

POSTFLEDGING DISPERSAL, HABITAT USE, AND HOME-RANGE SIZE OF JUVENILE WOOD THRUSHES

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ABSTRACT.—Although the availability of suitable postfledging habitat potentially is pivotal to juvenile Neotropical migratory birds, data on dispersal, habitat use, and home-range size are limited. We used radio telemetry to study the postfledging ecology of juvenile Wood Thrushes (*Hylocichla mustelina*) in the Ozark Mountains of southern Missouri. Natal home ranges were in mature oak-hickory forest, and natal home-range size ranged from 2.6 to 24.8 ha. Juveniles dispersed independently from their natal home ranges to post-dispersal ranges, with a mean dispersal direction of $185.2 \pm \text{SD of } 77.2^\circ$ and a mean distance of 2.08 ± 1.48 km. Habitats used after dispersal differed from natal habitats and included early successional oak-hickory and pine forests, mid-successional pine forest, mature riparian forest, and forest/field edges. These habitats were characterized by a dense understory and thick ground cover. Post-dispersal home-range size averaged 1.53 ha. Our data suggest that in large tracts of mature deciduous forest, a mosaic of early and mid-successional forest stands, along with mature riparian forest, will accommodate both the breeding and post-dispersal habitat requirements of Wood Thrushes and other Neotropical migratory birds. Received 21 January 1997, accepted 21 August 1997.

THE HABITAT REQUIREMENTS of Neotropical migratory birds are of increasing concern as breeding, wintering, and migration stopover habitats continue to be altered or destroyed (Martin and Finch 1995). Research on the habitat requirements of migratory birds has focused on habitats needed for successful nesting during the breeding period (Martin 1992, Donovan et al. 1995, Robinson et al. 1995) and survival during the wintering and migration periods (Conway et al. 1995, Moore et al. 1995, Petit et al. 1995, Sherry and Holmes 1996). Although these studies have examined habitats essential to the reproduction and survival of migratory birds, there remains a significant gap in our knowledge of habitat needs during the period between fledging and migration.

For juvenile migrants that are produced early in the breeding season, a period of several months may elapse between the time of fledging and arrival at coastal migratory stopover sites (Able 1972, Buskirk 1980, Anders et al. 1997). The quality of habitats available during this period potentially is critical to the survival of juveniles because they must obtain enough

food to build up fat reserves for migration and at the same time avoid predation (Moore et al. 1993). The inexperience of juveniles in foraging and avoiding predators makes the availability of suitable postfledging habitat especially important. Despite this importance of the postfledging period, data on movements, spatial-use patterns, and habitat use by juvenile passerines are limited.

Postfledging dispersal and habitat use have been studied in several species of nonmigratory birds and short-distance migrants using capture/recapture or resighting techniques (Holleback 1974, Woolfenden 1978, Dhondt 1979, Perrins 1980, Wolf et al. 1988, Sullivan 1989, Lens and Dhondt 1994, Zann and Runciman 1994). However, extensive movements of juvenile migrants from their natal areas have precluded mark/resighting studies on Neotropical migratory species. We studied the postfledging ecology of juvenile Wood Thrushes (*Hylocichla mustelina*) using radio telemetry. By tracking juveniles from the time of fledging, we obtained information on natal habitat use and home-range size, distance and direction of movements from the natal area (i.e. postfledging dispersal), and habitat use and home-range size in areas used after postfledging dispersal.

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METHODS

Study area.—Study sites were located in Carter, Reynolds, and Shannon counties in the Ozark Mountains of southern Missouri. This area contains contiguous mature and managed oak-hickory forest, with more than 80% forest cover in an area of 2 million ha (Geissman et al. 1986, Spencer et al. 1992). Most of the mature forest is even-aged as a result of extensive clearcutting during the early 1900s and is interspersed with young forest stands resulting from recent timber harvests. Nonforested land consists mainly of cattle pastures and small towns. Our study was conducted primarily on state forests. Forest management guidelines on these lands allow for the cutting of 10 to 12% of the forest each decade. Most timber harvesting is done by clearcutting, resulting in even-aged successional stands ranging in size from 1 to 8 ha (Missouri Department of Conservation 1986, Brookshire and Hauser 1993).

