

## BREEDING AND POST-BREEDING HABITAT USE BY FOREST MIGRANT SONGBIRDS IN THE MISSOURI OZARKS<sup>1</sup>

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**Abstract.** We compared habitat use by forest migrant songbirds during the breeding and post-breeding periods in four Missouri Ozark habitats: mature upland forest, mature riparian forest, 9- to 10-year-old upland forest, and 3- to 4-year-old upland forest created by clear-cutting. Adult forest-ground species showed a decrease in abundance in all habitats during the post-breeding period, but hatching-year birds of one of the two forest-ground species were most abundant in early-successional forest during this time. Adults of the two forest-canopy species tended to increase in abundance in 3- to 4-year-old forest from breeding season to post-breeding season. During the breeding season, some forest species were detected with mist-nets in the two early-successional habitats, but infrequently or not at all with point counts in those habitats. Forest birds captured in early-successional habitats during the breeding season may have been nonbreeding floaters, or may have been foraging there from nearby territories in mature forest. Dense shrubs or young trees in early-successional forest may provide habitat for nonbreeding and post-breeding forest migrant songbirds in the Missouri Ozarks.

**Key words:** early-successional, habitat use, Missouri Ozarks, post-breeding, songbirds.

### INTRODUCTION

Neotropical migrant songbirds are the focus of much attention due to declines in some species (Robbins et al. 1989, Askins et al. 1990). Research on the breeding, wintering, and migration ecology of some species is quite extensive (Hagan and Johnston 1992, Finch and Stangel 1993). There may be other phases of this annual cycle, such as the post-breeding period, that are equally important to the long term stability and sustainability of songbird populations. We defined the post-breeding period in migratory birds as the period after nesting or fledging until the onset of fall migration. This period may last several months for hatching-year birds produced early in the breeding season and for adults that raise only a single brood per year (Faaborg et al. 1996, Anders et al. 1998). During this period, birds must build up fat reserves and, at the same time, avoid predation (Moore et al. 1993). Both hatching-year and adult birds may be vulnerable during this time because hatching-year birds have little experience foraging on their own, and

adults of many species undergo a complete pre-basic molt (Pyle et al. 1987, Ralph et al. 1993), which may hinder their ability to fly (Rimmer 1988, Vega Rivera et al. 1998a). The availability of quality habitat during the post-breeding period may be critical to survival.

Some recent studies of Wood Thrush (*Hylocichla mustelina*) using radio-telemetry indicate habitats used by hatching-year birds during the post-breeding period differ from habitats used by adults during the breeding season. Wood Thrush nest in mature upland forest, whereas hatching-year birds often move to early- and mid-successional forest after fledging (Anders et al. 1998, Vega Rivera et al. 1998b). Adult Wood Thrush also may move to early- to mid-successional habitats or forest edges after breeding (Rappole and Ballard 1987, Vega Rivera et al. 1998a).

Post-breeding habitat use by other forest-breeding Neotropical migrant songbirds remains largely unknown due to the difficulty in tracking individuals from breeding territories to post-breeding habitats, and in detecting non-singing birds (Faaborg et al. 1996). We examined breeding and post-breeding habitat use by forest Neotropical migrant songbirds. We used ANOVA

<sup>1</sup> Received 13 May 1999. Accepted 11 April 2000.

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models to determine the effects of habitat, time-of-season, age of bird, year, and the interactions of these effects, on the relative abundance of each species. We hypothesized that the abundance of post-breeding adult and hatching-year forest birds would be greater in early-successional habitats than in mature forest.

## METHODS

### STUDY AREA

This study was conducted in 1997 and 1998 on the Houston-Rolla Ranger District of the Mark Twain National Forest (Pulaski, Laclede, and Texas Counties), and on Horseshoe Bend Natural Area, a Missouri Department of Conservation managed property owned by the Lad Foundation (Texas County). This area is on the Ozark Plateau in south-central Missouri and is characterized by rolling terrain dissected by numerous streams. The area is heavily forested; the three-county area we worked in is approximately 54% forested (Miles 1990, Smith 1990). The forest is primarily mature, even-aged forest that regenerated after extensive clearcutting during the early 1900s. Young forest stands created by recent timber harvests are interspersed throughout the area. Non-forested land consists of cattle pastures and small towns.

