

POSTBREEDING MOVEMENTS AND HABITAT USE OF ADULT WOOD THRUSHES IN NORTHERN VIRGINIA

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ABSTRACT.—We report movements and habitat use during the postbreeding period of radio-tagged adult Wood Thrushes (*Hylocichla mustelina*) at the United States Marine Corps Base, Quantico, Virginia, from May to October 1993 to 1995. Thirty of 61 radio-tagged adults stayed on the study area up to two months after they finished reproductive activities. During this time they underwent molt. Of these 30 birds, 11 (6 females and 5 males) molted in the same sites where they nested, 4 males moved to stands of deciduous saplings adjacent to their nesting territories, and 15 (4 females and 11 males) moved to molting sites 545 to 7,291 m from their nesting territories. We found no clear patterns that sex or reproductive success were related to the probability of moving away from nesting sites to molt, nor that the location of molting adults was correlated with the presence of fruiting plants. However, structural attributes of the vegetation that may enhance predation avoidance, such as the number of woody stems, the density of the understory, and the number of deciduous saplings, were significantly higher in molting sites than in nesting sites. We hypothesize that during molt, Wood Thrushes may need access to “safe havens” where protection from predators is enhanced. Our study strongly suggests that a conservation strategy that focuses on identifying and protecting nesting habitat is inadequate if the events and needs during the postbreeding period are not considered as well. Received 14 October 1997, accepted 18 September 1998.

THE POSTBREEDING PERIOD for Nearctic-Neotropical migrants, defined in this study as the interval from the end of reproduction to departure for migration, has received almost no attention. Indeed, except for anecdotal and circumstantial evidence, we lack basic information on the ecology and behavior of most passerines during the postbreeding period. One of the major reasons for this lack of information is that after reproduction, adults become secretive and are less likely to be caught, seen, or heard (Sealy 1979, Evans Odgen and Stutchbury 1996). Yet, the postbreeding period, which can last up to three months, is critical, not only because of its inherent ecological importance, but also because of its implications for conservation. During this period, individuals of most migrant species must find appropriate food and cover to successfully replace their plumage and to accumulate fat reserves in preparation for migration.

It has generally been assumed that after completing reproductive activities, most migrants

remain on their nesting territories where they undergo prebasic molt and accumulate fat prior to migration (Pyle et al. 1987). Individuals of some species are known to abandon their territories after reproduction and before starting molt or during the early stages of molt (e.g. Sealy 1979, Nolan 1978, Cherry 1985, Bocetti 1993). However, most of these reports were from observations of birds with unknown breeding histories, and no information was given regarding the factors that may influence departure from nesting sites.

We used radio tracking to document the postbreeding movements and habitat use of adult Wood Thrushes (*Hylocichla mustelina*). Radio-tracking studies have been criticized because cost and logistical constraints limit the number of individuals that can be monitored. We recognize that the problems inherent in small sample sizes apply in our study. However, radio tracking allowed us to obtain unique information that is otherwise difficult to obtain (Koenig et al. 1996).

We address two specific questions: (1) Do adult Wood Thrushes remain on their nesting territory to molt, or do they move elsewhere? (2) Are the characteristics of the nesting site

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different from those of sites used for molting? The reproductive ecology of Wood Thrushes is relatively well known (Roth et al. 1996), and some information has been published on movements, behavior, survival, and habitat use of juveniles during the postfledging period (Anders et al. 1996, 1998; Vega Rivera et al. 1998b). However, information on the behavioral ecology and habitat requirements of adults after breeding is not available. This information is urgently needed because of the conservation status of this species throughout most of its range (Hunter 1992).

STUDY AREA AND METHODS

Our study area was the 242-km² United States Marine Corps Base at Quantico (MCBQ), Virginia, 55 km southwest of Washington, D.C., on the eastern edge of the Piedmont Plateau (38°40'N, 77°30'W). About 75% of the MCBQ is forested. The most common forest cover types include a mix of American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), and oak (*Quercus* spp.; 60% of area); a mix of Virginia pine (*Pinus virginianus*) and oak (19%); and pure Virginia pine (21%). MCBQ forests are contiguous with extensive woodlands of the adjacent Prince William Forest Park, providing a combined forest coverage of 324 km². Within the forested area, however, gypsy moth (*Lymantria dispar*) damage and forestry practices have resulted in a diversity of canopy closures and seral stages.

