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PASSERINE BREEDING AND POST-FLEDGLING HABITAT USE IN RIPARIAN AND UPLAND TEMPERATE FORESTS OF THE AMERICAN MIDWEST

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Abstract. Riparian forests are thought to be important habitat for fledglings in a diversity of temperate-forest passerines, yet few studies have examined this hypothesis. The main objective of this study, conducted in temperate deciduous forests in Michigan's Lower Peninsula, was to compare bird use of riparian and upland forests during and after breeding. Using mist-nets, we quantified populations in accordance with the Monitoring Avian Productivity and Survivorship (MAPS) protocol. Nets were set up in both riparian and upland forests in a paired sampling design. After fledging, we captured juveniles, including those of the Ovenbird (*Seiurus aurocapilla*), at a rate higher in riparian than in upland forests. The trend for adult Ovenbirds was similar. For riparian breeders, we found no difference in capture rates over time between upland and riparian forests; these species appeared to stay in riparian forests after fledging. Our results suggest that riparian forests are important habitat for passerines during the period following fledging; they need to be considered accordingly during conservation planning.

Key words: *passerine birds*, *post-breeding dispersal*, *riparian forest*, *Ovenbird*, Seiurus aurocapilla.

Uso de Hábitat por Aves Paseriformes durante la Cría y luego de la Etapa de Volantón en Bosques Templados Ribereños y de Tierra Firme en el Medio Oeste Americano

Resumen. Los bosques ribereños han sido considerados como hábitat importante para los volantones de una diversidad de aves paseriformes de bosques templados. Sin embargo, pocos estudios han examinado esta hipótesis. El objetivo principal de este estudio, realizado en bosques deciduos templados en la Península Baja de Michigan, fue comparar el uso de hábitat de las aves de bosques ribereños y de tierra firme durante y después del período de cría. Usando redes de niebla, cuantificamos las poblaciones de acuerdo con el protocolo de Monitoreo de Productividad y Supervivencia de Aves (MAPS por sus siglas en inglés). Las redes fueron colocadas en muestras pareadas en bosques ribereños y de tierra firme. Luego del emplumamiento, la tasa de captura de los juveniles, incluyendo aquellos de *Seiurus aurocapilla*, fue mayor en el bosque ribereño que en el de tierra firme. La tendencia para los adultos de *S. aurocapilla* fue similar. Paras las aves que criaron en los sitios ribereños, no encontramos diferencias en las tasas de captura a lo largo del tiempo entre bosques de tierra firme y ribereños; estas especies parecen permanecer en los bosques ribereños luego de emplumar. Nuestros resultados sugieren que los bosques ribereños son hábitats importantes para las aves paseriformes durante el período post-emplumamiento; por ende, estos hábitats necesitan ser tenidos en cuenta a la hora de planificar para los esfuerzos de conservación.

It is well established that the condition and quality of a habitat are particularly important during the breeding season, when birds are strongly dependent on habitat-specific nesting sites to complete reproduction (Probst 1986, Brewer et al. 1991, Wiens 1992). However, recent studies are revealing that (1) post-breeding habitats may differ from breeding habitats and (2) post-breeding habitats' condition is as important as breeding habitats' condition for both juvenile and adult survivorship (Vega Rivera et al. 1999, Pagen et al. 2000, King et al. 2006).

Although a wealth of detailed information has been published on North American birds' requirements of breeding habitat, there are comparatively few data available on use of post-breeding habitat (Verner 1992, Vega Rivera et al. 1999, King et al. 2006). Recent studies indicate that after nestlings fledge, a variety of passerine species disperse into early-successional forests (Anders et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006). Furthermore, some studies suggest that this dispersal is species- or age-specific (Vega Rivera et al. 1998, 1999, Pagen et al. 2000). However, despite the importance of understanding passerines' use of the landscape after breeding, very little is known about songbirds' movement into and use of riparian forests during this time (Verner 1992, Machtans et al. 1996, Vega Rivera et al. 1998).

This study quantifies and compares the presence of passerines in upland and riparian deciduous forest during and after the breeding period. By employing a paired-samples mist-netting protocol, we tracked both adult (after hatch-year) and juvenile (hatch-year) birds over two seasons. The results of this study expand the knowledge of birds' use of habitat in the post-reproductive

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season in the North Temperate Zone and highlight the importance of riparian forests for avian conservation.