We studied bird abundance in four habitats: mature upland forest, mature riparian forest, 9- to 10-year-old upland forest, and 3- to 4-year-old upland forest. Three sites (replicates) of each habitat were surveyed during 1997, and three different sites of each habitat were surveyed in 1998 for a total of 24 sites in two years. Study sites were 2.5 to 5.2 ha, surrounded by forest, and spatially dispersed throughout the study area (Pagen 1999).

Vegetation characteristics such as canopy cover, basal area, and ground cover were significantly different among the four habitats (Pagen 1999). The mature upland and mature riparian sites had not received any silvicultural treatment for at least 50 years. Both 3- to 4-year-old and 9- to 10-year-old forest were created by clearcutting and had abundant natural tree regeneration. The 3- to 4-year-old and 9- to 10-year-old forest had on average 10% and 79% canopy closure and a 2.5-m and 5.8-m canopy height, respectively. Mature upland and riparian forests had approximately 90% canopy closure and a 19-m canopy height (Pagen 1999). Upland sites

were in mixed oak forests, dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.). Dogwood (*Cornus florida*), cherry (*Prunus serotina*), and sassafras (*Sassafras albidum*) also were present in these forests. Common shrubs included black raspberry (*Rubus occidentalis*), poison ivy (*Toxicodendron radicans*), fragrant sumac (*Rhus aromatica*), and buckbrush (*Symphoricarpos orbiculatus*). Riparian sites were dominated by elm (*Ulmus* spp.), box elder (*Acer negundo*), maple (*Acer* spp.), and sycamore (*Platanus occidentalis*). Ash (*Fraxinus* spp.), paw paw (*Asimina triloba*), and hackberry (*Celtis occidentalis*) also were present, and spicebush (*Lindera benzoin*) was the most common shrub. Ground cover was dense with forbs such as nettle (*Laportea canadensis*), giant ragweed (*Ambrosia trifida*), and wingstem (*Verbesina* spp.).

### BIRD SURVEYS

We surveyed bird communities by point counts and constant-effort mist-netting. We used the point count method because of its ability to locate breeding birds (Ralph et al. 1995). We used mist-netting because many Neotropical migrant songbirds are nearly silent during the post-breeding period (Faaborg et al. 1996), and visibility can be poor in early-successional habitats because of dense vegetation. Although problems associated with mist-netting and point counts are well documented, use of both methods should reduce problems (Rappole et al. 1993, Gram and Faaborg 1997).

*Point counts.* We conducted point counts five times at each site between 21 May and 17 August 1998, with approximately 2.5 weeks between visits to a site. We located four evenly spaced point count stations at each site. Each point was surveyed for 10 min, and birds were recorded as inside or outside a 50-m radius circle. All birds heard or seen within the study site were recorded.

*Mist-netting.* We surveyed each site with 10 nets in 1997 and 12 nets in 1998. The distance between net lanes was kept constant between years. At each site, we located net lanes approximately 50-m apart and at least 25-m from any habitat edge. Net lanes were arranged as systematically as possible within each site so that they sampled comparable areas. Nets were 30-mm mesh, 12-m long, and approximately 2.6-m high. We surveyed birds five times between 22 May and 21 August in 1997, and five times between

21 May and 17 August in 1998, with approximately 2.5 weeks between visits to a site. Each visit entailed operating net lines for approximately 5.5 hr beginning 20 min before sunrise. We banded birds with a U.S. Fish and Wildlife Service aluminum band and recorded the species, age (hatching-year or adult), and sex. Breeding condition was noted as the presence/absence of a brood patch or cloacal protuberance. Banding protocol followed Ralph et al. (1993).

#### STATISTICAL ANALYSES

We selected six species for analysis that were among the most abundant and had small confidence intervals for mean detections in each habitat: Red-eyed Vireo (*Vireo olivaceus*), Northern Parula (*Parula americana*), Acadian Flycatcher (*Empidonax virescens*), Ovenbird (*Seiurus aurocapillus*), Worm-eating Warbler (*Helmitheros vermivorus*), and Kentucky Warbler (*Oporornis formosus*). We also analyzed two guilds of species because confidence intervals were particularly small when data for several species were pooled. These guilds were: forest-ground species (Ovenbird, Worm-eating Warbler, and Wood Thrush), and forest-canopy species (Red-eyed Vireo, Yellow-throated Vireo [*Vireo flavifrons*], Yellow-throated Warbler [*Dendroica dominica*], Northern Parula, Yellow-billed Cuckoo [*Coccyzus americanus*], and Scarlet Tanager [*Piranga olivacea*]). Kentucky Warbler, although clearly a ground bird, was not included in the forest-ground guild because it is known to breed in early-successional forest (Thompson and Fritzell 1990).

