

WINTERING WOOD THRUSH MOVEMENTS AND MORTALITY IN SOUTHERN VERACRUZ

JOHN H. RAPPOLE,¹ MARIO A. RAMOS,² AND KEVIN WINKER³

¹Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, Texas 78383 USA,

²World Wildlife Fund, 1250 24th Street N.W., Washington, D.C. 20037 USA, and

³Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 55455 USA

ABSTRACT.—Populations of wintering Wood Thrushes (*Hylocichla mustelina*) were studied from 1982–1988 at three sites in southern Veracruz, Mexico, with a combination of mist-netting, color banding, observation, and radio-tracking. We marked 335 thrushes, and attached radio transmitters to 61. Based on radio-tracking data and observations of behavior of banded individuals, the population was composed of two major categories, sedentary individuals and wanderers. Sedentary birds moved ≤ 150 m from point of capture during the tracking period; often they remained at the same site through an entire winter season and returned to that site in subsequent winters. Behavioral observations of sedentary individuals indicated that many were territorial, and defended their areas against intrusion by conspecifics. Wanderers moved > 150 m from point of capture, often within a few hours after capture. They were not aggressive toward conspecifics, and groups of several such wanderers were occasionally seen foraging within a few meters of one another. Of 34 sedentary individuals radio-tracked, 2 died during the monitoring period while 7 of 27 wanderers died. All deaths were attributed to avian or mammalian predators. Mortality rates (deaths/tracking day) were 0.026 for wanderers and 0.004 for sedentary birds. Received 28 October 1988, accepted 3 February 1988.

THE WOOD THRUSH (*Hylocichla mustelina*) is common in the wet, lowland tropical forests of Central America from southern Veracruz to Panama (Rappole et al. 1983). Populations arrive on migration from breeding grounds in eastern North America in October and depart in April. During the winter period many birds of both sexes defend territories and show seasonal site fidelity, returning to the same territory in subsequent winters. Other individuals are nonterritorial wanderers or "floaters" that show no site fidelity (Rappole and Warner 1980, Winker 1989).

Wood Thrushes are found primarily in undisturbed to moderately disturbed (as in selectively logged) wet, primary forest from sea level to 500 m (Winker 1989), but wandering individuals use a variety of other habitats that include riparian forest and various stages of second growth. Comparisons of movements and mortality rates between *wanderers*, which use several habitat types, and *site-faithful birds*, which hold territories mainly in primary forest, are critical to understanding the ecology of this species and others with similar winter social systems. Seventy species of nearctic avian migrants that winter in the Neotropics have been documented as demonstrating a territorial sys-

tem in winter, 20 of which are forest-related species (Rappole et al. 1983). Many of the 87 other forest-related, migratory species that winter in the Neotropics are likely to have a territorial system of resource exploitation in winter as well.

Carrying capacity of the tropical wintering grounds for the Wood Thrush is potentially affected by the conversion of large amounts of its primary habitat type. As tropical wet, lowland forest is cleared, it is probable that more thrushes will be forced to follow a wandering rather than a territorial mode of existence because marginal habitats are occupied mainly by wanderers, and support few or no territorial individuals on a long-term basis (Winker 1989). Survivorship of wandering versus territorial birds is unknown.

Determination of the movement patterns and mortality rates for territorial birds is relatively straightforward. Average distances moved are < 100 m in a day, usually centered on the territory (Winker 1989). Mortality rates for the sedentary birds could be calculated with any of the various models in which a portion of the population is captured, marked, and released (Seber 1982). Percentage of recaptures during a later sampling period provides an estimate of turn-

over that can be related to mortality, assuming that most individuals are sedentary during the sampling period (Tipton 1980). Clearly such a method will not provide accurate estimates of wanderer mortality because these birds are likely to leave a site within hours after capture and release (Winker 1989).

Radio-tracking provides information on relative movements and mortality rates in a population that has both sedentary and wandering components. We report the results of a study of movements and mortality rates in wandering and sedentary Wood Thrushes as revealed by radio-tracking.

METHODS

We worked at 3 sites in the Tuxtla Mountains of southern Veracruz. Site 1 was located near the village of La Peninsula de Moreno, 15 km east-northeast of the town of Catemaco. The site is undisturbed to moderately disturbed (some logging) rain forest on steep slopes along the Coxcoapan River. This forest type is labeled "Selva Alta Perennifolia" by Pennington and Sarukhan (1968). Dominant canopy species include *Nectandra ambigens*, *Brosium alicastrum*, *Poulsenia armata*, and *Terminalia amazonia*; subcanopy species include *Pseudolmedia oxyphyllaria*, *Faramea occidentalis*, and *Trophis racemosa*; the spiny palm (*Astrocaryum mexicanum*) is the dominant lower story species; and vines are the major ground cover. Elevation is 110 m. There is second growth along the river, and some clearing for crops and pasture 1–2 km from the site.

