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PARENTAL CARE OF FLEDGLING WOOD THRUSHES

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ABSTRACT.—We report the study of parental care of Wood Thrush (*Hylocichla mustelina*) fledglings from nest-leaving to independence. From 1993 to 1995, we captured, radio-tagged, and monitored the movements and behavior of 23 fledglings and their parents from 12 broods at the U.S. Marine Corps Base, Quantico, Virginia. For pairs that subsequently renested ($n = 5$), the family group of male, female, and fledglings, remained within 62 (±5 SE) m of the first nest after fledging. During the period of post-fledging parental care, mean maximum distance between parents was 70 (±14) m. Females attended the young 13 (±1.3) days before initiating the incubation of a second clutch. Males continued attending the fledglings for 6 (±0.7) more days until the young achieved independence and dispersed (28–36 days post-hatching). In final clutches ($n = 7$), brood care was divided between the parents, and the position of the fledglings relative to the nest depended on the parents' choice of molting site (in the nesting area or elsewhere). Division of the brood by the parents has been thought to be a strategy to reduce predation and increase foraging efficiency. However, in the Wood Thrush and other species, joint attendance of initial broods, but division of final broods, suggest that other factors could be important for the parents' decision of whether or not to split the brood. *Received 15 June 1999, accepted 13 Nov. 1999.*

Parental care in passerines is not restricted to the nestling stage, but extends beyond fledging. In fact, the duration of parental care after fledging of the young can be as long as that of the nestling period (Skutch 1986), and investment by the parents may be even greater during this phase than during the nestling stage (Drent and Daan 1980, With and Balda 1990). Therefore, documentation of postfledging dependence events is important not only for understanding parental investment patterns and mating systems, but also for understanding its role in reproductive success and population demography (Royama 1966, With and Balda 1990). Difficulties in observing the young after they have left the nest has limited the gathering of information on this stage of the life cycle (Weatherhead and McRae 1990).

The Wood Thrush is a relatively well-known species, but little has been published on the postfledging, pre-independence phase of its life cycle. Roth and coworkers (1996) devoted only one paragraph to this stage, and scattered observations are found in Brackbill (1958) and Anders and coworkers (1997). We reported elsewhere on movements of young following independence (Vega Rivera et al. 1998). In this paper we report the behavior of adult Wood Thrushes (*Hylocichla mustelina*) and their young from fledging until the young reach independence. Our main objective is to provide information on development of the young and on parental care during the post-fledging, pre-independence period. Specifically we report the extent to which the male and female parents were involved in the care of fledglings and how this behavior was affected by the status of the parents attending early or late broods.

STUDY AREA AND METHODS

We conducted the study at the Marine Corps Base (MCB), Quantico, Virginia (38° 30′ N, 77° 25′ W, area 243 km²). Native forest types cover about 75% of the base and are stands of Virginia pine *Pinus virginianus* (17%) and mixed forest (83%). Details of the study area and methodology can be found in Vega Rivera and coworkers (1998).

During the summers of 1993–1995, we captured, radio-tagged, and monitored the movements and behaviors of 23 fledglings and their parents from 12 broods. Nests were found by tracking adults that were previously captured and radio tagged and by checking likely nest sites. We radio tagged the offspring 2–3 days before they fledged. Transmitters (Model BD-2G, Holohil Systems Ltd., Ottawa, Canada; average life >120 days; range of detection 400–1000 m on the ground) were attached using a leg backpack-harness (Rappole and Tipton 1991). Radio-tagged birds were located every other day. Once a bird was located, we continuously monitored its behavior for up to 30 minutes. We recorded the type of substrate (ground, bush, tree),

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height of perch, spatial separation of young and parents, and interactions between parents and young. Individual and nest locations were recorded using a GIS generated map of the Marine Base and a global positioning system (Pathfinder Pro GPS, Trimble Navigation Ltd., Sunnyvale, California). A minimum of 75 fixes were obtained for each location, which were differentially corrected and averaged using PFINDER software, and entered as a coverage into the base's GIS database.