From May to October, 1993 to 1995, we captured, radio tagged, and monitored the movements and habitat use of 61 adult Wood Thrushes. Thrushes were captured in mist nets on a 10-ha grid located in mature deciduous forest and at active nests within the study area. Females and males in breeding condition (vascularized and/or edematous incubation patch or enlarged and turgid cloaca, respectively) were equipped with radio transmitters. Only individuals that were positively identified as reproducing (i.e. observed building a nest, incubating, or feeding young) and that survived until departure from the study area were included in the analyses. Therefore, sample sizes vary because birds were lost to migration, depredation, or their transmitters fell off.

Radio attachment and radio tracking.—We attached transmitters to thrushes using a harness around the legs (Rappole and Tipton 1991). The transmitter package, including harness, weighed approximately 2.1 g (model BD-2G, Holohil Systems Ltd.), which is 4 to 5% of the adult's body mass. Transmitters had an average life of >120 days and a range of about 1 km on the ground and 3 km from the air. During the nesting season, we noticed no differences in the be-

havior of radio-tagged birds compared with those without transmitters.

Radio-tagged birds were located every other day using hand-held receivers and 4-element Yagi antennas. We pinpointed locations by approaching each bird. Birds often responded to an observer's presence by moving before we could see them. Nevertheless, we made every effort to record the bird's initial position. Once a bird was located visually, we recorded information for up to 30 min on its activity (perching or foraging), substrate (ground, shrub, tree), and whether it was alone or with conspecifics. The geographic coordinates for each location were obtained using a global positioning system. At least 75 fixes were obtained for each location; locations were differentially corrected and averaged using PFINDER software and then entered as a "coverage" into the MCBQ geographic information system.

When a bird'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 to 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. Transmitters lost during any part of the year were monitored during all subsequent flights. Transmitter failure can be a cause of signal loss. However, our experience with these transmitters did not indicate that transmitter failure was a likely cause of signal loss. We recovered 30 transmitters that were still functioning after they had fallen off of the birds, or the birds had been depredated.

Movement patterns.—We calculated home-range sizes (95% minimum convex polygon) during the nesting and molting periods using birds located 20 or more times in each period. We considered consecutive locations for a given bird as independent because they were separated by a minimum of 24 h, which is sufficient time for movement between any two points in the area (White and Garrott 1990). For each individual, we determined the extent of overlap between home ranges. We categorized home ranges as separate sites ("nesting" and "molting") if home ranges overlapped $\leq 10\%$. Similarly, "nesting/molting sites" were sites whose nesting and molting home ranges overlapped $> 10\%$. We also calculated (1) mean distance between consecutive point locations, hereafter referred to as mobility; (2) mean distance from the arithmetic center of the home range to every location, hereafter referred to as mean distance; and (3) distance between home ranges, measured from the arithmetic centers of the respective home ranges.

Vegetation sampling.—We characterized the structure and composition of vegetation at nesting and molting sites by sampling four to five circular plots,

22.5 m in diameter (0.04 ha), centered at randomly chosen bird locations within each site. At nesting sites, however, one plot was centered at the nest position. The vegetation data from a given circular plot were used to describe the site of only one bird, regardless of the number of adults using the site. To characterize the structure and composition of a particular site, vegetation data were averaged across sample plots. For each plot, 44 vegetation variables were measured directly in the field or derived from field measurements (James and Shugart 1970). Correlations between these variables were calculated (using Pearson and Spearman rank correlation coefficients because of nonnormal 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 analyses. The criteria for retention were ease of ecological interpretation and precision of measurement. This procedure resulted in a set of 12 variables for analyses. A listing and descriptions of all 44 variables are given in Vega Rivera (1997).

The diet of Wood Thrushes changes from predominantly insects during reproduction to predominantly fruits in the fall (Conway et al. 1994; see also Martin et al. 1951). Therefore, as a correlative measure of food abundance, we recorded the presence or absence of fruits (on plant species consumed by Wood Thrushes) within a radius of 10 m of the bird's initial position.