**Point counts.** We calculated mean detections/10-min point count for each species from the four points surveyed during each visit to a site. We used all detections (aural and visual) within a 50-m radius for the calculations. Confidence intervals for mean detections  $\text{point}^{-1}$  for each habitat decreased when individual visits were pooled, so we classified visits 1 and 2 as "early season" (which approximates the breeding season), visits 4 and 5 as "late season" (which approximates the post-breeding period), and dropped visit 3 from the analysis.

We used a square-root transformation on point-count data to improve normality and constancy of variance (Neter et al. 1996). We analyzed the effect of habitat, time-of-season, and their interaction on mean detections  $\text{point}^{-1}$  us-

ing a repeated-measures ANOVA specified as a nested model (SAS Institute 1990). We considered factors in the ANOVA model significant at a  $P$ -value  $< 0.1$  to increase statistical power. We used the least-significant difference test (LSMEANS; SAS Institute 1990) to test for differences among the levels of each factor in the ANOVA and a sequential Bonferroni test (Rice 1989) to adjust the significance level of each test to control for experiment-wide error rates at a  $P$ -value  $< 0.05$ .

If post-breeding adult and hatching-year forest birds prefer early-successional habitats, we predicted a significant habitat  $\times$  time-of-season interaction in the ANOVA model, and that detections should be greater in 3- to 4-year-old forest and 9- to 10-year-old forest than in either of the mature forest habitats during the post-breeding period. However, because point counts are less effective later in the season (Skirvin 1981), we were mainly interested in using point-count data to determine abundance by habitat during the breeding season. Conclusions on post-breeding habitat use were based primarily on mist-netting results.

**Mist-netting.** We standardized net captures for each visit to a site as captures  $100\text{-net-hr}^{-1}$ . As with point counts, visits were pooled and classified as early or late season. We analyzed the same species and species guilds used in the point count analysis. We screened all data for normality and constancy of variance and log-transformed data prior to analysis (Neter et al. 1996). We analyzed the effect of habitat, time-of-season, age of bird, year, and their interactions on mean captures using a repeated-measures ANOVA (SAS Institute 1990). As with point counts, we used the least-significant difference test to test for differences among the levels of each factor, and the sequential Bonferroni test to control experiment-wide error rates.

We predicted a significant habitat  $\times$  time-of-season, and habitat  $\times$  time-of-season  $\times$  age class effect in the ANOVA model, and that captures of both adults and hatching-year birds should be greater in 3- to 4-year-old forest and 9- to 10-year-old forest than in either of the mature forest habitats during the post-breeding period. We also predicted that abundance of adults should decrease in mature forest and increase in early-successional habitats from early season to late season.

Forest-canopy species are often not detected

TABLE 1. Mean ( $\pm$  SE) abundance of forest birds detected with point counts during the breeding and post-breeding period in four habitats in Missouri, 1998. Numbers with different letters indicate significantly different means among habitats within a period ( $P < 0.05$ ); rows without letters are not different.

