

POPULATION DYNAMICS OF THE WOOD THRUSH IN SOUTHERN VERACRUZ, MEXICO¹

KEVIN WINKER

*Bell Museum of Natural History, Department of Ecology and Behavioral Biology,
University of Minnesota, 10 Church Street, SE, Minneapolis, MN 55455*

JOHN H. RAPPOLE

Conservation and Research Center, National Zoological Park, Front Royal, VA 22630

MARIO A. RAMOS

World Wildlife Fund, US, 1250 24th Street NW, Washington DC 20037

Abstract. The Wood Thrush *Hylocichla mustelina* (Muscicapidae: Turdinae) was studied on wintering grounds in the rainforest of southern Veracruz, Mexico, using mist netting, radiotelemetry, and field observation. Data were collected during three boreal winters (primarily November–March), and 46 individuals received transmitters. All sex and age classes were present, but difficulties in aging and sexing did not allow accurate determination of proportions. Telemetry showed two types of spatial use: “sedentary” ($n = 18$) and “wandering” ($n = 21$). Wanderers moved greater relative distances, had higher subcutaneous fat reserves, and seemed to incur greater mortality than sedentary birds. Analysis of eight specimens suggests that these two strategies are practiced by both sexes. Six birds that received transmitters remained unclassified due to insufficient data. One isolated bird showed intermediate behavior. Netting revealed a lack of sedentariness in part of the population throughout the winter. Movements were correlated with weather changes: cold, wet weather systems brought an influx of transients into the lowland forest site. Vocalization and playback data imply that during these weather systems aggression subsided. Home-range size of sedentary birds averaged 0.44 ha (0.12–1.03 ha). Some wanderers seemed to make movements of >2 km. Wanderers were estimated to constitute approximately 50% of the population. Because wanderers apparently occupy habitats which undergo intolerable fluctuations in suitability and appear to suffer higher mortality, we tentatively accept Brown’s (1969) critical density level 3 as a valid descriptor of wintering Wood Thrush densities in this region.

Key words: *Nearctic migrant; neotropics; rainforest; territoriality; nonbreeding ecology; radiotelemetry.*

INTRODUCTION

The rate of conversion of natural tropical habitats in the neotropics to agriculture is alarming (Myers 1980a, 1980b, 1981; Caufield 1984), and concern has been expressed over what effects this habitat loss may have upon both resident and migrant bird species that utilize these resources (Vogt 1970, Terborgh 1980). Discussion over the potential effects of tropical habitat loss on nearctic migrants that use these resources during the boreal winter (e.g., Morse 1980, Holmes and Sherry 1988) has been hampered by a lack of relevant data from nonbreeding populations. Thus far we lack even the demonstration of a mechanism for the winter-limitation of any

nearctic passerine wintering in the neotropics. One reason for this deficiency may be the shortage of studies in which individuals have been marked and followed.

The importance of studying individuals when investigating population-level phenomena has recently been emphasized (Łomnicki 1978, 1988; Hassell 1986), and we concur with this advice. The study of individuals is easier when movements are relatively restricted, making species in which individuals hold winter territories attractive subjects for study. Nonbreeding, insectivorous, passerine migrants are frequently territorial (see Rappole et al. 1983, p. 22–25 for a review; also Elgood et al. 1966, Price 1981), and territoriality has been suggested as the most common social system among wintering nearctic migrants. (Greenberg 1986).

The hypothesis that tropical wintering habitat

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loss may have a negative effect upon wintering populations of nearctic avian migrants would postulate that these migrants are experiencing conditions of high density relative to the carrying capacity of the most favorable part of their wintering environments. When examined in the context of Brown's (1969) critical density model of the role of territoriality in population regulation, this postulation results in two predictions about a population of territorial wintering migrants: (1) habitats of decreasing levels of suitability should be occupied by individuals of that population, and (2) a class of nonterritorials should exist. This study examines these predictions in a wintering population of Wood Thrushes (*Hylocichla mustelina*), through exploration of movements, and, indirectly, behavior at the individual and population levels.

The Wood Thrush breeds primarily in the United States east of Texas, Oklahoma, Kansas, Nebraska, and the Dakotas, and winters largely on the Caribbean slope from eastern and southern Mexico through Central America to Panama and northwestern Colombia (AOU 1983). During the breeding season it inhabits mesic deciduous forests. It winters primarily in moist lowland forests. This species was chosen for several reasons: (1) it is a nearctic migrant whose entire winter range is undergoing extreme habitat loss; (2) individuals are territorial on the wintering grounds (Willis 1966, Rappole and Warner 1980); (3) its preferred habitat is rainforest (Rappole and Warner 1980; Rappole and Morton 1985; D. W. Warner, unpubl. data); (4) it is a common and easily captured species in southern Veracruz (Rappole and Warner 1980, Ramos 1989); and (5) it is large enough to bear a 2-g radio transmitter.

