Premigratory Movements of a Long-DdistanceMmigratory Species: the Wood Thrush (*Hylocichla mustelina*)

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(ABSTRACT)

The postbreeding period in migratory bird species is an important, but often neglected, area of knowledge. From May-October of 1993-95, I studied the breeding and postbreeding ecology of 61 adults and postfledging movement of 43 juveniles in a radio-tagged population of Wood Thrushes (*Hylocichla mustelina*) on the U. S. Marine Corps Base, Quantico, Virginia (38^0 30' N, 77^0 25' W). Fledglings became independent from their parents at 28-36 days post hatching and dispersed 307-5300 m from their natal sites to join flocks of conspecifics. About half (46%) of the young birds stayed in one dispersal site until migrating, but the rest visited other sites. In 40 instances, 15 fledglings moved up to 6 km out of the dispersal site and, after 1-5 days, returned to the locality occupied before initiating the movement. After dispersal, fledglings' positions ($n = 556$) occurred in (1) second growth and sapling stage sites at the edge of forested areas [52%], (2) gypsy moth (*Lymantria dispar*) damaged deciduous forest [21.8%], (3) Virginia pine (*Pinus virginianus*) forest that had a heavy understory of young deciduous trees and an open canopy [15.6%], and (4) mature mixed forest [10.6%]. Most fledglings (73%) left the Marine Base in September at the mean age of 81 days. After finishing breeding, adult Wood Thrushes underwent molt that extended from late July to early October. Flight-feather molt lasted on average 38 days and may have impaired flight efficiency in some individuals. Of 30 observed adults, 15 molted in the same area where they nested, and 15 moved 545 to 7290 m from their nesting sites. Molting sites were located in areas with a larger number of pines, less canopy cover, fewer trees with dbh >38 cm, and a denser understory strata than nesting sites ($P < 0.1$). My data suggest that a conservation strategy that focuses on identifying and protecting nesting habitat in the temperate region, although important, is incomplete at best if the events and needs during the postreproductive and postfledging periods are not considered.

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INTRODUCTION

Current concern about the decline of several long-distance Nearctic-Neotropical migrant birds has emphasized the need to perform baseline studies that provide us with information on what abiotic, biotic, and behavioral factors are causing these declines (Finch 1991). The origin of these declines is controversial, but probably multiple factors acting in both the breeding and wintering grounds play important roles (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990). Studies of particular species on the breeding grounds have already evaluated components that may affect fitness such as nesting success, recruitment, return rates, habitat use patterns, and nest parasitism (e.g., Wilcove 1985; Holmes et al. 1986; Yahner and Scott 1988; Sherry and Holmes 1992). It is remarkable, however, that the post-breeding and post-fledging periods (respectively the periods between the end of the reproduction of adults and the start of independence from parents in juveniles, and departure for autumn migration) have received almost no attention. Other than anecdotal and circumstantial evidence, we lack basic information for most migrants (and passerines in general) concerning the ecology and behavior after breeding of adults and dispersal of fledglings, even when information for this period may be of critical importance in conservation efforts as well as in addressing an array of ecological questions (Weatherhead and McRae 1990, Morton et al. 1991).

This information is scarce for many species because, after reproduction, adult birds become secretive and less likely to be observed or caught and juveniles disperse after independence from their parents, making documentation of their activities difficult (Ginn and Melville 1983:29-30). Further, adults of some species move away from their breeding territory after reproduction (Nolan 1978, Rappole and Ballard 1987). In recent years there has been an increased interest in use of radiotelemetry for study of small birds, mainly because of the improvement in transmitter technology (i.e., smaller size). Transmitters are still relatively expensive and of limited range and life, but well-designed studies can yield information that otherwise would be hard to obtain.

In this study I used radiotelemetry to examine the ecology and behavior of the Wood Thrush (*Hylocichla mustelina*) during the post-reproductive period and fledgling stage. My objectives were:

1.   To determine the pattern and extent of the premigratory movements of adult and juvenile Wood Thrushes, as well as to evaluate differences in these patterns between sex classes.

2.   To determine differences in habitat use between the breeding and postbreeding periods in adults, and the postfledging dependence and independence stages in fledglings.

3.   To examine behavior and social interactions during the postbreeding period.

4.   To examine the pattern and chronology of molt and determine its relationship to reproduction and migration departure.

The Wood Thrush is an excellent model for this study for several reasons. First, the Wood Thrush is a long-distance Nearctic-Neotropical migrant of conservation concern. Declines in the numbers of Wood Thrushes have been reported at regional and local scales (Sauer and Droege 1992, Roth and Johnson 1993; 4% per year over the period 1978 through 1988). For this reason the Wood Thrush has been identified as a high priority for management and monitoring in the southeastern United States (Hunter 1992). Thus, evidence or information that helps us to elucidate the causes of this decline is desirable. Second, the Wood Thrush's breeding biology is relatively well known (Bent 1949; Longcore and Jones 1969; Bertin 1977; James et al. 1984); therefore a change in habitat use and behavior in the postbreeding period is easier to detect.

Wood Thrushes molt and accumulate fat before migration. Both of these activities have high energy demands and birds that can molt and feed in productive habitats may be more likely to survive migration. Knowing how and where these activities occur will elucidate specific management strategies.

METHODS

Study area

The area of study was located on the U. S. Marine Corps Base at Quantico, Virginia (hereafter Marine Base). The Marine Base is located 35 km south of Washington, D. C. on the eastern edge of the Piedmont Plateau physiographic region, along the west bank of the Potomac River. It covers an area of 24281 ha, 75% of which is forested. The most common forest cover types on the Marine Base include American Beech- (*Fagus grandifolia*) Yellow Poplar (*Liriodendron tulipifera*) -Oak (*Quercus* spp.) (11535 ha), Virginia Pine (*Pinus virginianus*) (3944 ha), and Virginia Pine/Oak (3682 ha). Furthermore, the Marine Base is contiguous with extensive woodlands at the adjacent Prince William Forest Park, providing nearly 32375 ha of continuous forest. Within the forested area, however, gypsy moth (*Lymantria dispar*) damage, clear cutting, and prescribed burning have resulted in a diversity of levels of canopy closure and seral stages.

The entire Marine Base has been mapped in the ArcInfo geographic information system (Environmental Systems Research Institute, Inc., Redlands, California, USA), and thematic cover layers, such as contours, roads, streams, water bodies, training areas,

hunted areas, and forest types, were available for this project. A forest stand is an area of forest represented by approximately the same species composition, forest age, and canopy closure. Forest type categories were those recognized by the Society of American Foresters (Eyre 1980).

Local topography is characterized by gently sloping terrain with some steep slopes with defined drainages. Average elevation is 120 m. The soils are generally clay loams with varying amounts of sand and gravel and are usually acidic, low in organic matter and poor in natural fertility (Natural Resources Conservation Report, Marine Corps Development and Education Command, Quantico, VA, 1975).

Field methods

From late May to mid-October of 1993-1995, I radio tagged and monitored the movements and behavior of 43 juvenile, 31 adult female, and 31 adult male Wood Thrushes. The field work involved 5 main activities: mist-netting birds, searching for and monitoring nests, radio tracking Wood Thrushes, performing behavioral observations, and sampling vegetation.

*Bird sampling and capture.--*Three 10-ha plots located in the south-central portion of the Marine Base were gridded to accommodate 50 mist-nets (4 shelves, 12 x 2.6-m, 36-mm mesh) at each plot. In June of each year, I mist-netted each plot for 1000 net hours (approximately 2 consecutive days in each plot). Thereafter, I mist-netted in one of the plots for 1000 net hours every 2 weeks, throughout October, to monitor population turnover. All captured birds received a U.S.F.W.S. aluminum band. Female and male Wood Thrushes in breeding condition were equipped with a radio transmitter and tracked thereafter. Birds with radio transmitters were used both to locate nests and to monitor breeding and postbreeding movements.

Wood Thrushes were designated as in "breeding status" by evaluating the presence and condition of the cloaca and brood patch. Females were radio tagged if the brood patch was vascularized and/or edematous. Males were radio tagged if they had a clearly enlarged and turgid cloaca and if they were recaptured twice in the same area, which suggested that they were probably resident there. Each captured Wood Thrush also was examined visually for presence of subcutaneous fat and recently molting feathers.

*Nest searching and monitoring.--*Active Wood Thrush nests were found primarily by tracking the radio-tagged individuals. I also looked for nests by making random walks and observing specific adult nesting behaviors and by methodically searching through the grids. Once I found a nest, I checked its status by observing it directly or using a mirror attached to a pole; thereafter, nest visitation was minimized to

avoid any potential detrimental effects on the breeding outcome. To monitor the nesting stage, I observed the female behavior at as great a distance as possible using binoculars unless failure was suspected and nest contents had to be verified.

   Radio attachment and radio-tracking.--At successful nests, I captured the offspring 2-3 days before they fledged. Parents that were not already radio tagged were captured by positioning 3 mist nets around the nest before handling the offspring. Under optimal conditions, I fitted all members of the family with radio transmitters, but more often I radio tagged only one member of the pair. The transmitter was attached using a backpack harness made of cotton thread 1 mm in diameter. I followed the technique devised by Rappole and Tipton (1991) which involves the placement of the transmitter on the synsacrum of the bird using a two-loop harness in the shape of a figure-8. When positioned properly, the transmitter moved freely on the bird's back and was almost completely covered by the feathers with the antenna projecting directly over the tail. Transmitters remained on the birds until they either fell off or were removed. Each transmitter weighed approximately 2.1 g (Model BD-2G, Holohil Systems Ltd., Ottawa, Canada), had an average life of >120 days and range of detection of about 400-1000 m on the ground, and 1-3 km from aircraft depending on altitude and topography.

   The weight of the transmitter and its attachment method should not alter the normal behavior of a radio-tagged bird if the study results are to be generalized to untagged birds. Cochran (1980) suggested that the package weight be between 3% and 5% of body weight. A similar argument for birds is presented in detail by Caccamise and Hedin (1985). The transmitters I used weighed 2.1 g and comprised 5.0-6.0 % of the nestling's body weight when attached and 4.2-5.0 % of adult body weight. Flight performance and behavior did not appear to be affected. In 1994, I recaptured 2 individuals on which transmitters were attached in 1993 with a stronger string than I normally used. Both birds still had the transmitters, had obviously survived 2 long-distance migrations, and did not show lacerations or any other sign of irritation.

   Radio-tagged birds were not followed during the first day of radio-tagging, but they were monitored every other day thereafter. Birds were located using a four-element Yagi antenna and a 12-channel receiver (Telonics Communications, Inc.). Tracking was done primarily on foot. I pinpointed locations by approaching each bird until it moved. The position of the locations were obtained using a Geographic Positioning System (Trimble Navigation Limited, Sunnvale, California, USA), in Universal Transverse Mercator coordinates along with date, time, and bird identification. At each position, I recorded 100 fixes. All fixes were differentially corrected and incorporated into the Quantico Marine Corps Base's ArcInfo GIS database, where they were checked for accuracy against my field notes.

Birds responded to the observers' presence, and they moved and perhaps modified their behavior before I could see them. I made a concerted effort to record the first position. After several weeks radio-tracking, I could estimate the position and mobility of a bird before I saw it.

Once a bird was located, I monitored, when possible, its behavior continuously for up to 30 minutes. I did not follow a special protocol for behavioral observations nor did I attempt to standardize the time of day for each individual. I recorded all behaviors of the fledglings, specifically the type of activity (foraging or perching), substrate (ground, bush, tree), height of perch, and interactions with conspecifics.

When birds moved out of their regular range, I looked for them first by driving along roads with a one-element antenna mounted on a car roof. If loss of contact with a radio-tagged Wood Thrush lasted more than 4 days, I also performed aerial radio-tracking. Aerial tracking was conducted with a Cessna 172 at 350-500 m above ground in an area of about 20800 ha (or 7.5 km radius) around the bird's last known location. Two four-element antennas, mounted perpendicular to the fuselage on each wing strut, were connected to a switch box that allowed monitoring of each antenna separately. I regularly covered the entire Marine Base and adjacent Prince William Forest Park when looking for missing birds from the plane. I assumed that a bird had moved beyond the boundaries of the searched area when no signal was recorded by walking or driving around the last known location or during aerial tracking. Signal loss could also be due to transmitter failure, but my experience with Holohil transmitters did not indicate that transmitter failure was a likely cause. During the course of the study I recovered 30 functioning transmitters, 19 transmitters that had fallen from the birds and 11 from birds that had been killed by predators. Similarly, I recaptured 20 birds carrying transmitters that were still working; and with the exception of the 2 birds that carried their transmitters over a year, I never recaptured a bird carrying a radio that was not working.

Indices of activity and area used.--Three measures were computed and used as indices of bird activity for a given site/time interval: the size of the area that included all radiolocations of interest (AREA), the average distance between consecutive point locations (MOBILITY), and the average distance from the arithmetic center of the home range to every location (FCEN). Although "mobility" may underestimate real movements, it is still useful as a measure of relative movement if it correlates with real movements.

No attempt was made to determine the breeding territory of males, understanding the breeding territory as the area actively defended by a territorial male (Brown 1964). The area and boundaries of a given home range were calculated by the minimum convex polygon method, using all radiolocations obtained during the interval of interest. Average

number of locations for calculation of fledglings' and adults' home ranges were 25 (range 20-50) and 20 (range 14-33) locations, respectively. Program HOME RANGE (DOS version, University of Idaho, Ackerman et al. 1990) was used for this purpose. Theoretically, sequential observations of an animal's position can be considered independent if observations are separated by sufficient time for the animal to move across the entire home range (White and Garrott 1990:147). This criterion was adequately satisfied by the Wood Thrush data.

*Vegetation sampling.--*Breeding habitat was described by sampling 3 to 5 22.5-m-diameter circular plots (0.04-ha) within each male's home range. One plot was centered at the nest site and the rest were centered at randomly chosen bird locations. I assumed that characteristics of the male's home range typify the habitat of both the male and his mate.

Vegetation structure and floristics at each circular plot were sampled using the method described in James and Shugart (1970, see also Noon 1981). In each circular plot the following variables considered important in describing Wood Thrush habitat were measured:

1. All trees were identified and counted in dbh categories of 3-8 cm, 8.1-15 cm, 15.1-23 cm, 23.1-38, 38.1-53 cm, 53.1-69 cm, and >69 cm. A special tree category was snags. A snag was defined as any dead, standing woody stem with a dbh ≥ 10 cm and a height ≥ 1.5 m.

2. Shrub density at breast height was estimated by counting the number of shrub stems on two 22.5 m x 2 m transects within the circle. Counted stems included the main stem (<3 cm dbh) and those stems branching from the main stem below breast height.

3. Foliage volume was estimated by positioning a 3-m pole (2 cm diameter) marked at 0.5 m intervals at the 20 points located at 2 m intervals along the transect lines used for measuring shrub density. I recorded the presence or absence of foliage touching the pole within each height interval up to 3 m. For height intervals above 3 m, I recorded the presence/absence of foliage above the pole in each of the following height intervals: (1) 3-6 m, (2) 6-10 m, (3) 10-15 m, and (4) ≥ 15 m.

During the post-breeding period and fledging stage, I characterized the habitat in only those sites where the birds stayed ≥ 5 days. At each site, I sampled the vegetation in 3 to 5 0.04-ha circular plots centered at randomly chosen bird locations. Number of plots sampled depended on logistic constraints. Vegetation was measured as described above. To characterize the vegetation composition and structure of a particular site, I pooled the

data from all sampled circles at that site and extrapolated the values of variables to values per ha. Pooling values of several sampled circles rather than using each circle as an independent unit should more accurately represent the area that the bird was using.

Forty-three vegetation variables either were measured directly in the field or derived from field measurements (Table 1). Because some variables may contribute similar information, I determined correlations of all 43 variables. Because some variables were non-normally distributed, I used both Pearson and Spearman rank correlation coefficients. Within each pair or group of correlated variables ($r \geq 0.7$), only one member of a pair and 1 or 2 members of a group were retained for subsequent analysis. The criteria for retention were ease of ecological interpretation and more precise measurement. This resulted in a subset of 12 variables that facilitated the interpretation of the analysis, without, I believe, losing information.

Some of these correlations between vegetation variables deserve comment. Vegetation profiles (10 categories) and tree dbh categories (6 categories), were grouped into 3 categories each. In both cases, the newly created categories were correlated significantly with each of the variables used to create the category ($r \geq 0.7$); therefore only the new categories were retained. Measures of basal area were all correlated ($r \geq 0.9$) among the respective tree density categories from which they were calculated, and therefore only total basal area (T_BA) was retained. Density of trees per ha (THA) was highly correlated with density of deciduous trees (D_DEC, $r = 0.96$) and density of trees dbh 3-15 cm (D_SA, $r = 0.98$). In other words, an increase in trees in a given site was mainly the result of an increase of deciduous saplings. The 3 variables were retained for illustrative purposes. D_DEC and density of Virginia pine trees (D_VP) were weakly correlated ($r = 0.22$). Sites with a predominance of Virginia pine trees in the upperstory had a dense understory and midstory of deciduous saplings. D_VP was, however, correlated with density of trees dbh 15-38 cm (D_BC, $r = 0.62$), which indicates that most pines were that size.

Landscape analysis.--I used the program HOME RANGE to determine the arithmetic center of each home range, which is calculated as the arithmetic mean of x and y coordinates of locations. From the arithmetic center, I calculated the distance to the nearest mature (dbh >38 cm) deciduous and deciduous-pine forest, distance to the nearest creek, distance to the nearest road (<10% canopy cover), and distance to the nearest forest edge or opening (≥ 0.4 ha). In addition, I generated a circle of 300 m radius around the arithmetic center. Within each circle, I measured the total distance covered by roads and creeks using ArcView (V. 2.1, Environmental Systems Research Institute, Inc., Redlands, California, USA). I used 300 m as the measure of the radius of the circle because few locations in any given site were >300 m from the arithmetic center of the home range.

*Statistical analysis.--*The distribution of each variable, vegetative and physical, was evaluated for normality by graphically examining skewness and kurtosis, and by testing for normality using the Shapiro-Wilk test (SAS Institute 1988). Because of the lack of normality of most variables, nonparametric tests were preferred. The first step in comparing habitat characteristics between natal and dispersal sites was to screen the variables by making univariate comparisons (Wilcoxon two-sample test and Kruskal-Wallis 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. I used Multiresponse Permutation Procedures (MRPP, Mielke and Berry 1982) test. This method tests whether 2 sets of locations come from a common probability density distribution. The approach is nonparametric, making no assumptions about the shape of the underlying distribution. In this test I included variables that were significant ($P \leq 0.1$) in the univariate tests. The BLOSSOM software (National Ecology Research Center, Fort Collins, Colorado; Sauson et al. 1991) was used to perform the tests.

Additional statistical tests used during the analysis of the data are mentioned when appropriate. In all statistical tests a probability of 0.1 or less was accepted as significant, but I reported actual *P* values for descriptive purposes. Means are given as mean ± standard error. Because the mean is a measure of central tendency heavily influenced by extreme values, for comparative purposes, I also used box plots to show graphically the degree of dispersion on the values of variables. The upper and lower edges of the box are located at the sample 25th and 75th percentiles. The center horizontal solid line is drawn at the sample median and the dotted line is at the sample mean. The central vertical lines extend from the box to a distance at most 1.5 interquartile ranges. Any value more extreme than this is marked with a zero.

Throughout the dissertation, individual Wood Thrushes are referred to by a specific letter prefix followed by 3 numbers. The letter prefix refers to the individual's age/sex category: M = adult male, F = adult female, HY = fledgling or juvenile, and U = adult of unknown sex.

This dissertation is divided into 3 major chapters. The first chapter includes information on adults, both during the reproductive and post-reproductive periods. The second chapter includes information on the fledglings. In Chapter 3, I analyze the relation between reproduction, molt, and migration.

TABLE 1. Codes and descriptions for habitat variables measured at MCB Quantico, Virginia, 1993-95.

Mnemonic	Variable
1) THA	Density per ha of trees >3cm dbh
2-8) D_S-F	Density per ha of trees 3-8 cm, 8-15 cm, 15-23 cm, 23-38 cm, 38-53 cm, 53-69 cm, >69 cm dbh
9) D_SA	Density per ha of trees 3-15 cm dbh
10) D_BC	Density per ha of trees 15-38 cm dbh
11) D_DEF	Density per ha of trees >38 cm dbh
12-18) BA_S-F	Basal area per ha of trees 3-8 cm, 8-15 cm, 15-23 cm, 23-38 cm, 38-53 cm, 53-69 cm, >69 cm dbh
19) BA_SA	Basal area per ha of trees 3-15 cm dbh (m^2/ha)
20) BA_BC	Basal area per ha of trees 15-38 cm dbh (m^2/ha)
21) BA_DEF	Basal area per ha of trees >38 cm dbh (m^2/ha)
22) D_DEC	Density per ha of deciduous trees $\geq$3-8 cm dbh
23) BA_DEC	Basal area per ha of deciduous trees $\geq$3-8 cm dbh (m^2/ha)
24) D_VP	Density per ha of Virginia pine trees $\geq$3-8 cm dbh
25) BA_VP	Basal area per ha of Virginia pine trees $\geq$3-8 cm dbh (m^2/ha)
26) D_SG	Density per ha of dead trees $\geq$3-8 cm dbh
27) BA_SG	Basal area per ha of dead trees $\geq$3-8 cm dbh (m^2/ha)
28) TSP	Number of tree species
29) WS	Number of woody stems per ha < 3 cm dbh
30) T_BA	Total tree basal area (m^2/ha)
31) PVEG_0.5	Percent vegetation cover - 0-0.5 m
32) PVEG_1.0	Percent vegetation cover - 0.5-1.0 m
33) PVEG_1.5	Percent vegetation cover - 1.0-1.5 m
34) PVEG_2.0	Percent vegetation cover - 1.5-2.0 m
35) PVEG_2.5	Percent vegetation cover - 2.0-2.5 m
36) PVEG_3.0	Percent vegetation cover - 2.5-3.0 m
37) PVEG_6.0	Percent vegetation cover - 3.0-6.0 m
38) PVEG_10	Percent vegetation cover - 6.0-10 m
39) PVEG_15	Percent vegetation cover - 10-15 m
40) PVEG_>15	Percent vegetation cover - >15 m
41) PVEG_U	Percent vegetation cover - understory (0-3 m)
42) PVEG_M	Percent vegetation cover - midstory (3-10 m)
43) PVEG_C	Percent vegetation cover - canopy (>10 m)

Table 1. (Con't)

44) D_OPEN	Distance from the arithmetic center of the home range to the closest opening >1 ha	
45) D_CREEK	Distance from the arithmetic center of the home range to the closest creek	
46) D_FOREST	Distance from the arithmetic center of the home range to the closest mature deciduous or deciduous-pine forest (>70 cm dbh).	
47) ROADS	Total length of roads in a 300 m radius circle centered in the arithmetic center of the home range	
48) CREEKS	Total length of creeks in a 300 m radius circle centered in the arithmetic center of the home range	

CHAPTER 1
PREMIGRATORY MOVEMENTS AND ECOLOGY OF ADULT WOOD THRUSHES

(Abstract)

From May-October 1993-1995, I studied the breeding and postbreeding ecology and habitat use of 61 radio-tagged adult Wood Thrushes (*Hylocichla mustelina*) at the U.S. Marine Corps Base of Quantico, Virginia. Wood Thrushes arrived at the Marine Base in late April-early May. Most adults in the population completed their breeding activities by early August. Eight female Wood Thrushes renested 4 to 10 days after nest failure. Fledglings from adults that renested were attended by both parents. Females attended the young 10 to 17 days before initiating the incubation of the second clutch. Males continued attending the fledglings for 3 to 7 days until fledglings' independence. In single or last clutches, the care of the brood was divided between the parents. During breeding, birds restricted activities to a mean area of 2.6 ± 0.5 ha (95% convex polygon). Of 61 adults radio tagged during the study, 6 were killed, 7 lost their transmitter, and 18 could no longer be located within the study area before molting. The rest (10 F and 20 M) stayed at the Marine Base for molting. Of these, 15 molted in the same area where they nested, and 15 moved 545 to 7290 m from their nesting sites. In general, molting sites were located in areas with more pines, less canopy cover, fewer trees dbh >38 cm, and a denser vegetation in the understory strata than nesting sites ($P < 0.1$). During molt, birds restricted activities to a mean area of 1.4 ± 0.3 ha (95% convex polygon). Identification of the forces behind the selection of the molting sites is complex and the variability among individuals further complicates the problem. Yet, it was evident that for the Wood Thrush, the ecological processes operating before and after reproduction are different and, therefore, information on the reproductive period can not be extrapolated to the postreproductive period.

Introduction

The perceived decline of several species of Nearctic-Neotropical migrants in recent decades (Robbins et al. 1989b, Sauer and Droege 1992) has resulted in an increased concern about the long-term future of these species. The study of the "breeding season," generally referred to as the interval of time during which migrant birds reside in the Nearctic zone, has provided important information. In fact, conservation strategies for migrant species in North America are mostly based on events occurring within this season (Morton 1992). These studies, however, have been focused primarily on the nesting period and they have rarely addressed the postbreeding period.

The postbreeding period in migratory bird species is defined in this study as the interval between the end of reproduction and start of autumn migration. For most migrant passerine species, information about this phase of the annual cycle is unavailable. One of the major reasons for this lack of information is that after birds finish reproducing, they become "secretive" and less likely to be caught, seen, or heard (Ginn and Melville 1983:29-30) making documentation of this phase difficult. Yet, the study of this period, which in some species lasts up to 3 months, may be important, not only because of its intrinsic biological value, but also because of its implications for conservation. During this period individuals of most migrant species must find the appropriate conditions, i.e., food and cover, that allow them to successfully replace their plumage and accumulate fat prior to migration.

It has been generally assumed that during the postbreeding period most migrants stay on the nesting territories where they engage in molt and accumulate fat before autumn migration (Pyle et al. 1987), but apparently individuals of some species abandon their territories after reproduction is over. Such a shift has been postulated for Kirtland's Warbler (*Dendroica kirtlandii*, Bocetti 1993), Prairie Warbler (*Dendroica discolor*, Nolan 1978), Swainson's Thrush (*Catharus ustulatus*, Cherry 1985), and Northern Oriole (*Icterus galbula*, Sealy 1979). Most of these reports are the results of recoveries of banded birds and their value is limited because they represent only a point in the spatial and temporal distribution of the birds.

In this chapter, I report the use of radio tracking to study the movements of adult Wood Thrushes on the breeding grounds. The main objective of the study was to document the movements, behavioral ecology, and habitat use of adults during the postreproductive period. A second objective was to learn more about the nesting ecology of the species. Information on reproductive and postreproductive events is reported in this chapter to facilitate comparisons between the two periods.

The Wood Thrush is an open-nesting, migratory passerine species that breeds in

the United States east of Texas, Oklahoma, Kansas, Nebraska, and the Dakotas, and in southern Canada, and winters on the Caribbean slope from eastern and southern Mexico through Central America to Panama and northwestern Colombia (AOU 1983). During the "breeding season," the Wood Thrush has been identified as a common inhabitant of many types of mature deciduous forest within its geographic range (James et al. 1984). The nesting biology of this species is relatively well known (Bent 1949, Longcore and Jones 1969, Bertin 1977, James et al. 1984) and some information has been reported about the habitat use and social organization on the migratory stopover sites (Winker 1995) and wintering (Rappole et al. 1989, Winker et al. 1990) grounds. However, information about the behavioral ecology and habitat requirements during the postbreeding period is essentially lacking.

Specific questions I address in this chapter regarding the postbreeding period are (1) do males and females stay in the nesting territories to molt or do they move elsewhere?; (2) are the characteristics of the nesting site different from those of sites used for molting?; (3) do pairs stay together after reproduction is over or do they split?; and (4) do males remain territorial when molting?

Reproductive activities for the Wood Thrush have been reported to occur from late April and early May to late July and early August (Longcore and Jones 1969, Delaware; Oberholser 1974:664-665, Texas; Rappole and Ballard 1987, Georgia). On the wintering grounds in southern Mexico, autumn arrival occurred from mid-October to mid-November (Winker et al. 1990). Therefore, about 2 months of the annual life cycle of this species is unknown. Documentation of this interval of the Wood Thrush annual cycle not only would fill a gap in information on its basic biology, but also would provide us with a better understanding of the habitat requirements of this species that is essential to formulate effective conservation plans.

METHODS

From May to October of 1993 to 1995, I captured, radio tagged, and monitored the movements of 61 adult Wood Thrushes (30 F and 31 M) at Quantico Marine Base, northern Virginia. A detailed description of the methods and equipment used in this study can be found in the general methodology. Here, I will give only information that was not mentioned previously.

For timing of breeding, molting, and date of departure from the Marine Base, I relied heavily on radio-tracking data. Direct observation of radio-tagged birds allowed me to record if a bird was breeding (either incubating, brooding nestlings, or caring for fledglings) or molting. Incipient molt was difficult to observe from a distance; therefore, for most birds I approximated the beginning of the molting period by back-dating 15 days

from the time I observed the birds in heavy molt. I base this approach on the observation of 4 individuals captured before they started molt and captured again later in heavy molt, in which 13-16 days elapsed between captures. Additionally, in 8 of 15 birds that changed locality after reproducing, a similar period elapsed between the day they moved to the new locality and the day they were observed in heavy molt.

Starting dates of incubation and/or hatching were extrapolated from known dates for 2 pairs in which incubation was found to require 14 days and fledging to require 12 and 13 days, respectively. Timing for these events agrees with published information (Brackbill 1958, Longcore and Jones 1969).

