

PATTERN AND CHRONOLOGY OF PREBASIC MOLT FOR THE WOOD THRUSH AND ITS RELATION TO REPRODUCTION AND MIGRATION DEPARTURE

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ABSTRACT.—Documentation of the schedule and pattern of molt and their relation to reproduction and migration departure are important, but often neglected, areas of knowledge. We radio-tagged Wood Thrushes (*Hylocichla mustelina*), and monitored their movements and behavior on the U.S. Marine Corps Base, Quantico, Virginia (38° 40' N, 77° 30' W) from May–Oct. of 1993–1995. The molt period in adults extended from late July to early October. Molt of flight feathers lasted an average of 38 days ($n = 17$ birds) and there was no significant difference in duration between sexes. In 21 observed and captured individuals, all the rectrices were lost simultaneously or nearly so, and some individuals dropped several primaries over a few days. Extensive molt in Wood Thrushes apparently impaired flight efficiency, and birds at this stage were remarkably cautious and difficult to capture and observe. All breeding individuals were observed molting 1–4 days after fledgling independence or last-clutch predation, except for one pair that began molt while still caring for fledglings. Our data indicate that energetics or flight efficiency constraints may dictate a separation of molt and migration. We did not observe Wood Thrushes leaving the Marine Base before completion of flight-feather molt. Departure of individuals with molt in body and head, however, was common. We caution against interpreting the lack of observations or captures of molting individuals on breeding sites as evidence that birds actually have left the area. We argue also that current reports on overlapping of molt and migration based on observations of molting individuals out of the breeding range could be misleading because some individuals may leave the breeding area to molt in other places before starting a true migration. Received 30 June 1997, accepted 18 March 1998.

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 (Roth et al. 1996 and citations therein). Despite this, information about its molt is limited and details on how molt is integrated with reproduction and migration departure are lacking. Separation of reproduction, molt, and migration within the annual cycle is considered an evolutionary strategy to reduce energetic stress (Payne 1972, Ginn and Melville 1983), but exceptions exist. Overlap of reproduction with flight-feather and extensive body molt is apparently common in tropical species (Payne 1972, Foster 1974). In temperate regions, its occurrence has been reported in some species that breed at high latitudes where food resources are abundant only briefly (Payne 1972). Joint occurrence of molt and migration is less common, except for species with a

slow, diurnal migration with frequent feeding stops (e.g., hirundinids; Niles 1972).

The scarcity of information about timing and patterns of 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). Because 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 difficult. Consequently, molt data often come from observations and/or recoveries of individuals of unknown breeding history or when known, these relationships have not yet been investigated. 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 radiotelemetry-based studies can provide information that otherwise would be difficult to obtain.

The objectives of the study were (1) to provide information on the patterns and chronology of the prebasic molt in the Wood Thrush,

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and (2) to discuss the interaction between reproduction, molt, and migration departure.

For the Wood Thrush, a long-distance migrant of conservation concern (Hunter 1992), identification of the schedule of molt and its relation to reproduction and timing for migration are important for a better understanding of its biological cycle. Also, identification on how the molt process may modify the behavior of individuals and their vulnerability to predation may be critical to the conservation of this species.

STUDY AREA AND METHODS

The study was conducted at the U. S. Marine Corps Base in Quantico, Virginia, which is located 56 km southwest of Washington, D.C. on the eastern edge of the Piedmont Plateau physiographic region, along the west bank of the Potomac River (Hunt 1967). The Marine Base covers an area of 24,364 ha of which 75% is forested. The most common vegetation types included American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus spp.*) (47.5% of the forested area); Virginia pine (*Pinus virginianus*, 16.2%), and Virginia pine/oak (15.2%).

From May to October 1993–1995, we captured, radio-tagged, and monitored the movements and behavior of 42 juvenile and 61 adult Wood Thrushes as a part of a larger study on the behavioral ecology and habitat use of this species during the breeding and postbreeding periods (Vega Rivera 1997). During the breeding season, we captured and radio-tagged females and males positively identified as reproducing (i.e., those whose nests were found or who were associated with fledglings). Juveniles were captured during the nesting period by locating active nests, and during the postfledging period by mist-netting.