Species	Period	Habitat			
		Mature	Riparian	9-year-old	3-year-old
Red-eyed Vireo	Breeding	0.71 $\pm$ 0.23a	0.42 $\pm$ 0.04a	0.13 $\pm$ 0.07b	0.00 $\pm$ 0.00b
	Post-breeding	0.71 $\pm$ 0.00	0.29 $\pm$ 0.23	0.50 $\pm$ 0.26	0.00 $\pm$ 0.00
Northern Parula	Breeding	0.04 $\pm$ 0.04	0.25 $\pm$ 0.14	0.08 $\pm$ 0.08	0.00 $\pm$ 0.00
	Post-breeding	0.00 $\pm$ 0.00	0.08 $\pm$ 0.04	0.13 $\pm$ 0.13	0.04 $\pm$ 0.04
Acadian Flycatcher	Breeding	0.04 $\pm$ 0.04a	0.50 $\pm$ 0.21b	0.00 $\pm$ 0.00a	0.00 $\pm$ 0.00a
	Post-breeding	0.08 $\pm$ 0.08a	0.38 $\pm$ 0.13b	0.00 $\pm$ 0.00a	0.00 $\pm$ 0.00a
Ovenbird	Breeding	0.12 $\pm$ 0.15	0.00 $\pm$ 0.00	0.29 $\pm$ 0.29	0.00 $\pm$ 0.00
	Post-breeding	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	0.04 $\pm$ 0.04	0.04 $\pm$ 0.04
Worm-eating Warbler	Breeding	0.08 $\pm$ 0.08	0.04 $\pm$ 0.04	0.04 $\pm$ 0.04	0.04 $\pm$ 0.04
	Post-breeding	0.04 $\pm$ 0.04	0.13 $\pm$ 0.00	0.13 $\pm$ 0.00	0.07 $\pm$ 0.17
Kentucky Warbler	Breeding	0.00 $\pm$ 0.00	0.08 $\pm$ 0.04	0.17 $\pm$ 0.08	0.08 $\pm$ 0.04
	Post-breeding	0.00 $\pm$ 0.00a	0.25 $\pm$ 0.07b	0.13 $\pm$ 0.07ab	0.13 $\pm$ 0.07ab
Forest canopy guild	Breeding	1.00 $\pm$ 0.30	0.88 $\pm$ 0.07	0.46 $\pm$ 0.08	0.29 $\pm$ 0.04
	Post-breeding	1.13 $\pm$ 0.25	0.58 $\pm$ 0.18	1.12 $\pm$ 0.33	0.08 $\pm$ 0.04
Forest ground guild	Breeding	0.29 $\pm$ 0.15	0.04 $\pm$ 0.04	0.46 $\pm$ 0.40	0.04 $\pm$ 0.04
	Post-breeding	0.17 $\pm$ 0.17a	0.17 $\pm$ 0.04a	0.17 $\pm$ 0.08a	0.21 $\pm$ 0.15b

well with mist-nets in habitats with a high canopy (Karr 1981, Petit et al. 1992), so a comparison among habitats may be biased (Remsen and Good 1996). Therefore, we only interpreted results of the ANOVA for differences in the abundance of canopy species within habitats over time and between adults and hatching year birds in the same habitat.

Red-eyed Vireo, Acadian Flycatcher, Ovenbird, Worm-eating Warbler, and Kentucky Warbler were detected regularly with mist-nets in at least one of the two early successional habitats during the early season. To determine why these forest breeding birds were present in early-successional habitat, we determined the frequency of breeding condition and sex of adults captured during the early season in mature forest and in early-successional habitats. We also calculated the frequency of recaptured adults in mature and early-successional forest during the breeding season. We calculated recapture frequencies for visits 1–3 rather than for just visits 1 and 2 to increase the likelihood of recapturing birds that remained in the area during the breeding season.

Due to small sample sizes and potentially low statistical power, we considered  $P$ -values of  $\leq 0.1$  as significant.

## RESULTS

Based on point count detections, one species (Red-eyed Vireo) and one guild (forest canopy species group) had significant habitat  $\times$  time-of-

season effects ( $P < 0.1$  and  $P < 0.01$ , respectively). Three species (Northern Parula, Ovenbird, Red-eyed Vireo) and both guilds had significant habitat  $\times$  time-of-season effects for mist-net detections (all  $P < 0.05$ ), and four species and one guild had significant age-of-bird  $\times$  habitat  $\times$  time-of-season effects (Kentucky Warbler  $P < 0.01$ ; Ovenbird  $P < 0.1$ ; Wood Thrush and Worm-eating Warbler  $P < 0.05$ ; forest-ground species group  $P < 0.1$ ). Non-transformed point count and mist-netting data for each species and guild are presented in Table 1 and Figure 1.