As noted in the general methodology, characterization of the bird's nesting and dispersal sites was obtained by combining all 0.04 ha circular plots sampled within the boundaries defined by the radiolocations. When a circular plot was located in the area of overlap of 2 or more birds' home ranges, the plot was assigned for analysis to only 1 home range. In summary, 77% (or 24) of the sites were characterized by ≥ 5 plots and 23% (or 7) by 4 plots.

Distance between sites was measured from the arithmetic centers. Date of dispersal, if not known exactly, was considered to be the mid-point between the last date the bird was known to be in the area and the date the absence was noted.

RESULTS

Breeding events

*Breeding chronology.-*Wood Thrushes arrived at the Marine Base in late April-early May. All females and most males mist-netted in early June had either a vascularized brood patch or an enlarged cloaca, respectively. This suggests that initiation of reproduction occurred soon after females arrived. Nestlings from the first clutches fledged in late May or early June. The earliest observation of a fledgling was 2 June. The bird could not fly, which suggests that it had left the nest only 2 to 4 days before. Accordingly, the earliest date that a female Wood Thrush could have started incubation was 8-10 May. Timing for initiation of second or third clutches were associated with the success or failure of previous clutches. The latest record of breeding Wood Thrushes occurred in 1994. On 9 August, I found a nest of a radio-tagged male with 3 eggs. This male and his mate finished attending fledglings on 13 and 15 September, respectively. The span of the breeding season for this population covered the period from early May to mid-September, although most adults in the population completed their breeding activities by early August (Figure 1.1).

Female Wood Thrushes commonly renested after nest failure (Figure 1.1). On average 7.4 ± 0.8 d ($n = 8$) elapsed between the loss of a clutch and the beginning of the incubation of the replacement clutch. If the construction of the nest, which is done by the female only, takes about 5 days (Bent 1949:109, Bertin 1977), then females must have started almost immediately to build a new nest after failure. I only documented 1 case of a female successfully raising 2 clutches; however, 4 females initiated a second clutch after they had successfully raised young in a previous clutch. This suggests that fledging 2 clutches may not be a rare occurrence.

*Attendance of fledglings.-*Fledglings of adults that renested were attended by both parents. In 3 pairs with 1, 2 and 3 fledglings, respectively, there was not an apparent division of labor; both parents attended and fed the young. In 5 additional pairs that raised at least 1 young, I could not determine if both parents attended the young because at that time I had radio tagged only 1 member of the pair. Once females started the construction of the next nest, their involvement in the attendance of the fledglings decreased until it ceased when females started incubation. On average, females attended the young 13 ± 1.3 d ($n=5$, range 10-17 d) before they initiated incubation of the second clutch. Once females started incubation, the males continued to attend the fledglings for 6 ± 0.7 d (range 3-7 d) until fledglings' independence. During the time that fledglings were still attended by one or both parents, they remained together and were always ≤ 200 m from the nest.

In single or last clutches, 5 in this study, the care of the brood was divided between the parents, with each parent feeding only certain individuals of the brood. Males and females not only divided the brood, but also they were spatially separated. Figures 1.2 and 1.3 show the area used by 2 pairs during the attendance of the fledglings and molt. When there was spatial overlap between males and females, e.g., M603 and F509, it did not occur at the same time.

Mate switching and desertion.- During June-August, radio signals of 15 females and 3 males were lost after nest failure. I assumed these birds left the Marine Base. Of these, 13 females and 1 male left in June (6) and early July (8). Because these birds disappeared at a time in the season when other birds were still initiating nests, it is probable that some of these birds renested elsewhere. After nest failure in 8 radio-tagged pairs, the female renested with the same male on 7 occasions. They renested 122 ± 26.4 m (range 16-190 m) from the previous nest. This average did not include a pair that moved 4.3 km to renest. This pair fledged 1 young from their first nest, renested 95 m from the first nest and moved 4.3 km to initiate a third nest after the nestlings of their previous clutch were predated.

I only identified 1 female switching to a different male after nest failure. This

female moved 1470 m from her previous nest to initiate a new clutch. Switching of mates by females was probably more common, but I could not document it because several females moved out of the Marine Base. I positively identified the first mate for 6 of the 15 radio-tagged females that left the Marine Base at mid-season. During the next 2-3 weeks before they left and/or started molting, none of these 6 males was associated with a subsequent nest, although 3 of them were seen with other birds. Three of these males were left attending a single young.

All successful females ($n = 8$), i.e., females that fledged at least 1 young, renested with the same male. Subsequent nests were located at an average distance of 69 ± 13.8 m (range 17-117 m) from the previous nest.

*Reproductive success.-*Nest predation was high. Of 50 Wood Thrush nests found over the 3 years of study, including 14 replacement nests, 34 (68%) failed. I could not identify the cause of failure. In 82% of unsuccessful nests, failure occurred during the nestling stage.

*Mobility and behavior.-*During reproductive activities, average distance between consecutive radiolocations (mobility) of 23 adults (13F and 10M) was 114 ± 9.0 m, and distance from arithmetic center (FCEN) of home range was 107 ± 8.0 m. Wood Thrushes restricted their movements to an area of 3.9 ± 0.6 ha (100% convex polygon) or 2.6 ± 0.5 ha (95% convex polygon). There were no differences between sexes for any of these values ($0.13 < P < 0.8$). During the pre-incubation period and before renesting, males and females of radio-tagged pairs moved together and generally moved over a larger area. Once the female started incubation, males concentrated movements around the nests. I did not detect "extra-territorial trips" such as those reported in males of other species (e.g, *Dendroica discolor*, Nolan 1978; *Fringilla coelebs*, Hanski 1992), but males' response to my presence and relatively infrequent (once/48 hrs) observations could have prevented me from observing this behavior.

The postbreeding period

During the postbreeding period, adult Wood Thrushes undergo prebasic molt. In Chapter 3, I address in detail the pattern and chronology of the molt. Prebasic molt was complete (i.e., included wing, tail, and body feathers) and lasted on average 51 d.

Of 61 adults radio tagged during the study, 6 were killed, 7 lost their transmitter, and 18 moved out of the study area before molting. The rest (10 F and 20 M) were observed molting at the Marine Base. Of them, 15 (6 F and 9 M) molted in the same area where they nested, and 15 (4 F and 11 M) molted in a different location. Of the birds that molted in the same area where they nested, 10 molted within the mature forest and 4 (all

males) molted in sapling growth located at the forest edge or as patches surrounded by forest. Birds that left the nesting area moved 2015 ± 520 m (range 545-7291 m) from their nesting sites. Of the 30 birds that stayed at the Marine Base for molting, 4 were positively identified as pairs. Three of these pairs moved out of the nesting area for molting. Males and females were 320 m, 2.1 km, and 4.8 km apart (as measured by the distance between the arithmetic center of their home ranges), respectively. The male and female of the pair that stayed on the nesting area for molting were separated by 320 m.

*Mobility and behavior.-*Once the adults started molting, they became very sedentary. Average distance between radiolocations (mobility) at this time was 67 ± 8.0 m (n = 23 ind.). Their movements were restricted to an area of 3.6 ± 1.7 ha (100% convex polygon) or 1.4 ± 0.3 ha (95% convex polygon), and the mean distance (FCEN) from the arithmetic center of this area to all locations was 68 ± 7.0 m. Comparison of these values with those when birds were reproducing are shown in Table 1.1.

Molting adults were difficult to observe. When tracked, they moved into dense patches of vegetation, frequently among the branches of fallen trees. Although I did not follow a formal protocol to test for territorial behavior in molting male Wood Thrushes, several lines of evidence suggest that this behavior was absent. First, I never observed a molting bird in any activity associated with territorial behavior such as chasing, singing, or calling. Further, on 10 occasions, to 4 different males, I played a 3-min tape recording of Wood Thrush songs and alarm calls. I did not observe any response from the molting birds. This same tape successfully caused breeding males to approach the speaker when I used it earlier in the breeding season. Second, I observed and captured 6 adults and 8 juvenile molting, non-marked Wood Thrushes on the same sites where 2 radio-tagged individuals were molting. Third, molting birds seem to experience impaired flight efficiency (see Chapter 3), which seems essential for territorial behavior. Last, starting in early autumn when several radio-tagged Wood Thrushes were still molting, there was an influx of birds that had reproduced elsewhere. The large number of Wood Thrushes foraging on fruits in the same sites where some birds were molting made territorial behavior most probably not cost-effective.

Habitat use

*Vegetation attributes.--*Univariate comparisons of pooled data among nesting, molting, and nesting-molting sites showed significant differences in 9 structural variables (Table 1.2, Kruskal-Wallis test, P < 0.05). Further, multivariate assessment of differences among sites, including the 9 variables, resulted in rejection of the following null hypotheses of (1) no difference among nesting, molting, and nesting-molting sites (MRPP statistic = -9.74, P < 0.001), (2) no difference between nesting and molting sites (MRPP statistic = -11.55, P < 0.001), (3) no difference between nesting and nesting-

molting sites (MRPP statistic = -2.38, P = 0.036), and (4) no difference between molting and nesting-molting sites (MRPP statistic = -5.21, P = 0.002). Box plots of the 12 variables (Figs. 1.4 and 1.5), show that (1) for 8 variables, variability in the range of values was greater in the molting sites than either nesting and nesting-molting sites, and (2) vegetation attributes of sites used for nesting-molting tended to be intermediate between nesting and molting sites (Fig.1.6).

To further clarify individual trends, I performed paired comparisons regarding vegetation attributes (Table 1.3). Only 12 individuals that changed location for molting, and for which information on both nesting and molting sites was available, were included in the analysis. General trends (i.e., analysis in pooled data) did not hold when birds were examined individually (Table 1.3). For instance, variables such as density of snags (D_SG), density of trees dbh 15-38 cm (D_BC), density of trees dbh >38 cm (D_DEF), midstory percent cover (PVEG_M) and total basal area (T_BA) were not significantly different in the analysis of pooled data, but there were significant differences for some individuals. In some variables the direction of the higher value (i.e., nesting or molting sites) differed among individuals, so no trend was apparent when data were combined across individuals even though sites differed significantly for some individuals. Similarly, understory percent cover (PVEG_U) was significantly different between nesting and molting sites in pooled data, but the difference was not significant for 7 of the 12 birds analyzed individually.

Number of tree species present in nesting, molting, and nesting-molting sites were 17, 23, and 18, respectively. There was not a clear pattern of differences between nesting, molting or nesting-molting sites regarding proportion of sites where the species occurred, contribution of each species to the overall composition, or proportion of times that the species was 1 of the 3 more numerous species in a given site (Appendix A).

*Landscape.--*Nesting and molting sites differed in distance to nearest deciduous and deciduous-pine mature forest (D_Forest) and distance covered by creeks (Creeks) (Table 1.4). Nesting sites were mostly located within forest and had more creeks within a 300 m radius circle. None of the other variables was found to be significantly different. Nesting-molting sites were, for most variables, more similar to the nesting sites. The individual distribution of nesting, molting and nesting-molting sites in the space defined by 3 of the 6 landscape variables is shown in Fig. 1.7.

I also examined differences among nesting, molting, and nesting-molting sites considering 4 variables simultaneously (distance to the nearest road, distance to the nearest mature deciduous or deciduous-pine forest, distance covered by road, and distance covered by creeks). I tested the following null hypotheses of (1) no difference among nesting, molting, and nesting-molting sites (MRPP statistic = -3.17, P = 0.011), (2) no

difference between nesting and molting sites (MRPP statistic = -4.11, *P* = 0.005), (3) no difference between nesting and nesting-molting sites (MRPP statistic = .829, *P* = 0.936), and (4) no difference between molting and nesting-molting sites (MRPP statistic = -3.43, *P* = 0.011).

Time of departure

After molt was completed, or almost completed, and before leaving the Marine Base, most adult Wood Thrushes maintained a similar pattern of movements and stayed in the same site. Ten females and 7 males left the Marine Base without an apparent change in their pattern of movements. For several of these birds, however, I observed an improvement in their flying capabilities at the end. Although they stayed in the same area, they moved faster when I tracked them and they moved to spots that were not visited before. These locations were always associated with the presence of fruiting trees.

For other individuals that molted at the Marine Base, a change in movements was more obvious. For example, 2 weeks before leaving the Marine Base, a male moved 500 m from his nesting-molting site to a site never visited before, stayed 2 days and then moved back to his previous nesting site (Fig. 1.8). Two males moved 4.4 km and 500 m from their molting site back to their nesting area, stayed 2 and 22 days, respectively, and then left the Marine Base. Four males that molted in sapling stands adjacent to or within their area, moved back to the forest 3, 8, 15, and 23 d before leaving the Marine Base. None of the birds that moved back to their nesting area showed any territorial behavior, nor did they show the same pattern of movement as when they were breeding and defending a territory (see Fig. 1.9 for 2 examples). They mostly restricted their activities to certain spots characterized by the presence of at least one big tree, mainly blackgum or flowering dogwood, covered with ripe fruits.

Adults that stayed at the Marine Base for molting apparently left the Marine Base suddenly. I never relocated them after they were regarded as missing. The earliest date for an adult to leave the Marine Base after molting was 15 September and the latest was 14 October. Most birds (*n* = 21), however, left between 22 September and 10 October.

DISCUSSION

Reproductive activities

The duration of reproductive activities for the Wood Thrush has been reported to be from late April and early May to late July and early August (Longcore and Jones 1969, Delaware; Oberholser 1974:664-665, Texas; Rappole and Ballard 1987, Georgia). At the Marine Base, some individuals continued reproductive activities into mid-September.

However, for most individuals the reproductive period extended about 12 weeks, from early May to early August.

   Renesting, double broodedness and attendance of fledglings.--My data suggest that double-broodedness is common in the Quantico population of Wood Thrushes. Brackbill (1958) found double broodedness to be the rule in 9 pairs that he studied in Baltimore, Maryland. A division of the attendance of single or final broods by parents also has been reported for the Wood Thrush (Bent 1949, Brackbill 1958), and Brackbill (1958) even suggested that there may be a similar division in the care of first broods.

   Division of the attendance of fledglings has been reported in several species of passerines (see references in Moreno 1984 and McLaughlin and Montgomerie 1985) and is thought to be an advantageous strategy for reasons such as reduced predation or improved foraging efficiency. Smith (1978), for example, argued that brood division allows parents to locate young more easily, to regulate food delivery to the young more efficiently, and to facilitate detection of danger. Mellen et al. (1992) speculated that a separation in home range in Pileated Woodpeckers (*Dryocopus pileatus*) when attending fledglings results because food or other resources may become limited when rearing young. For the Wood Thrush and other species (e.g., Prairie Warbler, Nolan 1978), joint attendance of first broods, but division of single or last broods suggests that besides reducing predation and increasing foraging efficiency, other factors such as mate guarding could be important. In first broods, splitting of the brood and physical separation between male and female would increase the risk of females engaging in extra-pair copulations, as suggested by Weatherhead and McRae (1990) in their study of American Robin (*Turdus migratorius*). Moller's (1991) observations of Barn Swallows (*Hirundo rustica*) indicated that mate guarding was not severely constrained by parental care, and the intensity of mate guarding during the fertile period was as high during second as during first clutches. When the pair does not breed again that season, however, mate guarding is unnecessary and by separating the brood and moving to different sites, parents may take advantage of more optimal exploitation of food resources and a reduction in the chances of complete predation of the brood because fewer birds are together.

   Within-season breeding dispersal.-- Within-season breeding dispersal is thought to be a strategy to gain rapid renesting, avoid predation, and/or avoid depleted resources (Jackson et al. 1989). For instance, Haas and Sloane (1989) stated that female Loggerhead Shrikes (*Lanius ludovicianus*) sometimes leave the breeding territory soon after their young fledged and may wander during mid-season to locate unpaired males. My data show that within-season breeding dispersal was fairly common in the Wood Thrush.

   The observation of 3 females leaving the males attending fledglings is the first

time this has been reported for the Wood Thrush. Desertion by one of the parents was tested experimentally in the Snail Kite (*Rosthramus sociabilis*) by Beissinger (1990). He concluded that desertion occurs when a single parent is capable of caring for the offspring alone. Jackson et al. (1989) mentioned that female desertion has been interpreted as a strategy to accelerate the process of starting a new clutch. In Prairie Warblers, they argued, female desertion to increase renesting speed is not advantageous because males assume care of fledglings when females attempt a new brood, freeing the females for rapid renesting without incurring a time cost of dispersal. A similar argument could apply for the Wood Thrush. Five double-brooded pairs for which chronologies were known had an average interval of 13 ± 1.3 d between fledging of the first brood and the onset of the incubation of the next clutch. Females whose nests were predated started incubation of a replacement clutch 7.4 ± 0.8 d after nest failure. Thus, by dispersing, a female Wood Thrush would gain about 6 days. The net gain, however, would be less because of the time used in moving to a new place and finding a new mate.

The predation-avoidance hypothesis predicts that more moves should occur after unsuccessful nests than after successful nests. My data do not show a clear trend. Eight pairs renested 69 ± 13.8 m from the previous nest after fledging at least 1 young. On the other hand, 7 females renested 122 ± 26.4 m from the position of a previously predated nest (Wilcoxon tests, $Z = -1.37$, $P = 0.171$). This last average does not include, however, a pair that moved 4.3 km from a previously predated nest, and a female that moved 1.4 km to renest with a new mate after failure of her previous nest.

The dispersal and renesting of a pair documented here is the first report of this behavior for the Wood Thrush. As mentioned earlier, this pair fledged 1 young in their first nest, renested 95 m from the first nest, and after the failure in this second nest, they moved 4.3 km to initiate a third nest. Another radio-tagged pair left the Marine Base on 27 June after nest failure, but I could not locate them. Haas (1995) reported that a pair of American Robins moved 2.4 km to renest within a season. In their work on Gray Catbirds (*Dumetella carolinensis*), Darley et al. (1971) found after nest failure, most female Gray Catbirds moved with their mates up to 450 m from their previous territorry. They suggested that dispersal by pairs is an advantageous strategy because of the time that would be lost in finding a new mate and re-pairing. Jackson et al. (1989), however, questioned this argument. According to them, previous studies, which they cited, show that for most species local habitats are already saturated by territorial males, some of them unmated, that would make the establishment of a new territory very difficult.

Selection of site for molting

Thirty radio-tagged adult Wood Thrushes molted at the Marine Base, 15 in the same area where they reproduced and 15 elsewhere. Capture of individuals outside their

breeding range during the postbreeding period often has been documented (Nolan 1978, Cherry 1985, Rappole and Ballard 1987, Bocetti 1993), and has been interpreted generally as a result of birds looking for better places to forage, molt, and accumulate fat (Rappole and Ballard 1987). For the Turdinae, Cherry (1985) presented data showing that some Swainson's Thrushes leave their breeding areas before starting to molt, or when they are still in the early stages of molt. He captured thrushes 30 to 250 km from their closest breeding range.

This hypothesis that states that adults leave the nesting area to look for sites where production of food is higher assumes that, (1) during the course of the breeding season, food resources in the nesting area are depleted or diminished to a point where it is not cost-effective to stay; (2) availability of food resources in the nesting sites was always low; (3) food availability changes seasonally and consequently, a "good quality" site early in the breeding season may not be good later in the season; or (4) post-breeding adults are food opportunistic, and they change their diet to use the abundant fruit resources available at that time.

The importance of food resources during the reproductive stage can not be doubted. Birds must have access to areas where food is adequate in quantity, quality, and availability. However, most evidence for food limitation around the nesting sites is correlative and availability of food resources is rarely quantified (Newton 1980). An often cited paper that favors the hypothesis of food depletion around the nest site is that of Greig-Smith (1982). He contended that Stonechats (*Saxicola torquata*) move to renest far from previously-successful nests because food around the nests has been depleted. Sullivan (1989) and Jackson et al. (1989), however, suggested that for the Yellow-eyed Junco (*Junco phaenotus*) and Prairie Warbler, respectively, resources in the nesting sites do not seem to be limited. To my knowledge, the idea that a bird cannot find enough food for its molt and therefore moves out of the nesting familiar area remains speculative. In this study, I did not quantify temporal or spatial differences in food availability, but I did record the presence or absence of fruits on plants of species consumed by Wood Thrushes. In general, production of fruits in forest edges and disturbed or otherwise young forest patches began in mid- and late July whereas in mature deciduous or deciduous-pine forest fruit production started late August and early September. I did not find any pattern that related the initial location of radio-tagged molting adults with the presence/absence of fruiting plants. This analysis, however, ignores the fact that Wood Thrushes still forage on insects during the molting period. The type and amount of invertebrates that compose the diet of molting Wood Thrushes is unknown.

I did not find a relationship between number of young fledged by the adults and their decision to stay or move out from the nesting area for molting. This analysis could be biased (1) if there were unnoticed breeding pairs in the area, (2) if foraging sites were

shared among reproductive adults, or (3) if foraging sites were not detected because they were located out of the nesting area. It is likely that the radio-tagged individuals were not the only Wood Thrushes nesting in the area. For instance, on a site where I mist-netted for 1000 net/hrs every 2 weeks from June to September, I captured 8 adult females and 26 adult males with a brood patch or an enlarged cloacal protuberance, respectively. All these birds, which were not radio tagged, were captured before 15 July and therefore could have been nesting within or close to the grid but I did not locate their nests. It was not uncommon to capture Wood Thrushes besides the parents when I handled nestlings for radio tagging. On one occasion, to capture the mate of a radio-tagged female, I set 4 nets 10 m from the nest (with 2-day old nestlings at the time). In the subsequent 20 min I captured the radio-tagged female and 4 unbanded males.

To my knowledge differences between nesting and foraging sites have not been documented for the Wood Thrush. In this study, during the nestling and fledging-dependence stages, parents seemed to forage <300 m radius from the nest or fledgling's position. My presence when tracking these birds, however, may have caused the adults to move closer to the nest or fledglings, therefore biasing my observations. That some breeding adults moved farther than 300 m from their nest is suggested by net captures. Four incubating females were captured 400-600 m from their nests and a male was captured 800 m from its nest with fledglings. It is possible that in this study the location of breeding adults may have been more related to nesting than feeding activities. Different locations of nesting and foraging sites have been documented for other species. Hermit Thrushes (*Catharus guttatus*) nest in sites with small white fir trees (*Abies concolor*) but do not use these areas for foraging (Martin and Roper 1988). Steele (1993) proposed that nesting sites may be more important than foraging sites in determining the habitat that Black-throated Blue Warblers (*Dendroica caerulescens*) select. These and other authors (e.g., Ricklefs 1969, Best and Stauffer 1980, MacKenzie et al. 1982, Martin 1988, Rotenberry and Wiens 1989) have suggested that for open-nesting birds, habitat selection during the breeding season is apparently most critically influenced by the availability of protected nest-sites because of high nest predation. The extent to which food availability influences habitat selection in molting Wood Thrushes remains unknown. The situation is further complicated by the fact that half of the 30 tagged Wood Thrushes stayed in their nesting areas to molt and half moved out. More detailed studies that document the type and amount of food items consumed by breeding and molting Wood Thrushes, the location and characteristics of foraging sites, and the availability of food resources and seasonal changes are necessary before conclusive remarks can be drawn.

Food availability is likely to be important in the selection of molting sites. However, selection of molting sites could also be related to other factors. My data are not strong, but suggest that neither sex or date of molt initiation was related to the probability

of staying in or moving out of the nesting area. There is a possibility that reproductive success was involved. Eighty percent of the birds that moved did so after the last nesting attempt failed, but only 50% of the birds that stayed failed in their last attempt. Similarly, 50% of the birds that stayed were attending fledglings before molting, but only 18% of the birds that left had fledglings. Reproductive status of females' mates and neighboring males may also have influenced the selection of molting site. After nest failure, males constantly followed their mates until they renested. A female ready to molt could find it difficult to settle and initiate molt if her mate or neighboring males constantly harassed her. On 3 occasions that I was able to track females the last day that they were in the nesting familiar area, I observed these females moving through different males' territories and males joining them while they were in their territories. Similarly, a male ready for molting after his mate left could find it difficult to do so in his nesting territory if neighboring males are still breeding and trying to expand their territories. For instance, a male moved 30 July to a sapling stand located about 300 m from his nest to start molting while at least 2 of his neighboring males were still singing. These interpretations are speculative, but they are important to mention because they could stimulate publication of similar observations.

Another factor that surely influenced the choice of molting site was vegetation structure. During the molting period the vulnerability of adult Wood Thrushes to predation may be high because of impaired flight efficiency (see Chapter 3) . Survival during this period can be enhanced by behavioral inconspicuousness and /or selection of safe areas. Vegetation attributes that may enhance protection, such as number of woody stems, percent vegetation in the 0-3 m understory interval, and number of deciduous saplings were significantly higher in molting than nesting sites. These attributes were mainly found in Virginia pine forest, young deciduous stands, and forest edges. Virginia pine stands were particularly good in providing molting Wood Thrushes with fallen trees and dense thickets into which they moved when I tracked them. The safety of sapling-deciduous stands was probably related to proximity of individual trees that could make it difficult for predators to move through, and perhaps also by breaking the image of chased birds. The importance of sapling stands as "safe zones" is suggested by the observation that breeding Wood Thrushes often moved to these places when I tracked them for a long time.

The appropriateness of some nesting areas to offer cover to molting birds is perhaps indicated by the fact that nesting-molting sites (7 in this study) were, to some extent, intermediate in characteristics between nesting and molting sites.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Wood Thrushes remained at the Marine Base about 2 months after they finished breeding. During this time, Wood Thrushes underwent molt. The availability of the appropriate habitat for molting has important implications for the survival of the individual. Wood Thrushes must have access to habitats that provide them with adequate cover to avoid predation and food resources to fulfill the energy demands during the molt process. A healthy plumage has important implications, not only for their future survival during migration and on wintering grounds, but also for their reproductive performance the following year.

So far, we have been relatively successful in identifying the characteristics of the habitats associated with the reproductive activities of Wood Thrushes and many other migratory species, as well as in establishing correlations between the characteristics of those habitats and the reproductive output or performance of birds. Yet, of habitat needs, social behavior, and ecology, during the postbreeding period, we knew essentially nothing. Roth and Johnson (1984), for instance, have done an excellent work in documenting the dynamics of a Wood Thrush population in a 15-ha woodlot in Delaware over 22 years. They throughly discussed the population dynamics in this forest fragment and its relation to regional trends. However, nothing is mentioned of the activities during the period after the fledging of young and beginning of migration.

My data show that the identification of the driving forces behind the selection of the molting sites are complex and that the variability among individuals further complicates the problem. Yet, it is evident that for the Wood Thrush, the ecological processes operating during the reproductive period are different from those operating during the postreproductive period, and therefore, information on the reproductive period cannot be extrapolated to the postreproductive period. My data suggest that a conservation strategy that focuses on identifying and protecting nesting habitat during the breeding season, although important, it is incomplete at best if the events and needs during the postreproductive period are not considered.

It has been assumed that during the reproductive period, birds remain in a relatively small area. Regarding the Wood Thrush, for example, Able et al. (1984) commented from their studies of homing behavior in this species that, "It seems unlikely that birds which spend nearly all of the time during the breeding season within a small territory would be familiar with landscape features in an area of over 900 km^2." At the Marine Base, individual Wood Thrushes were restricted to an area of about 4 ± 3 ha during reproductive activities. Some of these birds stayed and molted basically in the same area. Yet, several others moved up to 7290 m within the Marine Base. I have discussed in this chapter some possible factors, but the question of why some birds stayed

and why some moved remain unsolved. But whatever the reasons, the fact is that half of my birds shifted sites and molted in areas with characteristics different from those where they nested. Large forested areas with a mixture of forest associations and ages, as the Marine Base and Prince William Forest, apparently can provide nesting and molting habitat to the local Wood Thrush breeding population. In fragmented landscapes, forest fragments may be appropriate for nesting but not for molting, or at least not for all individuals breeding there. Some individuals may need to move and find appropriate habitat for molting elsewhere before starting migration. The individual costs of these movements in terms of time searching and finding adequate habitat (survivorship) have not been studied and, therefore, their effects on the perceived population declines in this species are unknown.

TABLE 1.1. Comparison of mobility (m), Fcen (m) and area used (ha) between "nesting" ($n = 23$) and "molting" ($n = 23$) radio-tagged adult Wood Thrushes. MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\bar{\times}$	SE	Z[b]	P
Mobility	Nesting	114.5	9.0	3.13	.002
	Molting	67.2	8.0		
Fcen	Nesting	107.4	8.0	2.72	.006
	Molting	68.2	7.0		
Area (100%)	Nesting	3.9	0.6	2.32	.019
	Molting	3.6	1.7		
Area (95%)	Nesting	2.6	0.5	1.88	.058
	Molting	1.4	0.3		

[a]Mobility: average distance between consecutive point locations; Area: size of the area which included all radiolocations of interest (100% and 95% convex polygon); Fcen: average distance from the arithmetic center of the home range to every location.

[b]Wilcoxon 2-sample test (Normal approximation with continuity correction of 0.5).