STUDY AREA

The Sierra de Los Tuxtlas, about 42,000 km² in size, is a rugged, mountainous region of volcanic origin situated on the Gulf of Mexico near the Isthmus of Tehuantepec, 90 km southeast of la Ciudad de Veracruz (Fig. 1). Average rainfall varies annually from 2,500 mm–4,500 mm, depending on location. The orographic effect of Los Tuxtlas on air masses moving inland from the gulf causes higher rainfall on the immediate gulf slope than on the surrounding lowlands (Goldman 1951, p. 269). This effect is noticeable during the periodic cold, wet weather systems that move into the area from the north from Novem-

ber through March. These systems, called *nortes*, usually last 2–6 days. Several normally occur each month. The rest of the year is divided into the dry season, late March through May, and the rainy season, early June to early November.

Annual temperature means range from 18–26°C, depending mostly on altitude. The highest peaks in the range, Volcan San Martin and Volcan Santa Martha, are more than 1,500 m above sea level. Temperatures at the lowland study site (elevation 150 m) during the 1984–1985 field season averaged 21°C from 11 December through 20 March, with a low of 12°C (12 December 1984, 7 January 1985) and a high of 31°C (31 January 1985). For a more detailed summary of the climatology and geography of Los Tuxtlas, see Andrle (1967), Lot-Helgueras (1976), and Soto-Esparza (1976).

The original vegetation of much of Los Tuxtlas was the "selva alta perennifolia" (tall, evergreen, tropical forest) of Miranda and Hernandez (1963) and Pennington and Sarukhan (1968). Los Tuxtlas marks the northernmost extent of such habitat in the Western Hemisphere. Other forest types existed or are still present in the region (see Andrle 1967, p. 168), but our work was conducted in selva, or rainforest. Deforestation has caused profound habitat change in Los Tuxtlas, and most of the area is now grasslands, pastures, citrus groves, and weedy fields, broken by tree rows and small forest remnants. Andrle (1966) estimated that one-half of the Sierra de Los Tuxtlas was still forested in 1962. Rappole and Warner (1980) estimated that less than one-third remained forested in 1975. Using recent Landsat imagery and air photos, we estimated that less than 15% was forested in February 1986. Very little lowland forest remains in this region.

The La Peninsula study site lies on an edge of the largest remaining tract of selva left in Los Tuxtlas (<60,000 ha), in the steep valley of the Rio de Coxcoapan, a fast-flowing, rocky mountain river, near the small village of Ejido La Peninsula de Moreno (Fig. 1). Selva at this site is characteristic of the plant community at an elevation of 150 m, having a canopy height of 20–30 m (with emergents to >40 m). Topography is varied (minor valleys and ridges), with streams and treefall gaps common. Additional netting was conducted in March 1985 on the Volcan Santa Martha in virgin forest beside the Rio de Suchiapan, at an altitude of about 470 m. Fieldwork was conducted during the periods of November