Study sites containing breeding territories of adult Wood Thrushes and natal areas of juveniles were located on five 400-ha sites used for the Missouri Ozark Forest Ecosystems Project (see Brookshire and Hauser 1993, Kurzejeski et al. 1993). The topography of these sites is characterized by steep, highly dissected ridges and narrow valleys. Study sites consisted primarily of mature upland forest, and dominant tree species included black oak (*Quercus velutina*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), hickory (*Carya* spp.), short-leaf pine (*Pinus echinata*), and flowering dogwood (*Cornus florida*). Study sites were expanded over the course of each season to include areas to which juveniles dispersed.

Field methods.—We placed radio transmitters on Wood Thrush nestlings on day 9, 10, or 11 of the 12-day nestling period. Fledging dates of radio-tagged nestlings ranged from 2 June to 16 July, incorporating both first and second broods of the season. Radio transmitters weighed 1.3 g and had a battery life of 35 days in 1994 and 1.6 g and a battery life of 60 days in 1995. Nestlings weighed 26 to 37 g at the time the transmitters were attached. Transmitters were attached dorsally with the antenna pointing toward the tail, and a harness of nylon elastic string was tied under each wing, leaving room for growth of the wings and pectoral muscles. All nestlings were banded with U.S. Fish and Wildlife Service numbered leg bands and two color bands.

We located radio-tagged individuals using programmable receivers and 3-element, hand-held Yagi antennas. Each individual was located daily, and locations were mapped on 7.5-minute U.S. Geological Survey topographic maps. Universal Transverse Mercator coordinates were later determined for each location. We rotated the order in which individuals were located each day, with time of location ranging from 0535 to 1925 hours CST.

Natal habitat use and home-range size.—Natal home

range was defined as the area used by a juvenile from the time of fledging through initiation of postfledging dispersal (see below). Natal habitats were identified in the field based on tree species, dbh, and canopy height. Additional information on age and size of forest stands and management techniques or natural disturbances that had affected habitat structure (e.g. clearcutting, fire) were obtained by overlaying maps of natal home ranges on Missouri Department of Conservation forest stand maps.

We determined natal home-range size using 95% minimum convex polygons (Mohr 1947) calculated by program CALHOME (Kie et al. 1994). To avoid underestimating natal home-range sizes, we omitted from analysis individuals that died on their natal ranges ($n = 24$), those for which radio transmitters apparently failed ($n = 4$), and those for which transmitters apparently fell off ($n = 4$). Thus, natal home-range size was determined only for individuals that were considered to have dispersed from the natal home range and for which we had daily locations up to the time of postfledging dispersal ($n = 15$). Because we lost radio contact with some individuals, we considered a juvenile to have dispersed if loss of radio contact occurred within two standard deviations of the mean age at which other radio-tagged individuals were known to have dispersed ($\bar{x} = 22 \pm 1.99$ days; Anders et al. 1997).

To determine whether natal home-range size was independent within broods, we calculated the coefficient of association of siblings within broods in which at least two juveniles survived to disperse (Cole 1949, White and Garrott 1990). In this analysis, a coefficient of association of 0 represents chance association, +1 indicates perfect positive association (individuals were always together), and -1 represents perfect negative association (individuals were never together; Cole 1949). Results of this analysis indicate that natal home-range size was not independent within broods, so we also calculated the mean natal home range size for each brood in which more than one juvenile was radio-tagged.

Dispersal distance and direction.—Postfledging dispersal was characterized by linear movements of individuals away from their siblings and existing home ranges to non-overlapping home ranges. After dispersal from the natal home ranges, the coefficient of association within all broods was 0. Thus, we analyzed dispersal movements of each individual separately. We measured distance and direction of dispersal from the center of the natal home range to the center of the post-dispersal home range (White and Garrott 1990). Directions of movements were analyzed using procedures for circular distributions (Zar 1996).

Post-dispersal habitat use and home-range size.—We defined arrival at a post-dispersal home range as the first point after which an individual no longer exhibited a linear, directional movement away from the

natal home range, but instead concentrated its daily movements around a central location. We identified post-dispersal habitats in which juvenile Wood Thrushes were located based on tree species composition, dbh, and canopy height. We obtained additional information from forest stand maps on age and size of the stands and management techniques or natural disturbances that had affected habitat structure.