METHODS

STUDY SITES AND SAMPLING DESIGN

The study took place at the University of Michigan Biological Station, located in Emmet County in the northern part of Michigan's Lower Peninsula (45° 33′ N, 84° 40′ W). Vegetation cover consisted of temperate deciduous forest with upland habitat dominated by even-aged 100-year-old stands of aspen (*Populus grandidentata* and *P. tremuloides*), while riparian habitat had a mixture of alder (*Alnus* sp.), honeysuckle (*Lonicera* sp.), and quaking aspen (*Populus tremuloides*), in addition to a number of less common plants (Barnes and Wagner 2003, Akresh 2007). In riparian habitats, these trees and shrubs formed a relatively open upperstory with a structurally complex dense understory affording many possible opportunities for birds to hide. In July 2006, we quantified vegetation characteristics (canopy cover and species diversity) in both upland and riparian forests at three Monitoring Avian Productivity and Survivorship (MAPS) stations by standardized vegetation-survey methods (see DeSante et al. 2006). We categorized the upperstory as ≥15 m, the middle story as 5–15 m, the understory as 0.5–5 m, and ground cover ≤0.5 m (DeSante et al. 2006). We compared the means and standard errors of the two forest types.

Following the MAPS program (DeSante et al. 2006), in 2006 and 2007 we operated three MAPS stations at three 20-ha sites along 5 km of the Maple River within the University of Michigan Biological Station (Fig. 1). Each site contained adjoining upland and riparian forests. Ten 12-m mist nets were set up in each site; nets were located approximately 50–100 m apart. All sites combined, 18 nets were located in upland habitat, 12 in riparian habitat along the Maple River. The sharp transition from riparian to upland forest allowed us to assign each net to a particular forest type unambiguously. The nets' locations and capture effort remained the same throughout the study. Each day a single site was sampled, allowing upland and riparian habitats to be sampled simultaneously. Each site was resurveyed approximately every 10 days, for a total of 12 times per site between 22 June and 6 August in 2006 and between 1 June and 3 August in 2007 (DeSante et al. 2006). Captured birds were banded with a United States Geological Survey metal band. We translated capture date into ordinal date, coded as the number of the days elapsed from the beginning of the year.

Because we were particularly interested in differences between captures of adult birds and those of juveniles, we grouped birds by age class. Recaptures, unprocessed birds, woodpeckers, and passerine species for which the sample size was ≤5 were not included in the analyses.

STATISTICAL ANALYSES

To test for an increase in capture rates over time in a given forest type, we ran a generalized linear mixed model for total adults, total juveniles, adult American Redstarts (scientific names in Table 1), and adult Ovenbirds by using the "glmer" function in the "lme4" library in R, version 2.8.1 (Bates 2008, R Development Core Team 2008). Because samples of other species were small, we were able to model adults of only the American Redstart and Ovenbird. By using a mixed model we were able to account for interdependence among captures in different nets within a site as well as for repeated-measures sampling at the same net over time (Crawley 2007, Bates 2008).

