

WOOD THRUSH POSTFLEDGING MOVEMENTS AND HABITAT USE IN NORTHERN VIRGINIA¹

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Abstract. We monitored 42 radio-tagged, fledgling Wood Thrushes (*Hylocichla mustelina*) to investigate movement and habitat use during the postfledging period. Fledglings' mean (\pm SE) age at dispersal from the natal sites was 32.5 ± 0.6 days post hatching. First dispersal sites were located 1.5 ± 0.3 km from the natal site. All young joined flocks of juveniles, except three birds that remained solitary. Sixteen birds stayed at the first dispersal site until departure on migration, whereas nine visited additional dispersal sites. On 40 occasions, 15 fledglings moved up to 6 km from their dispersal sites. Before late August, 96.7% of fledglings' locations occurred in: (1) second growth scrub/deciduous sapling sites located along forest borders and abandoned farms (59.4%), (2) gypsy moth (*Lymantria dispar*) damaged deciduous forest (24.4%), and (3) Virginia pine (*Pinus virginianus*) forest with heavy deciduous understory (12.8%). Fruiting trees and shrubs used as food sources by juveniles fruit earlier in these habitats. After late August, an increased number of fledgling locations (14.1%) occurred in mature deciduous or mixed forest, possibly tracking the later fruiting cycles of understory plants in these habitats. Twenty-four of 33 fledglings left the study area in September. Mean age at departure was 81 ± 5 days post hatching. We suggest that postfledging movements in Wood Thrushes are keyed by the availability of food resources and the presence of conspecifics, although other factors may play a role. We conclude that successful conservation of migratory species requires protection of habitats used during the postfledging period as well as those used during the nesting portion of the life cycle.

Key words: fledgling dispersal, Wood Thrushes, *Hylocichla mustelina*, habitat use, juvenile movements, radiotelemetry.

INTRODUCTION

We define the postfledging period in migratory birds as the time between independence from the parents until departure on migration. This period, which can be as long as two months in some species, is regarded as the least known and understood portion of the avian life cycle (Pärt 1990, Morton 1991, Baker 1993). The scarcity of information is due mainly to the difficulties of observing the young after they become independent; a time during which they may move

considerable distances from their natal site (Nolan 1978, Haas 1995). Because of the lack of data, the ecological and conservation importance of the postfledging period is unknown. We know that the young must find food and avoid predators while undergoing the prebasic molt, but for most species we do not know what shifts in social relationships or habitat needs occur as a result of these requirements. High mobility and mortality rates are considered characteristic of the postfledging phase (Baker 1993), and some authors have assumed that once the young disappear from the natal site they begin a slow southward, migratory movement (Hann 1937, Bent 1953, Pulich 1976). Others have reported that the young stay in the general vicinity of where they were hatched, but may move into different habitats (Nolan 1978, Rappole and Bal-

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lard 1987, Bocetti 1993). For the Wood Thrush (*Hylocichla mustelina*), the only information available is that of Powell et al. (1995, in Roth et al. 1996). They reported that after independence from the parents, fledglings dispersed and settled in places located 1–6.4 km from natal areas where they remained until migration.

In this study, we used radiotelemetry to document the patterns and distance of postfledging movements in Wood Thrushes and to determine differences between natal and dispersal sites. We use these data to assess the validity of various hypotheses on the significance of postfledging dispersal, and discuss the implications of these findings for the conservation of the Wood Thrush.

METHODS

The study area was located on the 243 km² U.S. Marine Corps Base at Quantico (MCBQ), Virginia, 56 km southwest of Washington, D.C. on the eastern edge of the Piedmont Plateau physiographic region along the west bank of the Potomac River. The most common forest cover types include American beech (*Fagus grandifolia*)-yellow poplar (*Liriodendron tulipifera*)-oak (*Quercus* spp.) (47.3%), Virginia pine (*Pinus virginianus*) (16.4%), and Virginia pine-oak (15.2%). MCBQ forests are contiguous with extensive woodlands of the adjacent Prince William Forest Park, providing a combined forest coverage of nearly 324 km². Within the forested area, however, forestry practices and damage by gypsy moths (*Lymantria dispar*) have resulted in a diversity of canopy closure and seral stages, with dense understory shrub layers occurring at openings. The MCBQ has been mapped into a geographic information system (GIS) using the program ArcInfo (Environmental Systems Research Institute, Inc., Redlands, California) with coverages including contours, roads, water bodies, and habitat types.