We found four major patterns of abundance: first, some species were more abundant in early-successional habitat than mature forest during the late season. Significantly more hatching-year Worm-eating Warblers were found in 3- to 4-year-old forest and 9- to 10-year-old forest than in mature upland forest during the late season (Fig. 1). Hatching-year birds of the forest-ground guild were more abundant in 3- to 4-year-old forest and 9- to 10-year-old forest than in either of the mature habitats during the late season (Fig. 1). Several other species were present in early-successional habitat during the late season as well. We did not compare differences in canopy species among habitats. Rather, we compared how abundance in each habitat changed from the early season to the late season. The number of adult Northern Parulas, Red-eyed Vireos, and forest-canopy birds tended to in-

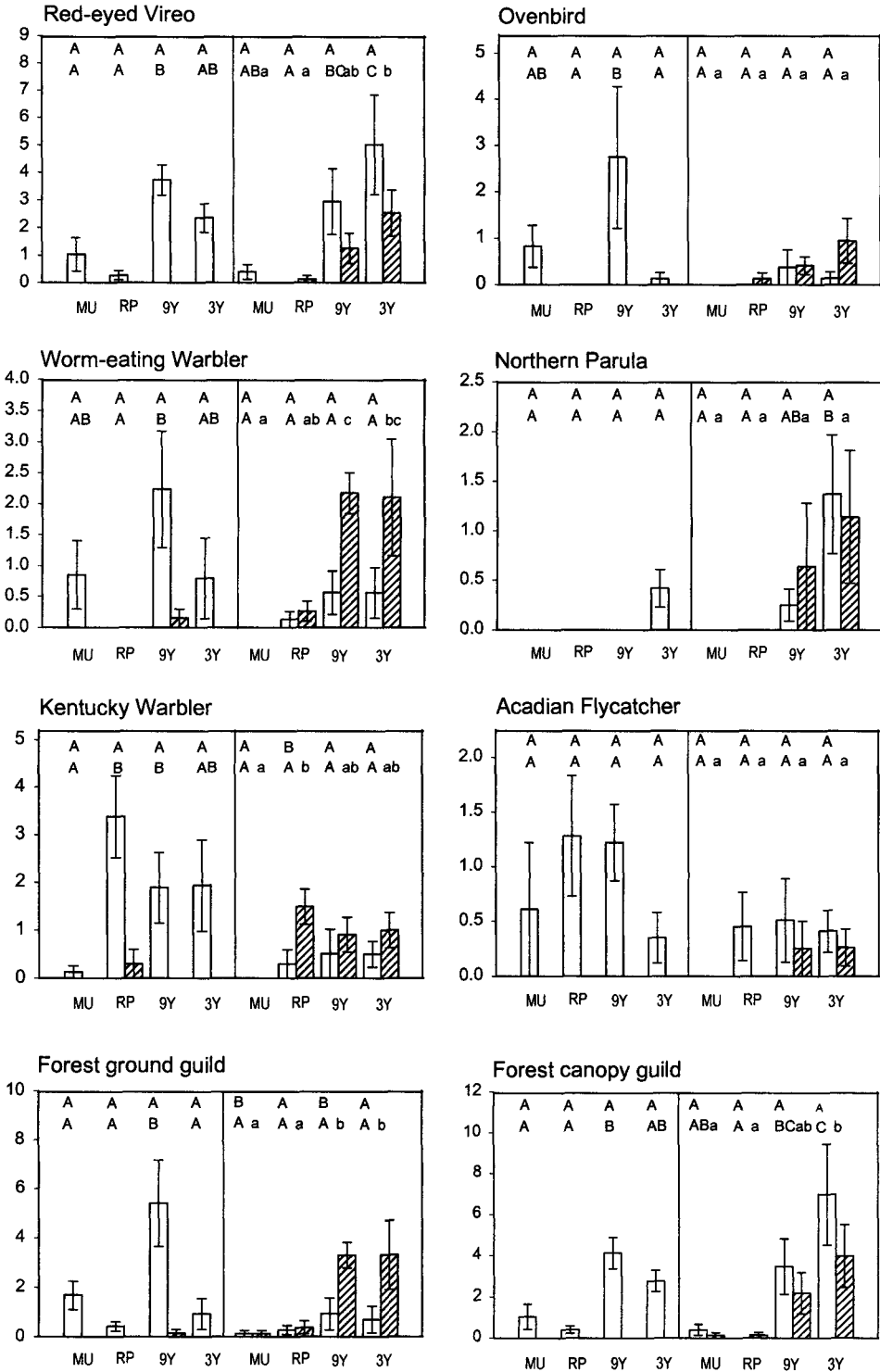


FIGURE 1. Mean abundance (1997, 1998) of bird species and guilds detected with mist-netting during breeding and post-breeding periods in mature upland forest (MU), mature riparian forest (RP), 9- to 10-year-old upland forest (9Y), and 3- to 4-year-old upland forest (3Y). Bars with the same letters are not significantly different at

crease in 3- to 4-year-old forest from early to late season (Fig. 1). Hatching-year birds of these three species/guilds also were present in the two early-successional habitats during the late season.