TABLE 1.2. Comparison of vegetation attributes among "nesting" ($n = 12$), "molting" ($n = 12$), and "nesting-molting" ($n = 7$) sites for radio-tagged adult Wood Thrushes. MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\overline{x}$		SE	Z[b]	P
THA	Nesting	1121	**a**	79	12.69	.001
	Molting	2059	**b**	262		
	Nesting/Molting	1514	**ab**	123		
D_DEC	Nesting	1016	**a**	80	7.12	.028
	Molting	1655	**b**	263		
	Nesting/Molting	1273	**b**	71		
D_VP	Nesting	34	**a**	9	10.89	.004
	Molting	318	**b**	57		
	Nesting/Molting	141	**ab**	59		
D_SG	Nesting	72		7	3.98	.136
	Molting	86		17		
	Nesting/Molting	100		7		
D_SA	Nesting	820	**a**	80	11.91	.002
	Molting	1732	**b**	280		
	Nesting/Molting	1137	**ab**	91		
D_BC	Nesting	250		9	2.71	.258
	Molting	328		40		
	Nesting/Molting	320		34		
D_DEF	Nesting	52	**a**	6	11.33	.003
	Molting	26	**a**	9		
	Nesting/Molting	115	**b**	52		
T_BA	Nesting	2353	**a**	110	7.52	.023
	Molting	2311	**a**	96		
	Nesting/Molting	2876	**b**	171		
PVEG_U	Nesting	14	**a**	1	16.36	.000
	Molting	25	**b**	2		
	Nesting/Molting	16	**a**	2		
PVEG_M	Nesting	68		3	0.49	.779
	Molting	67		3		
	Nesting/Molting	70		3		
PVEG_C	Nesting	59	**a**	4	17.31	.000
	Molting	29	**b**	4		
	Nesting/Molting	59	**a**	6		
WS	Nesting	2730	**a**	280	18.61	.000
	Molting	9848	**b**	1033		
	Nesting/Molting	4341	**a**	862		

[a] Name and description of vegetation codes are given in Table 1. Means with the same letter were not significantly different ($P > 0.05$, nonparametric multiple comparison for unequal samples, Zar 1996:227).
[b] Kruskal-Wallis test (Chi-Square Approximation).

TABLE 1.3. Results of statistical tests (Wilcoxon test) examining differences in vegetation attributes between "nesting" and "molting"sites for 12 radio-tagged adult Wood Thrushes. MCB Quantico, 1993-95[a].

ID	THA	D_DEC	D_VP	D_SG	D_SA	D_BC	D_DEF	PVEG_U	PVEG_M	PVEG_C	WS	T_BA
M902	M***	M**	M***	M	M***	M***	N**	M**	N	N*	M***	N
M919	M**	M**	M**	N	M*	N	N*	M*	N	N	M**	N
M546	M**	M*	M	N	M**	N	N	M	M	N**	M*	N
M514	M	M	M	N	M	N	M	M	N*	N	M	M
F904	M	M	M	N	M	M	N	M**	M	M	M*	M
F516	M*	M	M*	M**	M	M	M	M**	N	N**	M	M**
M928	M**	M	M	M	M**	M**	N	M	M	N	M**	M
M555	M**	M*	M**	N**	M*	M	N**	M	M	N**	M	N**
F509	M***	M	M**	M	M**	M*	N**	M**	N	N*	M**	N
M603	M**	M*	M***	M	M**	M**	N**	M	N*	N**	M**	N
F991	N*	N	N	N	N	N*	M	M	M	N	M	M
M933	M**	M*	M**	M	M**	M	N**	M	N**	N	M	N

[a] Names and description of vegetation codes are given in Table 1. N (nesting) and M (molting) indicate the site where a higher value occurred. * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.008$.

TABLE 1.4. Comparison of landscape parameters among "nesting" (*n* = 12), "molting" (*n* = 12), and "nesting-molting" (*n* = 7) sites for radio-tagged adult Wood Thrushes, MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\bar{x}$		SE	Z[b]	*P*
D_Road	Nesting	244	**ab**	40	5.41	.066
	Molting	188	**a**	36		
	Nesting-Molting	301	**b**	35		
D_Open	Nesting	197		44	1.39	.498
	Molting	256		37		
	Nesting-Molting	261		45		
D_Creek	Nesting	90		13	1.41	.495
	Molting	168		52		
	Nesting-Molting	82		15		
D_Forest	Nesting	0	**a**	.	15.45	.000
	Molting	139	**b**	46		
	Nesting-Molting	5	**a**	5		
Roads	Nesting	125		39	4.81	.090
	Molting	456		103		
	Nesting-Molting	181		54		
Creeks	Nesting	940	**a**	134	7.85	.019
	Molting	493	**b**	94		
	Nesting-Molting	879	**a**	123		

[a]D_Road, D_Open, D_Creek, and D_Forest are the distance from the arithmetic center of the home range to the nearest road, forest edge or opening ($\geq$ 0.4 ha), creek, and mature deciduous and deciduous-pine forest (dbh $\geq$ 38 cm), respectively. Roads and Creeks are the total distance of roads and creeks in a circle of 300 m radius. Means with the same letter were not significantly different (*P* >0.1), nonparametric multiple comparison for unequal samples (Zar 1996:227).
[b] Kruskal-Wallis test (Chi-square approximation).
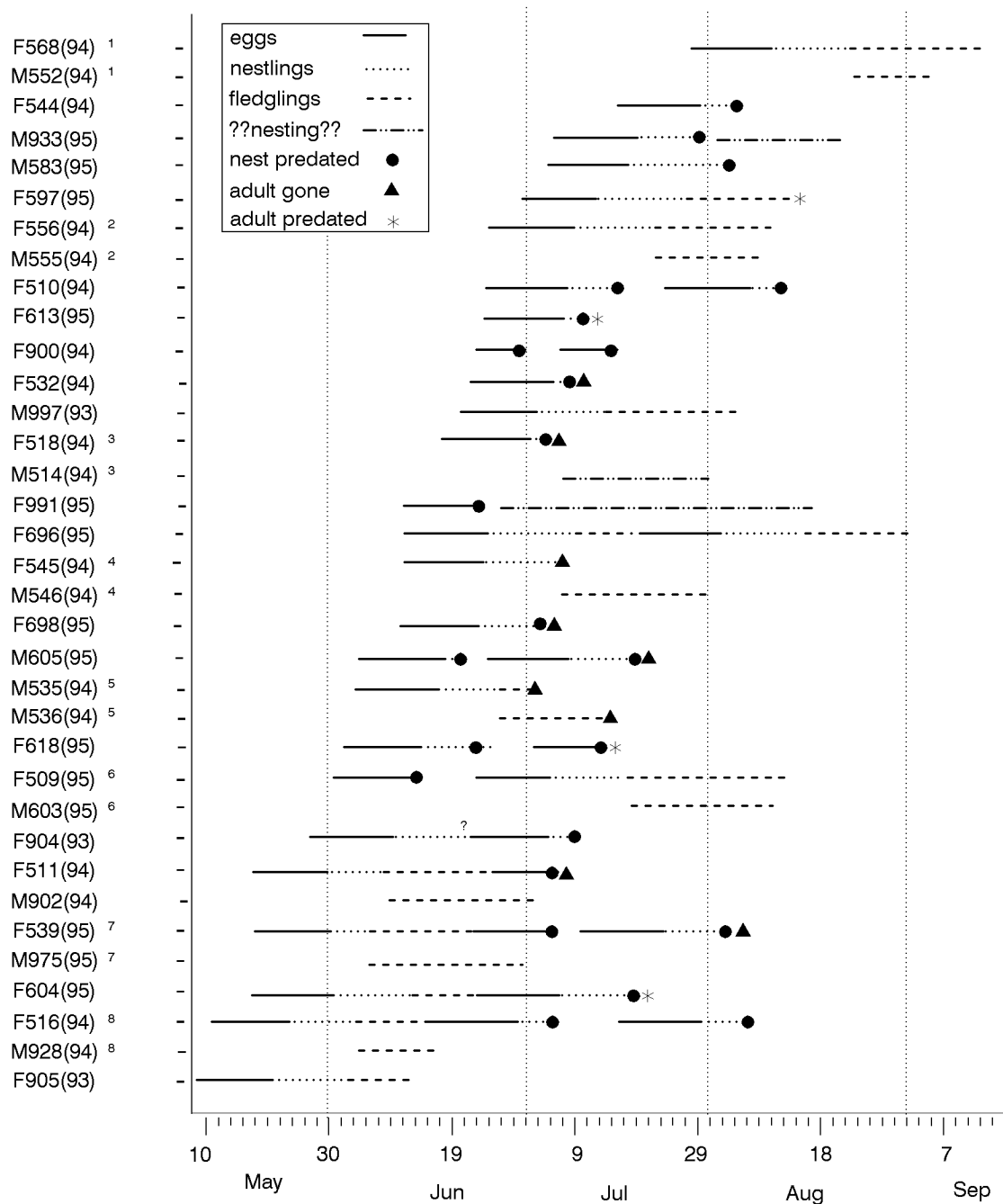
Fig. 1.1. Reproductive chronology of radio-tagged Wood Thrushes. Members of a pair are joined by a number. MCB, Quantico, Virginia, 1993-95.
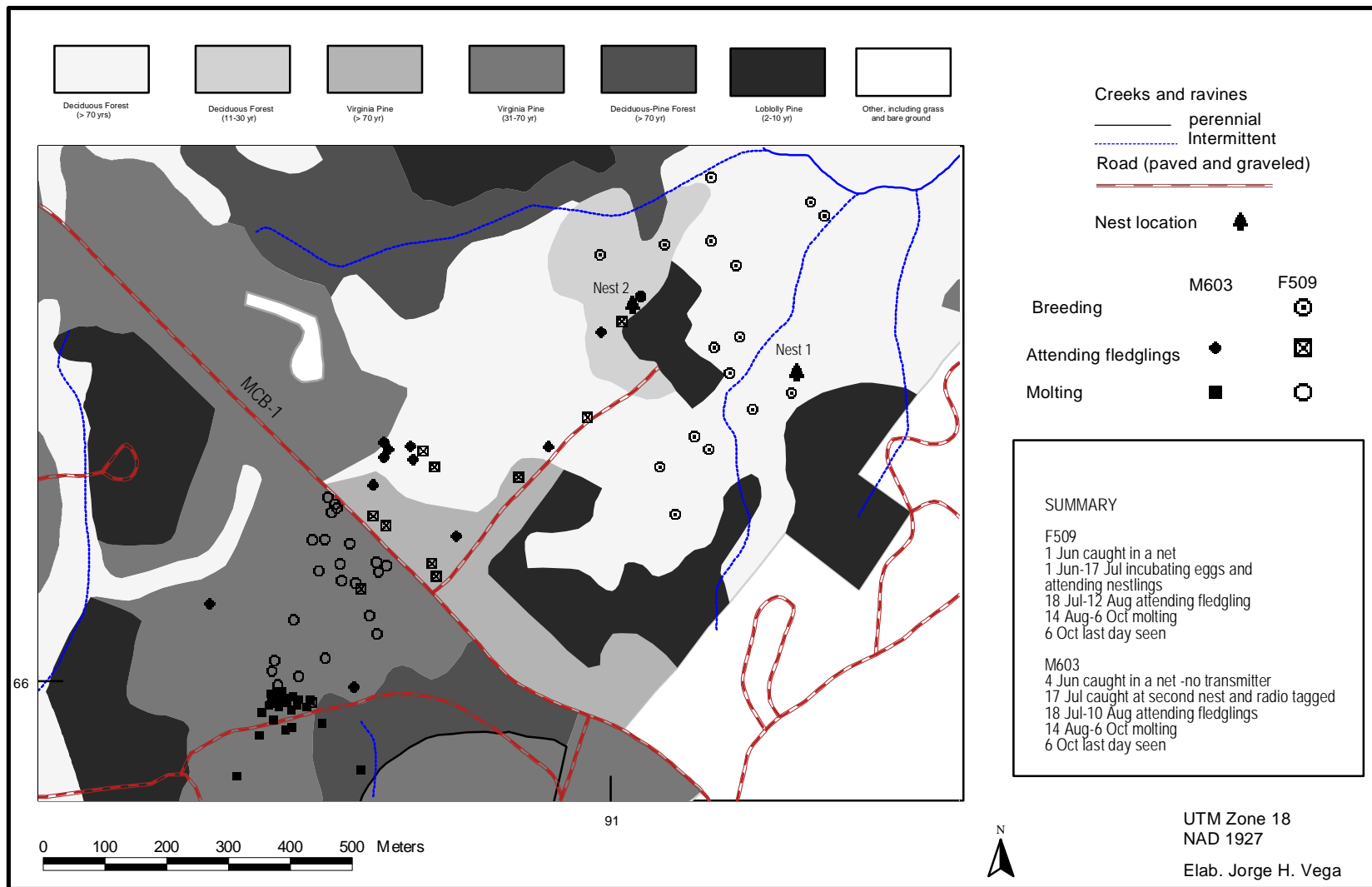
Fig. 1.2. Radiolocations of M603 and F509 during the reproductive and molting periods, MCB Quantico, Virginia, 1995.

Deciduous Forest (> 70 yrs)

Deciduous Forest (11-30 yr)

Virginia Pine (31-70 yr)

Deciduous-Pine Forest (> 70 yr)

Loblolly Pine (2-10 yr)

Other, including grass and bare ground

Creeks and ravines
perennial
Intermittent
Road (paved and graveled)

Nest location

M552   F568

Attending fledglings

Molting

F568 radiolocations - attending fledglings and molting

M552 radiolocations - attending fledgling and molting

18Jul

66

91

SUMMARY

18 July
M552 caught in net and radio tagged

9 August
Nest found, eggs

22 August
Three young radio tagged in the nest.
F568 caught by the nest

23 August-5 September
M552 attending one fledgling

23 August-14 September
F568 attending 2 fledglings

22 August-10 October
M552 molting. 10 Oct last day seen

5 September-14 October
F568 molting. 14 Oct last day seen

0   100   200   300   400   500   Meters

N

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NAD 1927

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Fig. 1.3. Radiolocations of F568 and M552 attending fledglings and molting, MCB Quantico, Virginia, 1994.
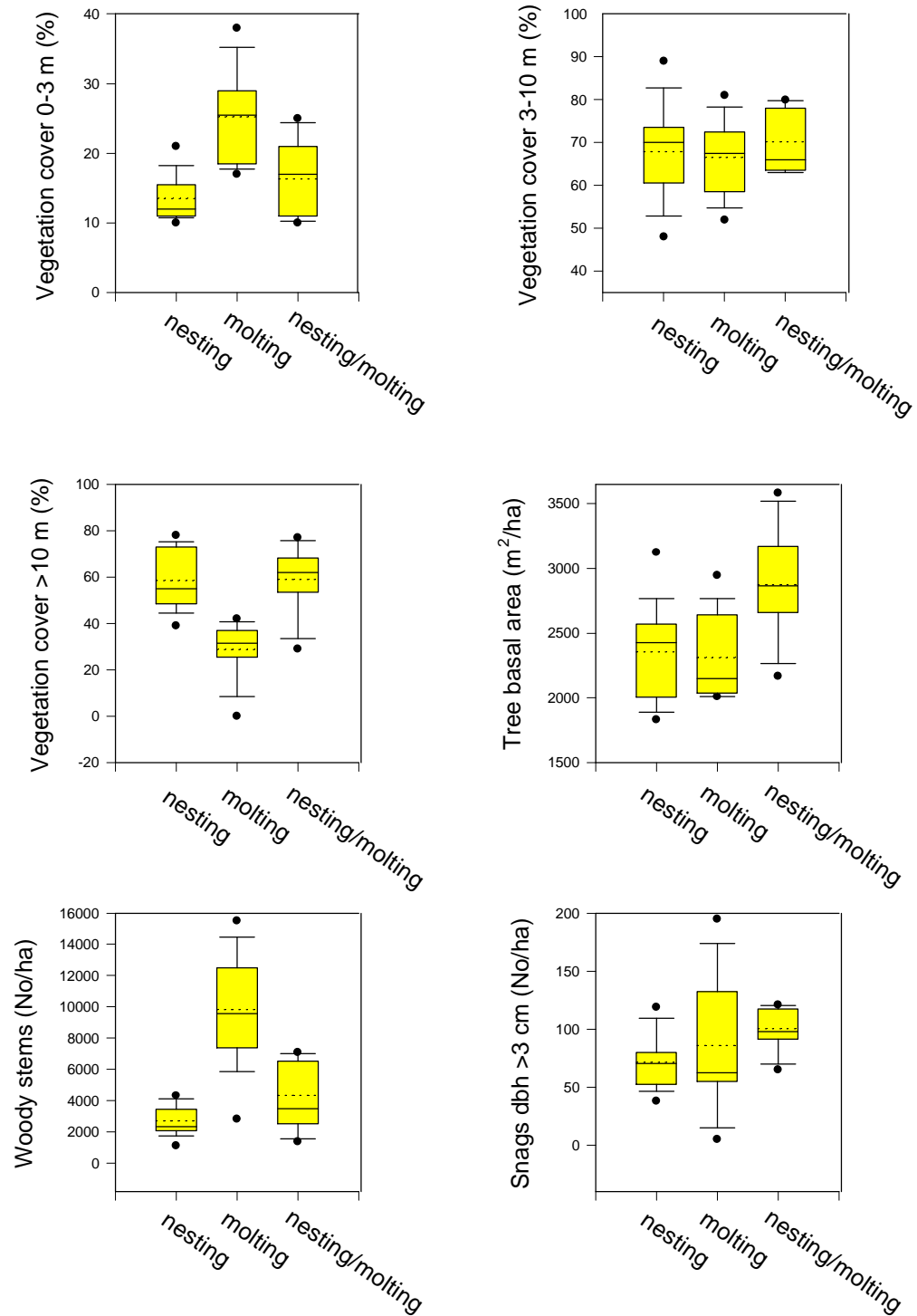
Fig. 1.4. Comparison of structural vegetation parameters among "nesting" (*n* = 12), "molting" (*n* = 12), and "nesting-molting" (*n* = 7) sites for radio-tagged adult Wood Thrushes, MCB Quantico, Virginia, 1993-95.
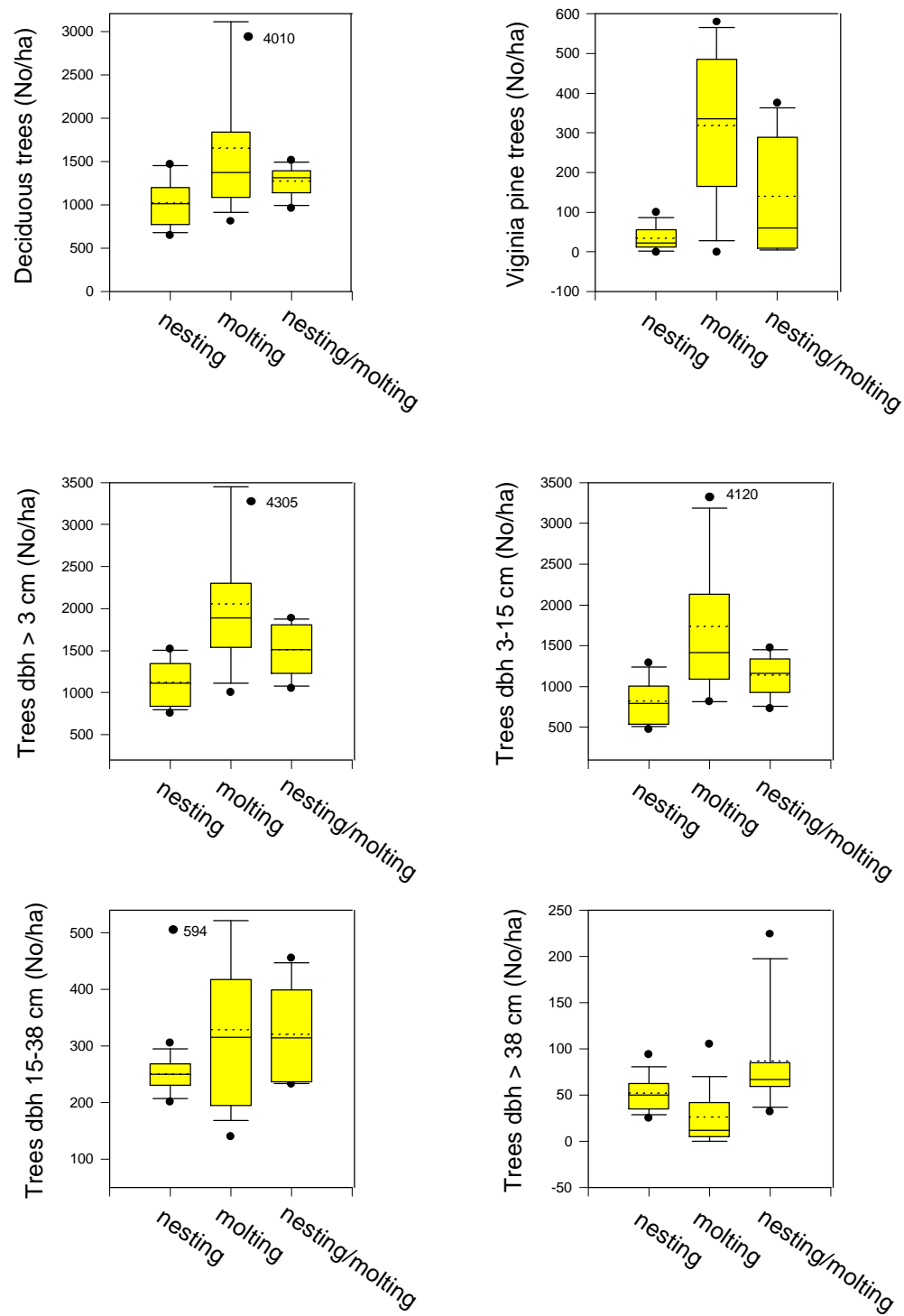
Fig. 1.5. Comparison of composition (deciduous vs. pine) and size (dbh 3-15, 15-38, >38 cm) of trees among "nesting" (*n* = 12), "molting" (*n* = 12), and "nesting-molting" (*n* = 7) sites for radio-tagged adult Wood Thrushes, MCB Quantico, Virginia, 1993-95.
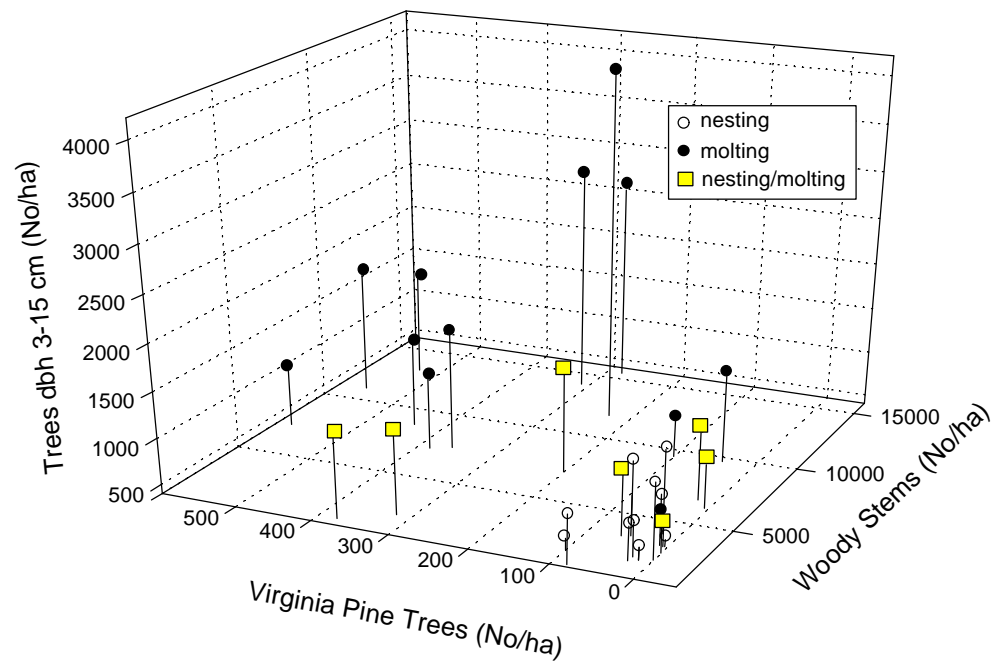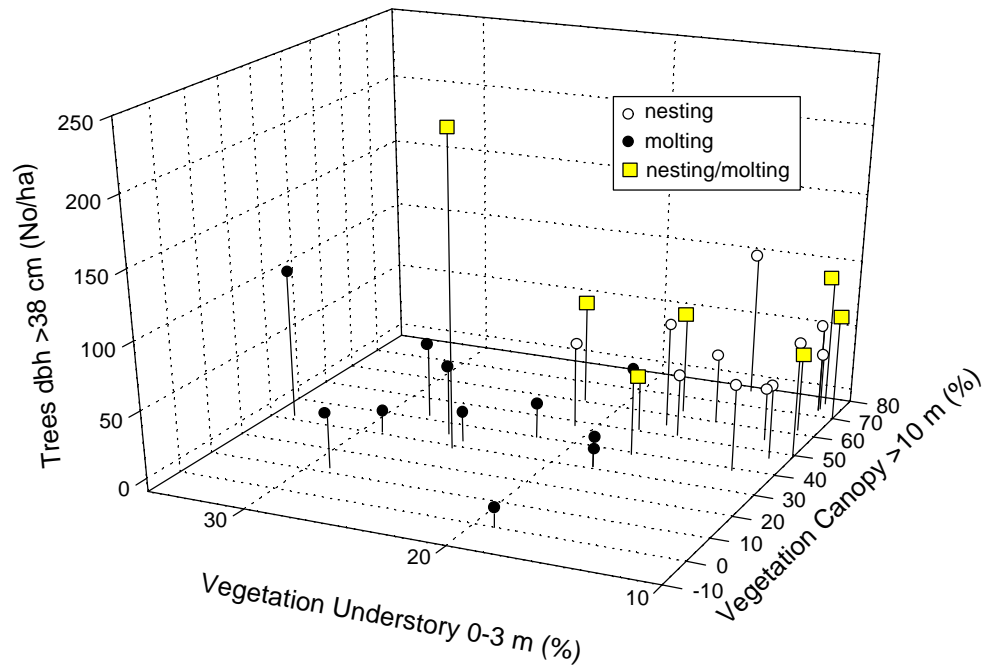
Fig. 1.6. Distribution of "nesting" (*n* = 12) "molting" (*n* = 12), and "nesting-molting" (*n* = 7) sites of radio-tagged adult Wood Thrushes, regarding six vegetation parameters, MCB Quantico, Virginia, 1993-95.
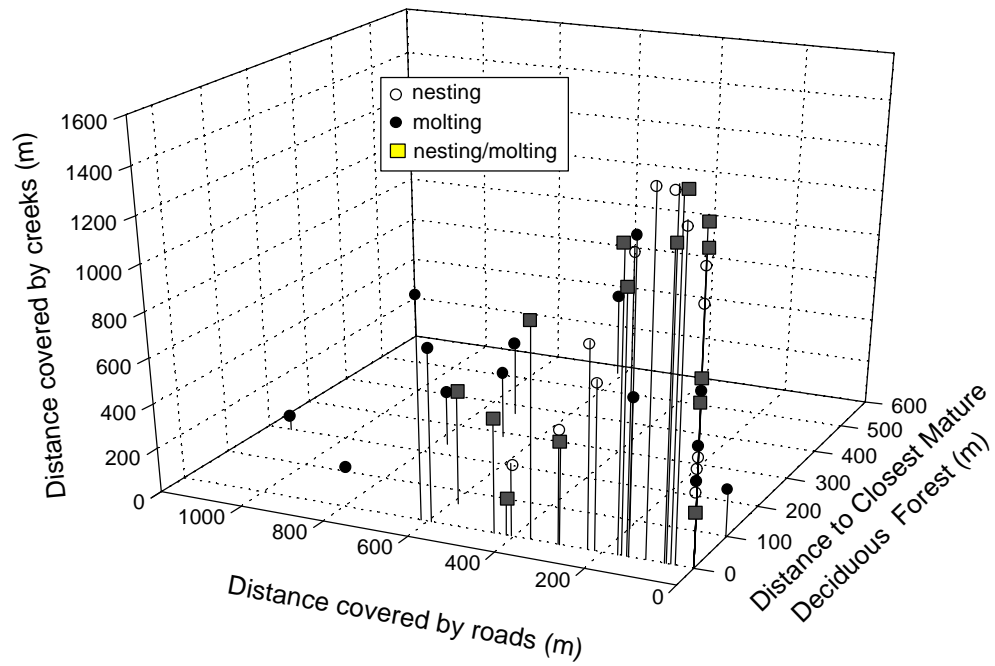
Fig. 1.7. Distribution of "nesting" (*n* = 12) "molting" (*n* = 12), and "nesting-molting" (*n* = 7) sites of radio-tagged adult Wood Thrushes, regarding three landscape parameters, MCB Quantico, Virginia, 1993-95.

Creeks and ravines

perennial

Intermittent

Road (paved and graveled)

Breeding ●

Molting ○

After molting ◉

Nests ▲

SUMMARY

6 June
Caught by the nest along with 4 fledglings and F539

6 Jun - 3 Aug
Engaged in reproductive activities. 3 Aug last day F539 is with male

3 Aug - 25 Sep
Molting

4 Oct
Last day seen

70

Prince William
Forest Park

New Branch Chopawamsic Creek

New Breckenridge Road

4Oct

26Sep

27Sep

91

0   100   200   300   400   500   600   700   800   900   1000   Meters

N

UTM Zone 18
NAD 1927

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Fig. 1.8. Radiolocations of M975 during the reproductive and molting periods, MCB Quantico, Virginia, 1995.

Deciduous Forest (> 70 yrs)

Deciduous Forest (11-30 yr)

Loblolly Pine (2-10 yr)

Virginia Pine (31-70 yr)

Deciduous-Pine Forest (> 70 yr)

Virginia Pine (> 70 yr)

Other, including grass and bare ground

Creeks and ravines

—————— perennial

- - - - - - Intermittent

Road (paved and graveled)

Nest location

66

Site of net capture M514

	M919	M514
Breeding	●	⊙
Molting	■	○
After molting	●	⊠

SUMMARY

M514
10 Jun Caught in a net; 21 Jun nest found
3 Jul nest empty, female gone
4 -31 Jul same general area. Could not find the nest or his mate
2 Aug - 6 Sep molting
7 - 29 Sep light molt head and body
29 Sep last day seen

M919
4 Jun caught in a net
5 Jun - 20 Jul associated with a female (two nests -predated)
21 Jul - 25 Aug molting
25 Aug1 Sep finish molt body
1 Sep radio on ground (harness broken)

91

0   100   200   300   400   500   Meters

N

UTM Zone 18
NAD 1927

Elab. Jorge H. Vega

Fig. 1.9. Radiolocations of M514 and M919 during the reproductive and molting periods, MCB Quantico, Virginia, 1994.