Site 2 was located near the village of El Bastonal, down the steep-sided canyon of the upper reaches of the Coxcoapan River, 19 km east-southeast of Catemaco in undisturbed rain forest. Species composition of the plant community is similar to Site 1. Elevation is 500 m. Tablelands southwest of the canyon have been cleared, but the canyon proper is undisturbed for several kilometers.

Site 3 was located near the Biology Field Station of the University of Mexico, 20 km north-northeast of Catemaco. This site is a mosaic of undisturbed, primary forest reserve, corn fields, bean fields, pastures, and isolated patches of heavily disturbed forest and second growth. Species composition of the primary forest is similar to Site 1. Elevation is 160 m.

Mist nets were set in each study site to capture the thrushes beginning at Site 1 where an 8.75-ha grid was established with 1 net every 50 m for a total of 48 nets. Netting was conducted at this site each winter from 1982–1987. We netted at Site 2 one season, January–March 1986. Nets were set in 2 lines of 10 nets each with 50 m between nets and lines. Details of net hours and netting periods for these sites are provided in Winker (1989). Site 3 was netted November 1986–

February 1987 and 10–22 January 1988 with 2 lines of 10 nets, 30 m between each net, and 50 m between each line, running along the northern boundary of the Biology Station. In 1988, we set a third line of 10 nets near the Biology Station Headquarters.

In 1988, we netted in all weather from dawn to dusk. Wood Thrushes move more during heavy rains associated with frontal systems (nortes) so it was vital to net during these periods. In addition, we had rain for a significant portion of 7 of the 12 days of our 1988 netting period. Faced with these conditions, we developed a system (umbrellas on poles, and towelling off hands and birds before removal) that, along with net checks at 20–30 min intervals, kept captives dry.

Each Wood Thrush captured was banded with a USFWS band and a unique combination of color bands for individual field identification. In addition, 61 of the birds were tagged with 2-g radio transmitters (4–5% of Wood Thrush body weight) (Custom Telemetry, Athens, GA). Each transmitter was 2 cm × 1 cm × 0.6 cm with a 23-cm whip, and powered by a silver chloride battery. Average battery life was 11.1 ± 8.8 days, based on mean time to signal disappearance in sedentary birds; this includes several transmitters in which the batteries were overheated, reducing battery life. A more reasonable estimate of battery life from later in the study would be 15–20 days.

Two attachment methods were used. From 1983–1987, we glued (Raim 1978) the transmitter to the bird's back using nonirritating eyelash glue (Winker 1989). In 1988, we introduced a harness design (Rappole et al. in prep). The bird was released at point of capture, within 1–2 h for gluing, and 15–20 min for harness.

Reception distance was highly variable depending on topography, intervening vegetation, aspect of the bird, and weather. In closed forest on flat ground, the signal from a perching bird could be picked up at a range of roughly 500 m (based on field tests of sedentary birds at known locations). We used a 4-element Yagi antenna attached to an LA-12, 12-channel receiver, and headphones for tracking. Locations were obtained by approaching until the signal moved or the bird was seen, and are therefore accurate within a circle 20 m in radius in most cases. During the first 3 yr, we attempted to make visual contact with every tagged individual at least once a day. From the fourth year on, we were sufficiently confident in our ability to detect a close, moving bird to dispense with the need for a daily, visual sighting, which reduced the amount of disturbance to individuals. Tagged birds were seen on ca. 10% of our location visits during this latter portion of the study.

Detection points were mapped on topographical maps (scale 1/10,000). Maps and radio-tracking detection points were digitized using the AutoCAD program (AutoDesk, Inc. 1985) for calculation of movement distances and areas of specific pieces of habitat.