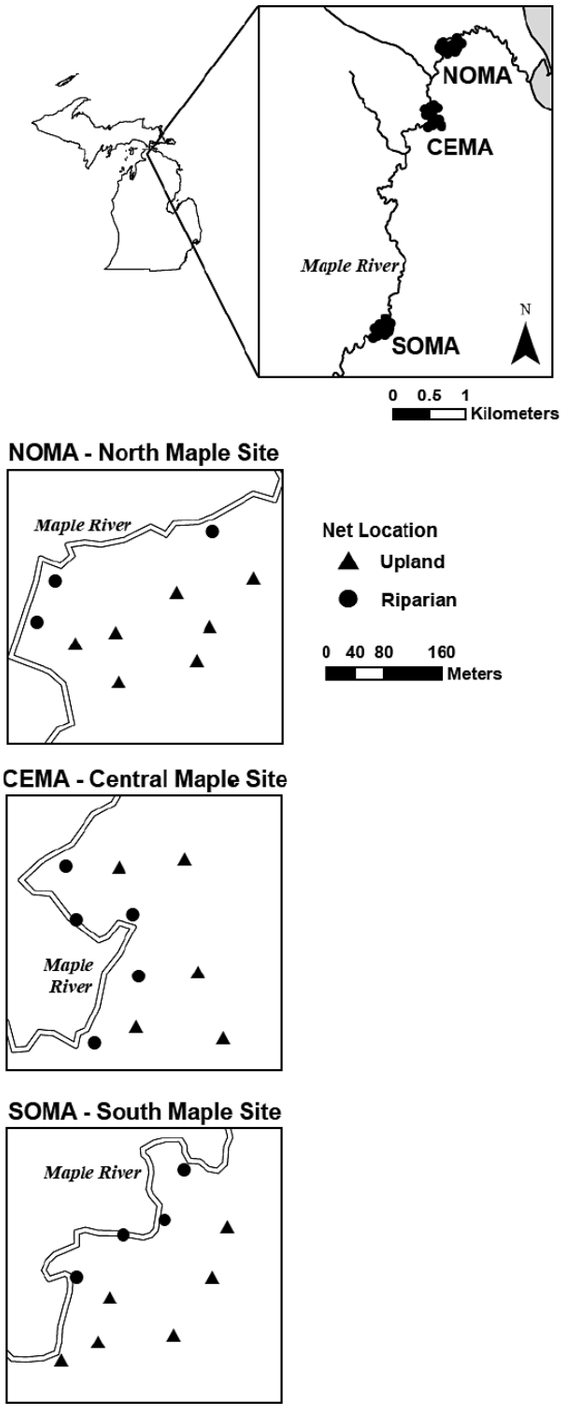


FIGURE 1. Map of the University of Michigan Biological Station site and net locations, Michigan. Nets were not classified as upland or riparian on the basis of distance to river but on vegetation at the net site.

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TABLE 1. Bird captures grouped by age class or habitat type. Total captures includes birds whose age was undetermined. For forest type, captures are standardized per 100 net-hours.

Species	Adult	Juvenile	Total	Upland	Riparian	Percentage of juveniles in riparian
American Redstart *Setophaga ruticilla*	103	35	174	4.2	15.7	89
Black-capped Chickadee *Poecile atricapillus*	34	59	108	4.2	7.4	59
Ovenbird *Seiurus aurocapilla*	68	26	102	4.6	6.0	73
Veery *Catharus fuscescens*	44	12	60	1.8	4.9	83
Song Sparrow *Melospiza melodia*	27	25	57	0.1	7.0	100
Nashville Warbler *Vermivora ruficapilla*	16	31	50	0.9	5.0	81
Common Yellowthroat *Geothlypis trichas*	25	13	41	0.2	4.9	100
Hermit Thrush *Catharus guttatus*	25	14	39	1.5	2.6	79
Cedar Waxwing *Bombycilla cedrorum*	28	3	32	0.4	3.4	100
White-throated Sparrow *Zonotrichia albicollis*	24	6	32	0.3	3.5	83
Chestnut-sided Warbler *Dendroica pensylvanica*	19	11	30	0.3	3.3	73
Red-eyed Vireo *Vireo olivaceus*	25	0	28	1.4	1.5	NA
Black-and-white Warbler *Mniotilta varia*	12	8	25	0.6	2.3	88
Rose-breasted Grosbeak *Pheucticus ludovicianus*	20	1	24	0.9	1.8	100
Mourning Warbler *Oporornis philadelphia*	16	5	21	0.1	2.5	80
American Robin *Turdus migratorius*	9	9	19	0.7	1.4	100
American Goldfinch *Spinus tristis*	17	0	17	0.1	2.0	NA
Canada Warbler *Wilsonia canadensis*	4	8	14	0.3	1.4	75
Eastern Wood-Pewee *Contopus virens*	6	7	14	0.5	1.0	100
Least Flycatcher *Empidonax minimus*	3	9	13	0.0	1.6	100
Swamp Sparrow *Melospiza georgiana*	4	7	12	0.2	1.3	71
Northern Waterthrush *Seiurus noveboracensis*	5	4	11	0.0	1.4	100
Great Crested Flycatcher *Myiarchus crinitus*	8	2	10	0.1	1.1	100
Gray Catbird *Dumetella carolinensis*	6	3	10	0.0	1.3	100
White-breasted Nuthatch *Sitta carolinensis*	4	4	10	0.6	0.4	25
Purple Finch *Carpodacus purpureus*	5	3	9	0.0	1.1	100
Red-winged Blackbird *Agelaius phoeniceus*	9	0	9	0.3	0.8	NA
Eastern Phoebe *Sayornis phoebe*	1	7	8	0.1	0.9	86
Golden-winged Warbler *Vermivora chrysoptera*	0	8	8	0.0	1.0	100
Common Grackle *Quiscalus quiscula*	7	0	7	0.3	0.5	NA
Indigo Bunting *Passerina cyanea*	5	1	6	0.2	0.5	0
Total	579	321	1000	24.4	89.3	81