CHAPTER 2
POSTFLEDGING DISPERSAL OF WOOD THRUSHES

(Abstract)

To investigate movement, habitat use and behavior of fledgling Wood Thrushes (*Hylocichla mustelina*) during the dependent and independent stages, 43 radio-tagged fledglings were monitored at the U. S. Marine Base Corps of Quantico, Virginia, during June-October of 1993-1995. Fledglings of first-broods stayed <200 m from the nest before dispersal. Fledglings of final or single broods stayed close to either the nest if the parents molted there, or they moved out of the natal area with the parents if parents molted elsewhere. At 28 to 36 days post-hatching, fledglings dispersed 307 to 5300 m from natal sites. All young joined flocks of juveniles, except 3 birds that remained solitary. Sixteen birds stayed in this first dispersal site until migrating, while 9 visited more than 1 site. On 40 occasions, 15 fledglings performed exploratory movements up to 6 km. After dispersal, fledglings' positions ($n = 556$) occurred in (1) second growth and sapling stage sites at the edge of forested areas [52%], (2) gypsy moth (*Lymantria dispar*) damaged deciduous forest [21.8%], (3) Virginia pine (*Pinus virginianus*) forest that had a heavy understory of young deciduous trees and an open canopy [15.6%], and (4) mature mixed forest [10.6%]. Fledglings left the Marine Base in September at the age of 81 ± 5 days. These results suggest that Wood Thrush fledgling movements were cued by the availability of food resources and the presence of conspecifics with which to socialize, but other factors, discussed here, may also play a role.

INTRODUCTION

The postfledging period in migratory birds, defined in this study as the time between achievement of independence and migration departure, is regarded by many authors as the least known and understood portion of the avian life cycle (Pärt 1990, Weatherhead and McRae 1990, Morton 1991, Morton et al. 1991; Baker 1993). This scarcity in information is due primarily to the difficulties of observing young after they have left the nest. Furthermore, after independence from the parents, fledglings disperse and may wander considerable distances from natal sites making documentation of their activities difficult (Haas 1995). The experiences to which fledglings are exposed and the responses that fledglings make during this phase could be of vital importance in determining the fledglings' lifetime reproductive success (Baker 1993). It is thus becoming increasingly apparent that postfledging dispersal and its variations, causes and consequences is not only an interesting problem with many behavioral, ecological, and evolutionary implications, but also a subject with relevant conservation consequences.

Study of the postfledging period is important for several reasons. First, this phase has been associated with high mobility and mortality rates (Baker 1993, Nilsson and Smith 1985). The postfledging dependence stage might be particularly critical for juvenile survival (Royama 1966, Sullivan 1989), and the probability of survival to independence was judged by Magrath (1991) to be an adequate estimate of relative probabilities of survival to breeding in many bird species. Because juvenile mortality may constitute a "bottleneck" in the annual cycle of a bird, it is important to identify causes of this mortality. Additionally, knowledge of postfledging survival is essential for the evaluation and understanding of different breeding strategies (Husby and Slagsvold 1992). Second, habitat requirements of fledglings might be specific. We do not know what the needs are of the young after they become independent from the parents and disperse from natal territories. We have assumed that fledglings require similar conditions to those found in the localities where they were born. There are, however, reports of fledglings visiting habitats different from those associated with the species nesting habitat (e.g., Bocetti 1993). Third, the documentation of this period would elucidate basic ecological and behavioral questions and review old assumptions and definitions (e.g., Morton et al. 1991, Reed 1993).

Why do the fledglings disperse?

Several hypotheses have been proposed to explain the dispersal movements of fledglings of migratory species.

*Breeding site selection hypothesis.--*This hypothesis states that young migratory birds assess habitat and choose potential breeding sites during continuous explorations in late summer and early fall, before autumn migration (Brewer and Harrison 1975, Van Balen 1979, Adams and Brewer 1981, Pärt 1990, Morton et al. 1991). This hypothesis is

an alternative to the older and generally accepted idea that the search for a breeding site and subsequent territorial establishment occurs soon after spring migration when birds arrive from their wintering grounds. Recent studies, however, have challenged this idea. For instance, Morton (1992) suggested that White-crowned Sparrow (*Zonotrichia leucophrys*) fledglings typically complete dispersal before migration. Adams and Brewer (1981) stated that breeding location of the Field Sparrow (*Spizella pusilla*) may be selected prior to their autumn departure. Eadie and Gauthier (1985) found that Bufflehead (*Bucephala albeola*) and Common and Barrow's Goldeneye (*B. clangula* and *B. islandica*) prospect for nest sites in the late summer of the year before they reach breeding age. These and other examples (Baker 1993) have prompted some authors (Baker 1993, Reed 1993) to suggest that the selection of breeding sites before migration might be a common occurrence for migratory species. Brewer and Harrison (1975) elaborated on the advantages of selecting a breeding habitat before autumn migration. They contended that this strategy might be advantageous because it would facilitate rapid commencement of breeding activities the following spring. They also argue that during the postfledging period, food supplies are high and energy demands low, a situation that allows young birds to dedicate time for the search of nesting habitats. Selection of breeding habitat prior to fall migration would be especially advantageous for species of migratory birds that breed in northern regions because proximate factors such as food and cover may not be available as cues to habitat selection in the spring, when territories of those species are established (Hildén 1965, Seastedt and MacLean 1979).

*Food search hypothesis.--*This hypothesis proposes that juveniles move out of their natal area primarily to access better sources of food (Morton 1991, Morton et al. 1991). This hypothesis also states that postfledging dispersal may allow birds to familiarize themselves with feeding sites that can be used in subsequent nesting seasons. A shortage of food supplies in the nesting sites has been recognized as an important factor that may be responsible for the breeding dispersal of adults (Greig-Smith 1982, Jackson et al. 1989). It also has been suggested that depletion of resources in the natal area may be responsible for the dispersal of fledglings and the subsequent aggregation of conspecifics in areas where food availability is high (Eden 1987).

*Navigational Target Hypothesis.--*This hypothesis proposes that premigratory movements of young birds allow them to become imprinted on or familiarized with local landmarks that would improve their ability to return from their wintering areas the following spring to at least some of those sites (Wiltschko and Wiltschko 1978, Able and Bingman 1987, Baker 1993). Wiltschko (1990) suggested that by exploring their surroundings, fledglings establish a directionally oriented map, by association of landmarks (e.g., visual, olfactory, magnetic), that can be used subsequently in spring migration for homing to the natal area.

*Socialization Hypothesis.--*According to this idea, young birds disperse and wander seeking flocks of conspecifics with which to socialize and migrate (Morton et al.

1991). Formation of flocks has long been recognized as an important way to locate patchy food supplies and to decrease the chances of predation (Hamilton 1971, Baker et al. 1981, Pöysä 1992). The postfledging period could also be an important learning window in which young birds interact with conspecifics and enhance their ability in dominance interactions and status and thus, their probability of survival in winter (Piper 1995).

In this study, I used radiotelemetry to (1) document the pattern and distance of premigratory movements of fledgling Wood Thrushes, (2) determine if vegetation and physical characteristics of natal and dispersal sites were different, (3) examine how the movement patterns of Wood Thrush fledglings can reject or support the different hypotheses of postfledging dispersal, and (4) discuss the implications of these findings for the conservation of the Wood Thrush in particular, and for Nearctic-Neotropic migratory species overall.

METHODS

During May to October of 1993-1995, I captured, radio tagged, and monitored 43 fledgling Wood Thrushes at the Quantico Marine Base, Virginia. Details about the study area and general methodology were given in the general methodology, and I will only add information pertinent to this chapter that was not previously mentioned.

Because most young were captured and radio tagged 1-2 days before they would have fledged naturally, their physical capabilities at that time varied not only because of individual differences, but also relative to the age at which they were radio tagged. To facilitate comparisons, age is given as the number of days after hatching, with day 1 as the day the nestling hatched. Day of hatching was extrapolated from 2 observed pairs in which incubation was found to require 13 days and fledging required 12 and 13 days, respectively. Timing for these events agrees with published information (Bent 1949:109, Brackbill 1958, Bertin 1977). I regarded fledglings as independent from their parents when I did not note any relation between both, such as feeding of the young, flying together, alarm behavior from the parents when I approached the fledglings, or when the fledglings dispersed by themselves from the natal area.

I characterized each site by combining all 0.04 ha plots sampled within the boundaries of that site. Eighteen sites (50%) were characterized by ≥ 5 plots, 6 (17%) by 4 plots, and the remaining 11 (33%) by 3 plots. Each 0.04 ha plot was used to characterize only 1 site. When more than 1 bird used or visited the same dispersal site, the site was considered for analysis only once. Vegetation structure and composition of natal areas were obtained using the locations of fledglings during the postfledging dependence stage.

Dispersal distance was defined as the distance between the arithmetic centers of

natal and dispersal sites. Distance between dispersal sites was measured as the distance between arithmetic centers. A new dispersal site was recognized if the site was situated ≥300 m from the previous one, and if the fledgling was known to spend at least 5 days in the new site. Movements of >300 m to sites where the fledglings stayed <5 days before returning to initial site were considered exploratory movements.

To detect trends in habitat use during the post-fledgling independence stage, I also performed an analysis on use of forest cover types. For this analysis, the original 34 forest cover types included in the Marine Base GIS-database, were reclassified in 4 forest type categories (pine, deciduous, pine/deciduous, and other) and age class (0-1, 2-10, 11-30, 31-70, >70 yr). Using ArcView computer software, I plotted all fledgling positions during the independence stage on the modified forest stand coverage and recorded the forest/age type at each position. The results of the analysis did not show a clear pattern (Appendix B).

RESULTS

The postfledging dependence stage

An account of the development of 18 individuals from 12 broods follows. It includes the interval from the date they were radio tagged until they become independent from the parents.

Behavior and flying capabilities.-- Fledglings radio tagged at 11 d of age or less could not fly; they stayed on the forest floor and made small jumps following the alarm call of the parents. From age 12 to 15 d, most fledglings were able to climb up bushes but they were still incapable of extended flight and could be captured by hand. During this time, they often perched quietly 1-5 m above the ground. When I approached them, they commonly froze and stayed immobile until I moved away. Sometimes, I could approach the fledglings up to 1 m before they moved. The parents exhibited alarm behavior (i.e., chipping and flying between perches) during these observations, but they did not come close enough to lead me to the fledglings' position. Sometimes the parents brought food to the young, but they did not feed them when I was nearby. At 16 d of age, the young became more active; they flew when I came within 7 m. They were able to fly distances >30 m between branches, flying low and close to the ground or higher in the mid-canopy. At this time, some young perched quietly in the mid-canopy while I observed, but they followed the parents' calls readily. At 17 d of age or older, they flew proficiently. At this age and after, fledglings were found commonly on the ground, but they moved up when I approached. There was variation among individuals. For example, one fledgling remained immobile for long periods at 19 d of age. On one occasion, during 40 min of observation, it did not move from a perch 4 m high. On the other hand, at 14 d of age another fledgling was moving easily between branches.

At 11-12 d of age, 9 nestlings had wing and tail measurements of 60 ± 3 mm and 15 ± 2 mm, respectively, including 10 mm sheath. One young within estimated age of 14 d had wing and tail measurements of 71 mm and 35 mm, respectively. The earliest age at which a young was observed in full plumage was 41 d. One young, captured at an estimated age of 46 d to replace the transmitter, had full plumage.

*Foraging.--*Unlike the young from other species, I only occasionally saw Wood Thrush fledglings begging for food, although they often were chipping when the parents did not feed them. Young soon started to feed independently. Early in the breeding season when trees with fruits were not available at the natal sites, fledglings began foraging by picking objects from the ground. Initially, this behavior was probably exploratory because the fledglings tried a variety of animal and plant items, such as insects, leaves, moss, flowers, and mushrooms. The first record of a young bird foraging by itself was at 17 d of age. After 20 d of age fledglings frequently fed by themselves, very often on fallen logs. Several days before they became independent, I observed fledglings on several occasions foraging on the ground accompanied by one of the parents. Fledglings born late in the season soon began foraging on fruits that were then abundant at the natal area. For instance, 3 siblings fledged in late August when fruiting trees in the natal site were common. At least 5 days prior to complete independence from the parents, these fledglings were spending much of the day foraging by themselves.

*Movements.--*There were 2 different strategies regarding attendance of the fledglings by the parents. If the parents intended to raise another clutch (6 pairs in my study), they kept the fledglings relatively near (within 200 m of the nest). For instance, during the postfledging dependence stage, 2 siblings were always close but separate from each other and never >100 m from the nest (Fig. 2.1). Both the male and the female attended all siblings until the female started a second nest, after which the male continued attending the fledglings for 8 more days. Similarly, 3 single fledglings from first broods were never >200 m from their nest until they dispersed (Fig. 2.2).

A different pattern was observed in fledglings from last broods (5 in this study). In those clutches, 1-3 days after fledging, the brood split and each parent fed different young. The distances that they moved from the nest varied depending on whether the parents remained in their territory for molting (3 clutches) or moved. For instance, 3 siblings started moving out of the nesting territory immediately after fledging and within 2 days of fledging were already >200 m from the nest. The male attended 2 fledglings (Fig. 2.3, movements of one of the fledglings) and the female attended one (Fig. 2.4). Similarly, another pair divided the attendance of their last brood, but both the female and male molted in the nesting area (Fig. 2.5).

In summary, during the postfledging dependence stage, mobility of fledglings was 73 ± 9.3 m ($n = 17$). They restricted their movements to an area of 1.6 ± 0.3 ha ($n = 17$). There was no trend for young that hatched earlier in the season to show larger mobility

($r = 0.46$, $P = 0.188$), or to use a larger area ($r = 0.46$, $P = 0.191$). Independence from parents occurred at 32.5 ± 0.6 d of age ($n = 18$). There was no trend for fledglings that hatched later in the season to become independent at a younger age ($r = 0.15$, $P = 0.545$). On average, 21 ± 0.7 d ($n = 18$) elapsed between radio tagging of fledglings and their independence. From the moment of dispersal, siblings' movements were apparently independent of each other. Only on one occasion, 2 siblings visited the same site, but they did so on different days.

Dispersal was apparently associated with the independence of the young from the parents. In 18 fledglings, dispersal occurred at the time that they were regarded as independent. There is a possibility, however, that fledglings, especially those whose parents started a second nest, were independent but stayed in the natal area a few days before dispersing. Once the female started incubation on the second nest, the male and fledglings were very close to her and it was not possible, using radiotelemetry, to detect if the male was still attending the young. Furthermore, the observer's presence might have caused a change in behavior of the birds. While observing these fledglings a few days before they dispersed, I did not see the male feeding young. A female, for example, attended her single, first-brood young during 16 days before she initiated a second nest. The fledgling did not move out of the natal area until 8 days later. During this time, it stayed no more than 100 m from the second nest. I never detected or saw the female or male approaching the young.

The postfledging independent stage

Postfledging dispersal.--Of a total of 29 fledglings from 18 broods that were radio tagged as nestlings or 1-2 days after fledging, 24 survived to independence. Of these 24 fledglings, 1 was killed before it dispersed, 3 were assumed to have dispersed from the Marine Base because lost radio signal, and 2 did not disperse from the natal area before migration. The remaining 18 did move out of their natal area and stayed within the Marine Base. The first dispersal site was located an average distance of 1539 ± 273 m (range 307 - 5300 m; $n = 18$) from the natal site. There was not a significant correlation between the distance of dispersal site and the date of dispersal ($r = -0.17$, $P = 0.492$). The hypothesis that Wood Thrush fledglings disperse with equal probability regarding direction was tested with Rayleigh's z test (Zar 1996:615). There was no significant trend in the direction of dispersal from the natal site ($z = 1.51$, $P > 0.2$, Fig.2.6). Eleven fledglings apparently moved at once from the natal area to their first dispersal site. Six fledglings, however, were observed stopping at 2-5 sites before reaching their first dispersal site. The movements to the dispersal sites of 3 of these fledglings are shown in Fig.2.7. Once fledglings were established in a dispersal site, there were no differences in mobility, size of the area used, or distance from center to that achieved in the natal sites, but variability of values in the dispersal sites was higher (Table 2.1).

*Dispersal site and patterns of movement--*Of 15 radio-tagged fledglings of known nests that survived until migration, 10 individuals were observed using 1 dispersal site; 3 individuals, 2; 2 individuals, 3; and 2 individual, 4. Of 10 fledglings radio-tagged after independence, 6 individuals used a single dispersal site (assuming that they were initially captured on their first dispersal site), 3 individuals, 2; and 1 individual, 3. Mean distance between consecutive dispersal sites was 1512 ± 181 m. Within the dispersal sites, fledglings moved an average distance between locations of 101 ± 11 m, and used an area of 2.81 ± 0.5 ha ($n = 32$ ind.). There was no trend for young that hatched earlier in the season to show a larger mobility ($r = 0.14$, $P = 0.418$), or to use a larger area ($r = 0.14$, $P = 0.425$).

During their stay at a given dispersal site, 15 fledglings performed exploratory movements. An exploratory movement consisted of a movement of >300 m out of the dispersal site and subsequent return, after 1-5 days, to the locality occupied before initiating the movement. I could determine the position of the fledgling in 11 of 40 exploratory movements that were recorded . Fledglings were found at an average distance of 1685 ± 527 m (range 400 - 6501 m) from the dispersal site.

Habitat use

*Vegetation.--*Twelve of the original 44 vegetation variables were selected for testing of differences between natal and dispersal sites; 7 of the 12 showed significant differences (Table 2.2). Multivariate assessment of differences between natal and dispersal sites including the 7 variables also showed significance (MRPP statistic = -4.92, $P = 0.003$). Matched-box-plots of each of 12 variables show that in general variability was higher in dispersal than natal sites (Fig.2.8 and 2.9).

Comparing natal and dispersal sites helped to identify general trends in the population. Individual differences, however, were reduced or diluted. These individual variations are important and, therefore, I show them graphically by plotting subsets of 3 variables. All but one of the variables selected to plot were those that showed significant differences between sites. Overall, natal sites had fewer pines, fewer woody stems, and fewer saplings (Fig. 2.10A). Dispersal sites generally were in areas with less canopy cover, fewer trees dbh >38 cm, and more vegetation in the understory strata (Fig. 2.10B). However, it is important to note that intermixing of natal and dispersal sites along these axes is clear. Thus, individual differences were additionally examined by performing comparisons for 16 individuals regarding the 12 variables (Table 2.3). Only those individuals with information on both natal and dispersal sites were included in the analysis. Table 2.3 shows that the outcome from the analysis of the pooled data did not hold for each individual. For example, only for 4 of 16 fledglings, the density of pines was significantly higher in the dispersal than natal sites and in 1 instance, there were significantly more pines in the natal than the dispersal sites. Percent of vegetation cover -canopy (PVEG_C), which was higher in natal than dispersal sites ($P = 0.007$) when data

were pooled, was significantly different for only 4 of the individual comparisons. This analysis is repeated for other variables in which the difference of natal and dispersal sites was significant in the pooled data.

Tree species richness was similar in natal and dispersal sites (14 and 13 species, respectively). There was not a clear pattern of differences between natal and dispersal sites regarding proportion of sites where the species occurred, contribution of each species to the overall composition, or proportion of times that the species was 1 of the 3 more numerous species in a given site (Appendix C).

*Landscape.--*Univariate analysis of pooled data showed that dispersal sites were closer to roads and openings than natal sites, but farther from mature deciduous forest (Table 2.4). Natal sites had less roads and more creeks (within a circle 300 m radius centered in the arithmetic center of the natal site) than dispersal sites (Table 2.4). This generality did not hold for all birds and some degree of overlap was observed (Fig. 2.11). I also examined differences between natal and dispersal sites regarding these 5 variables (distance to closest road, creek, and deciduous forest, and distance covered by roads and creeks) using a multivariate approach. The MRPP test revealed significant differences between natal and dispersal sites (MRPP statistic = -6.18, P = 0.0006).

Time of departure

Most fledglings left the Marine Base in September and early October (Fig. 2.12A). The average age of juveniles at departure from the Marine Base was 81 ± 5 d (n = 15, Fig 2.12B). There was a trend for fledglings that hatched later in the season to leave at a younger age (r = -0.71, P = 0.002). I observed certain behaviors in some fledglings before they left the Marine Base that deserve some comment. During September when several fledglings were leaving the Marine Base, fledglings that remained for 1-2 more weeks showed restless behavior. Eight fledglings over the course of several days moved distances of >300 m, making it difficult or impossible to define their position. Often the radio signal was lost only to reappear minutes later. These birds, however, did not change their location but remained in the same area. Also, 10 juveniles were observed making 1-3 long movements within 7 days of leaving the Marine Base. They moved an average distance of 1776 ± 230 m (n = 15, range 600-3219 m). The fledglings stayed 1-4 days in those sites and then disappeared (Fig. 2.13). Similarly, before leaving the Marine Base, 2 other juveniles moved to a new dispersal site, stayed 5 and 8 days, respectively, and then disappeared. There was also a tendency for fledglings to return to their more familiar site before leaving the Marine Base. Five juveniles that had been in a well-defined dispersal site were missing 1-3 days. They came back for 1 day to their dispersal site and then disappeared. For example, a fledgling moved 6.5 km from its dispersal site, moved back the next day and then disappeared. Similarly, 3 fledglings that were in a second dispersal site moved back to their previous, longer-term dispersal sites before they disappeared.

This increased mobility before leaving the Marine Base was not observed in all birds. Six juveniles disappeared suddenly. Three of these birds were never observed moving out of their only dispersal site. Considering all birds simultaneously, I did not detect a trend of increasing mobility late in the season for either mobility within natal sites ($r = 0.10$, $P= 0.253$, Fig. 2.14A), within dispersal sites ($r = 0.04$, $P= 0.420$, Fig. 2.14B), between dispersal sites ($r = 0.12$, $P = 0.226$, Fig. 2.14C), but a weak trend was detected when all movements were considered ($r = 0.12$, $P= 0.002$, Fig. 2.14D).

Survival of fledglings

Of 43 fledglings fitted with transmitters, 9 starved or were killed by predators. Three of them were found dead the day following radio tagging; 3, 10-19 days after radio tagging and before they became independent; 1, 5 d after dispersal; and 2, 3 weeks after dispersal. Three fledglings probably died of starvation because I found the bodies with no obvious injuries. In 4 instances, fledglings were predated by hawks. The transmitters of 2 fledglings were found in a nest of a Broad-winged Hawk (*Buteo platypterus)*. The hawk nest was located 1549 m and 3819 m from the last position of the fledglings, respectively. The transmitters and remains of another 2 fledglings were found closer to a Red-shouldered Hawk (*Buteo lineatus*) nest. The nest was located 766 m and 100 m, respectively, from the fledgling's last position. Another fledgling also was probably predated by a hawk because the transmitters and harness were intact. One fledgling was killed by a snake.

DISCUSSION

The postfledging dependence stage

Wood Thrush fledglings that were radio tagged at a time when they would naturally fledge were capable of short flights from branch to branch. However, I found 2 fledglings that could barely hop on the ground. Similar differences are reported in previous accounts about the flying capabilities of recently fledged birds. For example, Nolan (1974) reported that 2 young Wood Thrushes leaving the nest could barely hop, while Brackbill (1958) reported flights of about 16 m by young just out of the nest. My observation of 3 young jumping out the nest apparently following the call of the parents suggests that the parents may persuade the young to leave the nest at a younger age.

Transition to independence and dispersal

The process of transition to independence and the factors leading to the dispersal of the young is poorly understood, and this transition has been assumed to be a time of parent-offspring conflict (Trivers 1974), in which fledglings' insistence in being fed for a longer time may compromise the parents' ability to rear further young, and therefore the parents should force the dispersal of the young. Some authors argue that the dispersal of

the young is probably caused by the increasing aggression of the parents, especially the male, toward the young and of the young toward each other (i.e., Holleback 1974, Alonso et al. 1987). During my observations, I did not note any aggression among siblings or from parents to the young while they were with them. However, again, my presence could have modified their natural behavior.

Another hypothesis suggests that the decreasing amount of parental care, i.e., reluctance to feed the young, forces the young to become independent and disperse (Davies 1978). This hypothesis has been supported in several species where the behavior of fledglings has been studied (Davies 1976, Moreno 1984, Nilsson and Smith 1985). Although I did not quantify feeding frequency, I did observe in several pairs reduced or absent attention from parents to the young before dispersal. For instance, at the age of 25 d, a single fledgling was observed foraging on the ground; the parents did not arrive until 30 min after I arrived; I did not see the parents feed the young, neither did I see the young respond to the parents' presence. Six days later, the fledgling dispersed. Another single young remained in the natal area for 8 days after the female had initiated incubation on her second nest without, apparently, being attended. In several other instances, however, a close association between the young and the parent attending it was maintained until the same day that the young dispersed suggesting that fledglings may decide the time for dispersal without regard to the behavior or attendance of the parents; i.e., fledglings would disperse as soon as they are capable of flying and feeding by themselves. This idea has been suggested before. Nilsson (1990) suggested that young birds should disperse as early as possible to gain "dominance of site."

I observed other behavior regarding the dispersal of fledglings. Three males, which were left by their mates attending their single fledglings, moved with their young out of the natal area at an age when fledglings were expected to disperse. A male and its young moved 855 m from the last position in the nesting site. The next day, the male was back in his territory while the fledgling stayed in its first dispersal site. Another male and its young moved 400 m from the nesting site to a second-growth area. The young stayed at that site 33 more days and the male moved about 300 m from the young to a deciduous sapling stage area, and started molting. In another case, a male and the young moved 500 m from the last location in the nesting site (Fig. 2.7, position 22 July). The male came back to the nesting site 2 hours later, but the young kept moving further toward its dispersal site. Prior to the dates when these movements occurred, the young were moving with the male, therefore it is possible that fledglings follow the males to those sites. I cannot, however, eliminate the possibility that the fledglings moved by themselves and that the males follow them temporarily. These males were not attached to a mate at that time. Strong and Bancroft (1994) suggested that in White-crowned Pigeons (*Columba leucocephala*), adult birds may be leading young to safe feeding sites, and thus, habitat selection of young may reflect the experience of parents. They based their conclusion in the observation that some adults may have maintained contact with recently dispersed fledglings.

In 2 cases fledglings did not disperse from the natal area after independence. These fledglings may have remained in the natal area because of high abundance of fruits at the natal sites and because both adults attending these fledglings started molting before fledglings became independent.

Postfledging independence stage

The definition of a dispersal site was to a certain point arbitrary and may have some implications in the interpretation of details of my results, and so deserves some explanation. I assumed first that a fledgling had to stay in a new site at least 5 days for it to be considered a new dispersal site. Thus, 5 days was the period that I use to differentiate between dispersal and (1) movements I characterized as exploratory, and (2) movements performed when the birds were simply moving through. Also, I used a distance of 300 m as a cut off point to separate 2 dispersal sites. This value is about two-fold the mean distance from the arithmetic center of the home range for 11 fledglings (all locations considered) that used a single dispersal site ($\bar{x}$ = 113 m, SE = 4).

Habitat use

After dispersal, Wood Thrush fledglings underwent partial molt. Every juvenile handled in July and August was molting. The main challenge for young birds at this time is to find suitable habitat that provides them with enough food for feather growth and thermoregulation (Ginn and Melville 1983) and cover for protection from predators. Univariate and multivariate comparisons between natal and dispersal sites in pooled data show that, during the postfledging independence stage, Wood Thrush fledglings were using or visiting old second growth (located in old farms, forest edges, and gypsy moth damaged deciduous forest) and Virginia pine forest. Characteristics at these habitats, such as a dense understory and moderate open tree canopy, have been generally related to high production of insects and fruits and Wood Thrush fledglings may have taken advantage of this situation. Forest edges and openings have been associated with high rates of predation on eggs and nestlings of many forest-dwelling species (Askins et al. 1990), but their value as providers of protection for recently dispersed fledglings is unknown. Adult Wood Thrushes that were nesting often moved into sapling patches and dense understory in response to my close approach while I tracked them. Similarly, several molting adults moved to patches of deciduous saplings and Virginia pine forest. These observations suggest that these habitats may play a role for protection from predators.

When the habitat use analysis was done individually, i.e., when comparisons were done for each bird with data for both natal and dispersal sites, the general pattern did not apply to all birds. My results suggest that the importance of habitat factors involved in determining the selection of a site varies between individuals and within individuals temporally.

Leaving the Marine Base

The average age at departure of 21 fledglings tracked from the time they fledged until they left the Marine Base was 81 ± 5 d after-hatching. Most fledglings departed from late August to early October, with 47% leaving in September. On several occasions during September, fledglings were observed flying over a larger area than they usually did, and changing locations constantly. This behavior could be associated with the oncoming migration. Evans (1966), for instance, observed that Lesser Redpoll (*Carduelis flammea*) adults "become restless, feeding only for short periods, and spending most of the day at the tops of the trees surrounding the study area, or flying in wide circles overhead." Berttold (1993:129) mentioned that individuals ready for migration emit special calls that help to synchronize departure of conspecifics. Similar timing for leaving the Marine Base among Wood Thrush fledglings that occupied the same site was probable. For instance, on 6 September 1994, there were 5 radio-tagged Wood Thrush fledglings in a ≤5 ha second growth/pine forest patch. They all were gone from that site and from the Marine Base by 8 to 18 September. Next year, on the 13 of September there were 7 radio-tagged fledglings at the same site. All of them left that site, and 3 of them the Marine Base, between 12-22 September. Many other Wood Thrush fledglings were commonly observed at that site in both years, and they were gone by the same period.