Tracking procedures, like netting and radio-attachment techniques, evolved during the course of the study. During the first 3 yr, we concentrated on determining home range size and behavior of sedentary individuals (Winker 1989). Normally, locations of all birds were checked 2–3 times daily, but lost birds were followed only as time allowed. We began trying to follow these birds by airplane in 1985–1986, and continued this procedure through the 1988 season despite considerable logistical and meteorological problems. From the air, transmitter signals could be picked up 5–10 km away; however, the topography of steep canyons and ridges made tracking, even from the air, extremely difficult at sites 1 and 2. The topography at Site 3 is mountainous, but not as rugged. By 1988, we had perfected a system that confirmed the locations of all radio-tagged individuals at least hourly, regardless of the weather, from 30 min before dawn to dark (0530–1800). A list of "lost" birds was kept, and their transmitter frequencies were checked from key high points located within a 2-km radius of the release area. We regularly revisited the site at which the last signal was located. When these procedures failed, the bird's location was checked from the air. We lost only 2 of 25 birds by these procedures from 10–27 January 1988. This continuous monitoring from the ground plus weekly flights allowed contact with large numbers of wanderers simultaneously.

We selected 150 m as the critical movement distance to distinguish between sedentary individuals (≤ 150 m) and wanderers (> 150 m). Early work with sedentary individuals showed that most Wood Thrush territories do not contain boundary points > 150 m apart.

Our initial efforts to monitor the movements of wandering Wood Thrushes were largely ineffective for two reasons. First, the work was done at La Península and El Bastonal where a vertical ridge is seldom > 500 m away. It is difficult to locate signals, even from the air, in such terrain. The Biology Station terrain (Site 3) is much better suited to radio-tracking. Second, the time between checks allowed birds to move from the site.

We determined the date and cause of death where possible for transmitter-bearing individuals during the study. We compared the proportions of deaths in each of the movement classes. We calculated a daily survival rate for wanderers vs. sedentary birds based on number of deaths/transmitter-bearing day (Heisey and Fuller 1985) and a standard error (Johnson 1979).

There are five assumptions for these procedures. (1) We can determine the exact day of death (in most cases we determined hour of death). (2) The population is homogeneous, with each bird subject to the same probability of mortality. This assumption is probably not true. Immature birds are likely to have a higher mortality rate, but skull ossification in many immature thrushes is complete by December, so we had no reliable method to separate immature birds

from adults. (3) The daily mortality (or survival) rate remains constant from day to day. (4) The survival period for each tagged thrush is an independent event. (5) The inability to locate a signal and a radio-tagged individual's probability of survival are random and independent. Signal loss can be caused by transmitter failure, and movement beyond study area boundaries. Based on our experience, the main cause of transmitter failure was battery failure even for those that failed after 1–2 days, as indicated by recapture or resighting of radio-tagged birds that carried non-functional transmitters days or weeks after signal disappearance. Premature transmitter failure was caused by inadvertent overheating of the battery during activation, a fairly common occurrence early in the study. We found no evidence to indicate that predation caused transmitter failure. Most predators simply discard the transmitter in the normal process of consumption.

We identified the type of predator whenever possible. We identified a kill as avian if it had one or more of the following characteristics: (1) predator seen eating dead Wood Thrush, (2) head neatly removed from body, puncture wounds on body (interrupted meal), (3) feathers only (no bones or flesh) in a pile, (4) presence of feathers or bird feces under a perch site, (5) feathers stuck to wet vegetation and perch site. Observations used to identify mammalian kills included the presence of broken (mouthed) and matted chunks of feathers and flesh, broken pieces of bone and bits of flesh, and tooth marks on the transmitter.

RESULTS

We accumulated a total of 47,700 net hours from January 1983–January 1988 and captured 335 Wood Thrushes. Of the birds tagged with transmitters, 27 moved a straight-line distance > 150 m from their original point of capture while we followed them, and 34 did not move beyond that distance (Table 1).

Movements.—We used case histories to document the behavioral characteristics of wandering vs. sedentary individuals. Bird BS 353 (Fig. 1) was removed from Net 4 (480 m west of Dozer Patch) at 1445 on 13 January 1987. It was processed, released at point of capture at 1528, flew to a perch 20 m southeast of Net 4 and 7 m up, and preened until 1605. The thrush then began to move in 20–30 m flights until 1700, by which time it had moved 150 m southeast of the release point. Rappole waited until dark at 1800, but no further movement was detected.

He returned to the site at 0630 on 14 January 1987, and found BS 353's signal at the same spot

TABLE 1. Movement distances (m) and survivorship of wintering, radio-tagged Wood Thrushes.

Group (n)	Tracking days ($\bar{x} \pm SD$) ^a	Total days	Distance moved ($\bar{x} \pm SD$) ^b	Deaths	Daily survival rate	SE ^c
Sedentary (34)	13.2 \pm 11.9	450	96.1 \pm 34.9	2	0.996	0.003
Wanderer (27)	9.9 \pm 7.2	267	528.5 \pm 559.3	7	0.974	0.010

^a Mean number of tracking days/individual; SD = standard deviation.