Bird captures were classified as the response variable and were grouped by net and sampling date. For juveniles, we excluded data from the first eight ordinal dates, on which we did not catch a single juvenile bird, as juveniles presumably had not fledged or otherwise could not be captured in nets before 22 June. We classified net and site as random effects, with net as an effect nested within site (Crawley 2007, Bates 2008). We originally included a random effect of ordinal date on the slope of the linear regression (Crawley 2007, Bates 2008), but this random effect was not significant for all subsets modeled, and we removed it from all models. We assessed the significance of this random effect by using the ANOVA function in R (Crawley 2007). Our fixed effects were ordinal date, forest type, year, and the interaction term of ordinal date × forest type. Year was not significant for total adult birds and adult American Redstarts and was taken out of those models. For all models, we also included an "effort" offset, which took into account the number of hours a net was open on a given day (Neter et al. 1996). We fit the subset of total adults to a Poisson distribution. Because of small sample sizes for total juvenile birds and individual species, we used a binary transformation to create "presence/absence" data for these subsets and fit these data to binomial distributions. We classified significant variables in the models with $P < 0.05$.

RESULTS

We found differences between riparian and upland habitat in vegetation composition and percent vegetation cover (Table 2). Upland habitat had a more diverse upper story and greater vegetation coverage in the middle story, whereas in riparian habitat diversity and vegetation coverage in the understory layer and diversity of ground cover were greater.

We captured and included in our analyses 494 birds in 2006 and 506 birds in 2007, caught in 1979 net-hours. In 2006, 46% of birds captured were adults and 52% were juveniles. In 2007, by contrast, 69% of birds captured were adults and 12% were juveniles, though the age of 19% of the birds captured in 2007 was undetermined. We were able to identify the sex of 89% of the adult birds; 46% of these were females and 54% were males.

Despite 384 fewer net-hours in riparian forests, more birds, especially juveniles, were captured in riparian forests (71%) than in upland forests (29%) (Table 1). Although only 31 species were analyzed, 58 bird species were captured during the study, 40 in upland habitat, 55 in riparian habitat. Over the study, among the 31 species analyzed, for all except the White-breasted Nuthatch the capture rate per 100 net-hours was higher in riparian forest (Table 1).

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TABLE 2. Comparisons of canopy cover and plant diversity in riparian and upland forests at the University of Michigan Biological Station, by means and SE.

	Riparian	Upland
Upperstory canopy cover (%)	20.0 (11.5)	25.0 (13.2)
Midstory canopy cover (%)	31.7 (15.9)	53.3 (8.8)
Understory cover (%)	100 (0)	97.5 (1.4)
Upperstory diversity	2.7 (1.5)	4.7 (0.9)
Midstory diversity	5.7 (2.2)	6.8 (1.3)
Understory diversity	16.7 (1.7)	8.7 (0.9)
Ground-cover diversity	18.3 (1.7)	11.8 (0.4)

In both habitats capture rates of adults were relatively stable over time, with a slight decrease at the end of July (Fig. 2; Table 3). Capture rates of juveniles increased over time, especially in riparian forests. After young fledged, adult Ovenbirds were captured less in upland forest and more in riparian forest, while there was no apparent trend in adult American Redstarts by habitat over time. Recaptured birds were not included in the analysis, but of the 87 individuals recaptured once in a given year, 93% were adults, and 43% moved to a different forest type (Table 4).