A second pattern was that adults of some species/guilds decreased in abundance in all habitats during the late season. Numbers of adult Ovenbirds and Worm-eating Warblers in 9- to 10-year-old forest tended to decrease from the early to the late season (Fig. 1). Abundance of adult Kentucky Warblers and adult forest-ground birds also tended to decline in all habitats from the early season to the late season, with a significant decrease of Kentucky Warblers in mature riparian forest, and a significant decrease of forest-ground birds in mature upland forest and 9- to 10-year old forest (Fig. 1).

A third pattern was that some species were captured in both mature forest and early-successional habitat during the early season, but were only detected with point counts in mature forest habitats at that time. Detections point<sup>-1</sup> of Red-eyed Vireos were greatest in mature upland forest during the early season, with no Red-eyed Vireos detected in 3- to 4-year-old forest (Table 1). However, Red-eyed Vireos were frequently captured in the two early-successional habitats during the early season. Detections point<sup>-1</sup> of Acadian Flycatchers were significantly higher in mature riparian forest than in all other habitats during the early season (Table 1). No Acadian Flycatchers were detected with point counts in either of the two early-successional habitats. However, captures 100-net-hr<sup>-1</sup> of Acadian Flycatchers were not significantly different between habitats in either time-of-season (Fig. 1).

Finally, some species were detected with both point counts and mist-nets in mature forest and early-successional habitat during the early season. Detections point<sup>-1</sup> of Ovenbirds tended to be highest in 9- to 10-year-old forest, followed by mature upland forest (Table 1). Netting data showed a similar trend (Fig. 1). Significantly more adult Ovenbirds were captured in 9- to 10-year-old forest than in either 3- to 4-year-old forest or riparian forest during the early season.

Captures of adult Worm-eating Warblers also were greatest in 9- to 10-year-old forest during the early period (Fig. 1). The forest-ground guild showed no habitat differences with point counts, but captures of adults were higher in 9- to 10-year-old forest than in any other habitat during the early season.

Information on sex ratio, evidence of breeding condition, and frequency of recapture may help explain why individuals of six species were present in early-successional habitat during the early season (Table 2). Red-eyed Vireos and Kentucky Warblers had a more male-biased sex ratio in early-successional habitat than in mature forest, whereas Ovenbirds and Worm-eating Warblers were more male-biased in mature forest (Table 2). Red-eyed Vireos and Ovenbirds had a higher frequency of breeding condition in mature forest than in early-successional forest, whereas Kentucky Warblers had higher frequency of breeding condition in early-successional habitat. Acadian Flycatcher, Kentucky Warbler, and Ovenbird had a higher frequency of recapture in mature forest than early-successional habitat, whereas Worm-eating Warblers showed the opposite trend (Table 2). Because we could not reliably determine the sex of Acadian Flycatchers, we did not report the proportion that were male or in breeding condition.

## DISCUSSION

We found adult and hatching-year birds of several forest-nesting species in early-successional habitats during the post-breeding period and breeding season. Our results also highlight the value of multiple survey methods. Mist-nets detected non-singing individuals of several species in early-successional habitat (Red-eyed Vireo, Acadian Flycatcher), whereas point counts detected several canopy species in mature forest that could not be effectively netted in those habitats (Northern Parula, Red-eyed Vireo).

## POST-BREEDING SEASON HABITAT USE

Our prediction that forest birds would become more abundant in early-successional habitats during the post-breeding period was true for sev-

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$P < 0.05$ . The top rows of letters in each graph are comparisons of a habitat between breeding (left) and post-breeding (right) periods. The bottom rows of letters are comparisons among habitats within a period. Capital letters compare adults (open bars); lower case letters compare hatching-year birds (hatched bars).