^b Mean of farthest distance moved by an individual while carrying an active transmitter, measured as a straight line from point of release.

^c SE = standard error of the survival rate estimate, calculated using the formula from Johnson (1979: 653).

as on the previous night. The bird began to move at 0700, eliciting low intensity "bup bup bup" calls (Dilger 1956a, b), presumably the territory owner's response as it entered each new territory. By 0800, BS 353 had moved about 100 m south from its roost site, when its signal began to rapidly fade and was lost.

On 15 January 1987, we located BS 353's signal in an isolated forest patch on Wood Thrush Hill, 1.6 km northwest of its release point (Fig. 1). On 16 January, Rappole went into the site and located the signal at 0730. The signal rapidly faded, however, and disappeared again. All efforts to locate it on foot that day were futile. We relocated BS 353 on 21 January 1987, 0.8 km west-northwest of its last recorded location, 2.2 km from its release point. The same day at 1500 the bird was located on the ground in a patch of low (2-3 m), dense, stream-side second growth of nightshade (*Solanum*), *Balsa*, and bull nettle (*Cnidiosculus*), surrounded by corn fields. When we approached, the bird flew 180 m across the open corn field (bare dirt) into an isolated patch of primary forest on a ridge. The bird remained at this site until our departure on 1 February 1987.

A similar, long-distance movement was detected in BS 372 (Fig. 1). This bird was captured originally in Net 1 (380 m west of Dozer Patch) on 13 January 1988. It moved 50 m north of Net 1 on 15 January 1988, but was back near Net 1 on 16 January. On 17 January at 0830, the signal was gone. Intensive search throughout a 1-km radius of the site revealed no signal. On 19 January 1988, we located BS 372's signal near the village of Laguna Escondida, 1.4 km west-northwest of the capture site, but high winds prevented us from obtaining a precise location. The following day, 20 January, Rappole was unable to find the signal on the ground at the site where it had been the previous day. The signal was found on 21 January 1988 in disturbed rain forest in a ravine, 640 m north-

northwest from Net 1. On 22 January, the signal was picked up on the south side of Wood Thrush Hill in a thin hedgerow of trees bordering a corn field. At approach, however, the signal quickly faded. Efforts to relocate it were unsuccessful until 1115 on 25 January when the bird was located in an orange tree in the middle of a corn field on the northeast shoulder of Wood Thrush Hill, 1.7 km northwest of the original capture point.

Movement can be rapid on the ground as well. One individual (BS 363) was captured in Net 3 at 1700 on 21 January 1987, 420 m west of Dozer Patch. Since it was too late to release it after we attached the transmitter, we released the bird the next day, at Net 3 at 0827 in a light rain. The bird moved immediately and flew out of the primary forest site into a thin hedgerow of trees (5 m wide) that bordered the road to the village of Laguna Escondida. It moved along this hedgerow, flitting and foraging, at a rate of ca. 80 m per hour, finally settling in an isolated patch of heavily disturbed (grazed) forest at 1200, 290 m north of the original capture site. We located the bird at this site daily thereafter until we departed on 1 February 1987.

Wood Thrush territories average 0.42 ha in rain forest habitat in the Tuxtlas (Winker 1989). Wanderers, however, tended to aggregate in second growth areas along the edge of our primary forest sites at much higher densities. As an example, BS 372, BS 373, and BS 374 were all captured in Net 1 on 14 January 1988. They were joined in this tract on 15 January by BS 381, who was captured in Net 4 at 0920 the same day. A fifth, untagged bird was observed near Net 1 on this day as well. BS 381 left the tract on 16 January (Fig. 2), but the others remained in the narrow band (50 m) of second growth north of Net 1 until 17 January when they dispersed to other sites. BS 381 moved from the Net 1 area 360 m east to a tract of heavily disturbed (cut, grazed) second growth where a

