Means are for the four species with data for all three clearcut treatments and for all seven species in each treatment.
[b] Log-likelihood G test among treatments; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

nest predation rate in thinned plantations, because several species (e.g., Black-and-white Warbler, Pine Warbler, Northern Cardinal) that occurred in other treatments incurred greater nest predation in thinned treatments.

Increased nest predation in thinned plantations may also have been caused by a greater abundance of predators. Thinned stands had greater structural diversity than other treatments (D.R.B., personal observation). Typically, thinning opens the canopy, which promotes growth of an extensive shrub layer (Dickson et al. 1995). Thinned plantations in our study had distinct canopy and shrub layers (D.R.B., personal observation). Other stands, with the exception of regenerating stands, typically lacked a distinct shrub layer. Single-tree selection stands had a shrub layer, but it was more patchily distributed (mean number of shrubs ± SE, 45.3 ± 2.3) than in thinned stands (53.7 ± 1.8). In addition, ground-cover types (e.g., shrub, grass, leaf litter, bare ground) were more varied in thinned stands, whereas other stands tended to have either dense ground cover (regenerating stands) or sparse ground cover (mid-rotation, single-tree, and late-rotation stands). Thus, bird nests in thinned plantations may have suffered higher predation rates because thinning increased the structural diversity of the habitat, which allowed for the existence of a greater number of predators.

Variation in nest predation rates among treatments may also arise from a density-dependent response of predators to cumulative prey density (Gates & Gysel 1978; Martin 1988, 1996). Daily predation rate in this study was positively correlated with the relative abundance of birds (Fig. 1), suggesting that predators may show a functional response to prey density. Regenerating and thinned plantations had the greatest abundance of birds, late-rotation stands the least, and mid-rotation and single-tree stands supported an intermediate abundance of birds (Barber et al., unpublished data). Although predation rates differed only between two treatments, predation generally followed this same pattern (means in Table 3). Moreover, abundance of small mammals, which are thought to be one of the main groups of nest predators, also may have followed this pattern. In a study of small-mammal communities in streamside management zones (SMZs) and adjacent pine plantations in the Ouachita Mountains (Tappe et al. 1994), small mammal captures in winter were more frequent in pine plantations (2.5 captures per 100 trap nights) than in SMZs and older late-rotation stands (1.5). Within pine plantations, small mammal captures were higher in regenerating (2.8) and thinned (2.9) stands than in mid-rotation stands (1.6). All predators do not respond to prey in a density-dependent fashion, so patterns of predation rates are likely influenced by the suite of predators that occupy a particular habitat and the influence of habitat alteration on predator abundances (Tewksbury et al. 1998).