Because some adult birds were killed by predators, lost their transmitter, or left the study area before initiating molt, this analysis was based on observations of 30 radio-tagged individuals. Five of these birds were recaptured when molting. Additionally, we captured 13 molting adults for which we did not have previous data on reproductive activities. Information on juvenile molt was obtained from the capture of 23 molting individuals; 21 of these were captured after they had dispersed.

Adult and fledgling Wood Thrushes were fitted with radio transmitters attached using a backpack harness (Rappole and Tipton 1991). Each transmitter weighed 2.1 g (Holohil Systems Ltd., Woodlawn, Ontario, Canada) and made up 5–6% of the bird's body weight when attached. We detected no effect on the behavior of radio-tagged birds as compared with those without transmitters. Transmitters had an average life of at least 120 days, and could be detected at distances of 400–1000 m on the ground, and 1–3 km from the air.

Radio-tagged birds were located on foot on alternate days using a 4-element Yagi antenna and a 12-channel

receiver (Telonics Communications, Inc.). When a bird's signal could not be found at its previous location, we searched first along roads using a 1-element antenna mounted on the roof of a truck. If loss of contact lasted more than 4 days, we also performed aerial radiotracking with a Cessna 172 at 350–500 m above ground in an area roughly 7 km in radius centered on a bird's last known location. We assumed that a bird had left the study area if we could not detect its signal during the aerial search. Signal loss also could have been due to transmitter failure, but our experience with these transmitters indicates that transmitter failure was rare.

For all captured individuals, we recorded the stage (old, missing, in pin, emerging, full grown/new) of remiges and rectrices and the condition of body molt. Additionally, in 8 of the 18 adults captured in molt, we recorded the length of flight feathers. Primaries, which number 10 in Wood Thrushes (10th vestigial, not considered), were numbered one to nine distally from the carpal joint. The secondaries were numbered one to nine from the carpal joint inward to the body, including the tertials S7–S9. The six rectrix pairs were numbered one to six distally from the center of the tail. Molt on four regions of the body was scored using the terminology of Niles (1972).

We pinpointed locations by approaching each bird until it moved. When possible, we made continuous observations on the bird's behavior up to 30 minutes after locating it. Specifically, we noted the type of activity (foraging or perching), substrate (ground, bush, tree), and interactions with conspecifics. Direct observation of radio-tagged birds allowed us to record if a bird was involved with breeding activities (either incubating, brooding nestlings, or caring for fledglings) or molting. To obtain data on onset of molt and date of departure from the study area, we relied on radiotracking data. Incipient molt was difficult to observe from a distance; therefore, for most birds we approximated the beginning of the molting period by back-dating 15 days from the time we observed the birds in heavy molt. We based this approach on the observation that 13–16 days elapsed for four individuals captured before they started molting and later captured the first time they were observed in heavy molt. Additionally, for eight birds that changed locality after reproducing, a similar period elapsed between the day they moved to the new locality and the first day on which they were observed in heavy molt.

Throughout the paper, individual Wood Thrushes are referred to by a specific letter prefix followed by three numbers. The letter prefix refers to the individual's age/sex category: M = adult male, F = adult female, J = juvenile, and U = adult of unknown sex. Values presented are means \pm SE. In all statistical tests a probability of 0.1 or less was accepted as significant. All statistical analyses were performed using SAS (version 6.03 for PC) software.

RESULTS

Most Wood Thrushes arrived at the study area in late April and early May. Nestlings

from first and second clutches fledged in late May–early June and late July–early August, respectively. For most pairs, timing of clutches subsequent to the first was associated with the success or failure of previous clutches. The latest record of an adult attending fledglings was 14 September, but most adults (90%) in the population completed their breeding activities by mid-August.