For each juvenile Wood Thrush, we calculated the percent availability and percent use of each habitat that was available at the time of dispersal from the natal area (Allredge and Ratti 1986, White and Garrott 1990). For each individual, we defined available habitats as those occurring within a 300-m wide corridor connecting sequential daily locations, beginning with an individual's last location on its natal home range and ending with its last location on its post-dispersal home range. We assumed that dispersal movements between daily locations were in a straight line. Although the use of a 300-m wide corridor is somewhat arbitrary, we believe it is reasonable to assume that habitats within this area could have been sampled by juveniles. We identified habitats and measured habitat availability within these corridors using forest stand maps (Missouri Department of Conservation). We calculated percent use as the percentage of daily locations occurring within a specific habitat type. Post-dispersal home-range size was determined using 95% convex polygons (Mohr 1947) calculated by CALHOME (Kie et al. 1994).

RESULTS

Natal habitat use and home range size.—We radio-tagged 7 nestlings from 4 nests in 1994 and 42 nestlings from 13 nests in 1995. Of these, we followed 15 juveniles from fledging through dispersal from the natal areas (5 juveniles from 2 broods in 1994, 10 juveniles from 5 broods in 1995). All natal home ranges were in even-aged, mature oak-hickory forest characterized by dbh >20 cm and canopy heights ranging from 15 to 25 m. Stands ranged in age from 53 to 111 years.

Two different movement patterns were used by Wood Thrush family groups prior to dispersal. In five of the seven broods studied, home ranges were similar in character to territories defended by breeding males: movements were centered around the nest site, and areas within the home range were visited repeatedly up to the time of dispersal ("stationary" home ranges; Fig. 1). In the other two family groups (both in 1995), juveniles and adults moved progressively farther from the nest after

fledging ("drifting" home ranges; Fig. 2). Natal home ranges were occupied for a mean of 22.3 ± 1.99 days from the time of fledging to dispersal (Anders et al. 1997).

Natal home-range sizes were calculated based on a mean of 17 locations per individual. The mean coefficient of association of juveniles within broods on natal home ranges was 0.83, indicating that siblings remained together until the time of dispersal. Because natal home-range sizes within broods were not independent, we calculated the mean natal home-range size for each brood. Mean natal home-range size was 4.46 ha for broods with a stationary home range and 19.5 ha for broods with a drifting home range. Overall, natal home-range size ranged from 2.60 to 24.8 ha (Table 1).

Dispersal distance and direction.—We followed 12 juveniles from their natal home ranges to their post-dispersal home ranges (four juveniles from two broods in 1994, eight juveniles from five broods in 1995). In all cases, brood members dispersed separately from their natal areas. Mean dispersal distance was 2.08 ± 1.48 km (range 0.21 to 4.68 km). Dispersal generally was in a southerly direction, with a mean direction of $185.2 \pm 77.2^\circ$. On average, juveniles took four days to disperse from their natal home range to their post-dispersal home range (range 1 to 9 days). In two cases, we followed juveniles from an initial post-dispersal home range to a second post-dispersal home range (see Fig. 2). Typical dispersal movements of juveniles from natal to post-dispersal home ranges are illustrated in Figures 1 and 2.

Post-dispersal habitat use and home range size.—We identified post-dispersal habitat types and calculated home range sizes for 12 juveniles (four juveniles from two broods in 1994, eight juveniles from five broods in 1995). Habitat types used after postfledging dispersal included: (1) Early successional oak-hickory or pine forests resulting from clearcutting. These habitats were characterized by dense stands of young oaks and hickories 2 to 5 cm dbh or pines 2 to 8 cm dbh with canopy heights ranging from 3 to 5 m. Small openings in the canopy allowed for the dense growth of blackberry (*Rubus allegheniensis*) and grasses (Poaceae). (2) Mid-successional pine forest that had been burned periodically. This habitat consisted of mature trees >20 cm dbh with canopy heights from 20 to 25 m. The understory layer, consist-