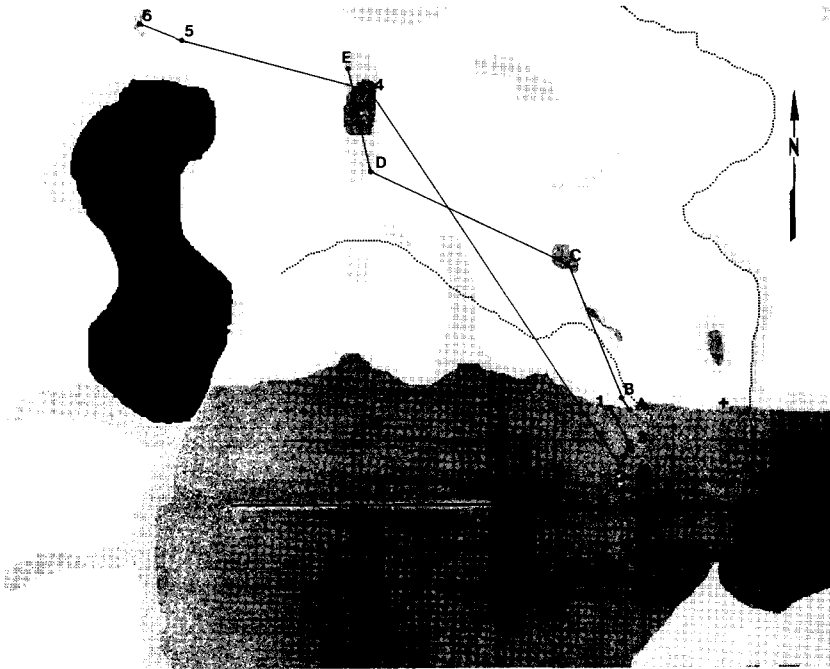


Fig. 1. Movements of Wood Thrushes, BS 353 and BS 372. The sequence of detection points for each bird is described in the text from release point to last detection consecutively: 1-6 for BS 353, and A-E for BS 372. White = cropland, hatching = second growth, black = water, gray = primary forest, dotted lines = roads; solid lines connect detection points; * marks Wood Thrush Hill; + marks Dozer Patch.

bulldozer was parked along a new road cut (Dozer Patch). BS 371, captured in Net 12 (270 m south-southwest of Dozer Patch) on 11 January at 1800, remained in the Net 12 area until 16 January 1988 when it moved to Dozer Patch with BS 381.

Birds that occupied these marginal, disturbed second growth sites made repeated forays into neighboring primary forest. As mentioned, BS 381 and BS 371 were captured in primary forest (nets 4 and 12, respectively) but moved to second growth at Dozer Patch. On the morning of 17 January 1988, both BS 381 and BS 371 had moved off from Dozer Patch into primary forest southwest across the Laguna Escondida road. They moved through a wide area of undisturbed rain forest that day (Fig. 2), but both were back in Dozer Patch at 1835 in the evening. The next day (18 January 1988), both birds were in Dozer Patch through the morning checks until 1123. At 1240, however, BS 381 was located 1.1 km west-northwest of this location in a farmer's backyard (Sinaca's Yard; bare dirt, a few citrus trees, pig leavings). BS 371 disap-

peared on 18 January and was not relocated until 21 January, 210 m north of Dozer Patch, in a piece of heavily disturbed primary forest. Rappole observed the bird as it foraged along a stream at 1300. It was attacked and chased by an unmarked Wood Thrush, but remained in the tract the rest of that day. On 22 January, Ramos found both BS 371 and BS 381 back in Dozer Patch. On 24 January, BS 371 spent the day in primary forest southwest of Dozer Patch, but was back there again in the evening. BS 381 disappeared for 2 days, but was found in Sinaca's Yard again on 26 and 27 January.

Similarly, BS 384 was originally captured in primary forest in Net 12 on 15 January 1988, moved to primary forest 320 m northwest, near Net 1 on 16 January, and was killed by a Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) in scrubby second growth along the Balzapote road, 560 m east of his previous location on 17 January 1988.

A number of wanderers collected in one of our primary forest sites, evidently in response to a large ant swarm. BS 377, BS 376, BS 383, BS