We captured Wood Thrush juveniles during the nesting period by locating active nests, and during the postfledging period by mist-netting. The work was conducted over three field seasons, May–October, 1993–1995. Active nests were found primarily by radio tracking tagged adults. Once a nest was located, contents were checked using a mirror attached to a pole. Thereafter, visits to the nest site were minimized. To monitor nesting stage, we observed female and male behavior using binoculars.

RADIO ATTACHMENT AND RADIO TRACKING

We attached transmitters to nestlings using a backpack harness (Rappole and Tipton 1991), two or three days before normal age of fledging. Transmitter packages weighed approximately 2.1 g (Model BD-2G, Holohil Systems Ltd., Ottawa, Canada), comprising 5–6% of the nestling's body weight when attached. They had an average life of > 120 days, and could be detected at distances of 400–1,000 m on the ground, and 1–3 km from the air. As reported in similar studies (Neudorf and Pitcher 1997), we detected no effect on behavior of radio-tagged birds as compared with those without transmitters. Radio-tagged fledglings were located on foot every other day using a hand-held 12-channel receiver and 4-element Yagi antenna. We pinpointed locations by approaching each bird until it moved (signal changed). The coordinates of each location were obtained using a global positioning system (GPS) (Pathfinder Pro, Trimble Navigation Ltd., Sunnyvale, California). A minimum of 100 fixes were obtained for each location, which were differentially corrected and averaged using PFINDER software, and entered as a coverage into the MCBQ GIS.

Birds often moved in apparent response to an observer's approach to within 50 m, but we made every effort to record the first location at which an individual was detected. Once a fledgling was located visually, we recorded type of activity (perching or foraging), substrate (ground, shrub, tree), and whether it was alone or with conspecifics. When possible, we made continuous notes on the bird's behavior for up to 30 min after location. When a fledgling's signal could not be found at its previous location, we searched first by driving along roads. If the signal was not found after four days, we performed an aerial search at 350–500 m above ground level from a Cessna 172 equipped with two, wing-mounted 4-element antennas. We assumed that a bird had left the study area if an aerial search covering a circle 7 km in radius centered on the bird's last known location failed to locate its signal. Signals lost during any part of the year were monitored during all subsequent flights.

Transmitter failure also is a cause of signal loss. However, our experience with these transmitters did not indicate that transmitter failure was a likely cause. Thirty of the transmitters

were recovered still functioning after they had fallen off, or their bearers had been killed by predators.

INDICES OF ACTIVITY AND AREA USED

Three parameters were used as indices of bird activity for a given site and time interval, where a "site" is defined as the area occupied by a bird over a specified time period. These parameters were as follows: (1) size of the area that included all radio locations (AREA), (2) average distance between consecutive point locations (MOBILITY), and (3) average distance from the arithmetic center of the home range to every location (FCEN). The area, boundaries, and arithmetic center of a given site were calculated by the minimum convex polygon method using all radio locations obtained during the interval of interest (minimum of five days) (HOME RANGE, Ackerman et al. 1990). Sequential observations of a bird's positions can be considered independent if the observations are separated by sufficient time for the animal to move between any two points in the area (White and Garrott 1990), a condition satisfied for our data by using locations separated by a minimum of 24 hr.

We define dispersal distance as the distance between the arithmetic centers of the natal and first dispersal sites. Distance between two dispersal sites was calculated as the distance between the arithmetic centers of each site, based on home range calculations. In reality, birds can move long, linear distances without establishing new home ranges, and some Wood Thrushes probably do behave in this way. However, our experience has shown that the majority of birds move a distance from the natal site and then settle for a period of days or weeks at a new site, which may be subsequently changed for a third or even fourth site. To measure this phenomenon requires making certain assumptions about space and time. For this study, the space/time assumptions used to decide when a bird had moved from one site to another were based on our experience with their movement patterns. Thus, we assumed that a dispersal site was distinct if it was a minimum of 300 m from a previous site and the bird stayed for more than five days.