Landscape measures.—From the arithmetic center of a bird's home range, we calculated the distance to the nearest (1) mature (dbh > 38 cm) deciduous and deciduous/pine forest, (2) creek, (3) road (<10% canopy cover), and (4) opening (≥ 0.4 ha). We also measured the total distance of roads and creeks within a 300-m radius around the arithmetic center of each home range.

Statistical analysis.—For analysis of vegetation and landscape attributes, we used information from 12 individuals for which we had data for nesting and molting sites, and 7 individuals that nested and molted at the same site. We were interested in both population and individual trends. Therefore, differences in vegetation attributes between nesting and molting sites were analyzed using pooled data and separately for each individual. To control the overall probability of Type I error in our analysis of differences among sites for pooled data and for each bird in paired comparisons, we adjusted significance levels using the Bonferroni method. With an *a priori* alpha level of 0.1 and 12 statistical tests, only alpha levels ≤ 0.008 were considered significant.

The distribution of each variable was evaluated for normality using the Shapiro-Wilks test (SAS Institute 1989); most variables were nonnormal. We first made univariate comparisons among habitat characteristics at nesting and molting sites using a Kruskal-Wallis test followed by a nonparametric multiple

comparison for unequal samples (Zar 1996:227) when appropriate. Next, we tested for between-group differences using multiple variables simultaneously with the multi-response permutation procedure (MRPP; Mielke and Berry 1982). MRPP is a nonparametric multivariate method that does not require assumptions of multivariate normality and homogeneity of variances. The strategy of MRPP is to compare the observed intragroup average distances with the average distances that would have resulted from all other possible combinations of the data under the null hypothesis. We included in this test seven variables that were significant ($P \leq 0.008$) in the univariate tests. We used BLOSSOM software to perform the MRPP tests (Slauson et al. 1991). We used Wilcoxon signed-rank tests for analysis of differences among paired nest versus molting sites. Other statistical tests are indicated in the text.

RESULTS

Of the 61 adults we radio tagged, 6 were killed, 7 lost their transmitters, and 18 apparently left the study area after nesting failure or fledgling independence. The remaining birds (10 females and 20 males) were observed molting within the study area. The prebasic molt was complete (i.e. flight feathers and body feathers were replaced), lasted 51 days on average, and was terminated by the time the adults left the study area (Vega Rivera et al. 1998a).

Movement patterns.—Of the 30 radio-tagged adults that molted in the study area, 11 (6 females and 5 males) molted in the same sites where they nested, and 19 molted in different sites. Of the birds that moved, 4 males used deciduous sapling stands adjacent to their nesting territories (see Fig. 1), and 15 (4 females and 11 males) used molting sites located $2,015 \pm \text{SE}$ of 520 m (range 545 to 7,291 m) from their nesting territories (Fig. 2). Males ($1,950 \pm 508$ m) and females ($2,090 \pm 1,303$ m) moved similar distances between nesting and molting sites ($t = 0.12$, $P = 0.905$). These movements were larger than the range of movements exhibited during the nesting season. Pairs moved 69 ± 14 m ($n = 8$) between successful nests and 122 ± 26 m ($n = 7$) between unsuccessful nests within a season. This average did not include a pair that moved 4.3 km to reneest, and a female that moved 1.5 km from her previous nest to initiate a new clutch with a different male (Vega Rivera 1997).