DISCUSSION

Our study found higher abundances of birds in riparian forest, as well as increases in captures of juveniles over time in riparian

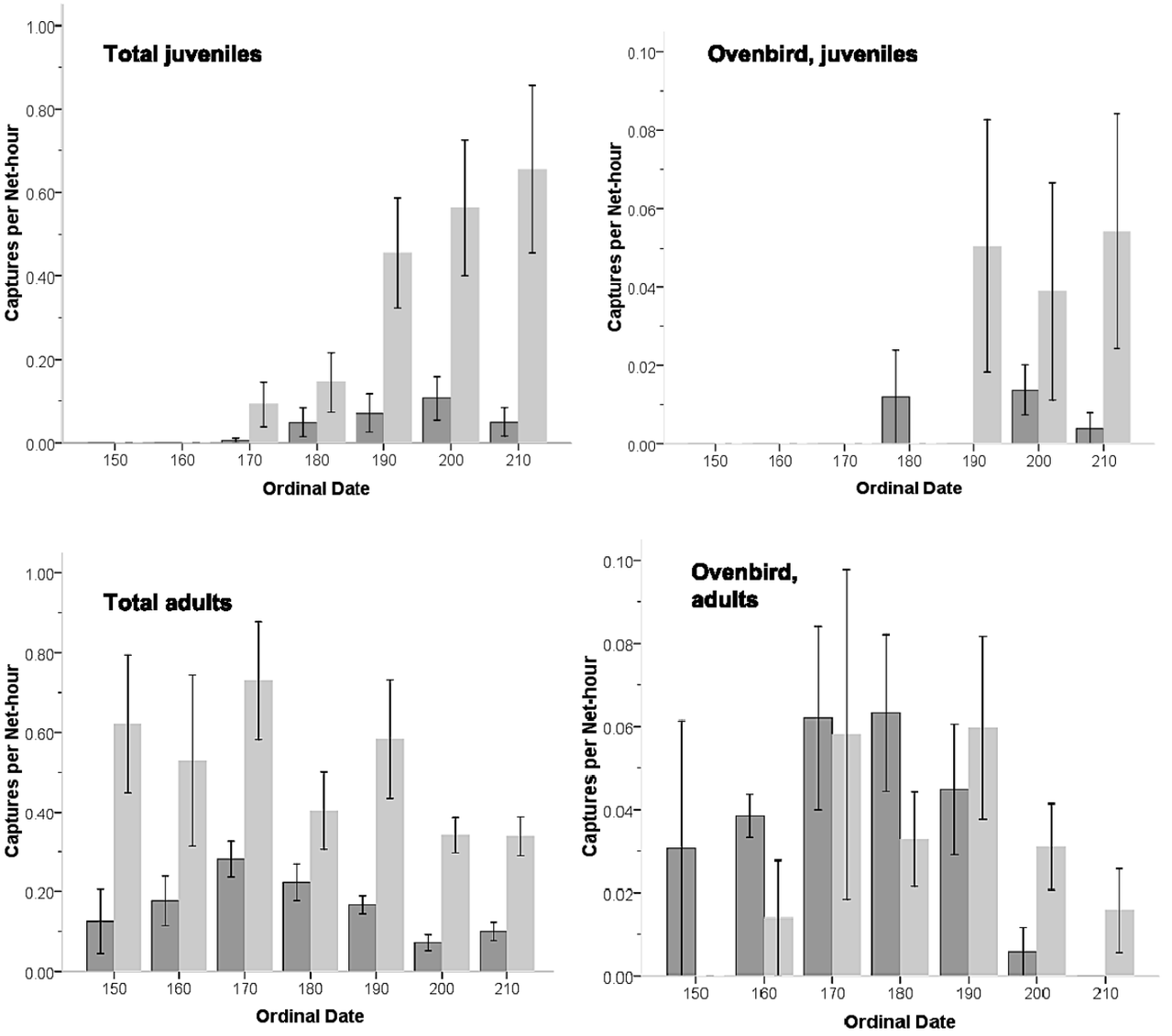


FIGURE 2. Capture rates of total adults and juveniles and adult and juvenile Ovenbirds per 10-day interval over time. Samples are captures for a given day at a site, in either riparian or upland forest, standardized per net-hour. Light gray bars represent captures in riparian forest, dark gray those in upland forest. Error bars are ±1 standard error.

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TABLE 3. Results of generalized linear mixed model for all adults, all juveniles, adult American Redstarts, and adult Ovenbirds. For adults, the number of observations is 353, for juveniles, 279.