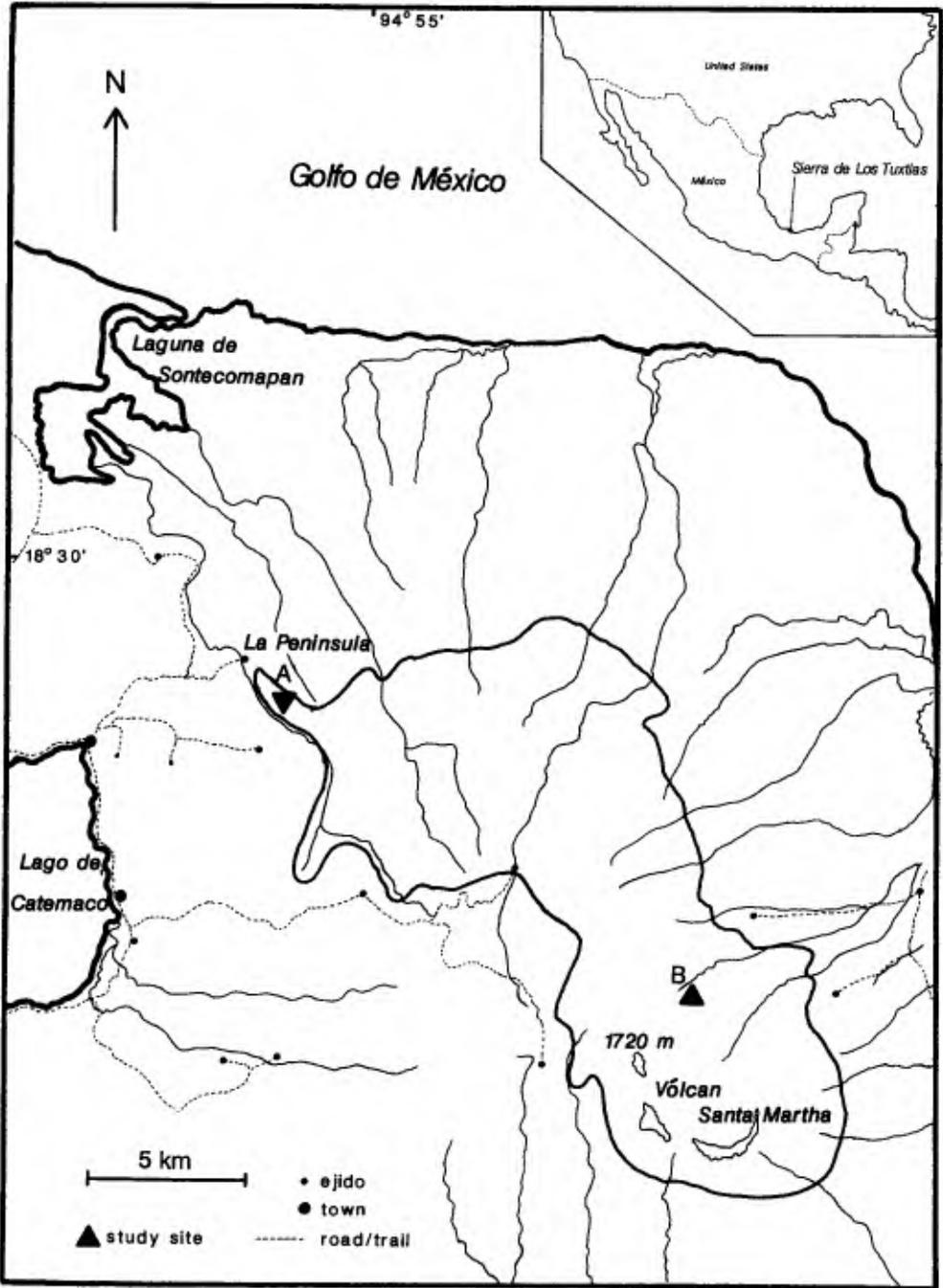


FIGURE 1. Location of study sites. Site A is the La Peninsula site; site B is the Santa Martha site. Enclosed area around the sites indicates current extent of relatively undisturbed forest. An ejido is a small agricultural community.

1982, January–March 1983, October 1983–January 1984, late March–early April 1984, and November 1984–April 1985.

MATERIALS AND METHODS

Study sites were mapped and gridded, and numbered flags were placed at 25-m intervals to facilitate plotting of precise locations both for radio locations and resightings. Nylon mist nets (12 × 2.6 m) were set at alternate grid points (50 m apart). Net spacing was chosen based on the estimated 0.5-ha average territory size of the Wood Thrush found by Rappole and Warner (1980, p. 363). On the La Peninsula site, 350 m × 250 m (8.75 ha), 48 nets were set, oriented perpendicular to the valley (approximately 50°). Nets were opened when weather permitted, and over 31,000 net hr were accumulated. The Santa Martha site (2.5 ha) was netted from 9–19 March 1985 with 16 nets (830 net hr).

Each Wood Thrush captured received a unique colored leg-band combination and an aluminum U.S. Fish and Wildlife Service band. Date, time, net number, age (when possible), molt condition, and subcutaneous lipid deposits were recorded for all birds. Lipid levels were estimated using the method of Helms and Drury (1960). Age was determined by skull ossification through mid-December, after which it became unreliable due to shrinking of the unossified regions. Examination of 85 museum specimens of known wintering birds taken from the area during the winters of 1973–1974 and 1974–1975 (see Ramos 1983) showed that aging by the presence or absence of wing bars or wing spots is inaccurate (Appendix I). Birds were released at the banding laboratory (on site) unless fitted with a transmitter, in which case they were released at the point of capture.

During the study, 46 Wood Thrushes were fitted with radio transmitters (average weight 2.0 g, Custom Telemetry, 185 Long View Drive, Athens, GA 30605). Expected transmitter life was 14 days. Transmitters were attached between 14 December and 15 February (all years). The attachment technique used was essentially that of Raim (1978), which involves the gluing of a primary cloth with artificial eyelash adhesive to the back of the bird, then the gluing of a secondary cloth, with transmitter attached, to the primary cloth. Attachment usually failed after approximately 40 days due to the regrowth of back feath-

ers. Two transmitters fell off after 2–3 days due to failure of year-old (i.e., not fresh) glue.

Transmitters were attached and birds released as quickly as possible at the point of capture; usual elapsed time was 1–1.5 hr. Only birds that appeared to be in good condition were selected to bear transmitters. Radio-tagged birds were located at least twice a day (morning and evening) when possible, using a four-element Yagi antenna and a 12-channel receiver (Custom Telemetry). Tracking was done on foot. Both triangulation and approaching a bird until it moved were used to pinpoint locations. Home-range sizes were estimated from these locations using the modified minimum area method of Harvey and Barbour (1965). The few points excluded by distance from inclusion in home-range size estimation were classified as extra-home-range forays, or “sallies outside the area” (see Harvey and Barbour 1965, p. 400; Burt 1943).