We defined initial broods as those followed by another nesting attempt and final broods as those with no subsequent nesting attempt. 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 laying dates using 13 days as an averaged incubation period (Roth et al. 1996; pers. obs.). We regarded fledglings as independent when no further parent-offspring interactions were observed, for example, feeding of the young, flying together, alarm behavior from the parents when we approached the fledglings, or when the fledglings dispersed from the natal area without being accompanied by the parents. Values presented are means ± SE. Because young from the same nest may not be thought of as independent, distance from nest and age of independence for siblings were averaged and considered for calculations as a single data point.

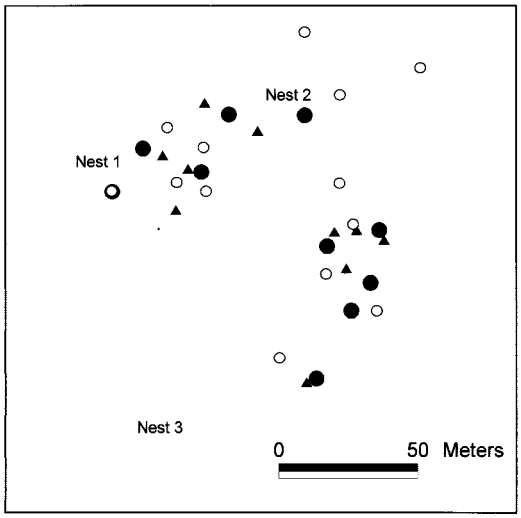

FIG. 1. Radio locations of a male Wood Thrush (○) and two fledglings (▲ and ●) from an early brood. Young were fledged from nest 1. Position of nest 2 and 3, which nestlings were depredated, are shown for reference.

RESULTS

Of 43 nests we monitored during the three years of the study (including replacements and second clutches), 25 were depredated: 5 (11.6%) during incubation, 9 (21%) at or within 1–2 days of hatching, 2 (4.2%) during the nestling period, and 9 (21%) at or within 1 day of fledging. In the remaining 18 nests (42%), at least 1 young was fledged for a total of 29 fledglings. Of these, 6 individuals (15%) were depredated within 5 days after leaving the nest. The rest (23 young or 85%) survived to independence. An account of the development of the young follows. Data for young of the same age were pooled.

Development of fledglings.—At 11 days of age, young could not fly and stayed on the forest floor. From age 12–15 days, most fledglings were able to climb bushes, but were incapable of extended flight. During this time, they often perched quietly 1–5 m above the ground, and froze when we approached them. At 16 days of age, young were able to fly at least 30 m between branches, close to the ground, or in the mid-canopy in response to parental alarm calls. By 17 days of age, most young flew proficiently, although one fledgling remained immobile for long periods at 19 days of age, while another moved very well between branches at 14 days of age.

We first observed fledglings feeding by themselves at 17 days of age, but it may have occurred earlier. Birds that fledged early in the season, when fruits were not available at the natal sites, foraged on the ground, often along fallen logs. Fledglings hatched later in the season, when fruits were abundant, depended heavily on fruits and spent most of the time foraging 5–10 m high in the trees.

Parental attendance and dispersal.—Adult Wood Thrushes followed one of two strategies regarding attendance of the fledglings. If the parents renested (5 pairs in our study), they kept the fledglings within 64 (±13) m of the nest (for an example see Fig. 1). Mean maximum distance between parents was 70 (±14) m. Of these pairs one had 3 young, two had 2 young, and two had 1 young. In families with more than one young, we did not notice division of the brood; both parents kept the young together and apparently attended all the young. Similarly, single young were attended by both parents. Once females started the construction of the next nest, her involvement in the attendance of the fledglings decreased and ceased altogether when they started incubation. On average, females attended the young