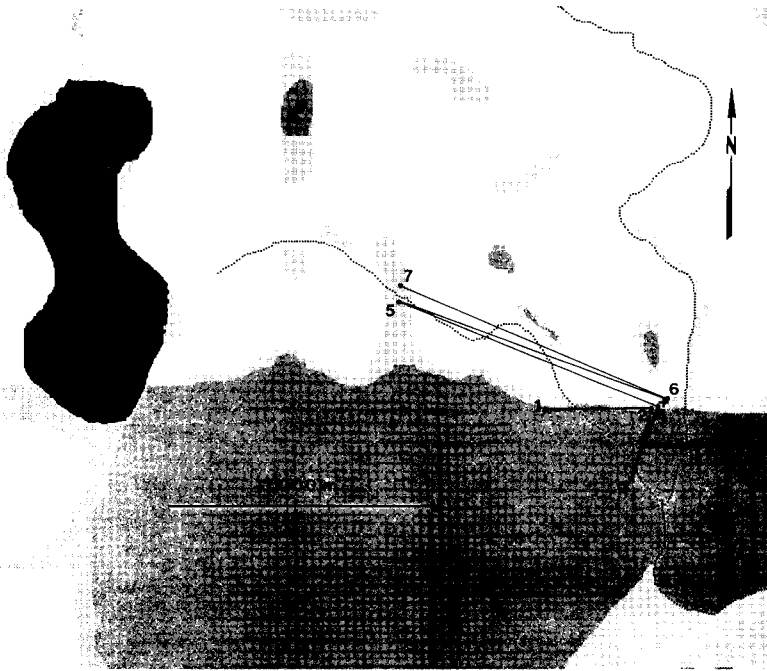


Fig. 2. Movements of Wood Thrush BS 381. The detection points described in the text are numbered 1-7 from release to last detection point. Shadings and symbols are the same as in Fig. 1.

380, BS 385, and BS 386 were all at the swarm, 240 m south-southwest of Dozer Patch at 0930 on 22 January 1988, along with individuals of a number of other species. BS 382 was 50 m east of this group. These birds were in and around the area for more than a week, despite the presence of Wood Thrushes that were calling and chasing in apparent attempts to maintain territories.

The signals of 9 birds disappeared in 3 days or less during the course of the study (1982-1988); the birds were never captured or detected again. Some of these disappearances may represent battery or transmitter failures. Others probably indicate birds that left the detection zone. Lost signals of 6 individuals (BS 372, BS 374, BS 353, BS 371, BS 381, BS 373) were re-detected at a later date. In all cases, their frequencies were checked several times each day from their last known location and from key elevated checkpoints. We are certain that these birds moved outside the detection zone and returned (in 4 cases to a previously occupied site, and in 2 cases to a new area).

At least 4 wanderers eventually settled in primary forest sites after moving considerable dis-

tances in a variety of habitats: LP 165, BS 353, BS 371, and BS 379. After this occurred, their movement patterns altered dramatically. They were found repeatedly at the same site, showed none of the skittish, wary behavior of wanderers, and seldom moved >50 m from a central point.

Mortality.—Nine radio-tagged birds died during the tracking periods. All were killed by mammalian or avian predators. Seven of 27 were identified as wanderers and 2 of 34 were sedentary birds (Table 1). These proportions are significantly different (Chi-square test, $P < 0.05$). The mortality rate, in bird deaths/tracking day (± 2 SE) was 0.026 ± 0.020 for wanderers and 0.004 ± 0.006 for sedentary birds; significantly different at the 90% level of confidence, but not at 95%.

Predation.—Six individuals were probably killed by avian predators, and 3 by mammalian. In 3 cases, we interrupted the predator: twice a Ferruginous Pygmy-Owl and once a Barred Forest Falcon (*Micrastur ruficollis*). Both these species were interrupted in other instances of avian predation as well. We were unable to identify the mammalian predators.

DISCUSSION

Movement characteristics of sedentary vs. wandering Wood Thrushes.—Radio-tracking indicated that most sedentary Wood Thrushes remained for long periods in one small area, an observation supported by banding data (Rappole and Warner 1980, Winker 1989). Individuals arrived at a site in mid- to late October, generally remained on the site until early April, and returned to the same site in subsequent winters. Sedentary birds made occasional forays, sometimes several hundred meters away from their home site. These forays normally lasted 1–2 h and were infrequent (1 per week or less). However Winker (1989) reported on two birds that left their sites for several days before returning.

Normally, sedentary individuals occupied an area that was not inhabited by any other Wood Thrush, though ant swarms, inclement weather, and the continuous efforts of wanderers to locate suitable territories in primary forest resulted in occasional concentrations of individuals (Winker 1989, Ramos 1983, Rappole and Warner 1980).

Wanderers showed a variety of movement patterns. Some individuals moved over a 2–3 ha area of rain forest for a period of hours or days, settled in an area of second growth for a day or two, and then moved back into primary forest. Others spent long periods (days, weeks) in second-growth patches before disappearing. Some were captured, radio-tagged, and left the detection area within a matter of hours.

Membership in either category, wanderer or sedentary, is not permanent. Banding data from earlier studies and radio-tracking data from this study showed several wanderers that became sedentary. None of these birds subsequently became wanderers again during our monitoring period. However, one sedentary individual (Rappole and Warner 1980) was forced to leave its small home site by aggressive neighbors. It was recaptured twice at nets far removed from its original home site before disappearing. A bird captured at 500 m elevation abandoned its home site, presumably because of inclement weather (Winker 1989).