During the 1984–1985 season, the date, time, type, and duration of every vocalization was noted. Additional observations were made by artificially stimulating presumably territorial individuals using a taped playback of calls used in agonistic interactions. Cassette tape sessions were conducted at various times of day, both with and without the presentation of a mounted conspecific model. The tape contained a repeated moderate to high intensity aggressive vocal confrontation between two individuals and was run for 12–15 min during each session, for a total of approximately 13 hr.

RESULTS

Despite being reported as uncommon in Veracruz (Loetscher 1955, p. 36), and rare in Mexico (Edwards 1972, p. 190), the Wood Thrush was the dominant understory forest species in this winter avian community, as indicated by mist-net captures (unpubl. data). During the study 217 Wood Thrushes were caught on the La Peninsula site. Many of these birds were recaptured or resighted periodically throughout the winter season, and several from one year to the next (Table 1). A disparity between captures and recaptures per 1,000 net hr for the 1982–1983 field season and the 1984–1985 and 1985–1986 seasons was due to an intensive November 1982 netting effort, during which migrants were still passing through. Wood Thrushes returned to Los Tuxtlas from mid-October to mid-November, and de-

TABLE 1. Wood Thrush netting results from La Peninsula.

Season	Captures	Recaptures	Previous season recaptures	Captures/1,000 net hr	Recaptures/1,000 net hr
1982-1983	81	80	0	10.54	10.42
1983-1984	40	14	3	5.76	2.02
1984-1985	96	42	3	6.59	2.88

parted around mid-April. Early and late dates were 16 October 1983 and 10 May 1985, although Ramos (1983, p. 20) recorded both slightly earlier and later dates in the region.

Because accurate determinations of age and sex were not possible on live birds throughout the winter, we determined the age and sex structure of the Wood Thrush population wintering in Los Tuxtlas by examining museum specimens taken from the area during the winters of 1973-1974 and 1974-1975 (mid-December-late March). Differences in age and sex proportions between these years were not significant, so the samples from both winters were pooled (age: $z = 0.599$; $P = 0.27$; sex: $z = 0.212$; $P = 0.29$; Wyatt and Bridges' [1967] test for differences between population proportions). Based on this sample, the population during those years was composed of 72% males and 28% females. Using only specimens collected earlier than mid-February (to eliminate the possibility of including fully ossified first-year birds), a more reliable age ratio was obtained—60% adults: 40% juveniles (Appendix I).

INDIVIDUAL MOVEMENTS

Radio-tracking results demonstrated two general, but distinct, types of movement among individual Wood Thrushes in Los Tuxtlas. We will use "sedentary" and "wanderer" as labels for these two behavioral categories. Movement alone was not always an accurate predictor of a bird's disposition, however, and several criteria were used to categorize each individual. Site fidelity and movement distances, patterns, and rates were found to be good separators, but capture records, agonistic behavior, and behavior when approached and flushed were also used. Table 2 shows the individualistic nature of birds fitted with transmitters and the various criteria used in categorizing each bird as "sedentary," "wanderer," or unknown. Sedentary individuals generally allowed a much closer approach by the tracker, and when flushed tended to move off

slowly, although occasionally in heavy rain wanderers behaved similarly.

Sedentaries. The movements of sedentary birds were much more restricted, both in rate and distance, than those of wanderers (Table 3). These restricted movements were reflected in a 78% recapture rate among sedentaries receiving transmitters. The mean length of within-season capture history for recaptured sedentaries was 38.6 days (first to last capture, Table 2). Since locations were only taken twice per day for most birds, the movement rates in Tables 2 and 3 were not accurate per-day figures; they were used as an index of movement based upon known locations.

The behaviors of well-known sedentaries (e.g., 213, 466 ['85], 1645, 1747, 1832, 1841, and 1645 and 1778 when in residence) and the behaviors of well-known nonterritorials, or wanderers (e.g., 1235, 1773, 1779, 1780, 1793, 1807, and 1856), were used as "templates" against which to compare other birds with fewer data. Not all birds tracked were classifiable as either sedentary or wanderer. Of the 46 birds which received transmitters, 18 were classed as sedentary, 21 as wanderer, and six were unclassified due to insufficient data (Table 2). The single bird from the Santa Martha site was also unclassified.

Figure 2 depicts the movements of a sedentary individual. Number 466 was present on the site in all three winters of the study, and was fitted with a transmitter in both the first and last years. The chronological sequence of locations shows that daily movements encompassed a large portion of what was eventually determined to be the home range. There was a great degree of overlap in the two areas of movement, but the third-year home-range center was 15 m away from the first-year center, suggesting that movement patterns had changed, and that perhaps home-range and/or territory boundaries are not entirely stable between years.

Home-range sizes for sedentary birds with transmitters varied from 0.12 to 1.03 ha, and

averaged 0.44 ha. The bird holding the 0.12-ha home range (no. 421) was found out of this area only once. For comparison, no. 1743 had a home range of 0.4 ha, yet was found out of this area four times. This may reflect differences in home-range quality: much of no. 1743's home range was rocky stream-edge and steep bank. Only two other extra-home-range forays were recorded among all birds with transmitters.