We used the number of days after hatching as an age parameter for timing of individual events. According to our observation and reports in the literature (Roth et al. 1996 and citations therein),

in Wood Thrushes, average incubation time is 13 days, and time from hatching to fledging is 12–15 days. We regarded fledged individuals as independent from their parents when we did not note any relation between parents and fledgling, such as feeding of the young, flying together, alarm behavior from parents during our observations, or when fledglings dispersed by themselves from the natal area.

VEGETATION SAMPLING

We characterized the structure and composition of vegetation at natal and dispersal sites by sampling three to five circular plots, 22.5 m in diameter (0.04 ha) centered on randomly-selected radio locations within each site (James and Shurgart 1970). The vegetation data from a given site were used only once, regardless of the number of fledglings using the site. To characterize the structure and composition of a particular site, the data from all sample plots were pooled. For each plot, 44 vegetation variables were measured directly in the field or derived from field measurements. Correlations between these variables were calculated (using both Pearson and Spearman rank correlation coefficients because of non-normal distribution), and within each pair or group of correlated variables ($r \geq 0.7$) only one member of a pair and one or two members of a group were retained for subsequent analysis. The criteria for retention were ease of ecological interpretation and precision of measurement. This procedure resulted in a set of 12 variables for analysis. A listing and descriptions of all 44 variables are given in Vega Rivera (1997).

To detect temporal trends in habitat use during the postfledging period, we also performed an analysis of habitat occupancy. Each natal and dispersal site occupied by a fledgling was associated with one of four habitat categories using the program ArcView (Environmental Systems Research Institute, Inc., Redlands, California). The habitat categories were as follows: (1) second growth scrub/deciduous sapling sites located along forest borders and abandoned farms, (2) mature (> 70 years old) deciduous forest damaged by gypsy moth, (3) mature mixed forest, and (4) mature pine forest.

LANDSCAPE ANALYSIS

From the arithmetic center of a given natal or dispersal site, we calculated the distance to the nearest locations of the following: (1) mature

(diameter at breast height, dbh > 38 cm) deciduous or deciduous/pine forest, (2) creek, (3) road (< 10% canopy cover), and (4) opening (> 0.4 ha). In addition, we generated a circle with a radius of 300 m around the arithmetic center. Within each circle, we then measured the total distance covered by roads and creeks.

STATISTICAL ANALYSIS

The distribution of each variable was evaluated for normality by examining for skewness or kurtosis graphically, and using the Shapiro-Wilk test (SAS Institute 1988). Because of the lack of normality for most variables, nonparametric tests were preferred. The first step in comparing natal and dispersal site habitat characteristics was to screen variables by making univariate comparisons (Wilcoxon two-sample test). Application of univariate models when several variables affect a response can lead to spurious results (Block and Brennan 1993), therefore, between-group differences were tested also for each variable simultaneously using Multiresponse Permutation Procedures tests (MRPP, Mielke and Berry 1982). This method tests whether two sets of locations come from a common probability density distribution. In this test we included variables that were significant ($P < 0.1$) in the univariate tests. The program BLOSSOM (Slauson et al. 1991) was used to perform the tests. In all statistical tests a probability of 0.1 or less was accepted as significant, but we report actual P values for descriptive purposes. Means are given as mean \pm standard error. Although 42 fledglings were radio-tagged during the study, sample sizes vary as birds were lost to migration, predation, or because the transmitters fell off the birds.

RESULTS

Sixty-five Wood Thrush juveniles were captured and banded, 42 of which were radio-tagged over the course of this study. Of these, 29 from 18 separate broods were tagged as nestlings or within one or two days of fledging. The remaining 13 were tagged after achieving independence. The natal sites and age are not known for these 13 birds. None of the 65 birds captured was recaptured or resighted in subsequent years.

MOVEMENTS TO AND WITHIN DISPERSAL SITES

Of 29 fledglings from known nests, 23 survived to independence. Of these, 2 stayed on their na-

tal site and 21 dispersed. Independence from parents occurred at 32.5 ± 0.6 days ($n = 18$) after hatching. There was no trend for fledglings hatched later in the season to become independent at a younger age ($r = 0.15$, $P > 0.5$). Based on movements of the young in three broods, the movement patterns of siblings from the natal site were apparently independent of each other. Distance between siblings' locations for any given day was > 300 m. Only in one instance did two siblings visit the same site, but they occupied the site on different days, indicating that their movements were independent.