TABLE 2. Proportion of birds captured with mist-nets that were male (Male), in breeding condition (BC), and recaptured (Recap) in mature forest (mature upland and mature riparian forest) and early-successional forest (3- to 4-year-old upland forest and 9- to 10-year-old upland forest) in the Missouri Ozarks, 1997 and 1998.

Species		Mature forest		Early-successional forest	
		Frequency	<i>n</i>	Frequency	<i>n</i>
Red-eyed Vireo	Male	0.50	10	0.65	34
	BC	0.90	10	0.77	43
	Recap	0.00	15	0.02	53
Acadian Flycatcher	Male	—	—	—	—
	BC	—	—	—	—
	Recap	0.45	11	0.00	12
Kentucky Warbler	Male	0.60	25	0.81	26
	BC	0.89	28	1.00	25
	Recap	0.32	25	0.15	41
Ovenbird	Male	0.83	6	0.67	21
	BC	1.00	6	0.95	22
	Recap	0.22	9	0.14	29
Worm-eating Warbler	Male	0.60	5	0.44	18
	BC	1.00	5	0.77	22
	Recap	0.00	7	0.07	41

eral species and, in particular, for hatching-year birds. In contrast, adults of each of the forest-ground species (Ovenbird and Worm-eating Warbler) showed no difference in abundance between habitats during the post-breeding period. We did not expect to detect many adults of these species with point counts because songbirds vocalize very little during the post-breeding period. However, mist-netting also detected few adult forest-ground birds in any habitat at this time.

There are several explanations for low detection rates of adult forest-ground birds during the post-breeding period. First, birds may be molting, which would constrain their ability to fly (Rimmer 1988, Vega Rivera et al. 1998a) and, in turn, to encounter nets. Vega Rivera et al. (1998a) found that adult Wood Thrush hid in dense vegetation during the post-breeding period and were very difficult to observe or capture. Second, the amount of movement and foraging may be reduced because adults no longer have to provision nestlings, leading to lower capture rates. Third, adults may have left the study area altogether. Adults sometimes leave breeding territories prior to migration (Nolan 1978, Rappole and Ballard 1987); Nolan reported several cases in which Prairie Warblers (*Dendroica discolor*) left territories soon after breeding to return from unknown locations in September or October prior to migration.

Adults of both Red-eyed Vireos and Northern Parulas tended to increase in abundance in 3- to

4-year-old forest from early to late season. This increase in abundance suggests that when no longer limited by nesting requirements, these species may move to other habitats. Morse (1967) reported that Northern Parulas in Louisiana began foraging in the forest understory after their young had fledged the nest. Because Northern Parulas reside in second growth habitats during the winter (Lynch 1989), it is not surprising that they would use early-successional habitats during the post-breeding period as well.

Anders et al. (1998) found juvenile Wood Thrush used early-successional habitat during the post breeding period; juveniles used early successional habitat proportionally more than its availability in the landscape and experienced no mortalities after dispersal there (Anders et al. 1997). The high density of vegetation in early-successional habitats may provide a greater abundance of food and shelter compared to mature forest habitats (Hollifield and Dimmick 1995). Birds may move into these habitats during the post-breeding period when they are no longer limited by nesting requirements that are found only in mature forest habitats.

#### BREEDING SEASON HABITAT USE

In several cases, forest migrant songbirds were as abundant or more abundant in early-successional forest than in mature forest during the breeding season (see also Thompson et al.

1992). For example, breeding season point counts and mist-netting indicated that Ovenbirds, Worm-eating Warblers, and the forest-ground bird guild were most abundant in 9- to 10-year-old forest, with lesser numbers in mature upland forest. Other species were detected with point counts almost exclusively in mature forest during the breeding season, but were detected with mist-netting in early-successional forest as well. Red-eyed Vireos, for example, may not have been detected with point counts in early-successional habitat during the breeding season either because they are difficult to see in dense vegetation, or because they are silent when in those habitats. We detected Acadian Flycatchers singing most often in mature riparian forest, but did not detect them singing in either of the two early-successional habitats. Netting data, however, showed Acadian Flycatchers were present in early-successional habitat during the early season.