Site fidelity

I mist netted for a total of about 20000 net/hr in my 3 10-ha mist-netting sites. During this time, I captured and radio tagged 43 fledglings within the grids. Additionally, I captured and banded 23 fledglings elsewhere within the Marine Base. None of them was recaptured or resighted in subsequent years. This result is not surprising. Low return rates of passerines banded as nestlings to the natal area are almost universal (Gauthreaux 1982). Using this kind of data to test for site fidelity has been questioned. It has been proposed that if young move out of their natal area before their first winter, then it is possible that they would be faithful not to their natal site but to sites they occupied as fledglings (Brewer and Harrison 1975, Haas 1995). This has been shown in several nonmigratory and migratory species (Nice 1937, Nolan 1978, Weise and Meyer 1979). According to my data, young Wood Thrushes did visit or become familiar with an area much larger that the parents' nesting area. For instance, a fledgling moved about 3.5 km to its dispersal site, was missing-exploring on 4 occasions, and 2 days before leaving the Marine Base, it returned to its natal area (Fig. 2.15). Therefore, fledglings were able to become familiar with a larger area than that used when they were dependent on the parents. Fidelity of Wood Thrush fledglings, thus, should not be measured only by inspecting if the return of young to their natal area, but to the area they visited when independent.

Why do Wood Thrush fledglings disperse?

That Wood Thrush fledglings moved out of the natal areas was evident in this study. It was also clear that during the postfledging independence stage, most fledglings visited several locations. The number of days that these birds stayed at a given site varied from 1-86 days. Furthermore, fledglings not only changed dispersal sites, but also made exploratory movements. On 11 occasions, I detected exploratory movements in 6 different individuals. These birds moved 400-6500 m, stayed 1-2 d, and moved back to their dispersal site. Additionally, 29 times, 15 fledglings were missing-exploring for 1-5 d. I regard these absences as exploratory because the birds returned to their former site. More exploratory movements were probably performed when fledglings moved from one site to another. Between the last day in a given site and the day they were located in other sites, on 20 occasions fledglings were missing for 1-28 days. I searched for birds the same day they were missing by walking and driving. Very often, because of logistic problems (e.g., military exercises, availability of plane and pilot), I could not fly until 6 d after the disappearance of the bird was noted. Thus, in some cases the possibility exists that the fledglings were already in the new dispersal site, but I did not locate them. For fledglings that were missing more than 6 d, this was improbable. Therefore, the probability exists that some fledglings visited sites outside the Marine Base and then returned.

The main hypotheses explaining the objective of these exploratory movements were previously mentioned in the introduction. Next, I will comment on how data on movements of Wood Thrush fledglings can be used to differentiate among these hypotheses (See Appendix D for summary of data as related to these hypothesis).

*Breeding site selection hypothesis.--*This hypothesis states that birds move out of their natal area to locate potential breeding sites. If a fledgling's main objective of exploratory movements is to look for potential breeding sites, then they should be visiting areas that were suitable for breeding. This was not the case for all Wood Thrush fledglings, or at least it was not apparent. First, a plot of all positions of dispersing fledglings and the breeding ranges of radio marked adults shows that only 5.5% of fledgling positions overlapped with known breeding ranges. Second, only once did I note an active nest while I was radio tracking fledglings. Third, many fledglings' positions were located in habitats that according to my observations of active Wood Thrush nests were most probably not suitable for breeding, such as second growth and saplings stage sites located in old farm areas and forest edges. This was mostly the case of some young that fledged early in the breeding season and moved to those sites. I did not see any sign of Wood Thrush breeding activity, nor did I observe or catch any adults at any of those sites, although males were singing in the adjacent forest. There were, however, many fledglings' positions (10.6%) in mature deciduous forest areas that were apparently appropriate for breeding. In conclusion, my results did not corroborate the hypothesis that the main purpose of the exploratory movements is the search of breeding sites.

Because selection of breeding sites is not apparent until the following spring, the ultimate test for this hypothesis would be to examine if fledglings returned to breed in any of the sites visited during the postfledging phase. This has been investigated indirectly. For example, Morton et al. (1991) observed that in male White-crowned Sparrows, the degree of philopatry appeared to be related to the amount of time those individuals spent in the study area the previous summer as juveniles. Nevertheless, even if the exact site for breeding is not chosen during the autumn explorations, which is most probably true, there should be an advantage for fledglings in gaining familiarity and local experience for potential breeding sites. Pärt and Gustafsson (1989, and citations therein) suggested that prior knowledge of an area increased the probability that an individual obtains a territory of high quality, and therefore has a direct effect in future breeding success. Similarly, Badyaeus et al. (1996) stated that for Wild Turkeys (*Meleagris gallopavo*), a better knowledge of an area, as reflected by a greater area covered prior to nesting, correlated with the quality of the selected habitat.

*Food search hypothesis.--*The possibility that Wood Thrush fledglings disperse to find sites where food resources were abundant is feasible. Adult Wood Thrushes fed the young largely with invertebrates (Bent 1949:110). According to my field observations, independent fledglings still consume invertebrates, but they largely forage on fruits if they were available. Based in stomach content analysis of 27 birds, in fall >70% of the Wood Thrush diet is fruits (Conway et al. 1994; see also Martin et al. 1951). My data suggest that the dispersal of fledglings, especially those from early-clutches, could have been performed to locate sites where food was more abundant. Although I did not quantify the production of fruits where Wood Thrushes were found, I did record the presence of fruits on trees or bushes, with special attention to those species on which Wood Thrushes were often foraging, such as blackgum (*Nyssa silvatica*), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum)*, and less in spicebush (*Lindera benzoin*), grape (*Vitis sp.)*, poison ivy (*Toxicodendron radicans*), greenbrier (*Smilax sp.*), and blueberry (*Vaccinium sp.*). Production of fruits in forest edges, young deciduous forest, old farm sites, and gypsy-moth damaged forested areas started as early as mid- and late-July. In Virginia pine and mature deciduous forests, on the other hand, production of fruits did not start until late August and early September, respectively. By mid-September, there were trees fruiting everywhere in the Marine Base. In support of a foraging hypothesis, early in the season, 27 of 31 fledglings dispersed to second growth, forest edges, and other sites with early fruit production. Late in the season fledglings were found anywhere, including the mature deciduous forest. For instance, 3 siblings became independent on 10-15 September; they were always found in mature deciduous forest. Another 2 siblings became independent in early September and dispersed to mature deciduous forest.

Another observation that may corroborate the idea of birds searching for food resources was the observation of fledglings, both from the same and different years, visiting the same locations. In Figure 2.16, I show 8 sites that were visited at least by 3 different radio tagged fledglings. Some of these sites (i.e., right upper corner) were

visited during the 3 years of the study. Most of these sites were gypsy-moth damaged forest, characterized by the presence of big trees, mainly white oaks, that were totally defoliated. Large dead trees create gaps where more sun light reaches the forest floor, causing an increase in understory growth, an increase in fruit production, and a higher concentration of foliage insects (Thurber et al. 1994).

This pattern, however, was not general. There were cases of 3 solitary fledglings that moved and stayed 10 or more days in second growth and sapling stage sites where I did not observe any trees, shrubs, or vines with fruits. These fledglings were commonly foraging on the ground presumably on invertebrates. I also observed fledglings moving from sites that still had many trees fruiting. Days later when I returned to those sites to sample the vegetation, there were still Wood Thrush fledglings at the site foraging on fruits.

Some authors have speculated that young move out of the natal areas searching for food supplies, because of a shortage of food occurs at those sites (Eden 1987). Greig-Smith (1982) suggested that Stonechats (*Saxicola torquata*) that successfully raised large broods move to renest perhaps to avoid local food depletion (but see Jackson et al. 1989). Some studies (Nilsson 1990, Kenward et al. 1993) have shown, however, that supplementary food may delay the dispersal of young, but they also found that young would disperse at their own accord, regardless of the food supply. Sullivan (1989) and Jackson et al. (1989) also suggested that, at least for the Yellow-eyed Junco and Prairie Warbler (*Dendroica discolor*), respectively, food does not appear to be limiting in the nesting sites. Do Wood Thrush fledglings disperse because a shortage of food supply in the natal area? While this study did not directly address this question, there are observations that deserve some comment. Five adult Wood Thrush pairs renested within 30-300 m meters from the nest where fledglings were produced. The adults must have assessed the availability of food in order for them to decide to renest. This suggests to me that if there was enough food in the natal site to support another brood, then fledglings could have stayed, at least until the new clutch hatched. This could not happen if either the diet of fledglings changed or adults drove the fledglings away, or at least facilitated their dispersal, to assure food supply for the coming young. According to my field observation changes in the diet could be an important reason for the observed habitat shifts of fledglings. A large proportion of the diet of fledglings after independence was fruits. As would be expected, most, but not all, first-brood fledglings dispersed from the natal areas, where fruits were not available at that time, to sites where production of fruits was high. On the other hand, 3 late-season broods stayed in the natal areas and foraged from fruits produced there. For instance, 2 siblings stayed in the area where their parents bred and molted until they left the Marine Base (Fig. 2.5).

Navigational target hypothesis.-- Baker (1993) argued that while fledglings' immediate needs, such as food and shelter, and search of areas suitable for breeding, shape in part the nature of the postfledging explorations, the creation of a "navigational

target" plays a major role. My data cannot directly address this hypothesis. However, given the high mobility observed in most Wood Thrush fledglings, this idea is feasible. Moreover, the observed ability of fledglings to return to previous sites found several kilometers apart, including their own natal site while they were at the Marine Base, is evidence that the young birds had some homing ability. It is not known whether the size of the area with which fledglings become familiar is large enough to be used for homing purposes the following spring when they return from their wintering ground. It is also not clear what kind of experience was necessary to achieve navigational ability, which specific clues were involved in this process (Able and Bingman 1987), and why some fledglings were relatively sedentary. The idea of the existence of a critical sensitive period in which fledglings develop a homing ability through on-site experience is very appealing. There are, however, experiments that indicate that exploration and familiar experience to an area were not necessary for homeward orientation (Able and Bingman 1987).

*Socialization Hypothesis.--*My data indicate this hypothesis is probable. In most occasions that I relocated radio-tagged juveniles, there were other untagged Wood Thrush fledglings with them. Agonistic interactions among members of these groups was strong, especially late in the season, when fledglings were finishing molt. It was common to observe young birds chasing each other and emitting alarm calls. These interactions could explain the movement of some fledglings out of a site that otherwise seemed suitable (i.e., food shortage was not apparent).

Flocking behavior of recently fledged birds has been reported in several species of passerines (Husby and Slagsvold 1992, Soler 1994) and is thought to increase foraging efficiency and decrease the chances of predation (Powell 1974). There is extensive literature that indicates that when birds depend on temporally and spatially patchy resources, foraging in groups increases the rate of food intake (Pöysä 1992, and citations therein). This behavior can be advantageous because individuals copy other group members' foraging behavior and therefore increase their own feeding rate and/or because groups attract other individuals to sites where food is abundant (Pöysä 1992). After independence, Wood Thrush fledglings depended largely on fruits, a resource that at least early in the summer at the Marine Base was temporally and spatially variable. Concentration of fledglings in sites where food resources are abundant would facilitate the location of those sites by recently dispersing birds.

According to Piper (1995), during this time young birds may be establishing rank dominance with lasting effect. Development of a dominance hierarchy in fledgling Wood Thrushes was not probable because individual composition of groups was not stable. The association of an individual with a group was temporary, and thus the composition and size of the group were variable. These interactions, however, are very important because they could provide young birds with winning strategies to be used in future contests, on both the wintering grounds and breeding grounds the following year. Furthermore, Wood

Thrush fledglings changed groups and changed from a group to solitary behavior, and there were also 3 individuals that did not join a group at all or did so only during 1-2 days. These observations suggested that the benefits of joining a group varied not only among individuals, but also temporally in individual cases.

Flocking behavior could also be important for safety purposes, e.g., to decrease the risk of predation (Hamilton 1971). After dispersing, fledglings move to unfamiliar areas and are probably still learning to forage by themselves. A juvenile's major challenge during this vulnerable period is stay alive. This can be met by selecting and concentrating in safe sites. Such sites were present within the Marine Base. There were sites where high concentrations of Wood Thrush fledglings occurred during most of the summer in the 3 years of the study. For instance, 2 fledglings in 1994 and one in 1995, all from different nests, dispersed to one of these sites. I captured and radio tagged 10 additional fledglings there. None of them was depredated. The 4 fledglings that were killed at or after independence, were apparently solitary the last time I checked them.

The analysis presented here suggests that searching for food and flocking behavior were the main forces that defined the pattern of dispersal and exploratory movements of Wood Thrush fledglings. Nevertheless, it also clear that the exploratory behavior may have been influenced by other factors, such as searching for breeding sites and creation of a navigational target. These factors are not mutually exclusive, and could all be important and they are probably combined to produce a complex array of movement patterns and behaviors. More detailed studies designed specifically to isolate and test these hypotheses are necessary. For instance, a direct measure of availability of food resources for fledglings in the natal and dispersal sites would be necessary, although not sufficient, to assess more accurately the importance of the food factor. Assessing the percent of fledglings that return to the "familiar area" although difficult to obtain, would certainly help to clarify the role of the exploratory movements in the search of potential breeding sites. Brawn and Robinson (1996) correctly stated that, "Lack of data on dispersal is a major gap in understanding the population dynamics of Neotropical migrants and prescribing effective conservation measures." Further studies should take a closer look at the type, degree, and results of agonistic interactions in sites with high concentration of fledglings. Sex differences in postfledging behavior are a key issue in this context, but they were not considered in this study because I could not differentiate between male and female fledglings. Male and female Wood Thrush fledglings are probably under different selection pressures, at least in some aspects, and therefore, their behavior should be expected to differ.

We also need to look for possible additional factors involved in the dispersal of fledglings. For instance, juveniles could be being forced to move out of prime breeding sites by adult males breeding there at that time. Two fledglings, for example, moved to <0.3 ha sapling corridors adjacent to forests. During the 2 and 6 weeks that they were there, they never ventured out of these sites. Even when they flushed repeatedly in

response to my close approach while I tracked them, they moved in circles, always staying within the boundaries of the sapling site. Brown (1978) reported the habit of adult Purple Martins (*Procne subis*), especially vagrant adults, in pursuing and attacking fledglings. They suggested that the parents led the fledglings away from the immediate nest vicinity to avoid these attacks. At the time that I observed Wood Thrush fledglings evidently avoiding moving out of sapling stage forest and forest edges, adult Wood Thrushes were commonly involved in territorial disputes in the adjacent forest. Later in the season, when adult Wood Thrushes started molting, they stopped any territorial behavior. If fledglings' movements were somehow restricted by the territorial adults, this would be the time for fledglings to move freely within the forest. I found that fledglings were more frequently found in mature forest sites later in the season. However, I can not 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.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The presence, type and extent of dispersal and exploratory movements reported in this study have important conservation implications. First, it was evident that, for whatever reasons, fledglings were visiting and staying in sites with different physical and vegetational characteristics from the sites where they hatched. Therefore, to succeed in the conservation of migratory species, we must consider not only protection of the nesting area, but all the array of habitat that Wood Thrushes fledglings visited during the postfledging period.

Second, my results suggest that small patches of breeding habitat, while they may fulfil the needs of parents, nestlings, and recently fledged young, may not be appropriate for fulfilling the needs of independent fledglings. Robbins, et al. (1989a), for instance concluded that the minimum-area requirements for breeding Wood Thrushes was 1 ha, although Hoover et al. (1995) consider that nesting success on fragments of that size would be extremely low. I report here that independent fledglings easily moved across areas covering 10000 ha and probably larger. The Quantico Marine Base and the adjacent Prince William Forest Park provide birds and other taxa with 32375 ha of mostly forested area, and offer a mosaic of habitats. It is, for instance, interesting that of the 23 Wood Thrush fledglings that dispersed, 19 remained within the Marine Base boundaries until September or early October, when they most probably started moving south to their wintering quarters in south Mexico and Central America. What would be the situation in a small forest patch? What differences would there be in the movement patterns and survival of fledglings that hatch in small patches of forest? If indeed, fledglings require special conditions or they are excluded from the natal areas, where would they go? Fledglings have certainly the flight abilities to travel distances on the order of kilometers to find appropriate sites, but this situation could increase the chances of predation.

Third, familiarity with an area has been recognized as an important factor

determining future breeding success and survival. At the Quantico Marine Base and adjacent Prince William Forest Park, during a period that lasted up to 3 months in some individuals, Wood Thrush fledglings were most probably able to identify prime breeding sites, high food production spots, and perhaps areas where risk of predation was lower. In some regions, heavy fragmentation of the landscape may prevent fledglings from obtaining that familiarity with an area with negative consequences for their future reproductive success.

The results reported here strictly apply only to the Wood Thrush and within this species to the population that breed in the Quantico Marine Base. However, it is possible that similar ecological behavior can be found not only in other Wood Thrush populations but also in other migrant species. Unfortunately we lack information for most migratory species regarding the ecology, behavior and needs of fledglings after they become independent from the parents (and this situation applies to sedentary species also). Thus, studies that address rate of movements, behavior, habitat use and selection, and mortality during the postfledging stage are urgently needed and should be a priority for future studies on migrant species.

TABLE 2.1. Comparison of mobility (m) and area used (ha) between "natal" ($n = 17$) and "dispersal" ($n = 32$) sites of radio-tagged Wood Thrush fledglings. MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\bar{x}$	SE	Z[b]	P
Mobility	Natal	73.0	9.3	-1.24	.215
	Dispersal	101.0	12.0		
Area	Natal	1.6	.3	-0.81	.419
	Dispersal	2.8	.5		
Fcentro	Natal	107.0	14.9	0.63	.526
	Dispersal	96.0	10.00		

[a]Mobility: average distance between consecutive point locations; Area: size of the area which included all radiolocations of interest; Fcentro: average distance from the geometric center of the home range to every location.
[b]Wilcoxon 2-sample test (Normal approximation with continuity correction of 0.5).

TABLE 2.2. Comparison of vegetation attributes between "natal" ($n = 17$) and "dispersal" ($n = 23$) sites for radio-tagged Wood Thrush fledglings. MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\bar{x}$	SE	Z[b]	P
THA	Natal	1320	88	-2.28	.021
	Dispersal	1768	172		
D_DEC	Natal	1170	59	-1.84	.064
	Dispersal	1471	162		
D_VP	Natal	66	29	-2.82	.005
	Dispersal	176	33		
D_SG	Natal	85	8	-1.45	.146
	Dispersal	121	15		
D_SA	Natal	1000	68	-2.62	.008
	Dispersal	1472	177		
D_BC	Natal	275	22	0.52	.603
	Dispersal	255	23		
D_DEF	Natal	57	7	1.82	.068
	Dispersal	40	7		
T_BA	Natal	2621	105	1.26	.208
	Dispersal	2462	108		
PVEG_U	Natal	15	1	-1.45	.249
	Dispersal	18	1		
PVEG_M	Natal	66	2	-0.79	.426
	Dispersal	68	1		
PVEG_C	Natal	55	2	2.69	.007
	Dispersal	42	4		
WS	Natal	3782	496	-2.62	.008
	Dispersal	7159	999		

[a] Name and description of vegetation codes are given in Table 1.
[b] Wilcoxon 2-sample test (Normal approximation with continuity correction of 0.5).

TABLE 2.3. Results of statistical tests (Wilcoxon Test) examining differences in vegetation attributes between "natal" and "dispersal'"sites for 16 radio-tagged Wood Thrush fledglings, MCB Quantico, 1993-95[a].

ID	THA	D_DEC	D_VP	D_SG	D_SA	D_BC	D_DEF	PVEG_U	PVEG_M	PVEG_C	WS	T_BA
HY515	N	N	D**	N	D	D*	N**	D	N*	N*	D	D
HY609	N*	N*	N	N	N**	N	D	D	N	D	N	N
HY611	D	D	D	N	D	N	D	D	D***	N	N	N
HY617	D	D	D	D	D	N	N	N	N	N	D	N
HY512	D***	D***	D	N	D***	D	N**	D*	D**	N**	D***	N
HY979	D**	D*	D***	D*	D**	D**	N**	D	D	N	D**	D
HY986	D**	D*	D***	D	D**	D	N**	D**	N	N	D**	N
HY533	D**	D**	D**	D**	D**	D	N	D	N	N	D**	D
HY547	D	D	D	N	D	N**	D	D	N	N	D	N
HY993	D	D	D	D	D	D	D	D	N	D	D	D
HY591	N	N	D	D	N	D*	N	D	N	N***	N	N
HY589	D	N	D	D	D	D	N	D	N	N	D	N
HY595	D	D	D	N	D	D	N	N	D	D	D	N
HY692	N**	N**	D	N	N**	N	D	N	D	N**	N	N
HY566	N	N	N	N	N	N*	N	N*	D	N	N	N
HY567	N	D	N*	N**	N	N*	D	D*	D	N	D	N

[a] Names and description of vegetation codes are given in Table 1. D (dispersal) and N (natal) indicate the site where the higher value occurred. * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.008$.

TABLE 2.4. Comparison of physical parameters between "natal" ($n = 21$) and "dispersal" ($n = 38$) sites for radio-tagged Wood Thrush fledglings. MCB Quantico, Virginia, 1993-95.

Variable[a]	Site	$\bar{x}$	SE	Z[b]	P
D_Road	Natal	335	37	3.63	.001
	Dispersal	164	21		
D_Open	Natal	245	41	1.96	.049
	Dispersal	154	20		
D_Creek	Natal	120	24	-1.07	.285
	Dispersal	154	21		
D_Forest	Natal	11	8	-3.95	.001
	Dispersal	155	28		
Roads	Natal	224	77	-3.53	.001
	Dispersal	663	62		
Creeks	Natal	784	118	2.55	.011
	Dispersal	492	48		

[a]D_Road, D_Open, D_Creek, and D_Forest are the distance from the aritmetic center of the home range to the nearest road, forest edge or opening ($\geq$ 0.4 ha), creek, and mature deciduous and deciduous-pine forest (dbh$\geq$70 cm), respectively. Roads and Creeks are the total distance of roads and creeks in a circle 300 m radius.

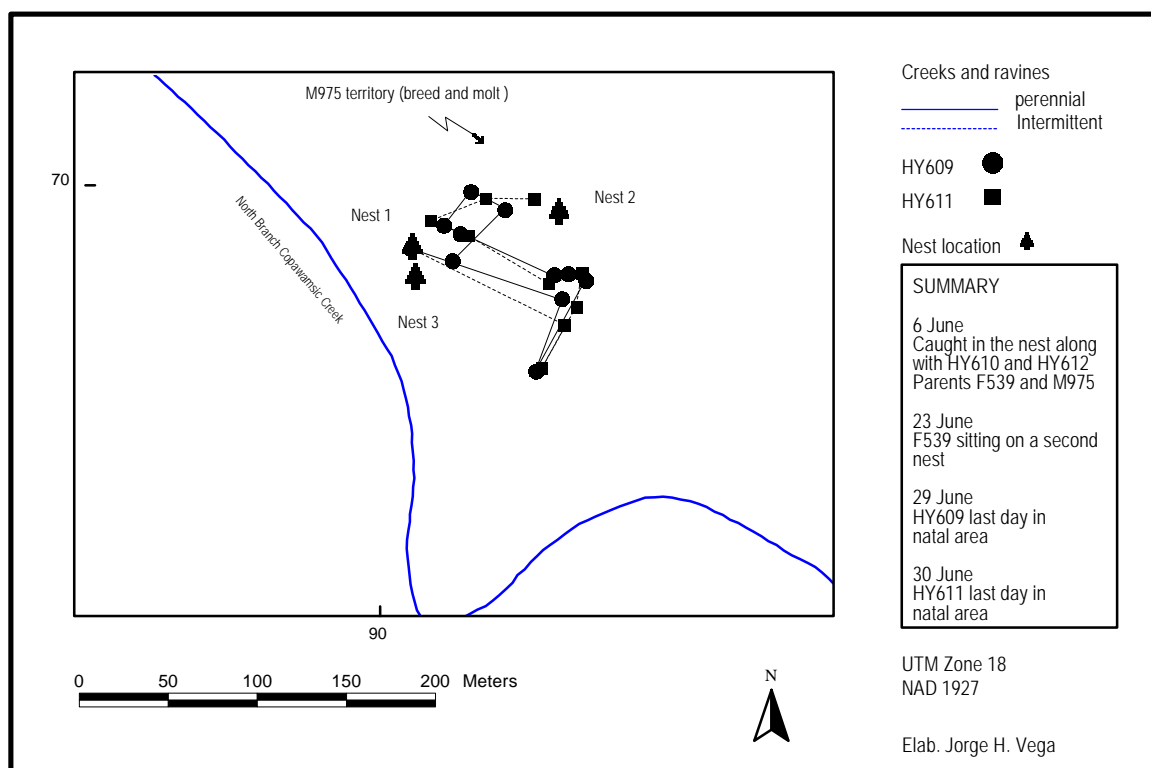[b]Wilcoxon 2-sample test (Normal approximation with continuity correction of 0.5).

Fig. 2.1. Radiolocations of HY609 and HY611 during the postfledging-dependence stage, MCB Quantico, Virginia, 1995.

Fig. 2.2. Radiolocations of fledglings HY512, HY533, and HY617 during the postfledging- dependence stage, MCB Quantico, Virginia, 1994-95.