Variable	Estimate	SE	t or z[a]	P	VE[a]	SD
All Adults						
Fixed						
Habitat	–0.088	0.88	–0.1	0.92		
Date	–0.0094	0.0028	–3.4	<0.001		
Habitat × date	–0.0052	0.0046	–1.1	0.27		
Random						
Net nested in site					0.14	0.37
Site					0.009	0.1
All Juveniles						
Fixed						
Habitat	10.7	5.2	2.1	0.04		
Date	0.09	0.02	4.6	<0.001		
Year	–1.55	0.35	–4.4	<0.001		
Habitat × date	–0.067	0.026	–2.5	0.01		
Random						
Net nested in site					0.49	0.7
Site					0.43	0.66
Adult American Redstarts						
Fixed						
Habitat	–5.88	2.96	–2	0.05		
Date	–0.0039	0.01	–0.4	0.7		
Habitat × date	0.024	0.015	1.5	0.12		
Random						
Net nested in site					0.33	0.57
Site					0.19	0.43
Adult Ovenbirds						
Fixed						
Habitat	7.67	3.21	2.4	0.02		
Date	–0.0039	0.014	–0.3	0.78		
Year	–0.96	0.35	–2.8	0.005		
Habitat × date	–0.041	0.017	–2.4	0.02		
Random						
Net nested in site					0.12	0.34
Site					0	0

[a] The t applies to the "all adults" subset; z applies to the remaining subsets.
[b] VE, variance explained by random variables.

TABLE 4. Movements of banded birds between forest types. Recaptured birds were standardized per 100 net-hours of the forest type in which the bird was recaptured. Recaptured birds captured more than once ($n = 10$) in a given year were omitted, in an attempt to exclude male "floaters."

	Upland to riparian		Riparian to upland	
Species	n	Captures standardized	n	Captures standardized
American Redstart	5	0.63	5	0.42
Ovenbird	4	0.5	3	0.25
All species	16	2.01	21	1.78

forest. We believe that this result for juveniles was due to their moving into riparian forests; however, we also present other possible explanations.

We captured a disproportionate number of juvenile birds in riparian forests. This trend included the Ovenbird, which nests in mature, interior forests with high canopy cover and not in riparian forest with low canopy cover and a shrubby, dense understory (Smith and Shugart 1987, Van Horn and Donovan 1994, Inman et al. 2002, King et al. 2006). On the basis of past studies (King et al. 2006, Vitz and Rodewald 2007) we hypothesize that Ovenbird fledglings quickly dispersed away from the nest and into protective habitats. Given the fledglings' initial poor flying abilities and predominately hopping locomotion, they were probably less likely to be captured in mist nets during the first days after fledging (Hann 1937, Vitz and Rodewald 2007). Once the fledglings became more competent fliers and were more likely to be captured in mist nets, we hypothesize that they had already moved into riparian forest.

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A high percentage of juveniles of other species were also captured in riparian forest, and we suspect that juveniles of other species that may nest in both upland and riparian forest moved into riparian forest. Among species that breed primarily in thick riparian vegetation, such as the Common Yellowthroat, Chestnut-sided Warbler, and Nashville Warbler (Richardson and Brauning 1995, Williams 1996, Guzy and Ritchison 1999), juveniles were captured primarily in riparian forest and therefore appeared to stay in riparian forest after fledgling. For unknown reasons, capture rates of juveniles were much higher in 2006. It is possible the birds of undetermined age captured in 2007 were predominantly juveniles, as these birds' capture rates also increased in riparian habitat over time (unpubl. data).

Despite relatively stable capture rates for all adults over time and no remarkable trend of movement of total recaptured adults, adults of some species may be moving into riparian forest after breeding. On the basis of a significant change in their presence over time, we suggest that adult Ovenbirds were moving into riparian forests later in the season. This is consistent with past observations of adult Ovenbirds dispersing from breeding territories in late July (Hann 1937, Pagen et al. 2000). We did not detect a similar trend for adult American Redstarts, and we are thus led to believe that adults of different species move in different patterns (Pagen et al. 2000). For riparian breeders such as the Common Yellowthroat and Chestnut-sided Warbler, our capture data suggest that adults of these species stay in riparian forest after juveniles fledge.