Some forest birds likely bred in early-successional forest. A forest bird likely bred in early-successional habitat if it was detected with both mist-netting and point counts (singing) in that habitat during the breeding season. Recapturing an individual bird at a particular site would also suggest a bird was territorial (breeding). For example, Ovenbirds and Worm-eating Warblers were detected by both mist-netting and point counts (singing) in 9- to 10-year-old forest, and Ovenbirds were recaptured at 9- to 10-year-old forest sites. Kentucky Warblers were detected singing and were recaptured in both early-successional habitats. We believe that Ovenbirds, Worm-eating Warblers, and Kentucky Warblers at least occasionally breed in early-successional forest, which is consistent with some other studies (Thompson and Fritzell 1990, Thompson et al. 1992). More detailed study of pairing success and nesting success among the habitats we studied is necessary to determine the quality of these habitats as breeding habitat for forest birds (Gibbs and Faaborg 1990, Morse and Robinson 1999).

Some forest birds in early-successional forest during the breeding season may be nonbreeding floaters (Brown 1969, Smith 1978). Early-successional habitats may be attractive to floaters because of the lack of conspecific breeding territories, and abundant food and dense cover (Hollifield and Dimmick 1995). Because these birds are not territorial, they do not sing (Hogs-

tad 1989), and hence would be easily missed by point counts (Brown 1969). Nonbreeding birds are most likely to be males (Brown 1969, Marra and Holmes 1997), are not always in breeding condition, and have a low chance of being recaptured because they are not territorial (Welsh 1975). Acadian Flycatchers and Red-eyed Vireos captured in early-successional habitat during the breeding season were likely floaters, although some captured during May may have been late transients (Rappole et al. 1993). Both species exhibited a low frequency of recapture in early-successional forest, had a lower frequency of breeding condition, and Red-eyed Vireos had a sex ratio biased toward males (Table 2).

Forest birds detected in early-successional forest during the breeding season also could be breeding in mature forest nearby and foraging in early-successional forest. Mature-forest breeding birds foraging in early-successional forest should show evidence of breeding condition, and may or may not show a male-biased sex ratio. Because they are central place foragers (Perrins and Birkhead 1983), they should have a greater chance of being recaptured at a particular site than a floater (Brown 1969). Worm-eating Warblers were occasionally recaptured at 3- to 4-year-old forest sites during visits 1 to 3, and did not exhibit a male-biased sex ratio during the early season. Therefore, it is possible that Worm-eating Warblers may nest in mature forest and occasionally forage in 3- to 4-year-old forest nearby, or may establish territories that overlap with both mature forest and early-successional forest.

#### CONSERVATION IMPLICATIONS

Maximizing the amount of mature forest habitat in the landscape at the expense of early-successional habitat may not always be desirable. Many Neotropical migrant songbirds typically described as forest species were present in early-successional habitats during the breeding season, post-breeding season, or both. Maximizing mature forest habitat ignores post-breeding habitat requirements, and may affect forest bird species that rely on early-successional habitat during the breeding season. Due to the very specific habitat requirements of early-successional bird species, this strategy will obviously impact them negatively as well. If increasing forest bird populations is a management goal, some mix of mature



and early-successional forest habitats may provide optimal habitat for most forest birds because it addresses both breeding season and post-breeding season habitat needs. The appropriate amount will vary depending on the extent and types of other land cover in the area, and specific conservation objectives. For example, in a fragmented agricultural landscape, increasing early-successional forest at the expense of mature forest may be detrimental because of a decrease in already limited nesting habitat and a potential increase in nest predation and parasitism rates for forest birds (Donovan et al. 1995, Thompson et al., in press). However, some early-successional habitat in a mostly forested landscape may be beneficial to forest birds because of foraging and shelter benefits without a significant effect on nest predation or parasitism rate (Thompson et al. 1996, Donovan et al. 1997).

#### ACKNOWLEDGMENTS

We thank Dan Walton and Esther Board for their assistance with field work, and John Faaborg for providing comments that greatly improved the manuscript. This research was funded by the USDA Forest Service North Central Forest Experiment Station, and is a contribution from the Missouri Cooperative Fish and Wildlife Research Unit (Biological Resources Division, U.S. Geological Survey; Missouri Department of Conservation; University of Missouri; and Wildlife Management Institute cooperating).

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