Previous studies examining the effects of silviculture on the nesting success of birds have mainly used artificial nests (but see King et al. 1996). Typically, nesting success is higher in clearcuts than in unmanipulated stands (Yahner & Wright 1985; Rudnicky & Hunter 1993). We can make few comparisons of nesting success between late-rotation and manipulated stands in our study because of our small sample sizes of nests in late-rotation stands, but we can compare nesting success in our stands to that found in other studies (Table 5). In general, most species nesting in our stands had nesting success equal to or greater than that found in earlier studies (Table 5). Daily mortality rates did not differ between our managed stands in westcentral Arkansas and unmanaged stands in the Ozark National Forest in northwest Arkansas for Indigo Buntings, Black-and-white Warblers, Worm-eating Warblers (Helmitheros vermivorus), and Kentucky Warblers (Oporornis formosus) (Li 1994) or between our stands and early-successional scrub habitat in central Texas for both Yellow-breasted Chats and Northern Cardinals (Barber 1993). Daily mortality rates
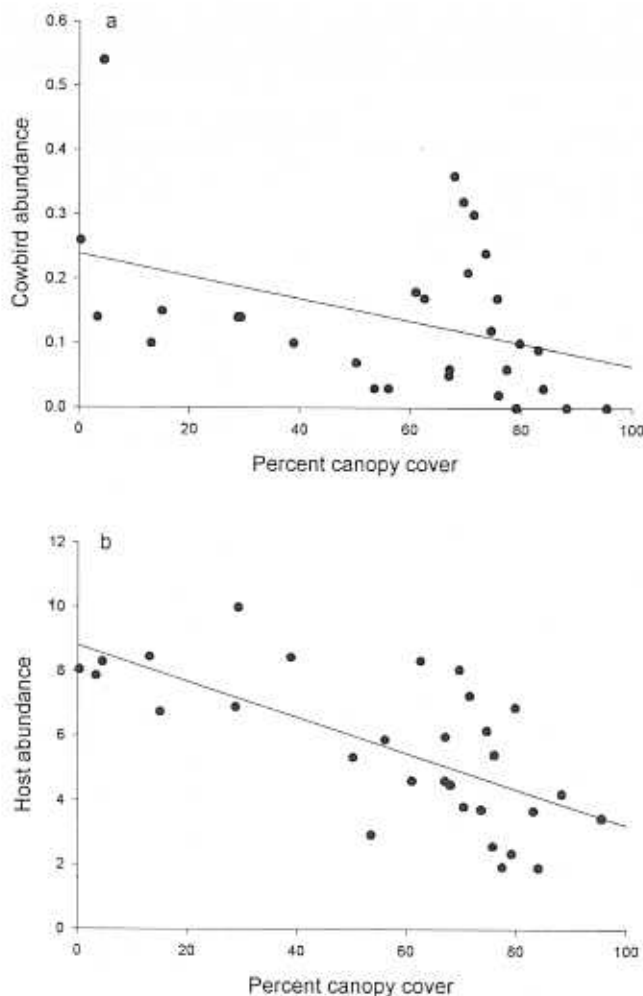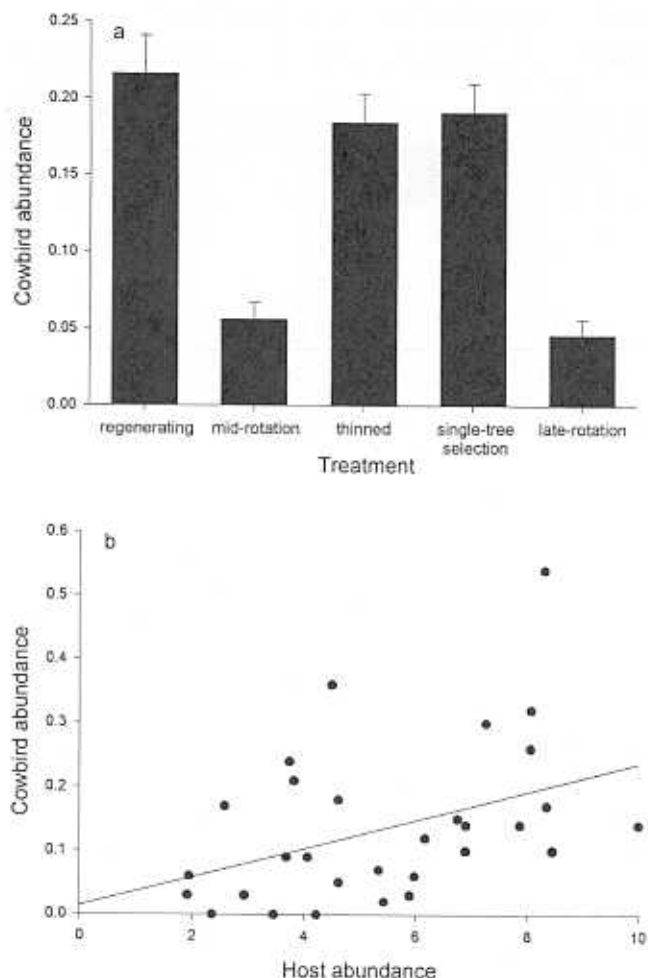
Figure 3. (a) Relative abundance of cowbirds among five different silvicultural treatments in the Ouachita Mountains of westcentral Arkansas, 1993–1995: regenerating, mid-rotation, and thinned plantations and single-tree selection and late-rotation pine-hardwood stands. Cowbird abundance is measured as the mean number of individuals detected per census point, and bars represent 1 standard error. (b) Relationship between cowbird abundance and host abundance. Cowbird and host abundance is measured as the number of cowbirds and total number of potential cowbird hosts detected per census point. Each point represents the mean cowbird and host abundance found in a single plot (48 ha average size) from 1993 to 1995.