Fig. 2.3. Radiolocations of HY589 during the postfledging period, MCB Quantico, Virginia, 1995.
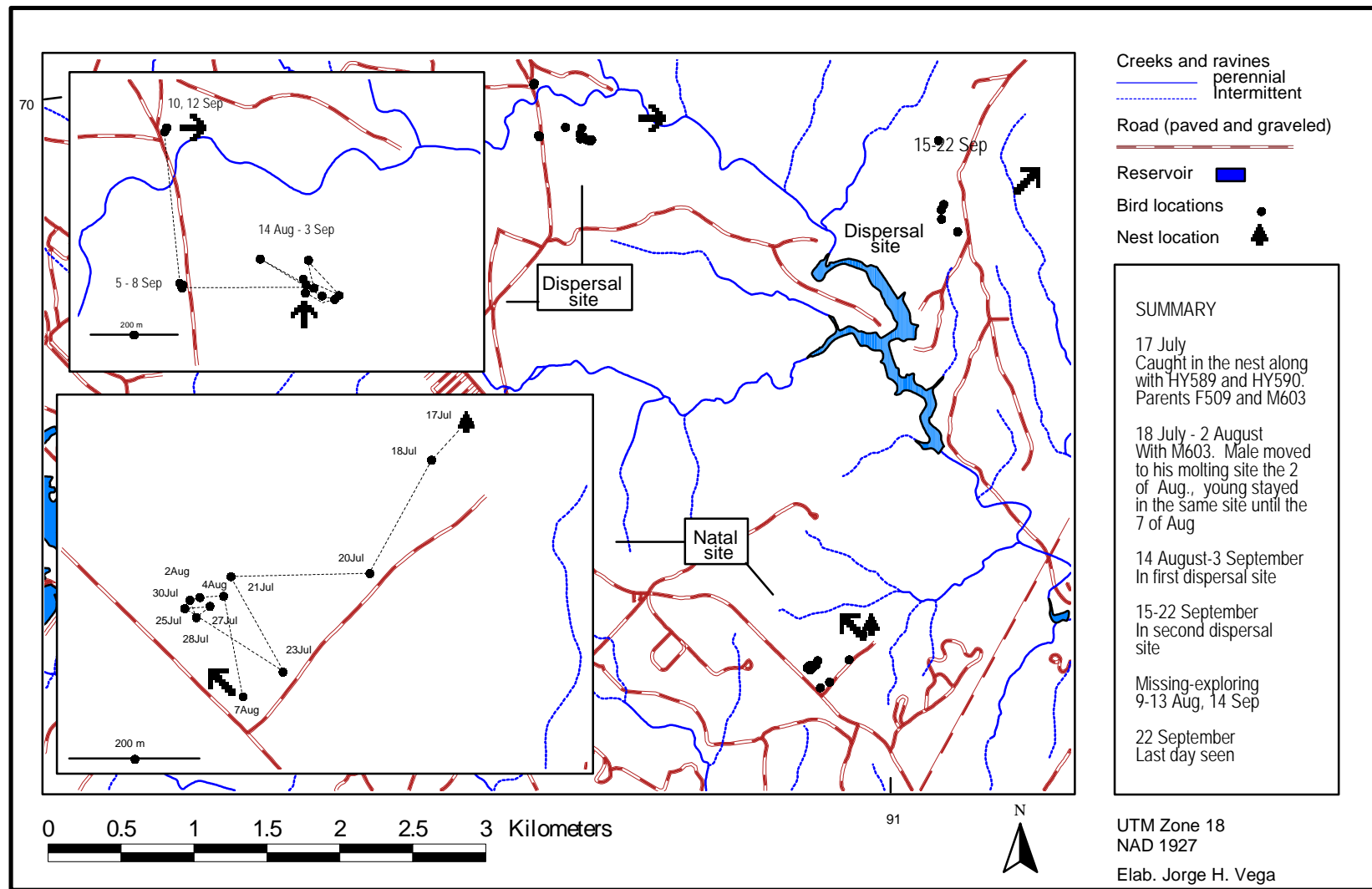
Fig. 2.4. Radiolocations of HY591 during the postfledging period, MCB Quantico, Virginia, 1995.
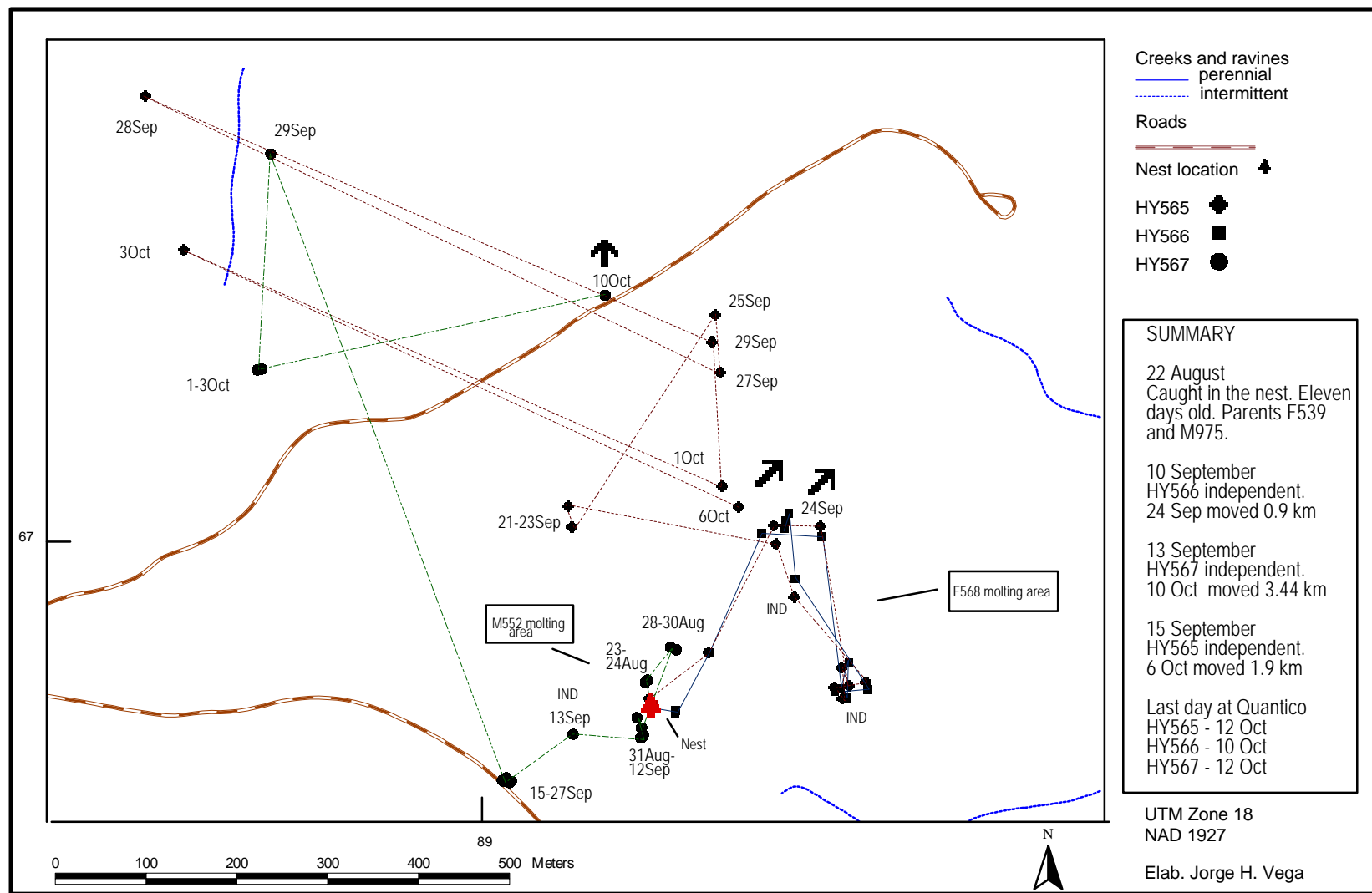
Fig. 2.5. Radiolocations of HY565, HY566, and HY567 during the postfledging period, MCB Quantico, Virginia, 1994.

Fig. 2.6. Compass direction and magnitude of observed dispersal events (Rayleigh Z=1.51, P =0.20), of Wood Thrush fledglings, MCB Quantico, Virginia, 1993-95.
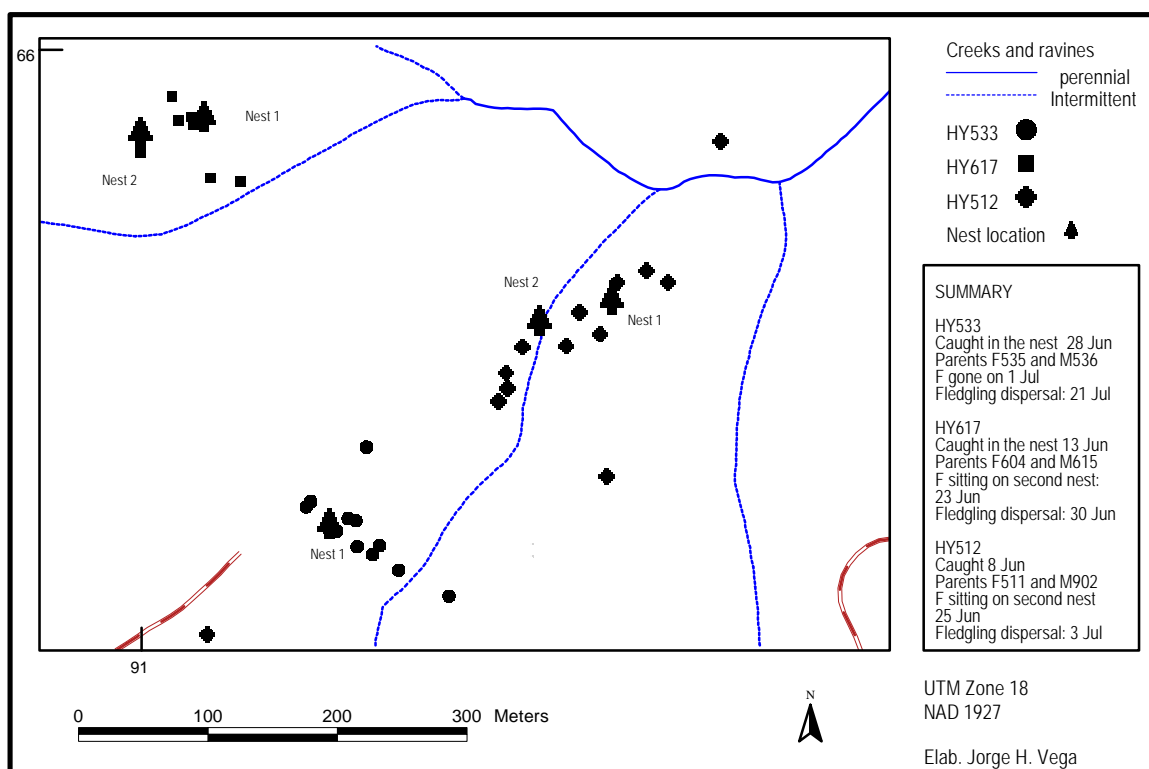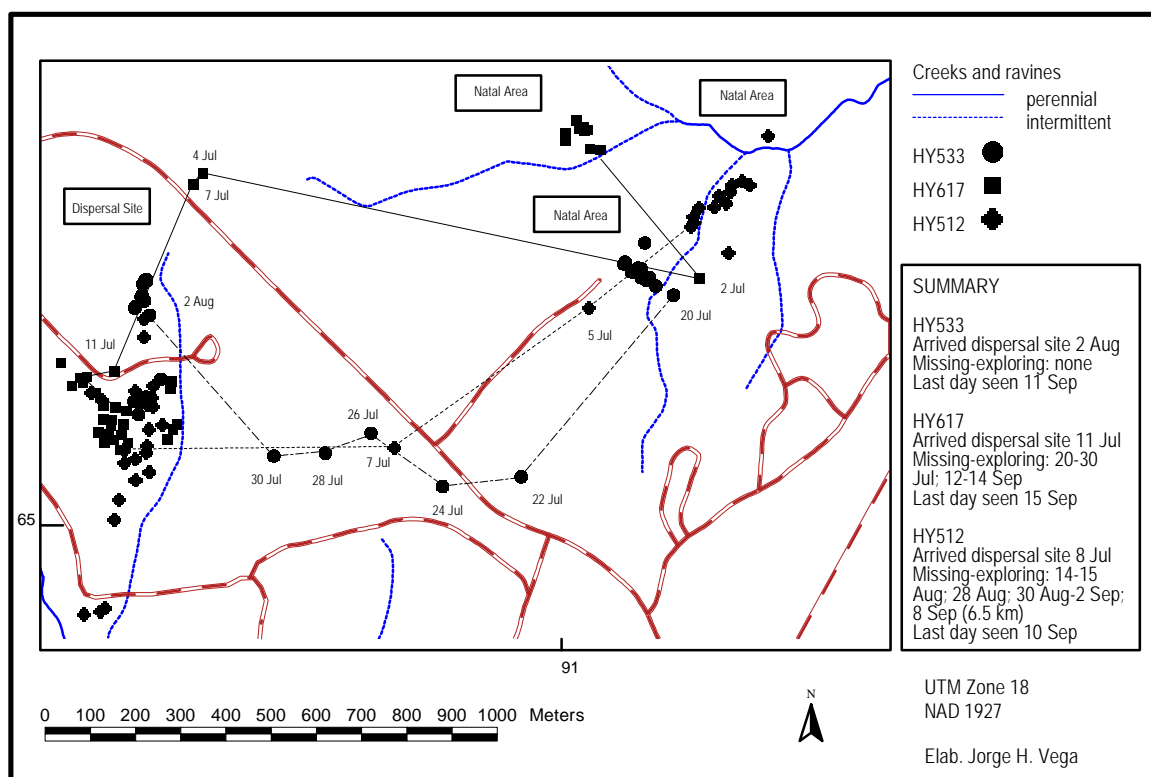
Fig. 2.7. Radiolocations of fledglings HY512, HY533 (1994), and HY617 (1995) during the postfledging period, MCB Quantico, Virginia, 1994-95.
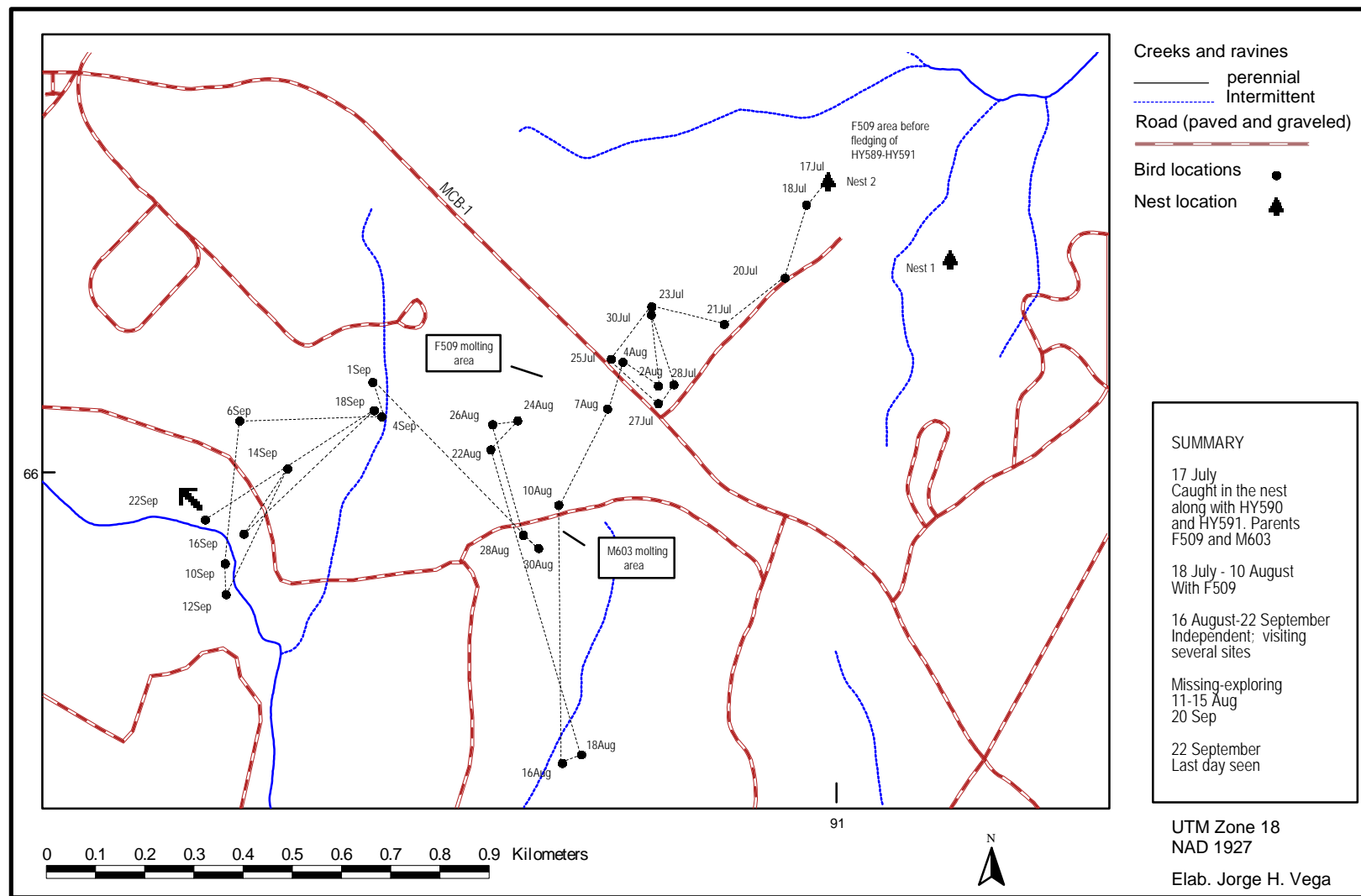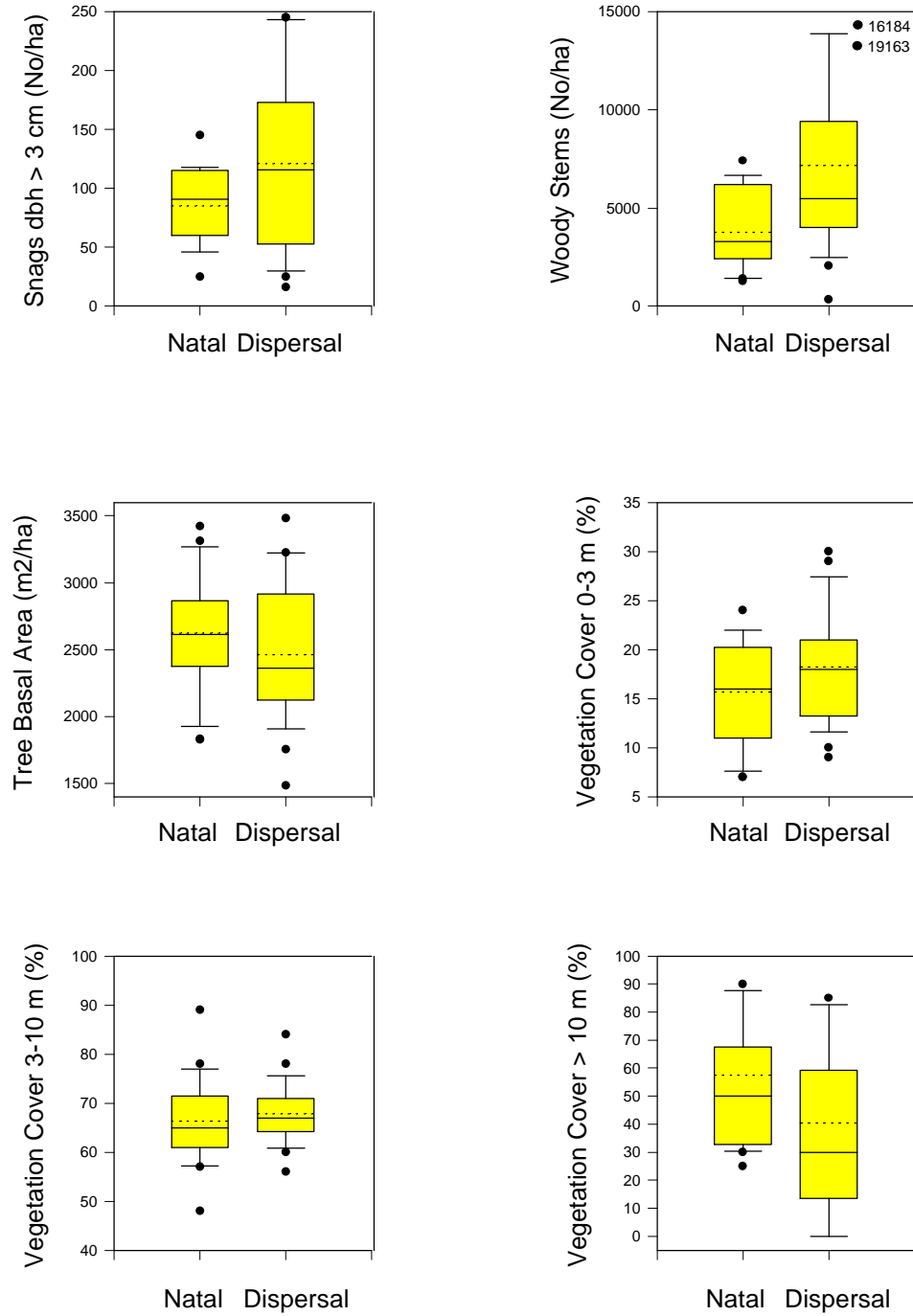
Fig. 2.8. Comparison of structural parameters between "natal" (*n* = 17) and "dispersal" (*n* = 23) sites for radio-tagged Wood Thrush fledglings, MCB Quantico, Virginia, 1993-95.
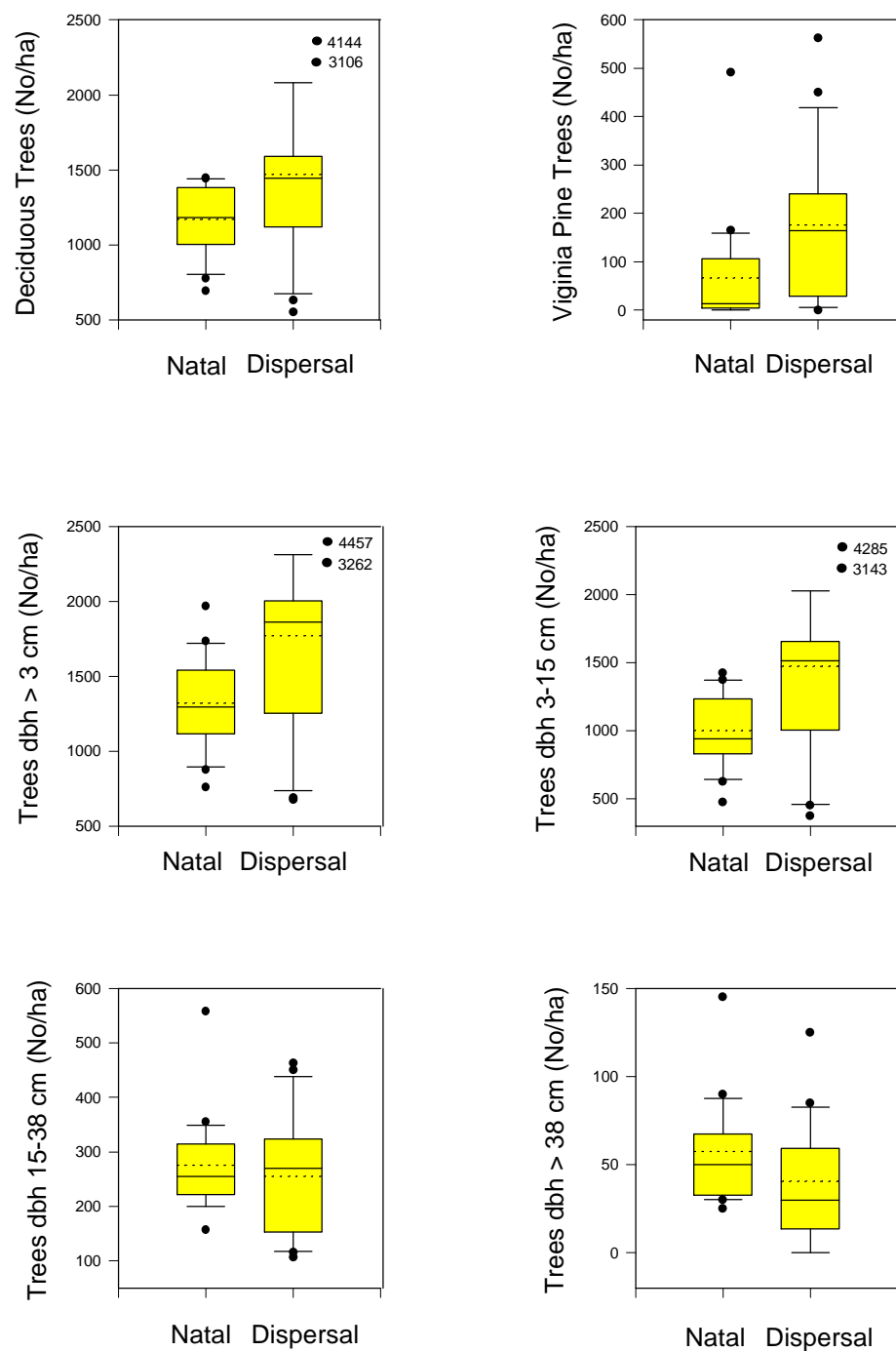
Fig. 2.9. Comparison of composition (deciduous vs. pine) and size (dbh 3-15, 15-38, >38 cm) of trees between "natal" (*n* = 17) and "dispersal" (*n* = 23) sites for radio-tagged Wood Thrush fledglings, MCB Quantico, Virginia, 1993-95.

A

B
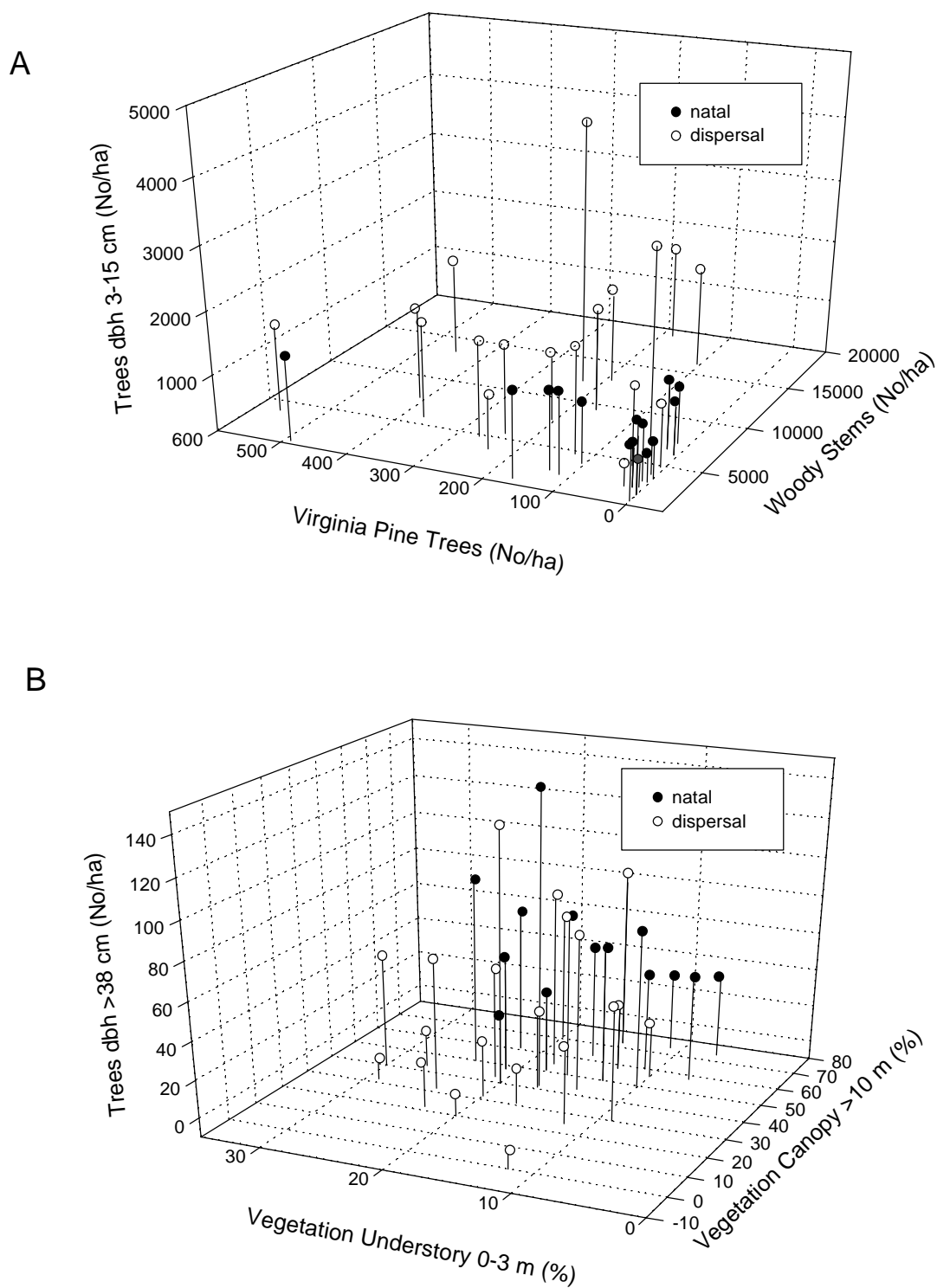
Fig. 2.10. Distribution of "natal" ($n = 17$) and "dispersal" ($n = 23$) sites of radio-tagged Wood Thrush fledglings, regarding six vegetation parameters, MCB Quantico, Virginia, 1993-95.
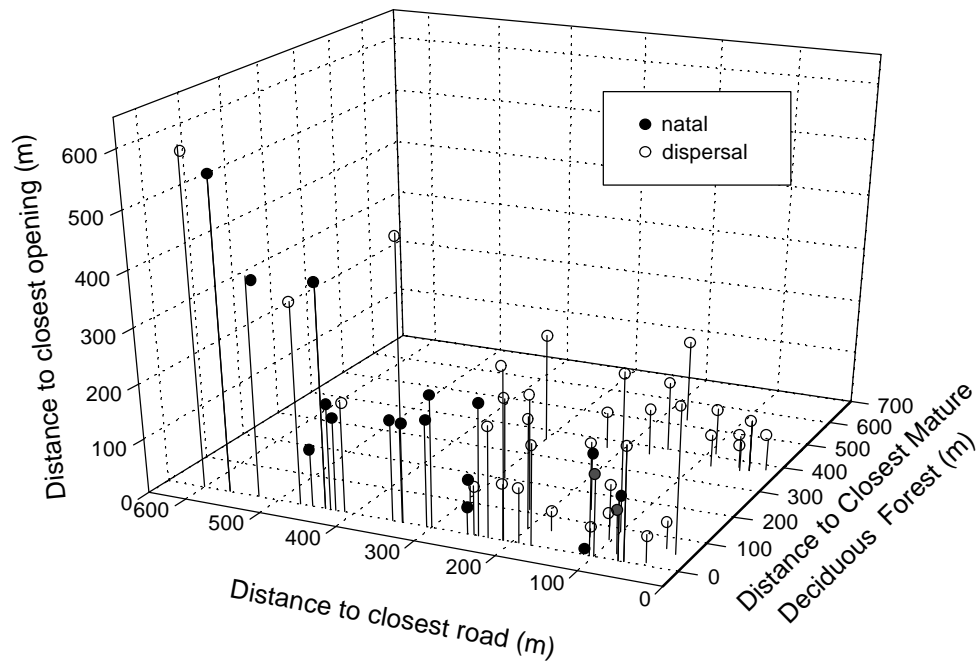
Fig. 2.11. Distribution of "natal" (*n* = 17) and "dispersal" (*n* = 23) sites of radio-tagged Wood Thrush fledglings, regarding three landscape parameters, MCB Quantico, Virginia, 1993-95.
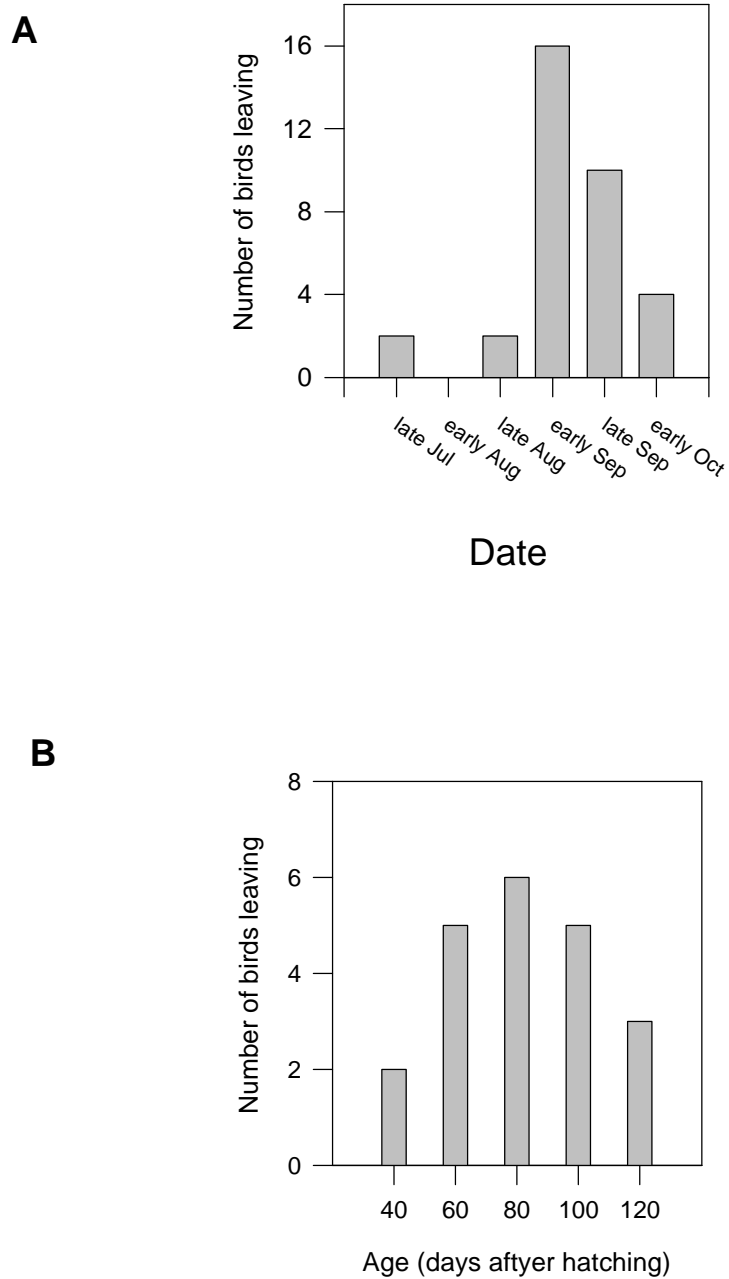
Fig. 2.12. (A) number of Wood Thrush fledglings leaving the Marine Base at two-week intervals, and (B) frequency distribution of age at the time of leaving, MCB Quantico, Virginia, 1993-95.