Two sedentary birds showed movements of a kind rarely described in wintering territorial systems. Each left its home range for several days (5 and 10), then returned again. Number 1645 took up residence in its home range upon return; no. 1778 (adult male) remained on its former range for 4 days, then departed again. It returned again 15 days later and was collected. Shortly after this, another bird (or perhaps two) took over the home range. The whereabouts of nos. 1645 and 1778 while gone was unknown, but they were at least 2 km away. The initial return of these two birds to the site coincided with the beginning of a *norte*, the same one that presumably caused a shift out of the riverine disturbed habitat by wanderer no. 1793 (see below).

Wanderers. Within the wanderer group, patterns were not consistent. Two very general types of movement emerged. In one type (Type 1, Movers; nos. 555, 1773, 1779, 1780), represented by Figure 3 (no. 1773), movements were largely random when near the study site, but those birds for which a final, distant signal was received (prior to total disappearance) were moving up the valley toward higher elevations and the interior of the forest tract.

The second general type of movement found among the wanderers (Type 2, Drifters; nos. 527, 1182, 1235, 1793, 1807, 1810, 1856) is represented by Figure 4 (no. 1793). These birds' movements were relatively localized compared with the wide-ranging movements of the mover group. Movement from the La Peninsula site to a nearby (ca. 150 m) disturbed riverine habitat and subsequent departure from the area was shown by six of the Type 2 wanderers.

Movements of all wanderers appeared to be correlated with adverse weather. Number 1793 was initially captured at the beginning of a *norte*, and its recapture 4 days later (transmitter attached) coincided with the end of this *norte*. Its subsequent movement from the small area it utilized in the riverine habitat coincided with the onset of the next *norte*, and its disappearance

upriver coincided with still another. The length of time no. 1793 stayed in the riverine disturbed area and the small space it used while there were not typical. It is possible that the bird was defending this space as a territory, but no change in behavior was observed, and, perhaps most suggestive, its flushing disposition did not change. These movements along the river may represent an attempt by a nonterritorial bird to "fit" itself into the territorial mosaic of the area by establishing residence on an edge. The marginality of the site it utilized along the river was twofold: it was young second growth (not forest), and was frequently flooded. The bird's eventual departure coincided with the *norte*-caused flooding of part of the small area it had been utilizing.

Wanderers included four individuals that disappeared almost immediately after transmitter attachment. These birds were similar to other birds subsequently classed as wanderers: they were newly captured birds, and their captures occurred at the end of *nortes*. Transmitter failure on all of these birds was considered improbable, for in each case the transmitter was activated on the day of attachment and was functioning perfectly before release. We interpreted these signal disappearances as large-scale movements out of the Coxcoapan valley. Including these four, a total of nine disappearances was recorded among the wanderers; three of these birds (nos. 1773, 1780, 1856) returned to the valley following disappearance, but none returned to the area utilized prior to departure. Home-range sizes were not estimated for wanderers because of their apparent transience.

The higher movement rate of wanderers resulted in a lower average number of tracking days per individual than among sedentary birds (Table 3). These high rates of movement were probably also responsible for a relatively low recapture rate (24%) and a short mean length of capture history (6 days) among transmitter-bearing wanderers which were recaptured (first to last capture, Table 2). These figures reflect the tendency of wanderers to leave our study site, and often, apparently, to leave the Coxcoapan valley. Once out of the valley, signals were never received, although checks were made daily from the highest available points, and periodically from the valley rim. These birds had to move at least 2 km to cause signal disappearance due to topography (apparatus was known to be suitable for at least 3–4 km line-of-sight), and were probably

TABLE 2. Vital statistics on Wood Thrushes receiving transmitters during the study. Transmitters were attached between 14 December and 16 February (all years). Groupings were based upon movement pattern (not shown), average distance moved per day, capture records, and behavioral disposition (see text for details).