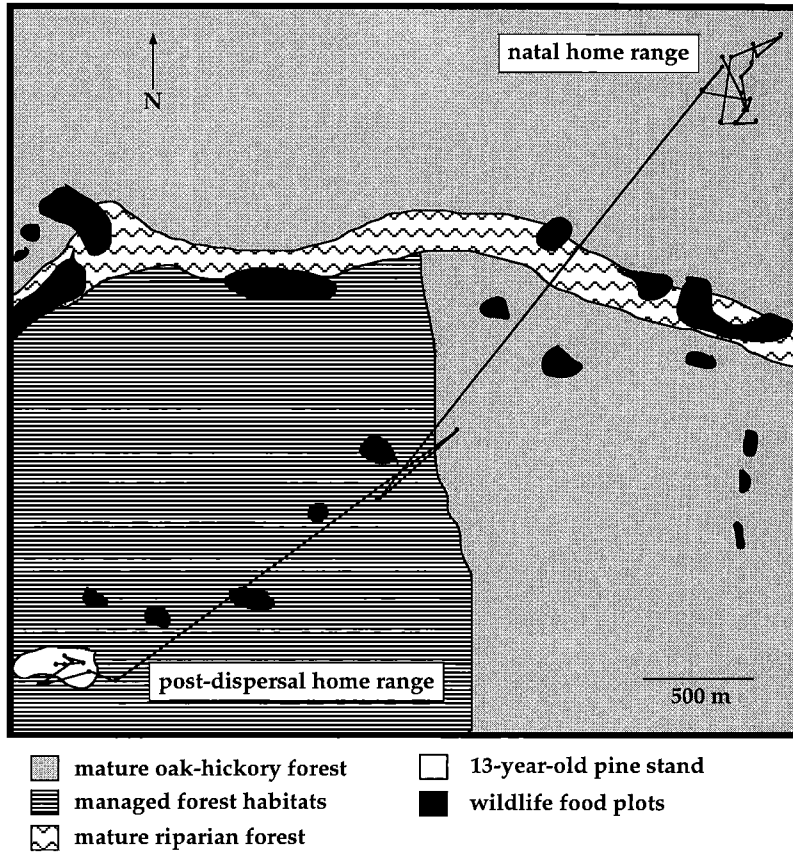


FIG. 1. Daily movements of a juvenile Wood Thrush from the time of fledging through arrival at the post-dispersal home range (juvenile 5 in Table 2). Natal home range is typical of a "stationary" home range. Each point represents a daily location, and points are connected in temporal sequence.

ing of oaks, hickories, and sassafras (*Sassafras albidum*), was dense in patches and ranged in height from 2 to 5 m. Ground cover was continuous and consisted of blackberry, poison ivy (*Toxicodendron radicans*), coralberry (*Symphoricarpos orbiculatus*), smooth sumac (*Rhus glabra*), and grape (*Vitis riparia*). (3) High-graded oak-hickory forest (forest in which most large trees had been cut for sale). This habitat contained a low density of mature trees >20 cm dbh. Canopy height was approximately 20 m but was open in large patches, allowing for the growth of a dense understory. Understory ranged in height from 3 to 4 m and consisted mainly of oaks, hickories, sassafras, blackberry, and poison ivy. (4) Mature riparian forest, which consisted primarily of sycamore (*Platanus occidentalis*) and black walnut (*Juglans nigra*) with dbh >20 cm and canopy heights ranging from 15 to

20 m. Ground cover was continuous, and a dense understory layer ranged in height from 2 to 4 m. (5) Forest/old field and forest/pasture edge. In these areas, forest edge was abrupt, with a dense canopy, understory, and ground cover. In edge habitats, juveniles always were located under the forest canopy. (6) Mature oak-hickory forest. In mature upland forest, juveniles were located in dense stands of 3 to 4 m understory trees along drainages, or in areas containing dense patches of ground cover 0.5 to 2 m high. Each juvenile that we tracked settled into one of the habitats described above, and its post-dispersal home range occurred entirely within that habitat.