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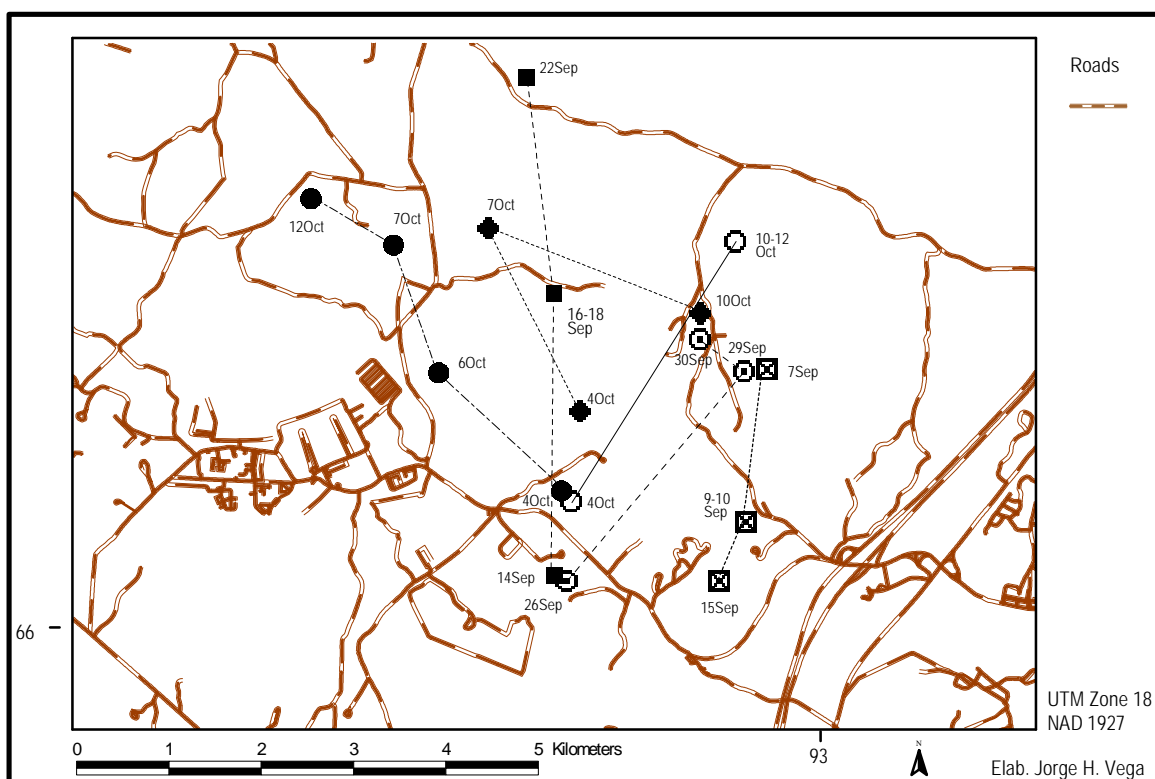
Fig. 2.13. Movements of six radio-tagged Wood Thrush fledglings within 3-7 days of leaving the Marine Base, MCB Quantico, Virginia, 1993-95.
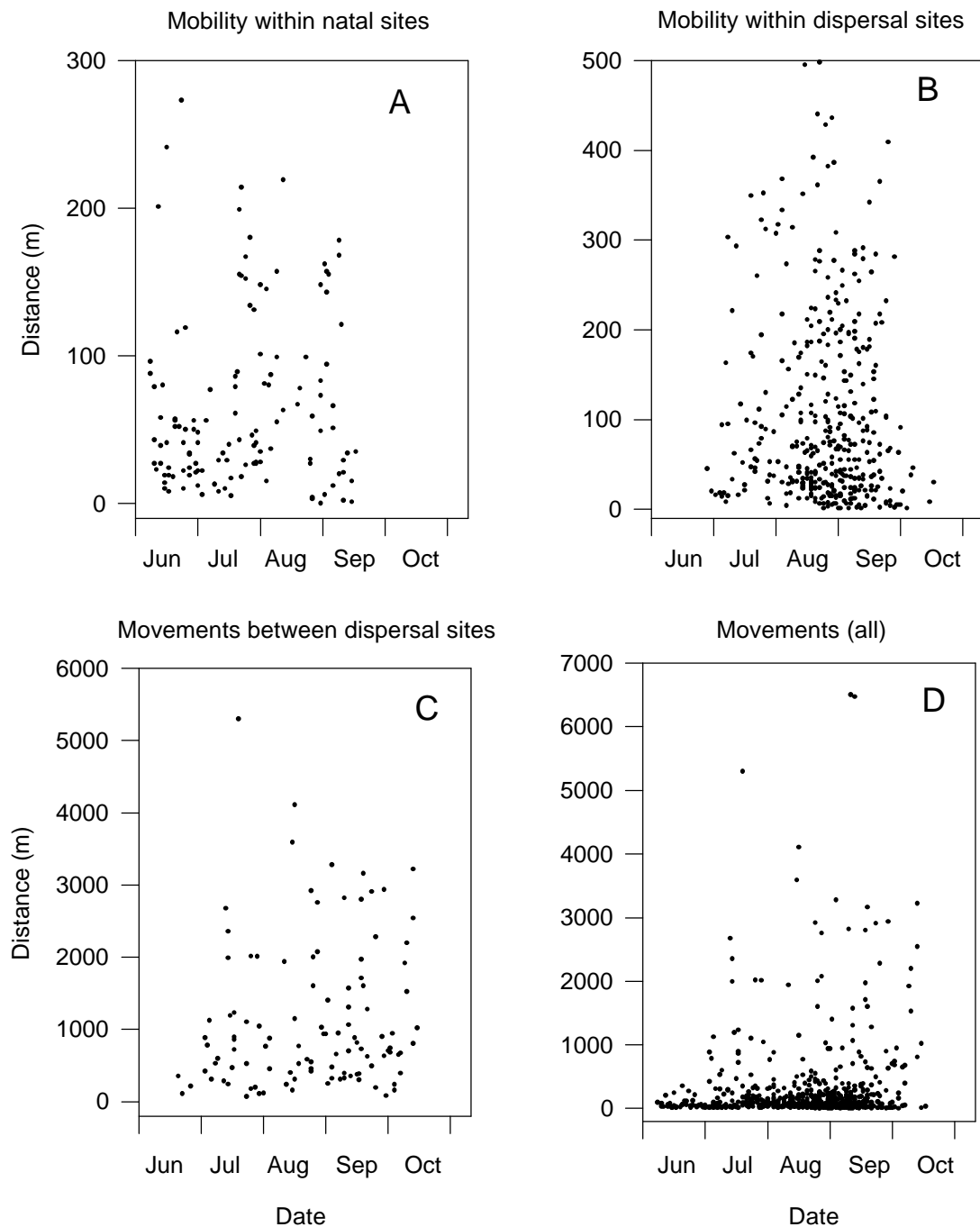
Fig. 2.14. Scatter plots of distance moved by radio-tagged Wood Thrush fledglings at (A) natal sites, (B) dispersal sites, (C) between dispersal sites, and (D) all movements considered, MCB Quantico, Virginia, 1993-95.

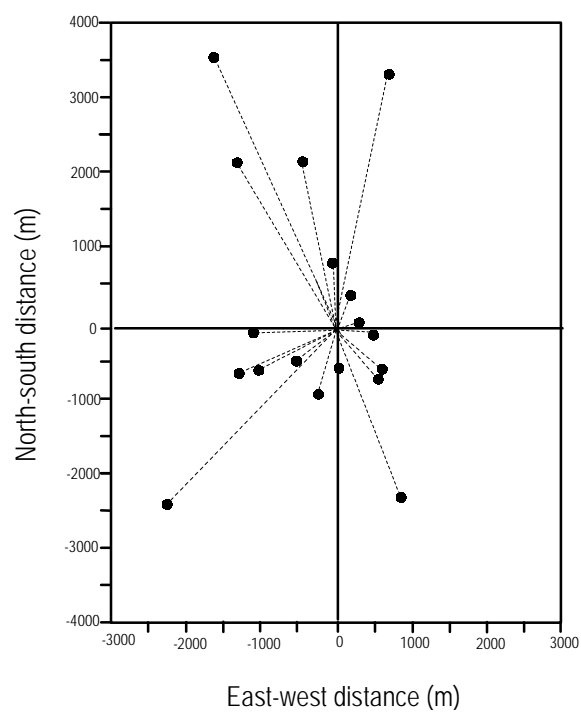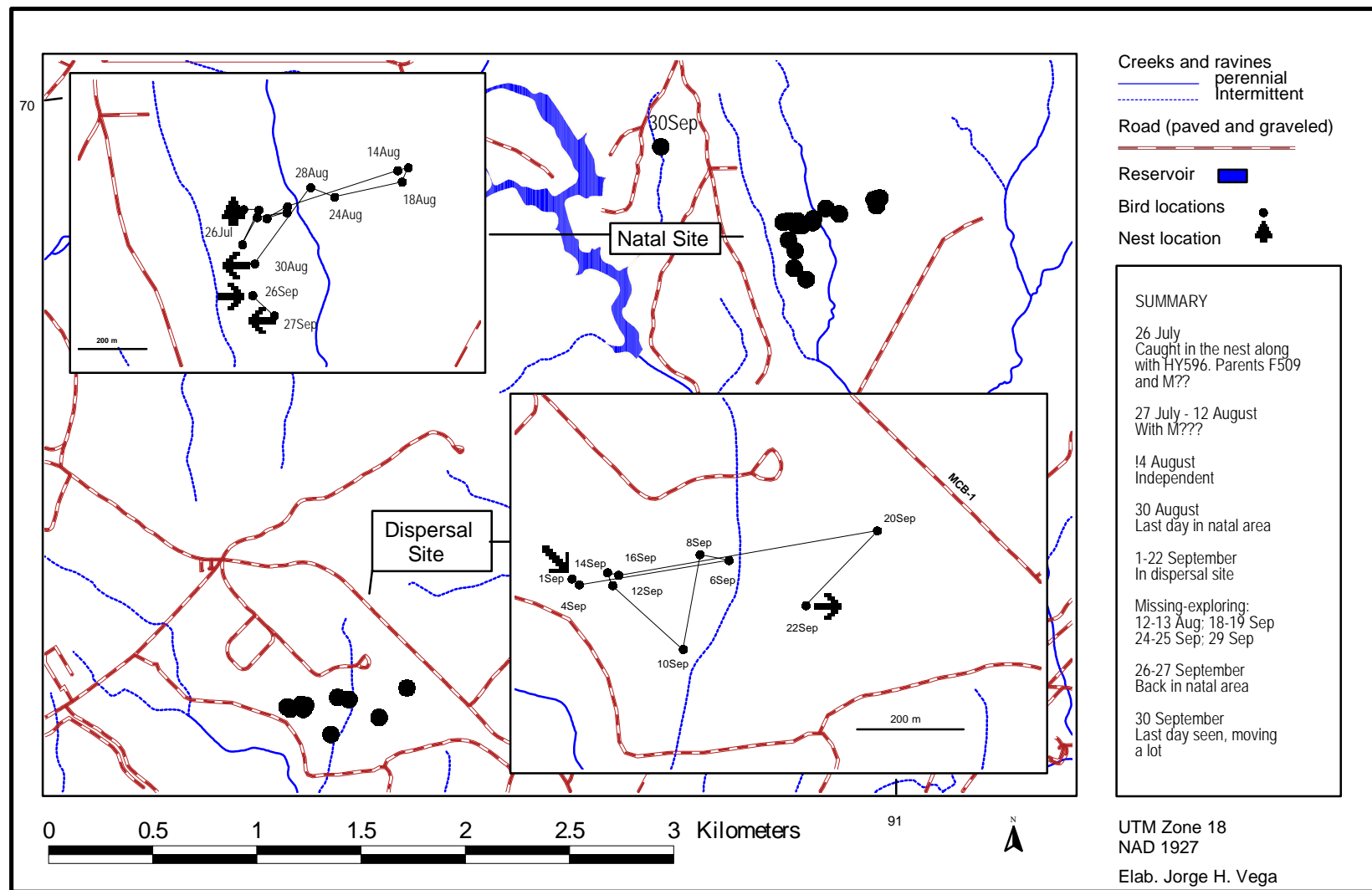Fig. 2.15. Radiolocations of HY595 during the postfledging period, MCB Quantico, Virginia, 1995.
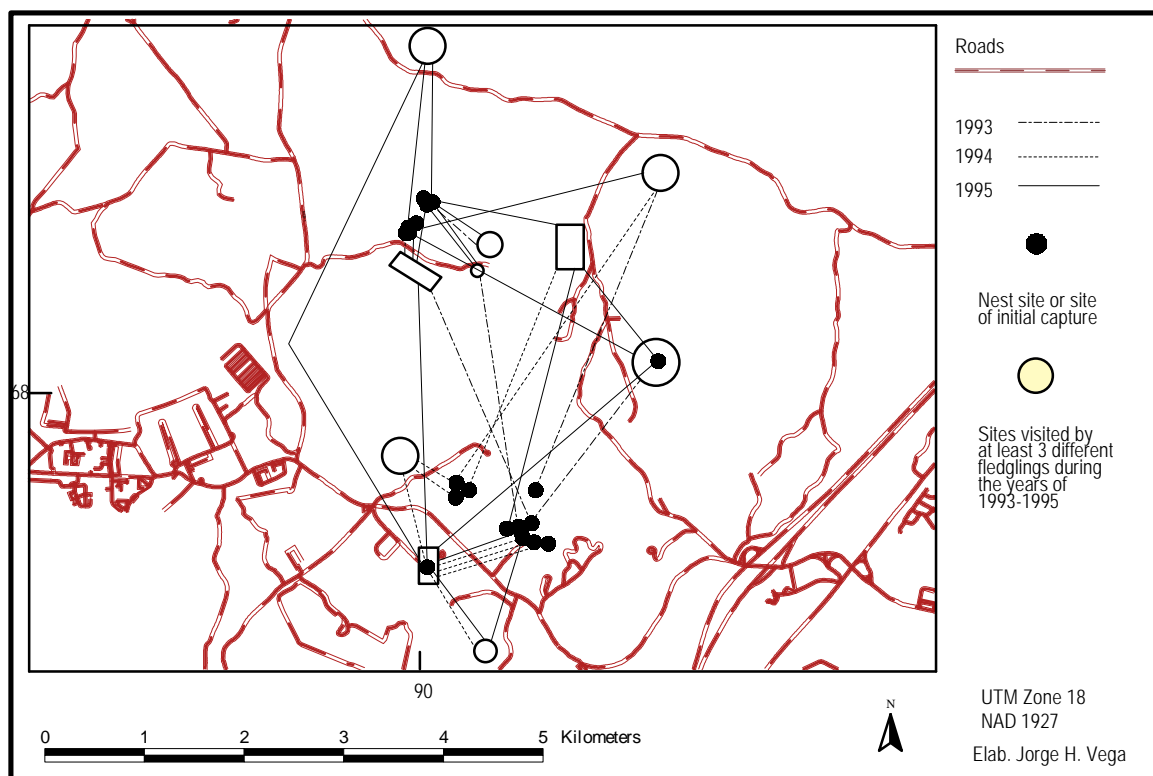
Fig. 2.16. Frequently used sites by radio-tagged Wood Thrush fledglings, MCB Quantico, Virginia, 1993-95.

CHAPTER 3
CHRONOLOGY OF REPRODUCTIVE ACTIVITIES, MOLT, AND MIGRATION FOR THE WOOD THRUSH

(Abstract)

Documentation of the schedule and pattern of molt, and its relation to aspects of reproduction and timing for migration is an important, but often neglected, area of knowledge. I radio tagged 104 Wood Thrushes and monitored their movements and behavior on the Quantico Marine Base, Virginia (38^0 30' N, 77^0 25' E) during May to October of 1993-95. The molt period in adults extended from late July to early October. In all observed and captured individuals, the rectrices were lost as a unit. Molt of flight feathers lasted an average of 38 days, and there was no significant difference in duration between sexes. Most breeding individuals were observed molting 1-4 days after fledgling independence or last-clutch predation. I suggest, however, that many birds began molt while still caring for fledglings. Energetic constraints may dictate a separation of molt and migration. My data favor this hypothesis. I did not observe Wood Thrushes leaving the Marine Base during flight-feather molt. Departure of individuals with molt in the body and head, however, was common. I argue that current reports on overlapping of molt and migration based on observations of molting individuals out of the breeding range could be misleading. In this study 15 females and 3 males left the Marine Base before molting. I suggest that Wood Thrushes left the breeding area to molt in other places before starting a true migration. I caution also against the interpretation of lack of observations or captures of molting individuals in the breeding sites as a justification to conclude that birds actually left the area. Extensive molt, such as that found in Wood Thrushes, apparently impairs flight efficiency, and birds at this stage are remarkably cautious, and consequently, extremely difficult to capture and to observe.

INTRODUCTION

The Wood Thrush (*Hylocichla mustelina*) is one of the most studied avian species in North America, and details about its natural history are relatively well known (Bent 1949, Longcore and Jones 1969, Bertin 1977, James et al. 1984). Despite this situation, information about its molt is limited (Bent 1949:112; Pyle et al. 1987:99), and details on how molt is integrated with reproduction and migration are lacking. Separation of breeding activities, molt, and migration within the annual cycle is considered an evolutionary strategy to avoid undue energetic stress (Payne 1972; Gin and Melville 1983:17), but exceptions exist. Overlap among these processes has been reported in numerous species (Payne 1972). For species such as the Wood Thrush, which undergo a complete prebasic molt before the autumn migration, identification of the schedule of molt and its relation to breeding and timing for migration is of paramount importance, not only for the in-depth understanding of the avian biological cycle, but also for conservation purposes.

The scarcity of information about timing and patterns for molt in Wood Thrushes and many other species is not unexpected. During the molt period, birds become secretive and less likely to be observed or caught, making documentation of activities during this period difficult (Ginn and Melville 1983:29-30). Further, individuals of some species move away from their breeding territory for molting (Nolan 1978, Cherry 1985, Rappole and Ballard 1987); following these individuals can be quite difficult. Consequently, molt data often come from observations and/or recoveries of individuals of unknown breeding history. In recent years there has been an increased interest in use of radiotelemetry for the study of small birds, mainly because of the improvement in transmitter technology (i.e., smaller size). Transmitters are still relatively expensive and of limited range and life, but well-designed studies can render information that otherwise would be hard to get (Rappole et al.1989; McShea and Madison 1992).

In this chapter I provide information on the schedule of reproduction, prebasic molt, and migration in a radio-tagged population of Wood Thrushes. My objective was to document the timing of these processes within the annual cycle and to discuss the relationships between molt, the breeding season, and timing for migration.

METHODS

For timing of breeding, molting, and date of departure from the Marine Base, I relied heavily on radio-tracking data. Direct observation of radio-tagged birds allowed me to record if a bird was breeding (either incubating, brooding nestlings, or caring for fledglings) or molting. Incipient molt was difficult to observe from a distance; therefore, for most birds I approximated the beginning of the molting period by back-dating 15 days from the time I observed the birds in heavy molt (see chapter 2, methods section for

details). When possible, start of incubation and/or hatching date were estimated by back-dating from time of hatching or fledgling. According to my observations of 2 pairs and reported information (Bent 1949:109; Bertin 1977), in the Wood Thrush incubation lasts 14 d and fledging occurs 13 d after hatching.

Estimate of duration and timing of molt were based on observations of 27 adults and 23 juveniles. All molting birds were radio tagged and were observed more than once over several days. In addition, I captured 18 adults (10 were radio tagged) and 23 juveniles (15 were radio tagged) when they were molting. In 8 of the captured adults, I recorded the stage (old, missing, in pin, emerging, full grown/new) and length of remiges and rectrices. Primaries, which number 10 in Wood Thrushes (10th spurious, not considered), were numbered 1 to 9 distally from the carpal joint. The secondaries were numbered 1 to 9 from the carpal joint inward to the body, including the tertials S7-S9. The 6 rectrix pairs were numbered 1 to 6 distally from the center of the tail. I recorded body molt in all captured juveniles and 8 adults. Molt on 4 regions of the body was scored using the terminology of Niles (1972): "*head* (capital track and the anterior, undivided portion of the ventral track), *breast* (middle portion of the ventral track immediately posterior to its bifurcation), *sides* (the dorsal edges of the postero-lateral branches of the ventral track beneath the wings), and *back* (roughly the anterior half of the dorsal track)." Niles (1972) also assigned an "active molt score" for each region: "0" for no active molt, "1" for moderate feather replacement, and "2" for relatively heavy feather growth.

RESULTS

Prebasic molt in adults

Molt patterns.--A composite pattern of molt in adult Wood Thrushes is inferred from 8 individuals caught when they were molting (Fig. 3.1) and from observations on 10 captured birds for which I did not measure flight feathers. None of these birds was recaptured; therefore I lack information on rate of growth.

Loss of P1 marked the beginning of molt in remiges. From there, molt proceeded sequentially, with P9 the last feather replaced. Similar size in pairs of growing remiges in 2 individuals suggests that replacement may have occurred simultaneously or very close in time. In 4 individuals molt of primaries in both wings showed some degree of asymmetry. Molt of secondaries S7-S9 (tertials) and S1-S6 was independent. Replacement of tertials apparently began at the same time as that of inner primaries. Order of replacement of tertials varied and was even asymmetrical between wings in 2 birds. Molt of S1-S6 started when replacement of primaries was very much underway. In 2 individuals, shedding of S1 occurred as P5 was out of the pin. Simultaneous replacement of 2 and 3 secondary feathers was observed in 2 individuals.

All observed individuals ($n = 27$) apparently lost all rectrices at once. They were observed without tail feathers ($n = 8$) or with even growth of feathers. Coincident with those observations, 5 birds captured when they were molting had growing rectrices of the same size, which indicates that rectrices were replaced simultaneously. Shedding of the rectrices occurred shortly after P5 was replaced and finished with the replacement of P9 or shortly after.

Body molt started before that of remiges and rectrices. Two males were captured showing body molt while still possessing all of their old flight feathers. By the time of the onset of molt in remiges and rectrices, body molt was extensive, and continued several days after molt of flight feathers was terminated. I base this statement on my observation of adults in full-new plumage still showing molt on the head, which was the last region to molt.

Molt chronology.--For most adult Wood Thrushes the onset of molt occurred in early August, but at least 2 birds commenced molt by 21 July (Fig. 3.2). The earliest capture of a molting adult was 27 July with moderate molt in *breast* and *sides*. The earliest and latest records of adults with completed molt were 16 September and 14 October, respectively. For most adult Wood Thrushes, the molt period extended from early August to late September (Fig. 3.2).

According to my observations, molt of rectrices and remiges lasted 38 ± 0.5 d ($n = 16$) with no significant differences between males (38.3 ± 0.6 d; $n = 9$) and females (37.1 ± 2.1 d; $n = 7$). Complete molt lasted 51.3 ± 1.4 d ($n = 21$) and was similar in duration for both males and females (52.2 ± 1.7 d, $n = 16$; and 48.4 ± 9 d; $n = 5$, respectively). My data suggest that Wood Thrushes that started molting earlier in the season extended the molt over a longer period ($r = 0.83$, $P = 0.001$).

Behavior during molt.--According to my observations on radio-tagged adults, heavy molt seriously impairs flight sustenance and maneuverability. I observed several molting birds that for several days could barely fly; for instance, while tracking a female, she moved 1 m up in a branch, from there she tried to fly up, but she could not, and fell down to the ground and disappeared hopping and flapping her wings. Molting adults, at least during the heaviest molt stage, were very difficult to observe and almost impossible to capture using mist nets. They hid on the ground, in the densest patches of vegetation where, on occasions, I had to approach within 3 m to make them move and ensure that they were alive. These changes in behavior were evident when I compared the mean distance between consecutive locations (128 ± 20 m and 63 ± 10 m, $P = 0.01$) and area used (3.6 ± 1.2 ha and 1.3 ± 0.3 ha, $P = 0.034$; 95% convex polygon) between the nesting and molting phases, respectively, in 15 adults.

Prebasic molt in juveniles

I captured 23 actively molting juvenile Wood Thrushes. The earliest date on which a juvenile in molt was captured was 27 July, an individual with incompletely grown rectrices and light molt on the *sides*. Nine more juveniles were captured from 9-20 August and 12 from 2-5 September. The latest date on which a molting juvenile was captured was 18 September. All juveniles captured had moderate to heavy general body molt. Of these birds only 2 were of known age; they were 82 and 64 d post hatching. One juvenile was observed with molt on the head at 90 d post hatching.

DISCUSSION

Molt in adults

The replacement of remiges in Wood Thrushes, including that tertiaries were molted ahead of the other secondaries, was typically of passerines (Dwight 1900). According to my observations, replacement of the tail as a unit occurs routinely in Wood Thrushes. Simultaneous molt of rectrices, although frequently observed in some species, is not a common pattern in passerines (Pyle et al. 1987:13). In Wood Thrushes, its occurrence was previously reported by Bent (1949:113). Comparison of the duration of the flight-feather molt with other members of the subfamily Turdiniae is not possible because of the lack of data. An exception is that reported by Cherry (1985) for Swainson's Thrushes (*Catharus ustulatus*). Based on calculation from recaptured individuals, he reported that this species required 32 d to complete flight-feather molt, which is close to the measure reported here for the Wood Thrush (38 ± 2.8 d).

*Sex differences in molt.--*It has been reported that in several passerine species adult males begin molt before adult females (e.g., Morton and Welton 1973, Mountain White-crowned Sparrows [*Zonotrichia leucophrys oriantha*]; Verbeek 1973, Water Pipit [*Anthus spinoletta*]; Rimmer 1988, Yellow Warbler [*Dendroica petechia*]; Norman 1990, Willow Warbler [*Phylloscopus trochilus*]). Perceived differences in the onset of molt between the sexes, however, could depend to some extent on interpretation of the data. In most instances, reported differences are based on averaged captures of molting birds of each sex rather than observed molt patterns in both members of known pairs. In studies where known breeding pairs have been identified, an earlier emancipation from parental care by one sex has been shown to correspond to an earlier molt schedule in that sex (Selander 1958, Morton and Welton 1973, Verbeek 1973, Sealy 1979, Tiainen 1981, Norman 1990). According to my data, it is possible that adult male Wood Thrushes commence molt prior to adult females. By 15 August, 76% of adult males had initiated molt, but only 50% of the adult females. However, according to my observations, independent of sex, all birds, except 1 male, started molting soon after they finished their breeding activities.

There are additional problems when sex differences on the onset of molt are based on birds of unknown breeding history. This difference could be the result of adult females abandoning the study area before they have molted. In this study, 15 females, but only 3 males that bred at the Marine Base, left before molting, so I did not get information on when they started molting. Further, if unmated males were present in the population, they would probably begin molt earlier than the breeding birds.

*Behavior during molt.--*Flight efficiency in adult Wood Thrushes was decreased because of extensive molt. Without exception all the birds I recorded molting lost all rectrices at once. Further, they dropped several primaries over a very short period. Simultaneous replacement of flight feathers in waterfowl resulting in temporary flightlessness is well known (Jehl 1990). In passerines, there are scattered reports that extensive molt may seriously impair flight efficiency and, consequently, cause flightlessness (e.g., Miller 1961, Haukioja 1971, Verbeek 1973, Rimmer 1988; but see Green and Summers 1975). This condition in passerines is probably more common than has been reported, especially among species at the northern limits of their distribution, where a short prebasic molt is a necessity (Haukioja 1971). Lack of reports is not surprising because this condition may be difficult to detect. In fact, most authors who report flightlessness associate this stage with extreme secretiveness (Newton 1966).