On average, the first dispersal site was located 1.5 ± 0.3 km from the natal site (range 0.3–5.3 km, $n = 18$). However, the initial dispersal for three birds whose signals were lost was likely beyond the boundaries of the study area (> 7 km). There was no significant correlation between distance from natal site to initial dispersal site and date of dispersal ($r = 0.17$, $P > 0.4$), nor was there a significant trend in direction of dispersal from the natal site (Rayleigh's Z-test, $Z = 1.51$, $P > 0.2$). Eleven fledglings apparently moved in a single day from the natal area to their initial dispersal site. Six fledglings, however, were observed stopping at two to five locations for various amounts of time before arriving at their initial dispersal site. Movements from natal to dispersal sites are shown for three individuals from separate broods in Figure 1.

After dispersal, all young joined flocks of juveniles, except three birds that remained solitary. The association of an individual with a group was temporary, and thus the composition and size of the group were variable. For most of the postfledging period, the number of observed agonistic interactions was minimal. However, by late August and September, interactions among juveniles, such as calls and chases were common. On 20 occasions that involved 10 of our radio-tagged juveniles, we observed birds chasing each other.

Of 15 radio-tagged fledglings of known nests that survived until migration, 10 individuals (67%) used a single dispersal site; 3 individuals (20%) used two separate dispersal sites; and 2 individuals used three and four dispersal sites, respectively. Of 10 radio-tagged fledglings from unknown nests, 6 individuals used a single dispersal site (assuming that they were initially captured on their first dispersal site); 3 individuals used two separate dispersal sites; and 1 individ-

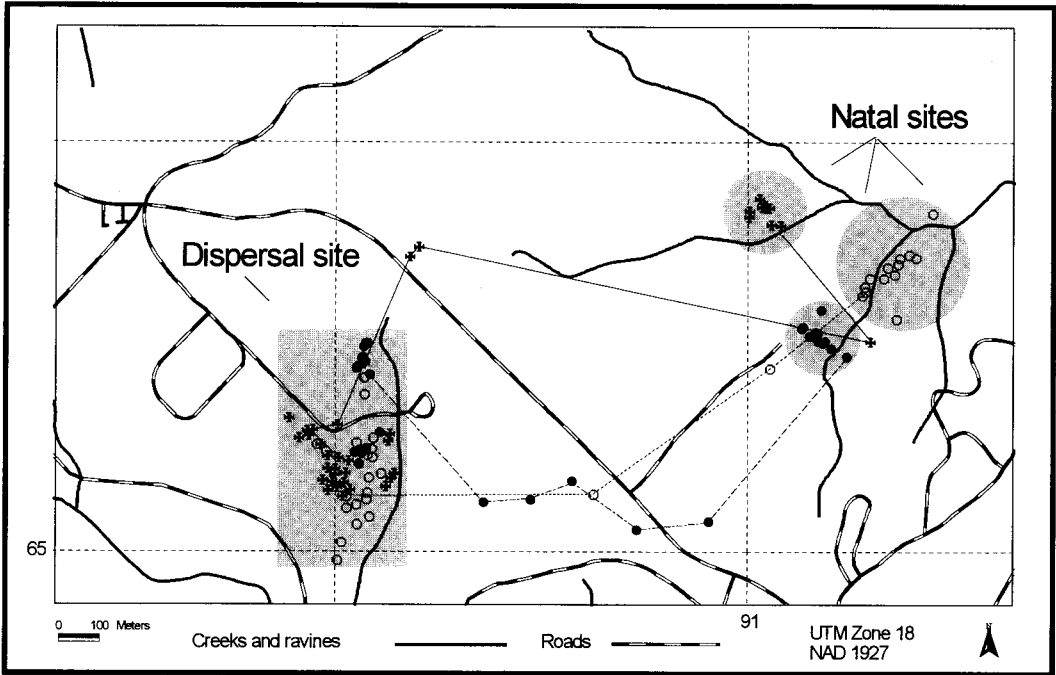


FIGURE 1. Radio locations of Wood Thrush HY512 (1994, open circles), HY533 (1994, solid circles), and HY617 (1995, crosses) during the postfledging period, MCBQ, Virginia, 1994–1995.