Figure 4. (a) Relationship between cowbird abundance and percent canopy cover. Cowbird abundance is measured as the number of cowbirds detected per census point. Each point represents the mean cowbird abundance and mean percent canopy cover in a single plot (48 ha average size) from 1993 to 1995. (b) Relationship between cowbird host abundance of birds and percent canopy cover. Host abundance is measured as the number of potential cowbird hosts detected per census point. Each point represents the mean host abundance and mean percent canopy cover in a single plot (48 ha average size) from 1993 to 1995.

in our study also were similar to rates predicted for Red-eyed Vireos (*Vireo olivaceus*), Northern Cardinals, and Indigo Buntings and were lower for Worm-eating and Kentucky Warblers in a 66% forested landscape (Robinson et al. 1995). Regenerating and thinned plantations, however, may be low-quality nesting habitat for some shrub-nesting species. The nesting success of White-eyed Vireos, Prairie Warblers, Common Yellowthroats, and Field Sparrows was low in both regenerating and thinned

plantations (Table 5) and was approximately half of that found for a broader array of shrub-nesting species (Martin 1993, 1995).

Two of three species that differed in cowbird parasitism rates among treatments had greater parasitism in thinned plantations (Table 4). The third species had greater parasitism rates in regenerating plantations. Overall, parasitism rates were similar in regenerating, thinned, and single-tree selection stands and lower in mid- and late-rotation stands. Cowbird abundance also was similar

Table 5. Summary of nesting success of bird species in other geographic areas compared with rates observed among different silvicultural treatments in this study.

Species (references[a])	n	other studies	Silvicultural treatment, this study					location of other studies
			regenerating	mid-rotation	thinned	single-tree selection	late-rotation	
Red-bellied Woodpecker (1)	56	82.0[b]	78.2					MS, OH
Eastern Kingbird (2)	109	47.0	58.2					KS, NY
Blue-gray Gnatcatcher (3)	42	24.4[b]	34.8		33.7			CA
Eastern Bluebird (4)	218	42.4	38.8					FL
White-eyed Vireo (5)	10	35.0	13.5	49.2	12.3			TX
Black-and-white Warbler (6)	66	50.4				61.6		AR
Prairie Warbler (7)	400	22.3[b]	15.8		20.5			IN
Kentucky Warbler (6)	27	45.4		52.6				AR
Worm-eating Warbler (6)	65	56.4		40.3				AR
Common Yellowthroat (1)	152	44.4[b]	17.1		18.1			MI
Yellow-breasted Chat (8, 9)	66	27.6	36.2		24.1			TX, MO
Northern Cardinal (8, 10)	290	18.8	16.2	20.3	37.7	58.2		TX, OH
Indigo Bunting (6, 9)	90	32.6	27.9	29.3	23.5	30.0	28.4	AR, MO
Field Sparrow (11, 12, 13)	363	43.8	22.5		21.1			IL, MI, WV

[a]References: 1, Martin 1995; 2, Murphy 1983; 3, Root 1969; 4, White & Woolfenden 1973; 5, D.R.B., unpublished data; 6, Li 1994; 7, Nolan 1978; 8, Barber 1993; 9, Annand & Thompson 1997; 10, Filliater et al. 1994; 11, Best 1978; 12, Evans 1978; 13, Wray et al. 1982.
[b]Simple percentage estimates rather than Mayfield estimates.

in regenerating, thinned, and single-tree selection stands, but was lower in mid- and late-rotation stands (Fig. 3a). Chritton (1988) also found higher densities of cowbirds in thinned loblolly pine stands than in unthinned (mid-rotation) stands. Opening the canopy may attract cowbirds for two reasons. Reduced canopy cover is associated with increased host abundance, and cowbirds increase with cumulative host density (Lowther & Johnston 1977; Barber & Martin 1997; Tewksbury et al. 1998). At the same time, cowbirds find hosts by perching in trees and watching adults build nests (Norman & Robertson 1975; Thompson & Gottfried 1976, 1981; Lowther 1979), and opening the canopy may increase the ease of such activities. Thinned plantations provide trees for cowbirds to perch in, and their open midstory may allow cowbirds to see host activity more easily. Single-tree selection stands also provide an abundance of perch sites for cowbirds and have a relatively open canopy, and Indigo Buntings suffered notably high levels of cowbird parasitism in these stands (Table 4). Thus, opening the canopy increases the number of forest birds but may also increase the risk of parasitism.