Despite our hypothesis that juvenile birds were moving into riparian forests, we present our results with caution, as there are possible alternative explanations. If more birds were breeding in riparian forest, or if the numbers breeding in the two forest types were equal but fledging success in riparian forest were higher, then more juvenile birds would likely be captured in riparian forest. But although we captured more total birds in riparian forests, we have no reason to believe that nesting success was higher in riparian habitats. Furthermore, only a movement of birds would explain the high number of juveniles captured in riparian forests of the Ovenbird and other species that nest primarily in upland forests (Smith and Shugart 1987, Van Horn and Donovan 1994). There is the possibility of birds being more easily captured in riparian forest because a greater proportion of the vegetation was at net level than in upland forest (Jenni et al. 1996, Remsen and Good 1996). This hypothesis would not explain the increase in captures over time, however, because the vertical distribution of vegetation did not change over the course of the project.

Since our capture rate of newly captured birds increased over time, our sites most likely were not closed with respect to immigration. Birds from outside our study sites presumably moved into the study sites in July and August (Machtans et al. 1996). As our study ended at the beginning of August, we are unsure of how long the birds stayed in riparian forests during the post-fledgling period. It is possible these forests are also being used as corridors for travel to other suitable post-breeding habitat (Machtans et al. 1996, Pagen et al. 2000).

Our results fit into a steadily improving understanding of juvenile birds' movement (Vega Rivera et al. 1998, King et al. 2006, Vitz and Rodewald 2007). Other recent studies have found that juvenile and adult passerines move from mature forest habitat toward edges, dense understory, and early-successional forests (Machtans et al. 1996, Anders et al. 1998, Pagen et al. 2000). These studies have presented two hypotheses, not mutually exclusive, that may explain the rapid dispersal of juveniles and upland adult breeders into early-successional and riverine habitats (White et al. 2005, Vitz and Rodewald 2007). The first posits that dispersal is driven by the higher availability of food resources (Rappole and Ballard 1987, Anders et al. 1998, Vitz and Rodewald 2007). Studies have found both higher fruit abundance and insect biomass in riparian forests during the summer and fall (Vega Rivera et al. 1998, Iwata et al. 2003, Mosley et al. 2006). Such protein-rich arthropod sources are of great importance for both growing juveniles and adults molting and building up fat reserves in anticipation of fall migration (Vega Rivera et al. 1998).

Alternatively, birds may be dispersing into riparian forests because of the protection from predators that these habitats afford (King et al 2006, Vitz and Rodewald 2007). Being inexperienced, fledglings are very susceptible to predation, and past research has shown juveniles' survival rates during the first 8 weeks after fledging to be very low (Anders et al. 1997, King et al. 2006). Molting adults and juveniles also suffer decreased flight mobility and are thus more susceptible to predation (Vega Rivera et al. 1999, Vitz and Rodewald 2007).

We found significantly more vegetative cover as well as higher plant diversity in the understory of riparian than in that of upland forest. Although upland forest also had high mean values for understory vegetation cover, the majority of this vegetation was bracken fern (*Pteridium aquilinum*), which provides less structural complexity than the woody vegetation found in the understory of riparian forest. Dense and structurally complex understory vegetation in riparian and early-successional forests can provide hiding places and escape routes from avian and mammalian predators (Anders et al. 1998, Vega Rivera et al. 1999, Vitz and Rodewald 2007) and can therefore increase survival rates of both fledglings and adult birds (King et al. 2006).

CONSERVATION IMPLICATIONS

This study adds to a growing body of evidence demonstrating the importance of riparian habitats for wildlife (Goforth et al. 2002, Bub et al. 2004). Although they cover only a small percentage of the landscape, riparian forests support among the most individual- and species-rich avian communities in the temperate zone with a number of taxa being restricted to such riverine vegetation (Saab 1999, Inman et al. 2002, Bub et al. 2004). In addition, continentwide studies have demonstrated the importance of riverside habitats as crucial stop-over sites for migrant birds (Lacki et al. 2004, Skagen et al. 2005).

Despite the significance of riparian forests for the preservation of biodiversity, these ecosystems currently face the intense pressures of logging, agriculture, industry, urban development, and disruption of hydrological cycles (Booth and Jackson 1997, Sweeney et al. 2004). Even small riparian forests, such as the one we studied, are used in both the breeding and post-breeding periods and thus help to play a role in the long-term persistence of avian populations (Bub et al. 2004). Many birds spend at least part of their fledging period in riparian as well as early-successional forests (Pagen et al. 2000, Vitz and Rodewald 2006); land managers need to include these habitats explicitly in their conservation and management plans.

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