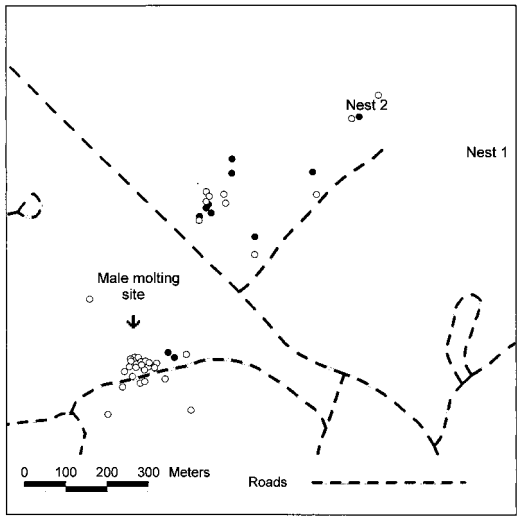

FIG. 2. Radio locations of a male Wood Thrush (○) and a fledgling (●) from a final brood on the Marine Corps Base, Quantico, Virginia. Young was fledged from nest 2. Position of nest 1, from which nestlings were depredated, is shown for reference.

13 (±1.3) days before initiating incubation of the second clutch. Once females started incubation, the males continued to attend the fledglings for 6 (±0.7) days until independence and dispersal.

In final broods (7 pairs; only 1 of these pairs successfully raised an initial brood) the strategy was different. For fours pairs, two with 2 young and two with 3 young, the brood was divided between the parents within 2–3 days of fledging with each parent subsequently feeding only specific individuals. Mean maximum distance between parents was 313 (±41) m. In two pairs, the female abandoned the study area within 4–6 days after fledgling of the young and left the male attending a single young. In a pair with two young, the male left the female attending them.

The distances that the young and the parents moved from the nest after fledging and before independence varied depending on whether the parents remained in their nesting area for molting (104 ± 5 m, $n = 5$ broods) or moved elsewhere (332 ± 156 m, $n = 2$ broods). For instance, the male of one pair with 3 fledglings moved out of the nesting territory with one of the offspring immediately after fledging, and 2 days after fledging they were more than 200 m from the nest (Fig. 2). The female remained in the vicinity of the nest site with the other two offspring.

There is no indication that fledglings from final broods become independent at an earlier age than those from earlier broods ($t = 0.02$, $P > 0.05$). Independence from parents occurred at 32.5 (±1.4, $n = 5$ initial broods) and 32.4 (±0.8, $n = 7$ final broods) days. After achieving independence, most fledglings dispersed 1.5 (±0.3) km from natal sites and joined flocks of conspecifics. There was no significant trend in direction of dispersal from the natal site (Rayleigh's Z-test: $Z = 1.51$, $P > 0.05$) nor was there a significant correlation between the distance of dispersal and date of dispersal ($r = -0.17$, $P > 0.05$). We did not note any aggression from parents toward the young or among siblings prior to dispersal. However, we observed another behavior related to dispersal of fledglings that deserves some comment. Three males, each attending a single fledgling, moved with their young out of the natal area at a time when fledglings were expected to disperse. One male and his single fledgling moved 855 m from the nesting site. The next day, the male was back in his territory, but the fledgling moved farther away. Another male and his fledgling moved 400 m from the nesting site to a second-growth area. The young stayed at that site 33 days. The male moved about 300 m from the fledgling to a deciduous sapling area and initiated molt. Similarly, a third male and his fledgling moved 500 m from the nesting site. The male returned to the nesting site 2 h later but the fledgling continued to move away.

DISCUSSION

Parental involvement during the post-fledgling, pre-independence period has been a topic of discussion because of its implications for reproductive strategies. Parents have three options regarding care of fledglings: (1) they can care for the brood together, (2) they can divide the brood with each parent providing care to a portion of the brood, or (3) one parent can care for the entire brood while the other departs or assumes other reproductive duties. We found adult Wood Thrushes employing all three strategies. Previous reports on Wood Thrush parental care mention that parents split the brood after fledging, but they remained within 200–400 m of their nests for 2–3