Molting adults were difficult to observe and

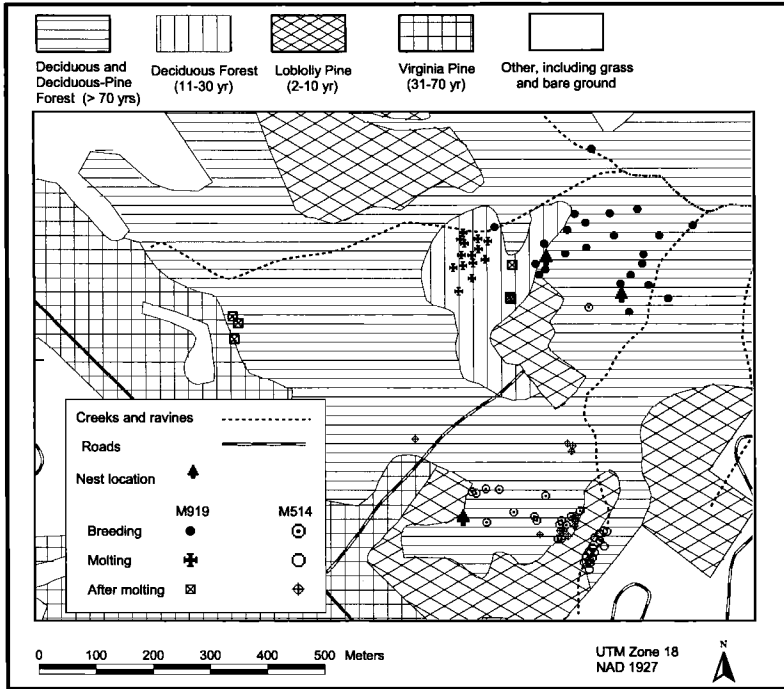


FIG. 1. Radio locations of two adult Wood Thrushes during reproduction, molting, and postmolting, Quantico, Virginia, 1995.

often resided in dense patches of vegetation, frequently among the branches of fallen trees (we often had to approach within 3 m to see them). This change in behavior was reflected in

the analysis of movements of 23 individuals. Once the adults started molting, they moved less (nesting vs. molting, respectively; mobility, 114 ± 9.0 m vs. 67 ± 8.0 m, Wilcoxon test, Z

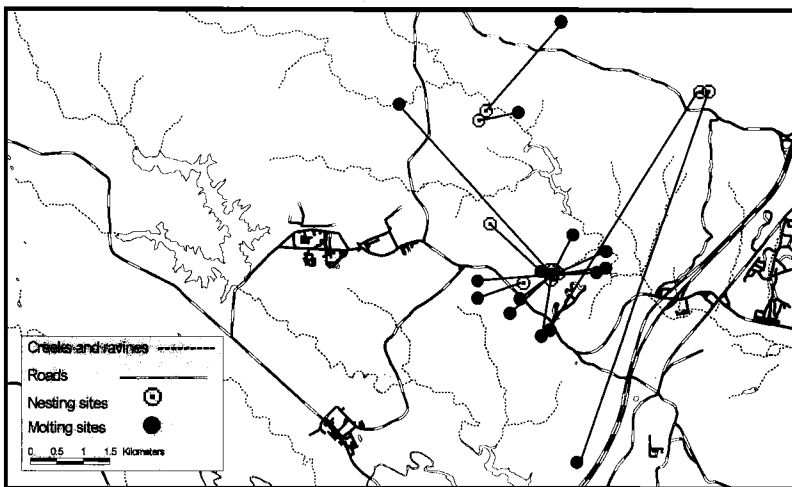


FIG. 2. Nesting (open circles) and molting (solid circles) sites of 15 adult Wood Thrushes that nested and molted in areas separated >500 m, Quantico, Virginia, 1993 to 1995.