We calculated percent use and availability of habitats after dispersal from the natal home range for 10 juveniles (four juveniles from two broods in 1994, six juveniles from four broods

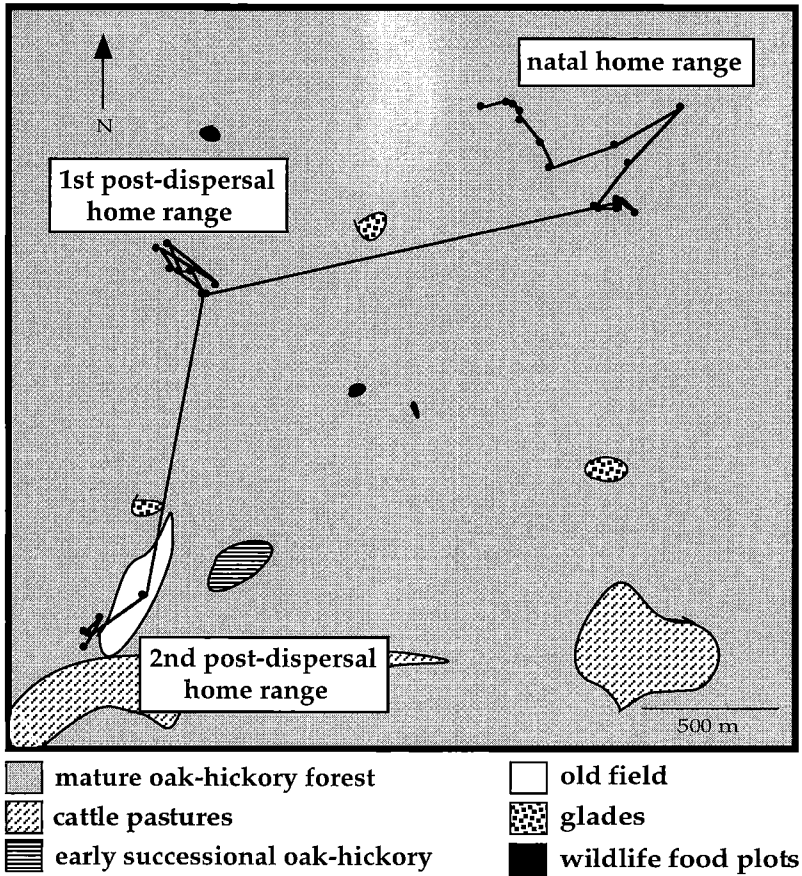


FIG. 2. Daily movements of a juvenile Wood Thrush from the time of fledging through arrival at post-dispersal home ranges (juvenile 9 in Table 2). Example shows a “drifting” natal home range and movement from an initial to a second post-dispersal range. Each point represents a daily location, and points are connected in temporal sequence.

in 1995). Two juveniles were excluded from this analysis. In one case, a juvenile dispersed through and settled into mature oak-hickory forest and did not sample other habitat types during the course of our study; in another case, a juvenile dispersed onto private land, for which necessary habitat data were not available. Calculation of percent use and availability of habitat types indicated that juveniles did not use habitats in proportion to their availability. Early successional oak-hickory and pine forests, mid-successional pine forest, high-graded oak-hickory forest, riparian forest, and forest/field edge were used proportionally more than their availability. Although two juveniles occupied post-dispersal home ranges in mature oak-hickory forest, this habitat type was used proportionally less than its availability (Table

2). Finally, we never found juvenile thrushes in old fields, pastures, glades, and wildlife food plots (“open” habitats; see Table 2).

Mean post-dispersal home-range size was 1.53 ± 1.60 ha ($\bar{x} = 9$ locations per individual), excluding the second post-dispersal ranges of two birds; home-range sizes in these second post-dispersal areas were 0.21 and 0.26 ha (Table 1). Post-dispersal home ranges were occupied for 4 to 30 days, but in some cases measurement of these periods was truncated because of transmitter failure.

DISCUSSION

During the first three weeks after fledging, juvenile Wood Thrushes remained on their natal home ranges in adult breeding habitat.

TABLE 1. Estimates of home-range size of juvenile Wood Thrushes in southern Missouri, 1994 and 1995. "Stationary" and "drifting" refer to two types of movement patterns exhibited by broods on their natal home ranges. After occupying an initial post-dispersal home range, two individuals moved to second post-dispersal ranges.