ual used three dispersal sites. Combining all 25 fledglings, mean distance between consecutive dispersal sites was 1.5 ± 0.2 km. Within a given dispersal site, fledglings moved an average distance between consecutive locations of 101 ± 11 m ($n = 32$), and used an area of 2.8 ± 0.5 ha ($n = 32$). Young that hatched earlier in the season did not show higher mobility ($r = 0.14$, $P > 0.4$), or use a larger area ($r = 0.14$, $P > 0.4$).

During their stay at a given dispersal site, 15 of 28 individuals (53%) (from known and unknown nests) performed exploratory movements. An exploratory movement consisted of a movement > 300 m from the dispersal site and subsequent return. We determined the location for 11 of 40 known movements, which were located a mean distance of 1.7 ± 0.5 km (range 0.4–6.5 km) from the arithmetic center of the dispersal site and lasted < 3 days. In 29 instances, the bird was known to have left the dispersal site, but we were unable to find the signal until it returned.

DEPARTURE FROM THE STUDY AREA

The average number of days post-hatching at which fledglings disappeared from the study

area was 81 ± 5 days ($n = 15$). Most fledglings departed between late August to early October, with 47% leaving in September. Fledglings that hatched later in the season left at a younger age ($r = 0.71$, $P = 0.002$). Of the 25 individuals tracked until departure, 10 were observed making long movements to new locations within 3–7 days prior to leaving the MCBQ (average 1.8 ± 0.2 km, range 0.6–3.2 km) where they stayed for one to four days before they disappeared. Five birds that had been using well-defined dispersal sites for some time disappeared for one to three days, came back to their dispersal site for a day, and then disappeared. Three birds that had been occupying a second dispersal site moved to their initial dispersal site, and then disappeared. Eight birds demonstrated patterns of increased, short-distance changes in location two to three weeks before departure. Over the course of several days, they moved constantly over distances > 300 m, making it difficult to define their position. Often the radio signal for these individuals was lost only to reappear minutes later. This type of behavior was not observed in all of the birds. Six birds disappeared after never having moved from their initial dispersal site.

TABLE 1. Comparison of vegetation attributes between "natal" (N; $n = 17$) and "dispersal" (D; $n = 23$) sites for radio-tagged Wood Thrush fledglings, MCBQ, Virginia, 1993–1995.

Variable	Site	$\bar{x} \pm SE$	Z^a	P
Trees per ha (≥ 3 cm dbh)	N	1,320 \pm 88	-2.28	0.02
	D	1,768 \pm 172		
Deciduous trees per ha (≥ 3 cm dbh)	N	1,170 \pm 59	-1.84	0.06
	D	1,471 \pm 162		
Virginia pine trees per ha (≥ 3 cm dbh)	N	66 \pm 29	-2.82	0.005
	D	176 \pm 33		
Dead trees per ha (≥ 3 cm dbh)	N	85 \pm 8	-1.45	0.14
	D	121 \pm 15		
Trees per ha (3–15 cm dbh)	N	1,000 \pm 68	-2.62	<0.01
	D	1,472 \pm 177		
Trees per ha (16–38 cm dbh)	N	275 \pm 22	0.52	>0.5
	D	255 \pm 23		
Trees per ha (> 38 cm dbh)	N	57 \pm 7	1.82	0.07
	D	40 \pm 7		
Tree basal area ($m^2 ha^{-1}$)	N	2,621 \pm 105	1.26	>0.2
	D	2,462 \pm 108		
% vegetation cover understory (0–3 m)	N	15 \pm 1	-1.45	>0.2
	D	18 \pm 1		
% vegetation cover midstory (4–10 m)	N	66 \pm 2	-0.79	>0.4
	D	68 \pm 1		
% vegetation cover canopy (> 10 m)	N	55 \pm 2	2.69	0.007
	D	42 \pm 4		
Woody stems per ha (< 3 cm dbh)	N	3,782 \pm 496	-2.62	0.008
	D	7,159 \pm 999		

^a Wilcoxon two-sample test (normal approximation with continuity correction of 0.5).