Of 61 adult birds radio tagged during the study, six birds were killed, seven lost their transmitters during nesting, and 18 (15 F and 3 M) left the study area after nest failure or fledgling independence. Of these, 13 females and 1 male left in June and early July, and 2 females and 2 males left in late July–August. Thirty (10 F and 20 M) adults stayed at the study area for molting. Of these, 11 (6 F and 5 M) molted in the same area where they nested; 4 males moved to deciduous sapling stands adjacent to their nesting territories and 15 (4 F and 11 M) moved 2015 ± 520 m (range 545–7291 m) from the mature deciduous or deciduous-pine forest where they had nested to Virginia pine forest, young deciduous stands, or forest edges where they molted.

Pattern of molt in adults.—A composite pattern of molt in adult Wood Thrushes is inferred from 18 captured individuals for which we recorded the molt stage. In eight of these birds, we measured remiges and rectrices (Fig. 1). None of these birds was recaptured, therefore we 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 adjacent growing remiges in five individuals suggested that replacement of these feathers may have occurred simultaneously or nearly so. In four 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 the inner primaries. The order of replacement of tertials varied, and was asymmetrical between wings for two

birds. Molt of secondaries, S1–S6, started when replacement of the primaries was already underway; shedding of S1 occurred as P5 was out of the pin. Simultaneous replacement of two or three secondary feathers was observed in three individuals.

Twenty-one individuals lost all rectrices at once. They were observed without tail feathers or with growing rectrices of the same size. Shedding of the rectrices occurred shortly after P5 was replaced, and finished with the replacement of P9 or shortly after.

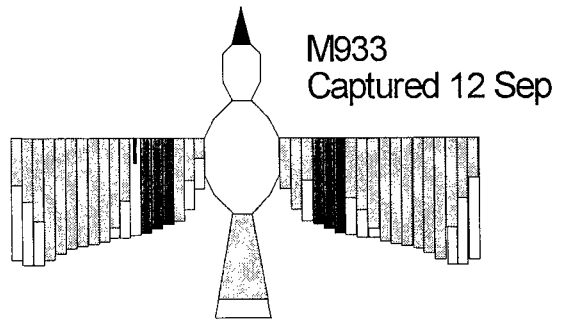
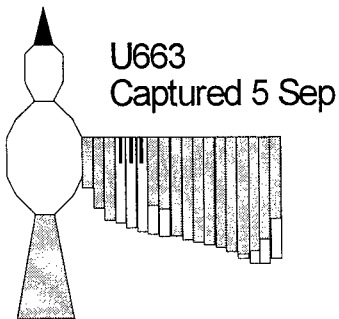
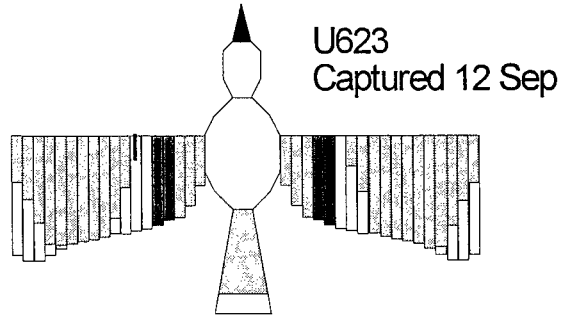
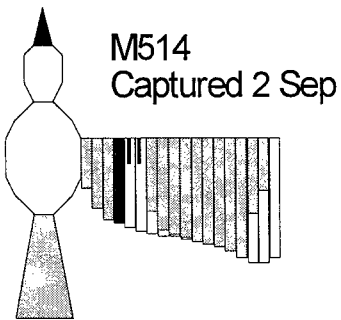
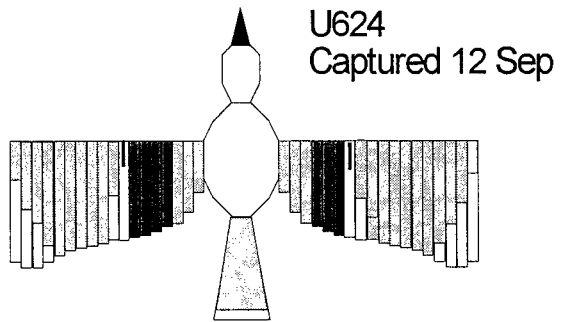
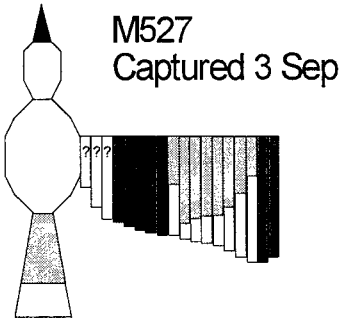
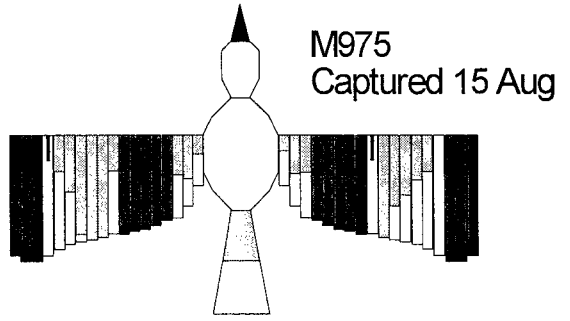
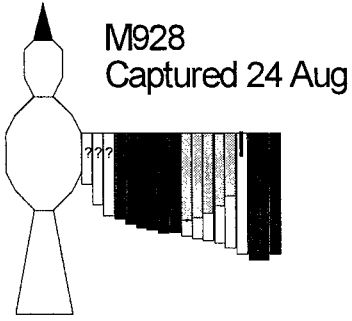
Body molt started before that of remiges and rectrices. Two males were captured showing body molt while still possessing all of their old flight feathers. By the onset of molt in remiges and rectrices, body molt was extensive, and continued at least 13 ± 1.4 days ($n = 12$) after molt of flight feathers was terminated or in its final growth stages. We base this statement on our observation of adults in full-new plumage still showing molt on the head the day before they left.