Movement pattern/home range	Area (ha)	
	$\bar{x} \pm SD$	Median (range)
	Natal	
Stationary ($n = 5$ broods)	4.46 \pm 1.62	5.28 (2.60–5.95)
Drifting ($n = 2$ broods)	19.50 \pm 7.44	19.50 (14.2–24.8)
Overall ($n = 7$ broods)	8.76 \pm 8.05	5.67 (2.60–24.8)
	Post-dispersal	
First ($n = 12$ individuals)	1.53 \pm 1.60	1.03 (0.06–5.63)
Second ($n = 2$ individuals)	0.24 \pm 0.04	0.24 (0.21–0.26)

Three weeks after fledging, they dispersed independently from their natal areas, moving an average of 2 km in a southerly direction. Most juveniles moved out of mature oak-hickory forest and settled into dense early and mid-successional forest (i.e. clearcuts), riparian forest, and forest/field edges. They remained on distinct home ranges in these habitats for up to four weeks (Figs. 1, 2).

Breeding territories of adult Wood Thrushes range in size from 0.08 to 2.8 ha (Roth et al. 1996), but radio-tracking of juveniles indicates that family groups use 2.6 to 24.8 ha before leaving the natal area (Table 1). If the use of such extensive areas by postfledging family groups is typical of other populations of migratory birds, then our understanding of the area required for the production of young by such species needs to be reassessed. To date, minimum-area requirements for most of these

species have been based only on the area required for pairing and nesting (Gibbs and Faaborg 1990, Porneluzi et al. 1993, Villard et al. 1993, Hoover et al. 1995).

On average, juvenile Wood Thrushes dispersed from their natal home ranges 22.3 days after fledging (Anders et al. 1997). Initial dispersal distances ranged from 0.21 to 4.68 km and were likely to be associated with the availability of appropriate post-dispersal habitats in which to settle. Although some juveniles moved only several hundred meters from their natal to post-dispersal areas, others moved several kilometers in order to find suitable post-dispersal habitats. Although it is possible that the radio transmitters affected dispersal movements, we observed no direct effects of the transmitters on flight ability.

The habitat types used by juvenile Wood Thrushes after postfledging dispersal differed

TABLE 2. Percent use and availability of post-dispersal habitats by juvenile Wood Thrushes. "Open" habitats include old fields, pastures, glades, and wildlife food plots.

Juvenile no.	Habitat type (% use/% availability)							
	Early successional oak-hickory or pine	Mid-successional pine	High-graded oak-hickory	Mature riparian	Forest/field edge	Mature oak-hickory	Open	
1	100/14.7					0.0/80.8	0.4/4.5	
2	92.3/48.6			7.7/10.4		0.0/41.0		
3	90.9/8.7			0.0/2.6		9.1/87.8	0.0/0.9	
4	81.5/3.6				3.7/0.6	14.8/94.2	0.0/1.6	
5	70.0/22.0			0.0/2.9	0.0/0.5	30.0/70.0	0.0/4.5	
6		75.0/11.0				25.0/89.0		
7			93.7/3.3			6.3/94.9	0.0/1.8	
8				85.7/17.3		14.3/79.8	0.0/2.9	
9					44.4/0.5	55.6/89.6	0.0/9.9	
10		16.7/11.0				83.3/89.0		

in most cases from the natal and adult breeding habitats. In our study, all natal home ranges were located in mature oak-hickory forest, and this habitat type was by far the most abundant available to juveniles after initiation of dispersal (Table 2). Despite the availability of mature upland forest, juveniles primarily used early and mid-successional oak-hickory and pine stands, mature riparian forest, and forest/field edges during the post-dispersal period (Table 2). Although it is possible that juvenile Wood Thrushes were excluded from mature forest by adult birds, we witnessed no encounters between adults and juveniles after dispersal from the natal areas. Furthermore, Wood Thrush densities are relatively low in southern Missouri, with the majority of mature forest being uninhabited by this species (Missouri Department of Conservation unpubl. data, A. Anders pers obs.). Thus, it is unlikely that juveniles were using other habitat types simply because they were excluded from mature forest by adults. We did not attempt to recapture juveniles to assess body condition in post-dispersal habitats; however, we had no mortalities of study individuals in any of the habitats (Anders et al. 1997). Consequently, we had no evidence that the post-dispersal habitats used by juveniles were suboptimal.