Considering the entire sample, there did not appear to be a trend of increasing mobility late in the season either within a dispersal site ($r = 0.04$, $P > 0.4$, $n = 391$) or between dispersal sites ($r = 0.12$, $P > 0.2$, $n = 113$), although there was a relationship when movements within and between dispersal sites were combined ($r = 0.12$, $P = 0.002$).

Similar timing for departure on migration occurred for some individuals that were occupying the same dispersal sites. Between 8 and 18 September 1994, five fledglings located at the same second growth dispersal site disappeared. Similarly, seven fledglings using the same dispersal site disappeared between 12 and 22 September 1995.

FLEDGLING SURVIVAL

Three of 20 fledglings from known nests that survived to independence and dispersed within the MCBQ were depredated within the first 10 days after dispersal, but only 1 of 13 fledglings radio-tagged after independence was found dead. Two fledglings were depredated presumably by Red-shouldered Hawks (*Buteo lineatus*), as their transmitters were found within 50 m of

an active nest. Their last previous locations were 100 and 766 m distant from the hawks' nest, respectively.

HABITAT USE

Seven out of the 12 vegetation variables showed significant differences between natal and dispersal sites (Table 1). Multivariate assessment of differences between natal and dispersal sites using these seven variables also was significant (MRPP statistic = -4.92, $P = 0.03$). Natal sites had fewer pines, fewer woody stems, and fewer saplings when compared with dispersal sites. Dispersal sites generally were located in areas with less canopy cover, fewer mature trees, and denser understory.

Univariate analysis of pooled data showed that dispersal sites were closer to roads and openings than natal sites, and farther from mature forest (Table 2). Within a 300 m radius of the arithmetic center of the natal or dispersal site, the distance covered by roads was larger on the dispersal sites, whereas the distance covered by creeks was lower (Table 2). Considering five variables (distance to road, distance to creek, distance to mature forest, meters of road, and

TABLE 2. Comparison of landscape parameters between "natal" ($n = 21$) and "dispersal" ($n = 38$) sites for radio-tagged Wood Thrush fledglings, MCBQ, Virginia, 1993–1995.

Variable ^a	Site	$\bar{x} \pm SE$	Z ^b	P
DRoad	Natal	335 \pm 37	3.63	<0.001
	Dispersal	164 \pm 21		
DOpen	Natal	245 \pm 41	1.96	<0.05
	Dispersal	154 \pm 20		
DCreek	Natal	120 \pm 24	-1.07	>0.2
	Dispersal	154 \pm 21		
DForest	Natal	11 \pm 8	-3.95	<0.001
	Dispersal	155 \pm 28		
Roads	Natal	224 \pm 77	-3.53	<0.001
Creeks	Dispersal	663 \pm 62		
Creeks	Natal	784 \pm 118	2.5	0.01
	Dispersal	492 \pm 48		

^a DRoad, DOpen, DCreek, and DForest are the distance from the arithmetic center to the nearest road, forest edge or opening (≥ 0.4 ha), creek, and mature deciduous and deciduous-pine forest (dbh ≥ 38 cm), respectively. Roads and Creeks are the total distance of roads and creeks in a circle 300 m radius.

^b Wilcoxon two-sample test (normal approximation with continuity correction of 0.5).

meters of creek), the differences between natal and dispersal sites were significant (MRPP statistic = -6.18 , $P < 0.001$). Early successional stages (shrub and deciduous saplings) associated with abandoned farms, roadsides, and forest openings were used commonly by fledglings early during the postfledging period. Use of these habitats declined as the season progressed, and by late August, use of mature deciduous and mixed forests had increased significantly (Fig. 2). For the entire postfledging period, habitat occurrence by fledglings, calculated by pooling and plotting all fledglings' radiolocations, was as follows: (1) second growth, 52%, (2) mature deciduous forest (damaged by gypsy moth), 21.8%, (3) mature Virginia pine forest, 15.6%, and (4) mature mixed forest, 10.6%. No birds were recorded using loblolly pine (*Pinus taeda*) habitat, although it covered about 1,100 ha in the study area.