Molt chronology in adults.—The earliest record of a molting adult was of a male captured on 27 July with moderate molt on breast and sides. The earliest and latest records of adults observed having completed molt were 16 September and 14 October, respectively. For most adults, the molt period extended from early August to late September (Fig. 2). Mean date for onset of molt was 10 August (± 2.1 days; females 15 August ± 3.4 days, $n = 10$; males 7 August ± 2.6 days, $n = 17$).

Molt of rectrices and remiges lasted 38.4 ± 0.7 days ($n = 17$) with no significant differences (*t*-test, $t = -0.90$, $P > 0.10$) between males (38.9 ± 0.8 d; $n = 11$) and females (37.5 ± 1.6 d; $n = 6$). Complete molt lasted 52.0 ± 1.1 days ($n = 21$), and was longer (*t*-test: $t = -1.80$, $P < 0.10$) in males (53.2 ± 1.1 days, $n = 15$) than females (49.2 ± 2.3 days; $n = 6$). Our data suggest that Wood Thrushes that started molting earlier in the season extended the molt over a longer period (Pearson correlation: $r = -0.83$, $P < 0.001$; $n = 21$; Fig. 3).

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FIG. 1. Molt stage of adult Wood Thrushes captured Aug.–Oct. 1995–1996 in Quantico, Virginia. Dark bars represent old feathers; light-grey bars represent new full-grown and partially growing feathers; narrow-dark bars represent pin feathers. Birds with one wing had symmetrical molt. All birds had heavy feather growth on body.