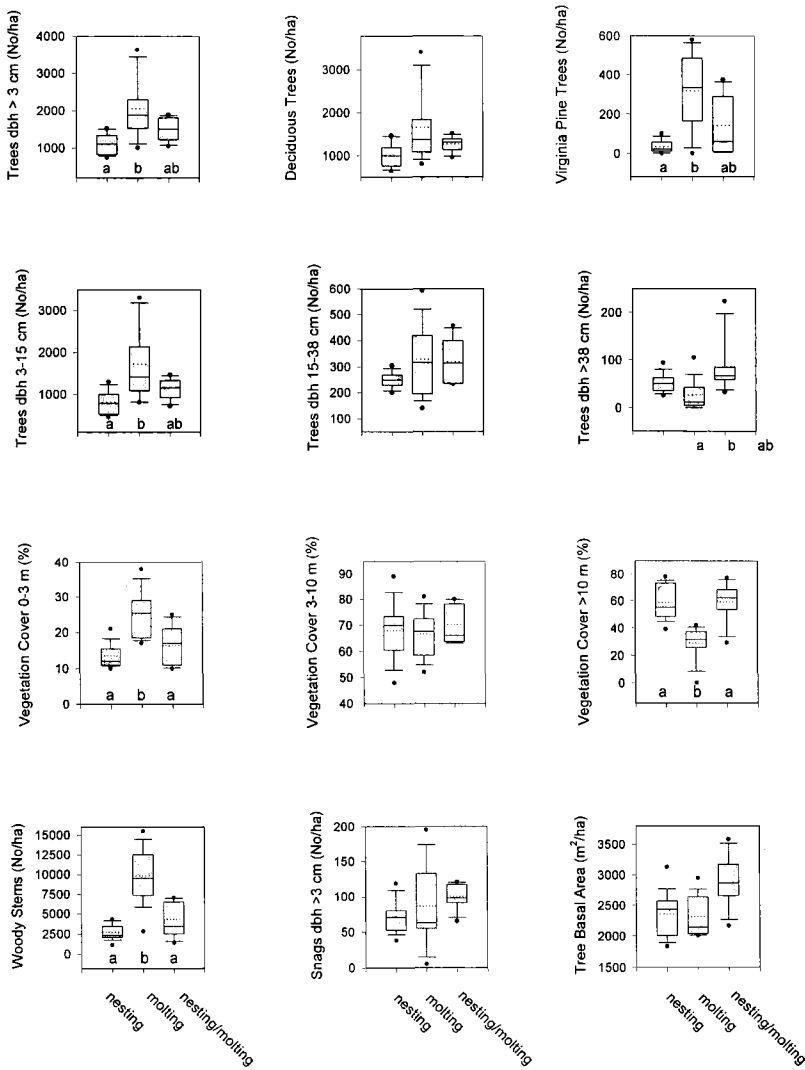


FIG. 3. Comparison of structural vegetation parameters among “nesting” ($n = 12$), “molting” ($n = 12$), and “nesting/molting” ($n = 7$) sites for radio-tagged adult Wood Thrushes, Quantico, Virginia, 1993 to 1995. Box plots with the same letter were not significantly different ($P > 0.05$, nonparametric multiple comparison for unequal samples).

$= 3.13$, $P = 0.002$; mean distance, 107 ± 9.0 m and 67 ± 8.0 m, $Z = 2.72$, $P = 0.006$) and restricted their movements to a smaller area (95% convex polygon; 2.6 ± 0.5 ha during nesting vs. 1.4 ± 0.3 ha during molting; $Z = 1.88$, $P = 0.058$).

Habitat attributes.—Seven structural vegetation variables differed significantly among nesting, molting, and nesting/molting sites (univariate comparisons of pooled data; Fig. 3). Note also in Figure 3 that for most variables the

range of values was higher on the molting sites than on either nesting or nesting/molting sites, and the range of values for sites used for nesting/molting tended to be intermediate between nesting and molting sites. MRPP analysis that included the seven variables revealed that the three kinds of sites differed significantly ($\delta = -9.77$, $P < 0.001$) and that all pairwise comparisons were significant (nesting vs. molting sites, $\delta = 11.59$, $P < 0.001$; nesting vs. nesting/molting sites, $\delta = -2.36$; $P = 0.023$;

TABLE 1. Results of statistical tests (paired comparisons, Wilcoxon signed-rank test) examining differences in vegetation attributes between "nesting" and "molting" sites for each of 12 radio-tagged adult Wood Thrushes. Nesting (N) and molting (M) indicate the site where a higher value occurred.

Bird ID	Vegetation traits ^a											
	Total trees	Deciduous	Virginia pine	Snags	Small trees	Medium trees	Large trees	% veg. 0 to 3 m	% veg. 3 to 10 m	% veg. >10 m	Woody stems	Basal area
514	M	M	M	N	M	N	M	M	N*	N	M	M
546	M**	M*	M	N	M**	N	N	M	M	N**	M*	N
555	M**	M*	M**	N**	M*	M	N**	M	M	N**	M	N**
603	M**	M*	M***	M	M**	M**	N**	M	N*	N**	M**	N
902	M***	M**	M***	M	M***	M***	N**	M**	N	N*	M***	N
919	M**	M**	M**	N	M*	N	N*	M*	N	N	M**	N
928	M**	M	M	M	M**	M**	N	M	M	N	M**	M
933	M**	M*	M**	M	M**	M	N**	M	N**	N	M	N
F509	M***	M	M**	M	M**	M*	N**	M**	N	N*	M**	N
F516	M*	M	M*	M**	M	M	M	M**	N	N**	M	M**
F904	M	M	M	N	M	M	N	M**	M	M	M*	M
F991	N*	N	N	N	N	N*	M	M	M	N	M	M

*, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.008$.