DISCUSSION

Our observations are clear evidence that after independence from the parents, Wood Thrush fledglings dispersed from natal territories and settled in habitats different from those where they were born. These results are similar to those reported by Powell et al. (1995, in Roth et al. 1996). Powell et al. (1995) also mentioned that once fledglings settled, they remained within an area of 500-m radius. We found, however,

that fledglings not only shifted dispersal sites, but also made exploratory movements. The possibility also exists that some fledglings visited sites outside our study area, and then returned.

PURPOSE OF POSTFLEDGING MOVEMENTS

Behavior of young birds during the postfledging period has been a topic of considerable interest and speculation (Rappole 1995). We consider five hypotheses to explain juvenile postfledging movements: (1) migration commencement, (2) breeding territory selection, (3) socialization, (4) intraspecific competition, and (5) optimal foraging. Data gathered during the current study provide some insight into the relative significance of each of these hypotheses as explanations for Wood Thrush behavior in the Virginia Piedmont.

Migration commencement. Several authors have proposed that once the young reach independence or complete the prebasic molt, they commence a gradual, southward migratory movement (Hann 1937, Bent 1953, Pulich 1976). This conclusion is based upon two types of information: the disappearance of the birds from the breeding territory, and band recoveries from south of the breeding site. For instance, Rappole and Ballard (1987) captured a hatching-

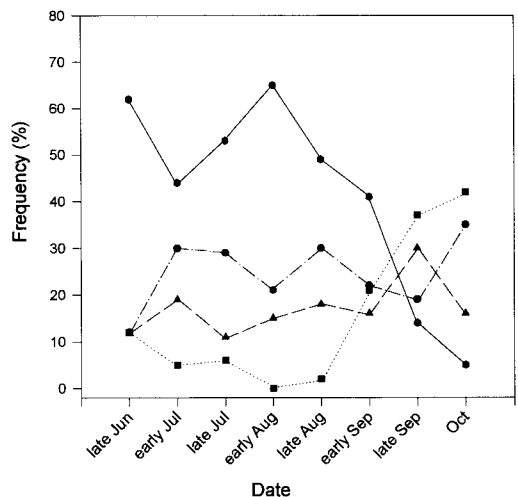


FIGURE 2. Frequency distribution (%) of positions of Wood Thrush fledglings by habitat type during the independence stage (hexagon: old farms, deciduous saplings, forest edges; circle: gypsy moth damaged forest; triangle: mature pine forest; square: mature deciduous and deciduous-pine forest;), at MCBQ, Virginia, 1993–1995.

year Black-and-white Warbler (*Mniotilta varia*) 100 km south of the nearest known breeding locality for this species in Georgia. The bird showed no evidence of being in a migratory state (no subcutaneous fat). Bocetti (1993) captured a hatching year Kirtland's Warbler (*Dendroica kirtlandii*) about 5 km from the nearest known breeding habitat. No pattern of southward movement was evident in the young Wood Thrushes followed during our study.

Breeding territory selection. Brewer and Harrison (1975) suggested that a major purpose of postfledging movements is for juveniles to familiarize themselves with available breeding habitat and to select possible territories to occupy during the next breeding season. Similarly, results from other studies suggest that fledglings prospect for breeding sites during the late summer prior to migration (Adams and Brewer 1981, Morton 1992, Baker 1993). If, as this hypothesis predicts, the main objective of dispersal movements was to scout for potential breeding territories, the birds should focus their visits on areas located in suitable breeding habitat. Most young Wood Thrushes spent the majority of their time in habitats not used by Wood Thrushes for breeding; therefore, our data do not support this hypothesis.

Socialization. Morton et al. (1991) proposed that a function of dispersal by young birds is to socialize in conspecific groups prior to migration. Our data demonstrate that fledglings tend to occur in the vicinity of other young Wood Thrushes at specific dispersal sites. What is not clear is whether the birds chose the site because of the presence of conspecifics, or for some other reason, e.g., quality of the food resources or predator-avoidance benefits. We also found that some Wood Thrush fledglings changed groups or changed from association with a group to foraging alone. In addition, three individuals did not join a group at all or did so only during 1–2 days. These observations suggest that potential benefits of joining a group may vary temporally.