Behavioral differences between wandering and sedentary Wood Thrushes.—There are marked differences in behavior, other than simply movements, between sedentary and wandering individuals. Many sedentary birds are intolerant

of conspecifics and defend their home site (territory) with a specific array of vocal and visual displays toward intruding individuals (Rappole and Warner 1980, Winker and Rappole 1988, Winker 1989). In contrast, most wanderers are floaters, i.e. "An individual member of a largely territorial population who is not defending a territory, and whose movements encompass an area significantly larger than those of the average territorial conspecific" (Winker 1989). On four occasions, wanderers released at point of capture were attacked and chased out of sight by a Wood Thrush of unknown status. Bird BS 353 was continually moved along through primary forest by vocal displays of apparently sedentary individuals. On three occasions, we observed known wanderers to be attacked and chased by other Wood Thrushes while foraging, with no preliminary vocal or visual display.

Differences in mortality rates between wandering and sedentary Wood Thrushes.—Wanderers suffer significantly higher mortality rates than sedentary birds. It was not until January 1987 that we recorded any deaths in individuals that had moved ≤ 150 m from point of capture, despite following many known territory holders (through recapture and resighting as well as radio-tracking) for months during the winter. The first documented death in this class (BS 324) was probably not a territorial individual. It was originally captured in primary forest at Net 9, 640 m west of Dozer Patch on 4 January 1987, resighted 50 m west of the capture point in primary forest-second growth edge on 11 January, and again in edge 60 m east of Net 9 at 1000 on 14 January. It was found dead in 3-yr-old second growth, evidently killed by a Barred Forest Falcon, 110 m north of Net 9 on 14 January at 1130.

Only one other death of a sedentary bird was recorded. BS 383 was killed by a Ferruginous Pygmy-Owl on 27 January 1988 near Net 19. This bird was 1 of the 7 birds associated with the ant swarm that used Net 19 area for 10 days. It is probable that this bird also was not a territory owner.

As in several other studies of birds and mammals, we found mortality in wandering Wood Thrushes to be higher than that of sedentary individuals (Jenkins et al. 1963, Errington 1963, Andelt 1985). Based on these and other studies of vertebrate dispersal, a logical prediction is that the majority of the wandering birds should be young of the year, particularly because win-

tering migrants appear to return to the same site annually (Rappole et al. 1983). With the cutting of large amounts of primary forest, however, increased numbers of adult, territorial birds are likely to be forced to wander. Unfortunately, we were unable to test the question of age ratios in the different movement categories because skull pneumatization was complete or nearly so by December, when we began most of our work.

We do not assume that the transmitters had no effect on a bird's ability to elude predators. It seems likely that transmitters do affect predation rates (Odom et al. 1982). Our initial hypothesis was that if two classes of birds, one sedentary and the other wandering, are tagged with radio transmitters of the same type and in the same manner, there will be no difference in mortality rate between the groups. Our test of this hypothesis indicates that it is false. We propose that the higher mortality rate in wanderers occurred because this class of individuals tends to move large distances into unfamiliar surroundings while searching for undefended, suitable habitat that can support them for an entire winter season. These birds are more vulnerable to predation than sedentary individuals, particularly in early morning, late evening, and at night when occupation of a well-protected roost site is important (Odom et al. 1982). In addition, time spent traveling from one site to another (as documented for BS 381, BS 353, and BS 372) is time not spent foraging.

The occurrence of wanderer mortality rates that are considerably higher than those of sedentary conspecifics implies that the wanderer strategy is followed by necessity rather than choice. We propose that wanderers search for sites suitable to establish a territory that will increase probability of over-winter survival. We predict that as destruction of tropical habitats continues, the numbers of wandering birds will increase, and that populations of these species will decline to levels at or near the carrying capacity of remaining preferred habitat. For the Wood Thrush, which winters primarily in the seriously threatened wet, lowland tropical forests of Central America, we predict a sharp decrease in population within the next decade.