^a Total trees (trees dbh >3 cm, no./ha); deciduous (deciduous trees dbh >3 cm, no./ha); Virginia pine (Virginia pine trees dbh >3 cm, no./ha); snags (dbh >3 cm, no./ha); small trees (trees dbh 3 to 15 cm, no./ha); medium trees (trees dbh 15 to 38 cm, no./ha); large trees (trees dbh >38 cm, no./ha); % veg. (percent vegetation cover); woody stems (no./ha); and basal area (m²/ha).

molting vs. nesting/molting sites, $\delta = -5.24$, $P = 0.002$). Bonferroni correction applied to these results did not change the conclusions (adjusted $P = 0.026$). These results further supported our conclusion of perceived differences between nesting and molting sites.

Results of the analysis on individual birds generally agreed with those obtained from pooled data (Table 1). However, as expected, there was individual variation (i.e. nonsignificant individual differences for variables that were significant when data were combined across individuals). We did not find significant differences in species composition or density of trees among nesting, molting, or nesting/molting sites (Vega Rivera 1997).

Landscape measures.—Nesting ($n = 12$), molting ($n = 12$), and nesting/molting sites ($n = 7$) differed in (1) distance to nearest deciduous and deciduous/pine mature forest (0 m, 139 m, and 5 m, respectively; Kruskal-Wallis test, $H = 15.45$, $P < 0.001$); (2) distance to the nearest road (244 m, 188 m and 301 m, respectively; $H = 5.41$, $P = 0.066$); and (3) total distance covered by creeks (940 m, 493 m, and 879 m, respectively; $H = 4.81$, $P = 0.066$). None of the other variables was found to be significantly different. MRPP analysis of differences among sites considering the four variables simultaneously (Bonferroni adjusted $P = 0.026$) yielded differences among nesting, molting, and

nesting/molting sites ($\delta = -3.17$, $P = 0.011$); between nesting and molting sites ($\delta = -4.11$, $P = 0.005$); and between molting and nesting/molting sites ($\delta = -3.43$, $P = 0.011$). The difference between nesting and nesting/molting sites was not significant ($\delta = 0.829$, $P = 0.936$).

Departure.—After completing molt, most adults maintained similar patterns of movement and stayed on their molting sites. Ten females and seven males left the study area without an apparent change in movement pattern. In the remaining 13 individuals, a change in movement pattern was observed. For example, two weeks before leaving the study area, one male moved 500 m from his nesting/molting site to a site not visited before, stayed two days, and then moved back to his nesting site. Two males moved 4.4 km and 500 m, respectively, from their molting sites back to their nesting areas and then left the study area. Four males that molted in sapling stands adjacent to their nesting sites moved back to the forest 3, 8, 15, and 23 days before departure. None of the birds that returned to their nesting areas showed any evidence of territorial behavior, nor did they show the same pattern of movement as when they were breeding and defending a territory. They restricted their activities to sites characterized by the presence of at least one large tree covered with ripe fruits, e.g. blackgum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*),

and sassafras (*Sassafras albidum*), where we observed them foraging.

The earliest date that a radio-tagged adult left the study area after molting was 15 September, and the latest was 14 October. Most birds (70%) departed the study area between 22 September and 10 October.

DISCUSSION

The presence of marked individuals outside of their nesting areas during the postbreeding period has been documented often (Nolan 1978, Cherry 1985, Rappole and Ballard 1987, Bocetti 1993) and has been interpreted as a strategy of searching for places where food availability is high (i.e. the food-search hypothesis). Contrary to what we found regarding movements of fledgling Wood Thrushes (Vega Rivera et al. 1998b), we did not find any pattern that related the location of radio-tagged molting adults with the presence of fruiting plants. A potential problem associated with this analysis, however, is that it ignores the insect component of the Wood Thrush's diet (23% of diet in fall; Martin et al. 1951).