Intraspecific competition. It is possible that juveniles are not dispersing according to their own needs, but in response to the needs of more dominant individuals in the population (Winker et al. 1995). If young birds seek resources in short supply that are important to adults, e.g., food or breeding/nesting sites, then adults may force them to move into less desirable locations. Although we never observed an adult Wood

Thrush attacking a juvenile, the behavior of some juveniles in our study was suggestive of this type of pressure. For instance, four fledglings left natal sites to take up residence in a small (< 0.3 ha), narrow corridor of shrubs adjacent to prime, mature forest breeding habitat. The birds occupying this strip were not found venturing out of the site during the two to six weeks that they were there, and did not leave the site when tracked on foot, but circled around behind the tracker, always remaining within the strip. Later in the season when most adults ceased breeding, fledglings were more frequently found in mature forest. At this time, adults did not show evidence of behaviors used by Wood Thrushes to defend territory during the winter period (calls, visual displays, chases) (Rappole and Warner 1980). However, it was not possible to determine whether this pattern was the result of the end of the males' territorial behavior or because production of fruits in the mature forest started at that time.

Foraging optimization. According to this hypothesis, the main purpose of postfledging movements by juveniles is location of optimal foraging habitat. The pattern of fledgling movements observed seems to fit this explanation. Young Wood Thrushes have considerable need for food resources. They must undergo a pre-basic molt and accumulate sufficient fat reserves to commence migration. It appeared from our data that initial dispersal by juveniles was to leave mature forest habitat and enter earlier successional stages where they fed on invertebrates and fruits. Although we did not quantify fruit production, we did record the presence of fruiting trees and shrubs present in the vegetation plots. We also recorded the species of plants on which young birds were observed feeding. These included blackgum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), spicebush (*Lindera benzoin*), grape (*Vitis* sp.), poison ivy (*Toxicodendron radicans*), greenbriar (*Smilax* sp.), and blueberry (*Vaccinium* sp.). Individuals of these species started to produce fruit earlier (July–early August) in the habitats frequented by the young birds early in the postfledging phase (abandoned farm fields, forest edges, and openings in forests damaged by gypsy moths). Later in the season, fruits became available in more mature habitats, and many fledglings appeared to shift their dispersal sites accordingly.

Based on our data, we suspect that foraging optimization was likely the most important factor driving the postfledging movements of young Wood Thrushes. However, the fact that juveniles generally occurred in loose aggregations of conspecifics may indicate that predator avoidance or some other benefit of flocking also is a significant factor in postfledging behavior. These factors are not mutually exclusive, and could combine to produce a complex array of movements patterns and behaviors. More detailed studies designed specifically to isolate and test these hypotheses are necessary.

CONSERVATION IMPLICATIONS

The natural focus of conservation concern for a migratory bird species is on the breeding site; the place where the territory is established, the nest is built, and the young are fledged. Therefore, management strategies in North America are based on breeding season events (Morton 1992). This focus is convenient as it also is the period when birds are most easily censused. However, for Wood Thrushes in the Piedmont of Virginia, habitat needs appear to be more complex. Once young birds of this species reach independence, they move away from mature forest into patches of earlier successional stages at forest edges and clearings within forested areas where fruits are more readily available. This finding raises questions regarding how "breeding habitat" should be defined. We propose that "breeding habitat" be defined not simply as the habitat type where the nest is located, but include the habitats used by adults and young during the 30–60 days from the completion of breeding activities until departure on migration. At present, although we know that Wood Thrushes use such habitats, we do not know that they *require* them. The requirement may not be for a specific habitat type, but rather the occurrence of soft mast species within a certain radius of the nesting site.

We do not know how common intra-seasonal shifts in habitat requirements are for Neotropical migrant species. Nevertheless, it is clear that any consideration of the conservation needs of the Wood Thrush or any other migrant must at least consider the bird's needs during the postfledging period. Conservation programs based upon determining the amount of suitable breeding habitat available for a species (e.g., Finch 1991, Gains and Morses 1996), and habitat manage-

ment based on those needs, should consider the entire "breeding" season. We can no longer assume that those needs remain unchanged once singing stops.

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