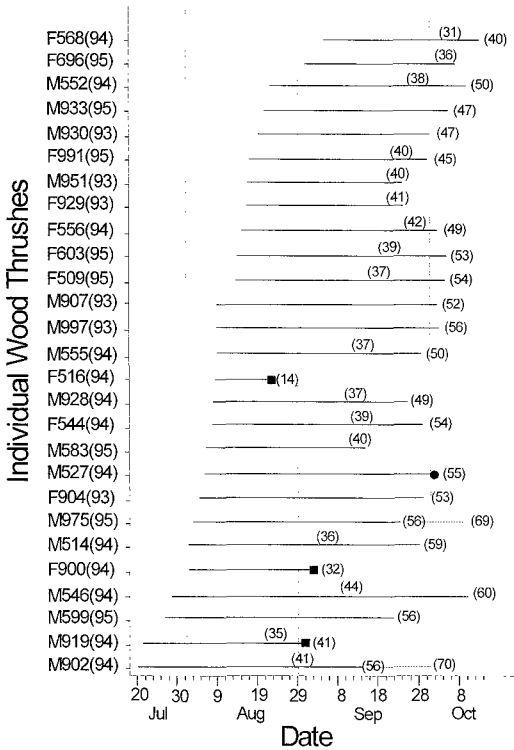


FIG. 2. Molt chronology in adult Wood Thrushes breeding in Quantico, Virginia. Numbers above and at the end of the lines indicate the duration (days) of flight-feather and complete molt, respectively. A dotted line represents a bird staying in the molting area after the end of the molt. A circle indicates that the transmitter fell off the bird. A square indicates that the bird was killed.

Adult behavior during molt.—According to our observations of radio-tagged adults, heavy molt seriously impaired maneuverability and ability to sustain flight. We observed five individuals that for at least 10 days could barely fly. For instance, while we tracked a molting female, she was observed to hop 1 m up a branch from which she attempted to fly but could not. She fell to the ground, and disappeared, hopping and flapping her wings. Molting adult Wood Thrushes, at least during the heaviest molt stage, were very difficult to observe, and almost impossible to capture in mist nets. They hid on the ground in the densest patches of vegetation where, on occasions, we had to approach within 3 m to make them move, and ensure that they were alive. These behavioral changes were also evident when

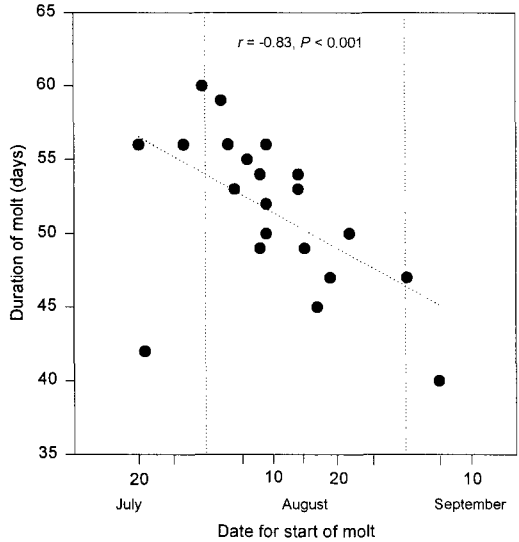


FIG. 3. Correlation between duration of molt (20 July = day 1) and date of onset of molt in adult Wood Thrushes (Pearson Correlation Coefficient; $r = -0.83$, $P < 0.001$).

we compared the mean distance between consecutive radiolocations in nesting versus molting sites for 23 birds (114 ± 9 m and 67 ± 8 m, respectively; Wilcoxon test: $Z = 3.13$, $P = 0.002$) and size of the area used (95% convex polygon, 2.6 ± 0.5 ha and 1.4 ± 0.3 ha, respectively; $Z = 1.88$, $P < 0.1$).

Overlap between reproduction and molt.—For molting birds for which we obtained breeding data, molt was initiated after reproduction was completed. For these birds, molt began 1–4 days after their young reached independence or after nest failure. We observed only one pair caring for fledglings while molting. This pair was captured when we radio-tagged their three nestlings, on 22 August. The male had general, light body molt. On 6 September, while still caring for one fledgling, the male had lost his rectrices and showed heavy general body molt. It was not until seven days later that the fledglings became independent. The female attended two of the three fledglings. At the time of capture she was not molting. On 14 September, while still caring for one fledgling, she was in heavy general body molt. Next day the fledgling had dispersed, and the female was without rectrices.