Because molting is a demanding process in terms of energy, the availability of sufficient food resources during the selection of molting habitat undoubtedly is important. However, our results suggest that the presence of adequate cover is equally important for Wood Thrushes (i.e. the predator-avoidance hypothesis) in the selection of molting sites. At our study area, the flight efficiency of some molting individuals was seriously impaired (Vega Rivera et al. 1998a). Therefore, a major challenge for molting Wood Thrushes was probably to escape predation. Two strategies can be adopted to enhance survival during molt: (1) behavioral inconspicuousness, and (2) selection of "safe havens." Anders et al. (1996, 1998) found that survival of juvenile Wood Thrushes was high when they reached "safe havens" three to four weeks postfledging. Our data suggest that vegetation attributes that may enhance protection, such as densities of woody stems, understory vegetation, and deciduous saplings, were significantly higher in molting and nesting/molting sites than in nesting sites. These attributes were mainly found in stands of Virginia pine and deciduous saplings, and along forest edges. Virginia pine stands were particularly good

in providing molting Wood Thrushes with fallen trees and dense thickets. Although our sample was small, depredation of birds was similar during reproduction (six birds, or 9.8%) and molting (two birds, 6.6%). We interpret this similarity as an indication that adult Wood Thrushes were successful in finding appropriate molting sites and as a result, the predation rate on molting birds was low.

Selection of molting sites also could be related to other factors. Our data are scarce, but they suggest that sex (Fisher's exact test, $P = 0.24$) was not related to the probability of staying in or moving out of the nesting area. Reproductive output may have influenced movements. Of 19 birds for which we had information on reproductive success (at least one young was fledged from the final clutch), 64% (7 of 11 birds) of the birds that moved did so after the last nesting attempt failed, but only 25% (2 of 8) that stayed failed in their last attempt. This difference was not statistically significant (Fisher's exact test, $P = 0.23$). Another possible factor influencing the pattern of movements was the date when reproduction ended and molt started. Birds that moved began molting earlier than those that stayed. Average onset of molt was 6 August (SE = 3.1) and 16 August (SE = 4.2) for birds that moved and stayed, respectively ($t = -1.81$, $P = 0.088$). More detailed studies are necessary to examine these hypotheses further.

Conservation implications.—Historically, studies on habitat needs of Nearctic-Neotropical migrants during the "breeding season" have focused on the nesting period. Implicit in these studies is the assumption that the birds reproduce and molt on the same sites; therefore, habitat requirements for nesting and molting are similar. For example, Robbins et al. (1989) concluded that the minimum-area requirement for breeding Wood Thrushes was 1 ha. In our study, less than half of the birds monitored during molt reproduced and molted in the same area. The remainder moved to molting sites located up to 7 km from their nesting territories. Regardless of the underlying reasons for these movements, the fact is that more than half of our birds shifted sites and molted in areas whose characteristics were different than those in which the birds nested. Molting Wood Thrushes may not be looking for specific forest types, but rather for habitats with certain struc-

tural characteristics that provide adequate food and cover.

Large forested areas with a mixture of forest types and ages (such as our study area) apparently can provide nesting and molting habitat for the local Wood Thrush population. Fragmented landscapes, however, may provide appropriate nesting habitat but not molting habitat. Some individuals may need to move to appropriate molting habitat before migration. The cost of these movements in terms of survivorship has not been evaluated, and their effect on the perceived population decline in Wood Thrushes is unknown (Haas 1995).

Researchers have been relatively successful in identifying habitat characteristics associated with reproduction in Wood Thrushes and many other migratory species. Consequently, conservation plans have focused on identifying and protecting nesting habitat (e.g. Finch 1991, Gains and Morses 1996). Without question, protection of nesting habitat is important. However, our data and the data of others for Wood Thrushes (Anders 1996, 1998; Vega Rivera et al. 1998a,b) show that habitat needs for reproduction are not always the same as those during the postbreeding period. Understanding these differences is essential if effective conservation measures for Nearctic-Neotropical migrants are to be established.

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