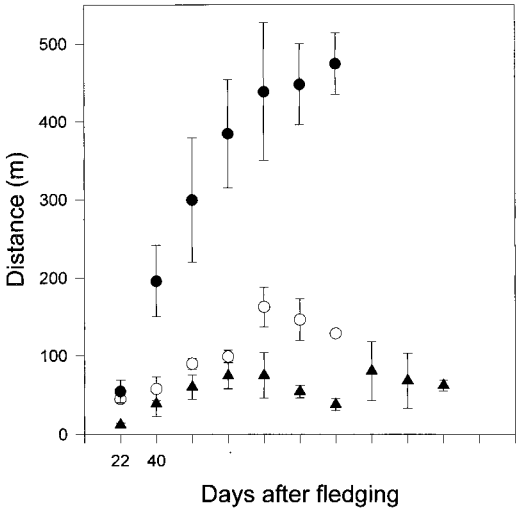

FIG. 3. Distance of young Wood Thrushes from their nests during the post-fledging, pre-independence period. ▲ represent initial nests (averaged from 5 broods); ○ represent final broods from parents that stayed in their nesting site to molt (averaged from 5 broods), ● represent final broods from parents that moved out of their nesting site to molt (averaged from 2 broods).

weeks later, while young were still attended by a parent (Roth et al. 1996). In contrast, we found that once fledglings left the nest, the distance that they moved depended on the parents' reproductive activities. If the parents were going to renest, then the entire family group (male, female, and fledglings) remained together and close to the nest. If adults had completed nesting activities for the year, then the position of the fledglings with regard to the nest depended on the parents' choice of molting site, whether on the breeding territory or elsewhere (Fig. 3).

Brood division between parents following fledging has been reported in several species of passerines and has been thought to be an advantageous strategy for reasons such as reduced predation or improved foraging efficiency (see references in Moreno 1984, McLaughlin and Montgomerie 1985). These explanations are incomplete because it is now clear that a range of post-fledging parental care patterns exist, not only for different species, but for individual pairs within the same species, and even for the same pair at different times in the season. Mate guarding may play an important role in accounting for these differences (Weatherhead and McRae 1990, Møller 1991). Brood division may entail fitness costs for the male because the physical separation between male and female as a result of splitting the brood may compromise the extent of mate guarding, and increase the risk of females engaging in extra-pair copulations. For single-brooded species, this should not be a conflict. However, for multi-brooded species, such as the Wood Thrush, the male's decision to attend a portion of an initial brood while the female attends the others may present a trade-off between the advantage of increasing the success of the present brood versus the advantage of assuring paternity for subsequent, same-season broods. Even so, there are reports where the extent of mate guarding was found to be similar between first and subsequent clutches (Møller 1991) or greater for final broods (Weatherhead and McRae 1990, Kopachena and Falls 1993). From our observations of radio-tagged pairs that re-nested, it was evident that male, female, and offspring were moving as a unit. We propose that by keeping all fledglings together and close to subsequent nests, males still may be able to monitor the activities of their mates. During final broods, mate-guarding becomes unnecessary and, as we observed, parents split the brood and moved apart. In agreement with this idea, division of single or final broods, but joint attendance of initial broods has been reported for other species (e.g., Prairie Warbler, *Dendroica discolor,* Nolan 1978; European Robin, *Erithacus rubecula,* Harper 1985; Blackbird, *Turdus merula,* Edwards 1985). Likewise, Ritchison and coworkers (1994) reported no differences in the percentage of extra-pair young in second broods, even when male Northern Cardinals (*Cardinalis cardinalis*) care for fledglings while females initiate another nest. Edinger (1988) proposed that when female Northern Orioles (*Icterus galbula*) stayed close to the nest, their mates may be in visual or auditory contact without close association. He observed that male mate following was significantly more frequent when females ranged more than 120 m from the nest.

Although our sample size is small and our evidence is circumstantial, we suggest that mate-guarding may play a role in parental care for Wood Thrushes. It is evident that more

work is necessary to fully understand the costs and benefits for different strategies regarding parental care. For instance, it is necessary to clarify whether or not division of the brood between parents is accompanied by physical separation of the pair. A combination of radio tracking, detailed behavioral observations, and DNA fingerprinting seems to be a promising approach.

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