Overlap between molt and migration de-

parture.—Twenty-three of 30 birds that bred and molted at the study area, and for which we had data, left between 15 September and 14 October. All of these birds had completed flight feather molt by the time they left. Five individuals were known to still have head molt in progress on the day before they left.

Prebasic molt in juveniles.—We captured 23 juvenile Wood Thrushes in moderate to heavy general body molt. The earliest date on which a juvenile in molt was captured was 27 July. This was 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 last date on which a molting juvenile was captured was 18 September. Juveniles left the study area in September and early October, with 47% leaving in September.

DISCUSSION

Molt in adults.—The replacement of remiges in Wood Thrushes, including the tertiaries which were molted ahead of the other secondaries, was typically passerine (Dwight 1900). Simultaneous molt of rectrices, which occurred routinely in our population, is not a common pattern in passerines (Pyle et al. 1987). In Wood Thrushes, its occurrence was previously reported by Weaver (1949). Roth and coworkers (1996) reported 3 adults that dropped all rectrices at once. The only other member of the Turdinae for which data are available is Swainson's Thrushes (*Catharus ustulatus*; Cherry 1985). Based on calculation from recaptured individuals, this species required 32 days to complete flight-feather molt, which is close to the measure reported here for the Wood Thrush (38 days).

Sex differences in molt.—Our data suggest that adult male Wood Thrushes commenced molt prior to adult females. Average date of onset of molt in males was eight days earlier than for females. These results agree with numerous reports for other passerine species (e.g., Verbeek 1973, Rimmer 1988, Norman 1990). In our population, the difference in onset of molt between the sexes could have been influenced by female dispersal. In this study, 15 females, but only 3 males that bred at the study area, left before molting. Thus, we did not get information on when those females started molting. Our observations of molting

individuals for which we had information on breeding activities suggest that emancipation from parental care by one parent corresponded to initiation in molt in that parent. This observation agrees with published information from studies of other passerine species where known breeding pairs have been identified (e.g., Morton and Welton 1973, Sealy 1979, Tiainen 1981).

Behavior during molt.—Flight efficiency in adult Wood Thrushes was reduced during extensive molt. Twenty-one birds on which we had observations lost all rectrices at once and five lost several primaries over a short time. 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 impair or even prevent flight (e.g., Haukioja 1971, Verbeek 1973, Rimmer 1988). Haukioja (1971) suggested that this condition in passerines is probably more common than has been estimated from captures or visual observations, but furtive behavior associated with this condition made its detection difficult.

Lack of observations or captures of molting individuals on their nesting sites have been used as justification for the conclusion that birds actually have left the nesting area (for instance Sealy 1979). We caution against this interpretation. In this study, if molting birds had not been radio-tagged, they would likely have passed unnoticed because they were furtive, silent, and flew very little. Capturing radio-tagged molting Wood Thrushes using passive mist netting was difficult. On several occasions, we surrounded molting birds with mist-nets and yet failed to capture them. Only active chasing of the birds toward the nets proved to be effective.

Reduced ability to fly may result in increased predation, but during this study only two radio-tagged adults were predated while molting, whereas six were predated when they were nesting. Survival during extensive molt can be enhanced by behavioral inconspicuousness and/or selection of safe areas (Jehl 1990). Both strategies apparently were adopted by molting Wood Thrushes; they were secretive and they molted in sites with vegetation attributes, such as a dense understory, that may have enhanced protection (Vega Rivera 1997).

Relation between reproduction and molt.—Separation of breeding and molt is considered a general strategy that allows these processes to occur with minimal nutritional stress (Payne 1972, Morton and Welton 1973, Ginn and Melville 1983; but see King and Murphy 1985, Murphy 1996). The initiation of molt while still caring for fledglings has been reported for several species (e.g., Rimmer 1988, Norman 1990, Zaias and Breitwisch 1990, Evans Ogden and Stutchbury 1996). In our study, all known breeding Wood Thrushes apparently began molt after their young reached independence or after nest failure, but two individuals were found molting while caring for fledglings.