ACKNOWLEDGMENTS

We thank the World Wildlife Fund, U.S., and in particular Tom Lovejoy, for financial support

throughout the entire study period. The Caesar Kleberg Wildlife Research Institute and the Instituto Nacional de Investigaciones sobre Recursos Bioticos provided release time for Rappole and Ramos, respectively, as well as logistical support in the field. The Mexican government (Department of Fauna Silvestre) and the U.S. Fish and Wildlife Service, Banding Laboratory, kindly provided necessary permits. The following individuals provided voluntary help in the field without which the work would have been impossible: Jose Luis Alcantara, Samantha Baab, Kevin Ballard, Sergio Barrios-Monterde, Isabel Castillo, Rick Coleman, Dave Delahanty, Doug Gomez, A. Hartlage, Jacinto Hernandez, John Howe, John Klicka, Coleman Nemerov, Mara Neri, Ben Robles, Steve Stucker, Nellie Tshipoura, and Jorge Vega-Rivera. Gene Morton, George V. N. Powell, and two anonymous referees made numerous helpful comments on the manuscript.

LITERATURE CITED

- ANDELT, W. F. 1985. Behavioral ecology of coyotes in south Texas. *Wildl. Monogr.* 94: 1-45.
- AUTODESK, INC. 1985. AutoCAD, version 2.1x of the AutoCAD drafting package. Sausalito, California, AutoDesk, Inc.
- DILGER, W. C. 1956a. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Auk* 73: 313-353.
- . 1956b. Adaptive modifications and ecological isolating mechanisms in the thrush genera *Catharus* and *Hylocichla*. *Wilson Bull.* 68: 171-199.
- ERRINGTON, P. L. 1963. Muskrat populations. Ames, Iowa State Univ. Press.
- HEISEY, D. M., & T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* 49: 668-674.
- JENKINS, D., A. WATSON, & G. R. MILLER. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.) in northeast Scotland. *J. Animal Ecol.* 36: 97-122.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651-661.
- ODOM, R. R., J. H. RAPPOLE, J. EVANS, D. CHARBONNEAU, & D. PALMER. 1982. Red-cockaded Woodpecker relocation experiment in coastal Georgia. *Wildl. Soc. Bull.* 10: 197-203.
- PENNINGTON, T. D., & J. SARUKHAN. 1968. Arboles tropicales de Mexico. Mexico, Inst. Nac. Forestales.
- RAIM, A. 1978. A radio transmitter attachment for small passerines. *Bird-Banding* 49: 326-332.
- RAMOS, M. A. 1983. Seasonal movements of bird populations at a Neotropical study site in southern Veracruz, Mexico. Ph.D. dissertation, Minneapolis, Univ. Minnesota.
- RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY III, & J.

- RUOS. 1983. Nearctic avian migrants in the Neotropics. Washington, D.C., U.S. Fish & Wildl. Serv.
- , & D. W. WARNER. 1980. Ecological aspects of avian migrant behavior in Veracruz, Mexico. Pp. 353–393 in *Migrant birds in the Neotropics* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.
- SEBER, G. A. 1982. The estimation of animal abundance. London, Griffin & Co., Ltd.
- TIPTON, A. R. 1980. Mathematical modeling in wildlife management. Pp. 211–245 in *Wildlife management techniques manual* (S. D. Schemnitz, Ed.). Washington, D.C., The Wildlife Society.
- WINKER, K. 1989. The Wood Thrush (*Catharus mustelinus*) on its wintering grounds in southern Veracruz, Mexico. M.S. thesis, Minneapolis, Univ. Minnesota.
- , & J. H. RAPPOLE. 1988. The relationship between *Hylocichla* and *Catharus* (Turdinae). *Auk* 105: 392–394.

The **Hawk Mountain Sanctuary Association** is now accepting applications for its thirteenth annual award to support student research on birds of prey. Support for this award is provided by Carl Zeiss Optical, Inc. Up to \$2,000 is available and will be awarded to one or two recipients. To apply, a student applicant should submit a brief description of his or her research program (five pages maximum), a *curriculum vitae*, a budget summary including other funding anticipated, and two letters of recommendation to **Dr. James C. Bednarz, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529 USA**. The deadline for applications is **15 November 1989**. The Association's board of directors will make a final decision in February 1990. Only undergraduate and graduate students in degree-granting institutions are eligible to apply. The awards will be granted on the basis of the project's potential **to improve understanding of raptor biology and its ultimate relevance to the conservation of raptor populations**. The funds are no longer restricted to studies in North America and **applications from anywhere in the world** will be considered.

The Hawk Mountain Sanctuary Association awarded its **1989 research grant** to **Suzanne M. Joy**, a M.S. candidate at **Colorado State University**. Her project is entitled "Nest-site characteristics and foraging behavior of Sharp-shinned Hawks in mature aspen and conifer habitats."