It is possible that reduced ability to fly may cause increased predation but it has not been investigated. Survival during this period can be enhanced by behavioral inconspicuousness and /or selection of safe areas, strategies which apparently were adopted by molting Wood Thrushes. During this study, only 1 radio-tagged individual was taken by a predator (a Red-shouldered Hawk *Buteo lineatus*) while molting. Molting Wood Thrushes were secretive and molted in sites that have vegetation attributes that could enhance protection, such as high number of woody stems, dense understory vegetation, and high number of deciduous saplings. These attributes were mainly found in Virginia pine forest, young deciduous stands, and forest edges. Virginia pine stands were particularly good in providing molting Wood Thrushes with fallen trees and dense thickets into which they moved when I tracked them.

Molt in juveniles

My information on prebasic molt in juvenile Wood Thrushes was limited. I captured juveniles molting from the end of July until early September. However, fledglings of later clutches with body-head molt were still present at the Marine Base until the middle of October. Based on my observations, it appeared that juveniles started the prebasic molt soon after they became independent from their parents. Juveniles from earlier clutches had probably completed the molt before they left the Marine Base in early September. Berthold (1993:90-91) mentioned that later-hatched juveniles accelerate their development processes (for example molt), which render them ready for migration at a younger age than their early-hatched conspecifics. According to my data, there was a

trend for juvenile Wood Thrushes that hatch earlier in the season to spend a longer time on the Marine Base that those that hatch later ($r = 0.66$, $P = 0.02$). There was not a trend, however, for later-hatched juveniles to became independent from the parents at a younger age ($r = 0.22$, $P = 0.68$).

Relationship among reproduction, molt, and migration departure

Relation between reproduction and molt.--Separation of breeding and molt is considered a general strategy that allows these processes to occur with minimal energetic stress (Payne 1972, Morton and Welton 1973, Ginn and Melville 1983). However, the initiation of molt in parents while still caring for fledglings has been reported for several species (e.g., Evans 1966, Lesser Redpoll [*Carduelis flammea cabaret*]; Green and Summers 1975, Snow Bunting [*Plectrophenax nivalis*]; Rimmer 1988, Yellow Warbler; Norman 1990, Willow Warbler; Zaias and Breitwisch 1990, Northern Mockingbird [*Mimus polyglotus*]). In this study, 9 known-breeding Wood Thrushes apparently began molt 1-4 days after their young reached independence or after nest failure. However, I recorded 2 individuals molting while caring for fledglings. A pair was captured on 22 August when I radio tagged their 3 nestlings. The male had light general body molt. On 6 September, while still caring for one of the fledglings, the male had lost the tail and showed heavy general body molt. It was not until 7 days later that the fledgling became independent. The female was not molting when captured. On 14 of September, she was observed still caring for 1 fledgling, although she was in heavy general body molt. The next day she lost her tail and the fledgling had dispersed.

It is possible that more Wood Thrushes started molting while still taking care of fledglings, but I was unable to document this situation because of my inability to visually detect incipient body molt without actually capturing the bird. When I recorded a bird as molting, it was the "notable molt" of Nolan (1978) that I recorded, i.e., bird with heavy molt in the head or with missing or growing flight feathers. Most birds in this condition, with exception of the 2 birds mentioned, were not in the company of fledglings, but obviously, they initiated molt earlier.

Incompatibility between molt and reproduction is thought to be a strategy to avoid nutritional stress (King and Murphy 1985). I suggest that Wood Thrushes attending the last brood of the season may initiate molt before fledgling independence with minimal nutritional stress for 2 reasons. First, close to independence, Wood Thrush fledglings feed mostly by themselves and, therefore, their demands for food from parents likely are low. Also, at this time, fledglings also are capable of full flight, and thus they are less vulnerable to predators, making the parental role in this aspect less critical. Second, at the Marine Base the onset of adult molt coincided with the initiation in production of fruits and berries, which according to my observation and reported information (Martin et al. 1951, Conway et al. 1994) are commonly eaten by Wood Thrushes in late summer and fall. For instance, 7 fledglings (from 3 broods) that became independent in late August

and early September were observed foraging by themselves on blackgum fruits at least a week before they became independent. I do not have information, however, in how much of the diet of molting birds was composed of invertebrates and fruits. Nor do I know whether fruits provide necessary structural components for feather production.

An overlap between care of fledglings and onset of molt would effectively prolong the potential reproductive period for an individual, and therefore would increase the probability of producing offspring (Foster 1974). For such species as the Wood Thrush, which feed extensively on fruits during the molt, a rapid and extensive molt may be energetically viable.

*Relation between molt and migration.--*At the time for migration, a bird must have fully functional flight feathers (Ginn and Melville 1983:17) and therefore, molt is scheduled in such a way that no migrant has to fly with gaps in its wings (Berthold 1993:137) . Rimmer (1988) found that most Yellow Warblers initiated migration during the final phase of remigial molt, "when flight efficiency was probably close to maximal." Although there are reports that individuals of some species migrate when still molting (e.g., Hyytiä and Vikberg 1973, Sealy 1979), no details are given regarding the extent of the molt or if this included flight feathers. Overlap between molt and migration is possible for some species. For instance, Niles (1972) suggested that molt-migration overlap, while unusual among long distance migrants, is typical of migrant hirundinids. He argues that a slow, diurnal migration with frequent feeding stops reduces energetic demands, and allows individuals to finish molt while migrating. According to my observations, I have no evidence that Wood Thrushes that molted at the Marine Base left the Marine Base before the replacement of remiges and rectrices was complete, or when only a terminal fraction of growth was occurring. Departure with body molt is apparently more common. Berthold (1993:137) stated that body molt is frequently still occurring during migration, but he added that "the most intense period of moult is generally before the onset of migration."

I suggest that records of molting individuals outside the breeding range may not be evidence of overlap between molt and migration. Cherry (1985) captured molting Swainson's Thrushes 30, 150, and 250 km from the closest breeding range. He stated that Swainson's Thrushes are unlikely to initiate actual southward migratory movement during the middle of molt. In this study, 8 adults left the Marine Base after nest failure or fledgling independence after mid-July and early August. These birds were not migrating, but were moving elsewhere to molt. I base this conclusion on the fact that intensive study of this species on the wintering grounds in Veracruz, Mexico, has demonstrated that arrivals occur from mid October to mid November (Winker et al. 1990).

Furthermore, I caution against the interpretation of lack of observations or captures of molting individuals on the breeding sites as justification for the conclusion that birds actually left the area (for instance Sealy 1979). In this study, if molting birds

were not radio tagged, they likely would have passed unnoticed because they were furtive, silent, and flew very little. Capturing radio-tagged molting Wood Thrushes in mist nets was difficult. I surrounded several molting birds with mist-nets and yet sometimes I failed to capture them.

Documenting the relationship between reproduction, molt and migration is especially important for species that molt before autumn migration. Major questions regarding the relationship among these events remain unsolved. For instance, segregation between reproduction and molt in the annual cycle in these species is thought to indicate metabolic incompatibility. Payne (1969) stated that this separation suggests that birds are limited by the availability of food. In northern Virginia, the Wood Thrush's cycle is suited to take advantage of the changing conditions in the breeding areas. They breed when insects, the main food supply for nestlings, are abundant, and molt when production of fruits, on which they depend heavily during this time, is at a peak. Discussion of whether the ultimate factors timing the annual cycle are associated with reproduction or molt is also debated. For *Zonotrichia capensis*, for instance, Wolf (1969) states that the ultimate factors in the timing of the annual cycle in this species were associated with breeding and that molt "is relegated, evolutionarily, to periods that are unfavorable for breeding," whereas Miller (1962) believed that the molt was the important factor in the annual cycle of his population and that it constrained breeding. From the conservation point of view, identification of where the molt takes place, what the habitat requirements are during this time, and how this process may modify the behavior of individuals and their vulnerability to predation is important.
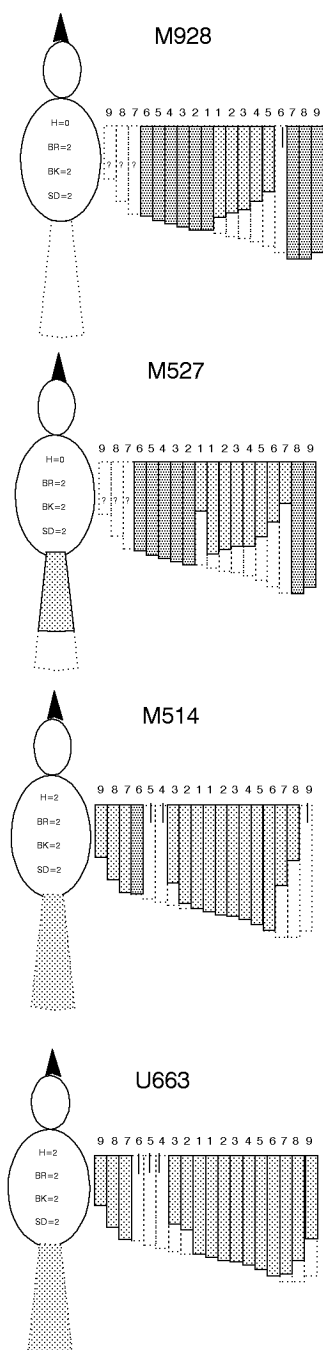
Fig. 3.1 Molt stage of adult Wood Thrushes. Light and dark gray bars represent emerging/ new and old feathers, respectively. Birds with only one wing had symmetrical molt. H=head, BR=breast, BK=back, and SD=sides. Body and head scores are "0" absent, "1" light, and "2" heavy. Numbers above the wings represent standard numeration of primary and secondary feathers. MCB Quantico, 1993-95.

M975

9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9
H=0
BR=2
BK=2
SD=2
9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9

U624

9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9
H=2
BR=2
BK=2
SD=2
9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9

U623

9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9
H=2
BR=2
BK=2
SD=2
9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9

M933

9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9
H=2
BR=2
BK=2
SD=2
9 8 7 6 5 4 3 2 1 1 2 3 4 5 6 7 8 9
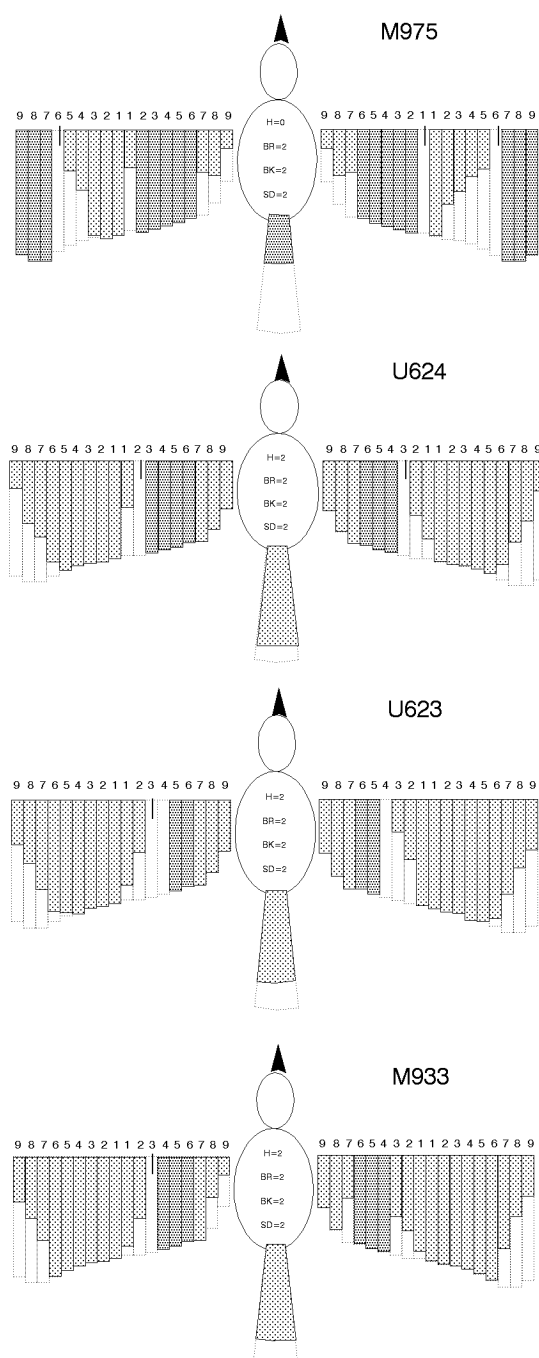
Fig. 3.1 (Con't)
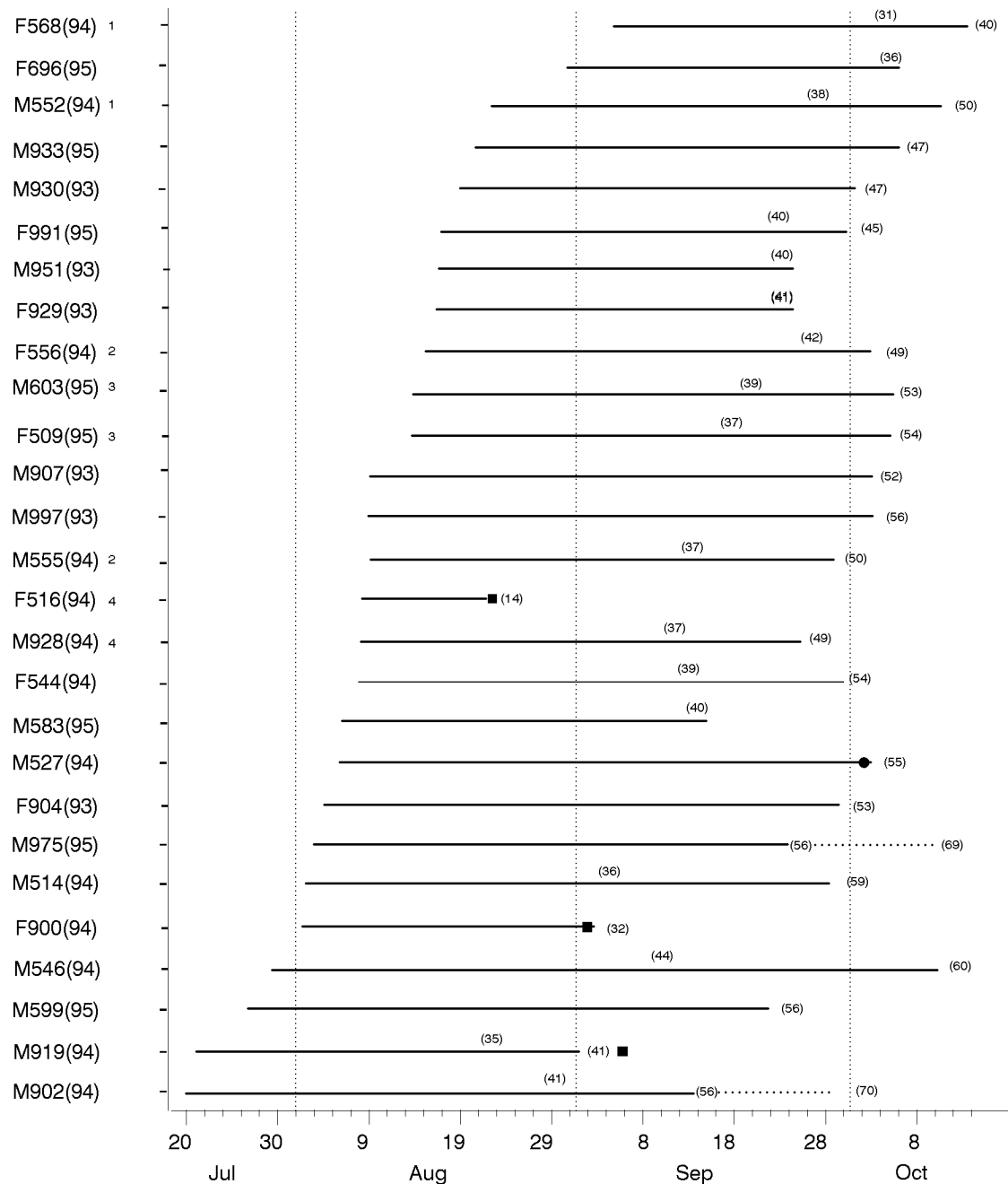
Fig. 3.2. Molt chronology of adult Wood Thrushes. The numbers above and at the end of the lines indicate duration (days) of flight-feather molt, and total number of days that the bird was observed molting, respectively. A dotted line represents a bird staying staying at the Marine Base after it finished molting. A circle and a square indicate that the transmitter fell off the birds or that the bird was killed, respectivy. Member of a pair have the same number MCB Quantico, Virginia, 1993-95.

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Comparison of tree species composition among "nesting"($n = 12$), "molting" ($n = 12$), and "nesting-molting" ($n = 7$) sites, for radio-tagged adult Wood Thrushes, MCB Quantico, Virginia, 1993-95.

Species	Site	Total[a]	N[b]	Dom[c]
Acer rubrum	Nesting	.071	1.0	.25
Red maple	Molting	.083	.92	.25
	Nesting-Molting	.131	1.0	.71
Aralia spinoza	Nesting	0	0	0
Devil's walkingstick	Molting	.002	.08	0
	Nesting-Molting	0	0	0
Betula nigra	Nesting	0	0	0
River birch	Molting	.004	.08	.08
	Nesting-Molting	0	0	0
Carpinus caroliniana	Nesting	.007	.58	0
American hornbeam	Molting	.022	.33	.08
	Nesting-Molting	.019	.71	.14
Carya sp.	Nesting	.033	1.0	0
Hickory	Molting	.013	.50	0
	Nesting-Molting	.029	1.0	0
Cercis canadensis	Nesting	.001	.08	0
Redbud	Molting	.002	.33	0
	Nesting-Molting	.001	.14	0
Cornus florida	Nesting	.154	1.0	.83
Flowering dogwood	Molting	.172	1.0	.75
	Nesting-Molting	.123	1.0	.42
Diospyros virginiana	Nesting	0	0	0
Common persimmon	Molting	.003	.25	0
	Nesting-Molting	0	0	0
Fagus grandifolia	Nesting	.255	1.0	.66
American beech	Molting	.116	.92	.33
	Nesting-Molting	.143	1.0	.83
Fraxinus sp	Nesting	.009	.58	0
Ash	Molting	.005	.58	0
	Nesting-Molting	.003	.57	0
Ilex opaca	Nesting	.074	.92	.08
American holly	Molting	.022	.92	0
	Nesting-Molting	.080	1.0	.14
Juniperus virginiana	Nesting	.002	.92	0
Eastern red cedar	Molting	.009	.66	0
	Nesting-Molting	.005	.57	0

Kalmia latifolia	Nesting	.005	.50	0
Mountain laurel	Molting	.003	.16	0
	Nesting-Molting	.061	.57	.14
Liquidambar styraciflua	Nesting	.055	.75	.08
Sweetgum	Molting	.128	.75	.50
	Nesting-Molting	.037	.42	0
Liriodendron tulipifera	Nesting	.093	1.0	.25
Yellow poplar	Molting	.123	.92	.25
	Nesting-Molting	.061	1.0	.14
Nyssa silvatica	Nesting	.104	1.0	.25
Blackgum	Molting	.025	.92	0
	Nesting-Molting	.137	1.0	.57
Pinus virginianus	Nesting	.032	.92	.08
Virginia pine	Molting	.161	.92	.50
	Nesting-Molting	.087	1.0	.28
Prunus serotina	Nesting	0	0	0
Black cherry	Molting	.016	.42	.08
	Nesting-Molting	0	0	0
Quercus alba	Nesting	.058	1.0	.33
White oak	Molting	.026	.75	0
	Nesting-Molting	.039	1.0	0
Quercus rubra	Nesting	.039	1.0	.16
Red oak	Molting	.044	1.0	.16
	Nesting-Molting	.033	1.0	0
Robinian pseudoacacia	Nesting	0	0	0
Black locust	Molting	.005	.08	0
	Nesting-Molting	0	0	0
Sassafras albidum	Nesting	0	0	0
Sassafras	Molting	.003	.58	0
	Nesting-Molting	.002	.42	0
Tsuga canadensis	Nesting	.005	.16	0
Eastern hemlock	Molting	.007	.08	.08
	Nesting-Molting	.001	.14	0

[a]Proportion made by the species from total of trees in nesting, molting, and nesting-molting sites.
[b]Proportion of sites where the species ocurred in nesting, molting, and nesting-molting sites.

[c]Proportion of times the species occurred as one of the three more numerous species.

Appendix B

Frequency distribution (%) of positions of Wood Thrush fledglings by forest/age types during the independence stage, MCB Quantico, Virginia, 1993-95.

APPENDIX C

Comparison of tree species composition between "natal"($n = 12$) and "dispersal"($n = 21$) sites, for radio-tagged Wood Thrushes fledglings, MCB Quantico, Virginia, 1993-95.

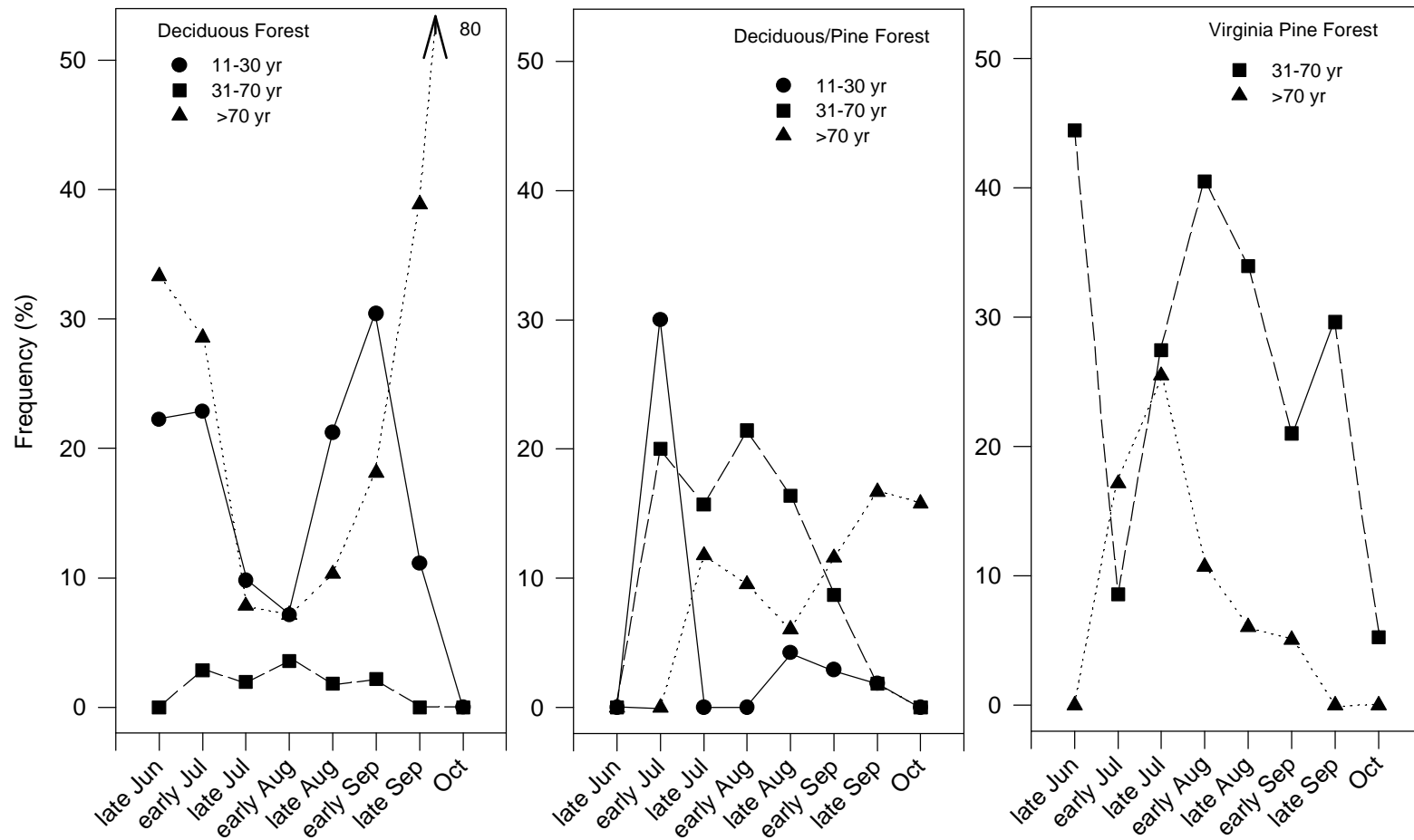| Species	Site	Total[a]	N[b]	Dom[c]
Acer rubrum	Natal	.105	.857	.428
Red maple	Dispersal	.098	.809	.286
Carya sp.	Natal	.035	.857	0
Hickory	Dispersal	.036	.476	0
Cornus florida	Natal	.133	1.0	.500
Flowering dogwood	Dispersal	.282	1.0	.857
Fagus grandifolia	Natal	.173	.928	.428
American beech	Dispersal	.174	.952	.666
Fraxinus sp.	Natal	.006	.357	0
Ash	Dispersal	.004	.428	0
Ilex opaca	Natal	.145	.857	.285
American holly	Dispersal	.032	.666	.047
Juniperus virginiana	Natal	.002	.428	0
Eastern red cedar	Dispersal	.006	.333	0
Kalmia latifolia	Natal	.036	.428	0
Mountain laurel	Dispersal	.027	.190	.095
Liquidambar styraciflua	Natal	.057	.571	.214
Sweetgum	Dispersal	.109	.333	.190
Liriodendron tulipifera	Natal	.077	.857	.071
Yellow poplar	Dispersal	.099	.904	.381
Nyssa silvatica	Natal	.132	.908	.428
Blackgum	Dispersal	.055	.714	.095
Quercus alba	Natal	.054	.857	.071
White oak	Dispersal	.035	.714	0
Quercus rubra	Natal	.034	.857	0
Red oak	Dispersal	.033	.714	.047
Sassafras albidum	Natal	.008	.428	0
Sassafras	Dispersal	.010	.381	0

[a]Proportion made by the species from total of trees in natal and dispersal sites.
[c]Proportion of sites where the species occurred in natal and dispersal sites.
[d]Proprtion of times the species occurred as one of the three more numerous species

Summary of hypotheses proposed to explain postfledging dispersal

BREEDING SITE SELECTION HYPOTHESIS

Young birds disperse to assess for potential breeding sites

Prediction 1.

During the postfledging period, fledglings will be more commonly found in suitable breeding habitats (i.e., mature deciduous and deciduous-pine forest).

▸ Most fledglings' positions (72.2%) were found in habitats probably not suitable for breeding (I did not see any sign of breeding activity, nor did I observe or catch any adult at any of those sites, although males were singing in the adjacent forest) such as second growth and saplings stage sites located in old farm areas and forest edges.

Prediction 2.

During the postfledging period, fledglings will be more commonly found in areas actively used for nesting (fledglings will use the presence of breeding birds as an indication of suitable breeding habitats).

▸ A plot of all positions of dispersing fledglings and the breeding ranges of radio marked adults shows that only 5.5% of fledgling positions overlapped with known breeding ranges. Only once I noted an active nest while I was radio tracking fledglings.

Prediction 3.

Fledglings that return to breed in the area where they spent the postfledging period, will settle first and in better territories than those fledglings that hatched elsewhere.

Prediction 4.

There will be a positive relation between the size of the area that a fledgling visited the summer it hatched and the quality of its territory the next spring.

FOOD SEARCH HYPOTHESIS

Young birds disperse to access better sources of food and to familiarize themselves with

feeding sites that can be used in subsequent nesting seasons.

Prediction 1.

Abundance of invertebrates and fruits consumed by juvenile Wood Thrushes will be higher in dispersal than nesting sites.

- ▸ I did not quantify the abundance of invertebrates and fruits in nesting or dispersal sites. However, I did record the presence of fruits on trees or bushes on which fledglings forage. Early in the season (before late August) trees and bushes with fruits where common in forest edges, young deciduous forest, old farm sites, and gypsy-moth damaged forested areas, where fledglings were primarily found (96.7% of total locations). Trees and bushes with fruits were rare in the natal sites. Late in the season when fruits were common in some areas with mature deciduous forest, fledglings' locations increased from 3.3% to 14.1%.

Prediction 2.

Dispersal sites will have a larger production of invertebrates and fruits consumed by juvenile Wood Thrushes than random-chosen sites.

Prediction 3.

Supplementation of food (given that the right food is provided and this is available for juveniles) in the nesting sites during the postfledging period will prevent young birds from dispersing.

NAVIGATIONAL TARGET HYPOTHESIS

Fledglings disperse to become imprinted on or familiarized with local landmarks that would improve their ability to return from their wintering areas the following spring to at least some of those sites.

Prediction

The amount of time and "exploration" that fledglings spent and performed during the postfledging period, will be positively correlated with the probability of their return to the area.

SOCIALIZATION HYPOTHESIS

Young birds disperse to seek flocks of conspecifics with which to socialize and migrate.

<u>Prediction</u>

During the postfledging period, fledglings will be found primarily in company of conspecifics.

▸   In agreement with this prediction, in all occasions that I relocated radio-tagged juveniles, there were other untagged Wood Thrush fledglings with them. However, there were 3 individuals that did not join a group at all or did so only during 1-2 days.

VITA

Jorge H. Vega Rivera was born in Mexico, D. F. on November 5, 1957. He attended public schools in Mexico City and graduated with a bachelor's degree in Biology from Universidad Autónoma de México. Jorge was a professor at the Science and Humanities College in Mexico City from 1979 to 1983, and a research associate at the National Research Institute for Biotic Resources (INIREB) in San Cristobal de las Casas, Chiapas, from 1983 to 1988. During the period of 1988 to 1990, he completed a Master's degree in Wildlife Management at Texas A&M University, Kingsville. He worked for two years as visiting researcher at the Conservation and Research Center, Smithsonian Institution in Front Royal, Virginia. In 1993, he began a doctoral program in the Department of Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University. Jorge completed requirements for his doctoral degree in May 1997.

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