Bird number	Tracking days	Average m/day	Home- range size (ha)	Aggres- sive display*	Submis- sive display ^b	Approaches to ≤ 25 m		Days† since first capture	First to last capture (days)
						Occur- rences	Attempts		
A. Sedentaries, La Peninsula									
165 (1983)	9.5	ca. 80.0	— ^c	—	—	3	3	82	733
213	12.5	49.6	0.93	—	—	7	8	84	84
390	9.0*	21.1	0.20	—	—	6	6	69	75
421	11.5	34.8	0.12	—	—	5	5	9	9
466 (1983)	6.5*	— ^d	0.20	—	—	—	—	0	737
466 (1985)	21.5	40.5	0.20	2	—	24	24	737	737
548	7.5*	26.7	0.30	—	—	5	5	0	25
1107	6.5*	33.1	0.35	—	—	3	3	38	38
1645 ^e	32.5 (23)	54.0	0.50	—	—	24	26	21	57
1694	6.5	49.2	0.25	—	—	10	10	3	3
1736	6.0	63.8	0.40	1	—	10	12	0	3
1743 ^f	13.5	99.3	0.80	—	—	3	7	0	0
1747	34.5	41.9	0.58	—	—	7	8	0	0
1778 ^g	42.5 (24)	52.7	1.03	?	—	15	17	0	43
1794	8.5	64.7	0.35	—	—	7	9	0	0
1832	24.5	45.2	0.45	1	—	12	14	12	12
1841	24.5	72.4	0.65	2?	—	17	20	0	4
1870	2.5 ^d	85.6	0.20	—	—	6	6	22	22
B. Wanderers, La Peninsula.									
460	1.0	388.0	—	—	—	0	0	0	
526	1.5	104.0	—	—	—	1	1	0	0
527	3.5*	62.9	—	—	—	0	1	0	0
555	2.5	— ^h	—	—	—	0	1	0	2
1182	6.0*	51.3	—	—	—	1	3	0, 8 ^b	0
1235	13.5*	41.8	—	—	—	0	7	0	8
1727 ⁱ	0.0	—	—	—	—	—	—	0	0
1728 ^j	1.5	—	—	—	—	0	1	0	0
1741 ^j	1.5	—	—	—	—	0	2	0	0
1773 ^k	5.5 (4.5)	421.9	—	—	—	1	7	0	0
1774	0.5	—	—	—	—	0	0	0	0
1779	8.5	103.5	—	—	—	0	2	0	0
1780 ^k	9.5 (5)	276.6	—	—	—	0	1	0	0
1793	19.5	164.3	—	—	—	1	7	4	4
1807	4.5	235.6	—	—	1	1	3	0	0
1810	2.5	116.0	—	—	—	0	2	0	2
1849	0.5	176.0	—	—	—	1	1	0	0
1850 ^l	0.0	—	—	—	—	—	—	0	0
1856 ^k	16.0 (11)	178.7	—	—	—	1	9	1	14
1872 ⁱ	0.0	—	—	—	—	—	—	0	0
1890 ⁱ	0.0	—	—	—	—	—	—	0	0
C. Unclassified birds, including single Santa Martha bird.									
077 ^l	5.0*	25.0	?	—	—	3	3	81	81
165 (1984) ^m	1.0	50.0	?	—	—	2	2	402	733
1130 ⁿ	3.0*	15.7	?	—	—	2	2	29	490
1204 ^o	?	—	—	—	—	—	—	0	0
1219 ^p	0.0	—	—	—	—	—	—	0	0
1238 ^q	4.0*	126.3	—	—	—	1	3	0	0
SM52 ^r	4.5	131.0	—	—	—	8	8	0	0

† Transmitter attached x days after bird's initial capture.

* Bird located only once per day.

^a Given either in a natural encounter or in response to taped playback.^b Immediate retreat in response to aggression.^c Readings mixed up with a *Habia gutturalis* bearing a transmitter, making movement estimate approximate and accurate home-range size estimate impossible.

TABLE 3. Comparisons between transmitter-bearing Wood Thrush sedentaries and wanderers.

	Sedentaries	Wanderers
Number of individuals	18	21
Total tracking days	280.0	98.0
Mean tracking days (SD) per bird	15.6 (11.6)	4.7 (5.7)
Mean distance (SD) moved per bird per day (m) ^a	53.8 (21.5)	178.5 (122.3)
Deaths	0	2

^a An index of movement based on a maximum of two radio locations per day. Sedentaries: $n = 17$; Wanderers: $n = 13$.

more distant, since valley-rim checks were unsuccessful. No wanderers were recaptured from one winter to the next.

During the study, two wanderers bearing transmitters were taken by predators, one by an unknown predator and the other by a raptor. Because the sample periods within the two groups (tracking days) were disparate, the effective "window" into the lives of sedentaries was much longer than for individual wanderers; we had nearly three times the sample period in the sedentary group, yet not one sedentary bird died while being tracked. This trend was substantiated during three subsequent years of data collection (Rappole et al. 1989; summarized in Discussion).

Although differences in movement rates made any quantitative assessment difficult, and therefore crude, we estimated that wanderers constituted approximately 50% of the Wood Thrush population at La Peninsula.

Collected birds. Six birds successfully collected to determine sex (two additional birds had gonads destroyed by shot), showed that sedentaries comprised birds of each sex (3 females, 1 male), and wanderers included one male and probably one female. Sedentaries in this sample consisted of two birds with radio and recapture histories

(1 male: no. 1778, 1 female: no. 1130), and two were shot when responding aggressively to playback of aggressive vocalizations (2 females). Wanderers in this sample were no. 1856 (male), and one probable wanderer, an unbanded female collected after a *norte*.

Subcutaneous lipids. Subcutaneous fat deposits upon initial capture were higher in wanderers than in sedentaries ($z = 5.49$, $P < 0.001$, Wilcoxon's rank sum test; Fig. 5).