Overall levels of cowbird parasitism in the Ouachita Mountains (12.1%) were similar to those found in other studies of forested landscapes (Hoover et al. 1995; Robinson et al. 1995; Hanski et al. 1996) but were lower than those found in studies of more fragmented landscapes (Robinson 1992; Hahn & Hatfield 1995; Robinson et al. 1995; Tewksbury et al. 1998). Predicted levels of parasitism for species in a 66% forested landscape (Robinson et al. 1995) were similar to (e.g., Indigo Bunting) or greater than (e.g., Northern Cardinal, Worm-eating Warbler, Kentucky Warbler) parasitism levels found in our study. Nest parasitism often decreases with

an increase in the amount of forested cover in the landscape (Robinson et al. 1995; Tewksbury et al. 1998), and cowbird abundance decreases with distance from forest edges (Brittingham & Temple 1983). Thus, cowbirds may not successfully invade extensively forested areas, even if the areas are managed by clearcutting (Thompson et al. 1992).

In summary, daily mortality and daily predation rates among two or more treatments differed for several species, but these differences were lost for all species after Bonferroni adjustments. When predation rates were averaged across species, thinned plantations had greater predation rates than single-tree selection stands. Thinned plantations also had higher levels of cowbird parasitism for two of seven species, which may contribute to nest failure. Thinned plantations may provide low-quality nesting habitat for several early-successional shrub-nesting species. Several shrub-nesting species had lower nesting success in thinned and regenerating plantations than found in other published studies. Moreover, the positive relationship between daily predation rate and relative abundance of birds suggests density-dependent predation. In contrast, many species nesting in either mid-rotation or single-tree selection stands had nesting success similar to that found in earlier studies. This suggests that some silvicultural treatments, such as single-tree selection, and some seral stages of even-aged management, such as mid-rotation stands, may provide suitable habitat for forest land birds. Future studies should address questions related to the source-sink dynamics of species in selected habitats and across managed forest landscapes. Although thinned plantations with open canopies may result in high predation and parasitism for some species, it is unknown whether the risks of preda-

tion and parasitism will decrease following canopy closure. Further study on how thinning affects predator abundance and diversity could be informative. Moreover, additional research is needed to elucidate the relationship between bird abundance and canopy cover and how these variables influence the relative abundance of cowbirds.

Acknowledgments

Literature Cited

Annand, E. M., and F. R. Thompson III. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management 61:159–171.

Barber, D. R. 1993. Effects of alternate host densities on Brown-headed Cowbird parasitism in Black-capped Vireos. M.S. thesis. University of Arkansas, Fayetteville.

Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. Condor 99:595–604.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

Chritton, C. A. 1988. Effects of thinning a loblolly pine plantation on nongame bird populations in east Texas. M.S. thesis. Stephen F. Austin University, Nacogdoches, Texas.

Dickson, J. G., F. R. Thompson III, R. N. Conner, and K. E. Franzreb. 1995. Silviculture in central and southeastern oak-pine forests. Pages 245–266 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

Evans, E. W. 1978. Nesting responses of Field Sparrows (*Spizella pusilla*) to plant succession on a Michigan old field. Condor 80:34–40.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation of Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

Friedmann, H., and L. F. Kiff. 1985. The parasitic cowbirds and their hosts. Proceedings of the Western Foundation of Vertebrate Zoology 2:226–304.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59:871–883.

Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape level: cowbirds prefer forests. Conservation Biology 9:1415–1424.

Hanski, I. L., T. J. Fenske, and G. J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk 113:578–585.

Haskell, D. G. 1995. Forest fragmentation and nest-predation: are experiments with Japanese Quail eggs misleading? Auk 112:767–770.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42–53.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. Technical report 24. U.S. Fish Wildlife Service, Washington, D.C.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk 112:146–155.

James, D. A., and J. C. Neal. 1986. Arkansas birds: their abundance and distribution. University of Arkansas Press, Fayetteville.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effect of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. Conservation Biology 10:1380–1386.