It is possible that more Wood Thrushes started molting while still taking care of fledglings, but we lack documentation because of our inability to detect incipient body molt without actually capturing the bird. When we recorded a bird as molting based on observations only, it was the “notable molt” of Nolan (1978) that we recorded, i.e., a bird with heavy molt on the head or with missing/growing flight feathers. None of the birds in this condition, with exception of the two birds mentioned, were in the company of fledglings.

In our radio-tagged population, reproductive effort was apparently extended to a point where it did not compromise the timing of molt and migration. Reproduction, from building of the nest to fledgling independence, took about 51 days. Molt of flight feathers took an average 38 days. If we consider that 91% of the adults left the study area between 22 September–10 October, then the latest any pair should have initiated a clutch was 25 June–13 July. These dates agree with our data. Except for one pair, which began nest building on 22 July, all breeding pairs initiated their last clutch before 13 July.

An overlap between care of fledglings and onset of molt would effectively prolong the potential reproductive period for an individual (Foster 1974, Evans Ogden and Stutchbury 1996). We suggest that Wood Thrushes attending the last brood of the season may initiate molt a few days before fledgling independence with minimal nutritional stress for two reasons. First, close to independence, Wood Thrush fledglings feed mostly by themselves; therefore their demands for food from

parents probably are low. Also, at this time fledglings are capable of full flight and thus they are less vulnerable to predators which makes parental role in this aspect less critical (Vega Rivera 1997). Second, at the study area the onset of adult molt coincided with a time when production of fruits and berries was high. Based on our observations as well as information in the literature (Martin et al. 1951, Conway et al. 1994, Roth et al. 1996), these resources are commonly eaten by Wood Thrushes in late summer and fall.

Relation between molt and migration.—Simultaneous occurrence of flight feather or extensive body molt and migration is considered incompatible because of the negative effects on flight efficiency and nutritional condition (Kjellén 1994). Indeed, for most species it is assumed that molt is scheduled so that migrant birds have fully functional flight feathers at the time of migration (Ginn and Melville 1983). Based on our observations, we have no evidence that Wood Thrushes molting at the study area left before the replacement of remiges and rectrices was complete. Departure with light body molt was not uncommon.

There are, however, reports that individuals of some species migrate while molting (e.g., Hyytiä and Vikberg 1973, Sealy 1979). We suggest that many records of birds showing flight feather or heavy body molt found outside the breeding range may represent relocation to special molting sites rather than migration. Rappole and Ballard (1987) proposed that birds of many species may move to special molting areas safer from predators and/or with better food resources than nesting habitats. Cherry (1985) captured molting Swainson's Thrushes 30, 150, and 250 km from the closest known breeding areas for the species. He concluded that Swainson's Thrushes are unlikely to initiate actual southward migratory movement during the middle of molt. In our study, 18 adults left the study area after nest failure or fledgling independence. These birds were probably not migrating, but were moving elsewhere to renest or initiate molt. We base this conclusion on the fact that intensive study of this species documents that transients do not arrive in south Texas until late to mid-September (Rappole and Blacklock 1995) or in Veracruz, Mexico, until early October (Winker et al. 1990).

We propose that birds that left the study area relocated some distance from their nesting sites to specific molting areas. They remained for several weeks in these areas while completing molt and preparing for migration, following a time sequence very similar to the birds that remained on the study area. Testing of this hypothesis will require additional studies.

ACKNOWLEDGMENTS

We thank Darl Fletcher and David Condoulis for excellent help with field work. We are grateful to the staff of the Natural Resources Branch at the Quantico Corps Marine Base, especially Tim Stamp, for their unconditional support and help during our work at the Quantico Marine Corps Base. J. B. Cruz, R. R. Root, and three anonymous reviewers provided comments on the manuscript. This research was supported by the U.S. Department of Defense, Legacy Program, as a grant to the Smithsonian Institution.

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