Santa Martha site. Only one bird was captured on the Santa Martha site, and this individual received a transmitter. Its movements were dissimilar from those of any other bird tracked. It moved about on the valley floor loosely, generally using the flatter terrain along the river. The area it covered was long (260 m) and narrow, unlike the home range of any sedentary mapped, but its flushing disposition matched the sedentary type, rather than that of wanderers (Table 2c). Without conspecifics in the area its movements were probably not constrained. It is noteworthy that one Wood Thrush was seen on this site the day before a *norte* came. Netting commenced during this *norte*, and no Wood Thrushes were seen, heard, or captured for the duration of this weather system (3 days). On the day fol-

←
^a Transmitter problems: broken antenna (466); experimental 0.7-g transmitter (1870); home-range sizes estimated from locations, resighting, and recapture data.

^b Bird left area, later returned. Tracking days in parentheses and average distance moved are values for resident period only. See text.

^c Newcomer which established a home range near study site.

^d Vocalization heard from vicinity of radio-tagged bird.

^e Only detections were 0.45 km from site. Movement between locations inestimable due to terrain.

^f First transmitter fell off after 3 days; new transmitter attached upon recapture, 3 days later signal disappeared.

^g Signal (and thus bird) disappeared shortly after transmitter attachment. Functionality of transmitter certain upon attachment.

^h Bird's only movements were due to long distance flushes (by tracker) prior to disappearance.

ⁱ Bird left valley (signal disappearance), later returned. Tracking days in parentheses and average distance moved are for resident period only.

^j Movements localized, but located on only 2 days in a 5-day period.

^k Sedentary by recapture record; problems with shorting out transmitter in heavy rain. Tracking record alone considered insufficient evidence for categorization. Before transmitter failure, no. 165 was found out of its home range, where it showed wanderer-type movement (moving rapidly and keeping well away from tracker) until returning to its home range, when it settled down again in its movements (moving slowly and circularly when pushed).

^l Sedentary by recapture record; transmitter fell off, however.

^m Transmitter found fallen off after 2 days, its position making the previous day's location uncertain.

ⁿ Functionality of transmitter upon release uncertain.

^o Signal behaved as though antenna had broken.

^p Individual from Santa Martha. Although the other birds in Table 2C are unclassifiable due to insufficient telemetry data, this individual simply does not fit into either category.

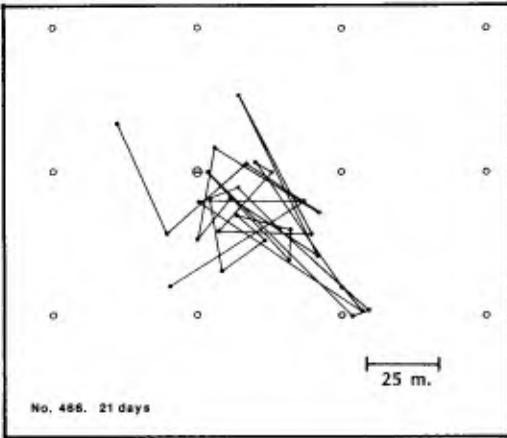


FIGURE 2. Movements of Wood Thrush sedentary individual no. 466 over 21 days (1985). ⊕ indicates capture location; open circles are nets. Black dots are connected in chronological order and show locations (maximum of two per day). Note relatively even use of space and narrow scope of movement pattern.

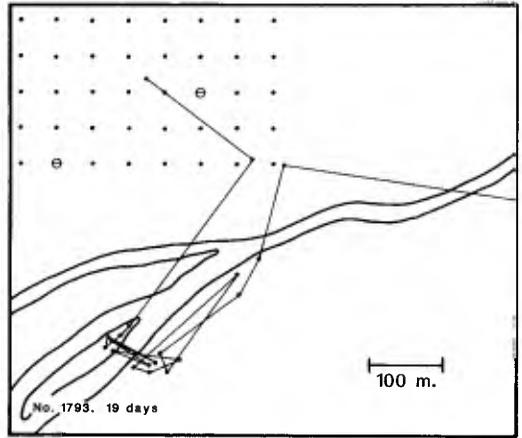


FIGURE 4. Movements of Wood Thrush wanderer no. 1793 over 19 days (example of a drifter). ⊕ indicates capture locations. Black dots are connected in chronological order and show locations (maximum of two per day); black dots not connected by lines are nets. Note relatively localized wanderings.

lowing this *norte*, this single Wood Thrush was captured and fitted with a transmitter. During the next *norte* no signal was found.