The composition of post-dispersal habitats varied to some extent, but structural features common to all of the habitats used were a dense understory and thick ground cover. In the early successional oak-hickory stands, regenerating oaks and hickories created a dense layer of cover, and stands of blackberry, poison ivy, sumac, grape, and young saplings created thick cover in the pine stands, mature riparian forest, and forest/field edges. Even the areas of mature oak-hickory forest used by thrushes contained understory or ground cover that was denser than in other areas of the forest due to gaps in the canopy or mesic conditions. In all of these habitat types, juveniles were located consistently on or near the ground within dense vegetative cover.

Two main threats to the survival of juvenile birds during the post-dispersal period are predation and food shortage. Dense vegetative cover may reduce the risk of predation, particularly by raptors. Cooper's Hawks (*Accipiter cooperii*) and Broad-winged Hawks (*Buteo platypterus*) depredated at least three of our 49

study individuals on their natal home ranges (Anders et al. 1997), and these species also may pose a predation threat during the post-dispersal period. It is unlikely that even these relatively small raptors could maneuver within most of the post-dispersal habitat types used by juvenile thrushes. In addition to providing protective cover, post-dispersal habitats used by juveniles may provide more abundant food resources than do areas of mature upland forest. Insect abundance may be higher in early and mid-successional forests and wooded riparian habitats because of increased vegetation density (J. Weaver pers. comm.). In addition, we observed several juveniles foraging extensively on blackberries during the post-dispersal period. The abundance of blackberries in early and mid-successional pine stands, forest/field edges, and wooded riparian habitats may attract juvenile birds to these areas.

Although we did not radio-track other species, we observed several other forest-breeding migrants in the early successional forests and riparian habitats in which we located juvenile Wood Thrushes. We observed several juvenile Red-eyed Vireos (*Vireo olivaceus*) in these habitats in addition to Ovenbirds (*Seiurus aurocapillus*), Worm-eating Warblers (*Helmitheros vermivorus*), Kentucky Warblers (*Oporornis formosus*), and Black-and-white Warblers (*Mniotilta varia*) of unknown age. Moreover, we have captured adults and juveniles of each of these species in young stands of oak-hickory and pine at the end of the breeding season. In Illinois, S. Robinson (pers. comm.) has captured Ovenbirds, Worm-eating Warblers, and Kentucky Warblers, some of which had been banded in mature forest, in group-selection cuts at the end of the breeding season. In addition, adult and juvenile Hooded Warblers (*Wilsonia citrina*) have been observed using dense riparian habitats, blackberry patches, and dense vegetation along the forest edge during the postbreeding period in Pennsylvania (Morton 1990, Evans Ogden and Stutchbury 1997). Although it is possible that juveniles of some of these species fledged from nests in early successional or riparian habitats (e.g. Kentucky Warblers; Thompson and Fritzell 1990, Kilgo et al. 1996), the presence of exclusively forest-breeding species, as well as the high densities of individuals in these areas, indicate that forest-breeding migrants other than Wood Thrushes are using

early successional, riparian, and edge habitats during the post-dispersal period.

Open habitats such as old fields, cattle pastures, glades, and wildlife food plots were not used by juvenile Wood Thrushes after dispersal from their natal areas (Table 2). Each of these habitats lacked the dense woody cover typical of habitats used by juveniles. However, several juveniles apparently moved across wildlife food plots and cattle pastures during the course of their dispersal movements, and two individuals settled in forest/field edges during the post-dispersal period. Wildlife food plots and cattle pastures in this area are relatively small and make up a small percentage of the habitat available to juvenile birds; however, larger openings of this type may affect juvenile dispersal in highly fragmented forests (see Lens and Dhondt 1994).

Data on post-dispersal habitat use by juvenile migrants indicate that the presence of early and mid-successional forest stands, mature riparian forest, and forest/field edge may be important to the post-dispersal habitat requirements of these birds. Forest management practices, as well as natural disturbances such as fire and wind, have the potential to increase the availability of early successional forest and forest edge habitats. However, increases in these habitat types occur only at the expense of forest-interior breeding habitat (Paton 1994, Thompson et al. 1995, Donovan et al. 1997). Management decisions concerning the post-dispersal habitats of migrants should take into account the tradeoffs between creating early successional habitats and reducing forest breeding habitat. Our results suggest that in large tracts of mature deciduous forest, a mosaic of early and mid-successional forest stands, along with the protection of mature riparian forest, may accommodate both the breeding and post-dispersal habitat requirements of Wood Thrushes and other Neotropical migratory birds.

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