Li, P. 1994. Breeding productivity, microhabitat requirements, and parental care of Neotropical migrant birds in the Ozarks of Arkansas. Ph.D. dissertation. University of Arkansas, Fayetteville.

Lowther, P. E. 1979. Nest selection by Brown-headed Cowbirds. Wilson Bulletin 91:118–122.

Lowther, P. E., and R. F. Johnston. 1977. Influences of habitat on cowbird host selection. Kansas Ornithological Society Bulletin 28:36–40.

Martin, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. Proceedings of the National Academy of Science of the United States of America 85:2196–2199.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 in J. Hagan and D. W. Johnston, editors. Ecology and conservation of Neotropical migrants. Smithsonian Institution Press, Washington, D.C.

Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. Nature 380:338–340.

Martin T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Martin, T. E., I. J. Ball, and J. Tewksbury. 1996. Environmental perturbations and rates of nest predation in birds. Transactions of the North American Wildlife Natural Resources Conference 61:43–49.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Mayfield, H. 1975. Suggestions for calculating nesting success. Wilson Bulletin 87:456–466.

Murphy, M. T. 1983. Nest success and nesting habitats of Eastern Kingbirds and other flycatchers. Condor 85:208–219.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithological Monographs 26.

Norman, R. F., and R. J. Robertson. 1975. Nest searching behavior in the Brown-headed Cowbird. Auk 92:610–611.

Nour, N., E. Matthysen, and A. A. Dhondt. 1993. Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. Ecography 16:111–116.

Powell, D. S., J. L. Faulkner, D. R. Darr, Z. Zhu, and D. W. MacCleery. 1993. Forest resources of the United States, 1992. General technical report RM-234. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Reitsma, L. 1992. Is nest predation density dependent? A test using artificial nests. Canadian Journal of Zoology 70:2498–2500.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions in Zoology 9:1–48.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408–418 in J. Hagan and D. W. Johnston, editors. Ecology and conservation of Neotropical migrants. Smithsonian Institution Press, Washington, D.C.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Root, R. B. 1969. The behavior and reproductive success of the Blue-gray Gnatcatcher. Condor 71:16–31.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

Rudnicky, T. C., and M.L. Hunter Jr. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. Journal of Wildlife Management 57:358–364.

Sauer, J. R., and R. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:217–223.

Smith, K. G., R. S. Dzur, D. G. Catanzaro, M. E. Garner, and W. F. Limp. 1998. State-wide biodiversity mapping for Arkansas. Arkansas gap analysis final report. Center for Advanced Spatial Technologies, University of Arkansas, Fayetteville.

Tappe, P. A., R. E. Thill, M. A. Melchiors, and T. B. Wigley. 1994. Wildlife values of streamside management zones in the Ouachita Mountains, Arkansas. Pages 122–138 in Riparian ecosystems in the humid U.S.: functions, values and management. National Association of Conservation Districts, Washington, D.C.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Habitat fragmentation in a western landscape: breeding productivity does not decline with increasing fragmentation. Ecology 79:2890–2903.

Thompson, C. F., and B. M. Gottfried. 1976. How do cowbirds find and select nests to parasitize? Wilson Bulletin 88:673–675.

Thompson, C. F., and B. M. Gottfried. 1981. Nest discovery and selection by Brown-headed Cowbirds. Condor 83:268–269.

Thompson, F. R., III, W. D. Dijak, T. G. Kulowiec, and D. A. Hamilton. 1992. Breeding bird populations in Missouri Ozark forest with and without clearcutting. Journal of Wildlife Management 56:23–30.

Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201–219 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Vickery, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Is density an indicator of breeding success? Auk 109:706–710.

White, S. C., and G. E. Woolfenden. 1973. Breeding of the Eastern Bluebirds in central Florida. Bird-Banding 44:110–123.

Wray, T., II, K. A. Strait, and R. C. Whitmore. 1982. Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. Auk 99:157–164.

Yahner, R. H., and B. L. Cypher. 1987. Effects of nest location on depredation of artificial arboreal nests. Journal of Wildlife Management 51:178–181.

Yahner, R. H., and A. L. Wright. 1985. Depredation on artificial ground nests: effects of edge and plot age. Journal of Wildlife Management 49:508–513.