POPULATION-WIDE MOVEMENTS

The apparent correlation between individual behavior and weather is evident at the population

level through netting and vocalization data. The 1984–1985 field season was the most thoroughly netted; in the following analyses the 3 days during this season on which nets were open for less than 4 hr were excluded. These days gave misleading capture rates, since most captures occurred in the morning (when nets were open

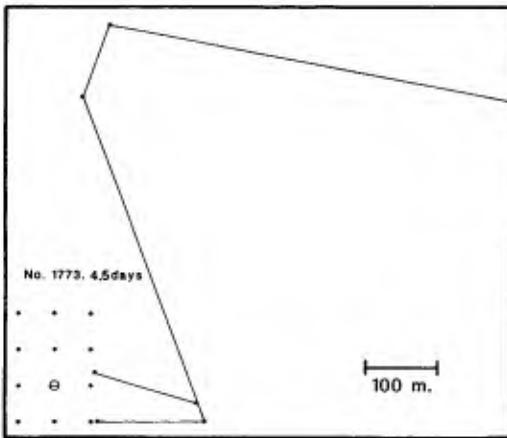


FIGURE 3. Movements of Wood Thrush wanderer no. 1773 over 4.5 days (example of a mover). ⊕ indicates capture location. Black dots are connected in chronological order and show locations (maximum of two per day); black dots not connected by lines are nets. Note long distances between locations and broad scope of movements.

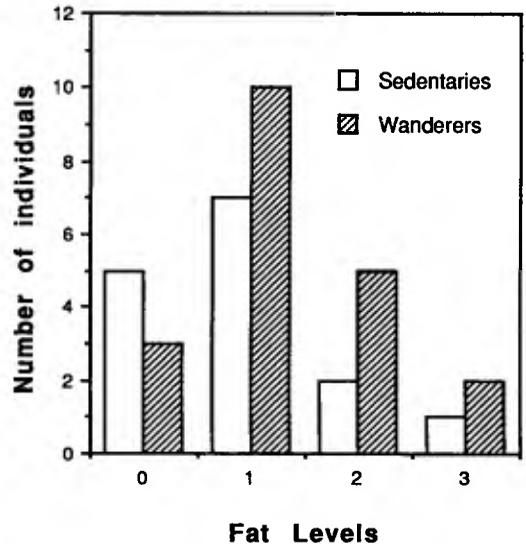


FIGURE 5. Comparison of subcutaneous lipid deposits between transmitter-bearing Wood Thrush sedentaries and wanderers.

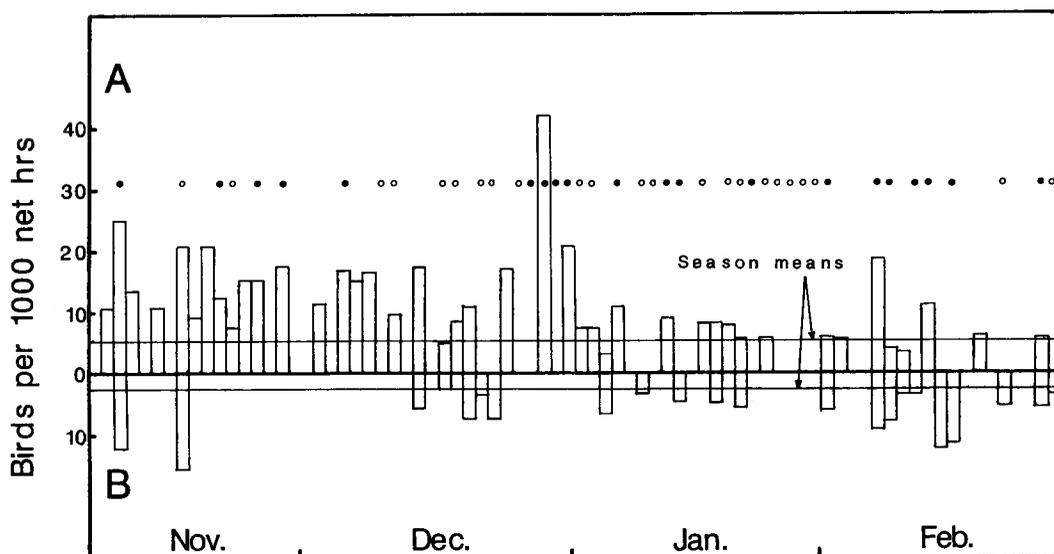


FIGURE 6. Captures (A) and recaptures (B) of Wood Thrushes for the 1984–1985 field season, by day, expressed as birds per 1,000 net hr. Fine horizontal lines denote season means. Closed circles represent rainy days and open circles represent sunny days.

these days). Netting results confirmed the relationship between movements and weather reported for Los Tuxtlas by Ramos (1983). Significantly more Wood Thrushes were captured during days associated with *nortes* (rainy days: $n = 22$, $\bar{x} = 10.12$, $SD = 7.62$), than on days with good weather (sunny days: $n = 27$, $\bar{x} = 4.40$, $SD = 3.80$; captures and recaptures included, $z = 2.83$, $P = 0.005$, Mann-Whitney U -test). No correlations were found between capture rates and either minimum or maximum daily temperatures. Figure 6 shows the distribution of captures, recaptures, and weather events during the 1984–1985 field season. The recapture rate of Wood Thrushes was also higher on rainy days (excluding days upon which no birds were recaptured: $z = 2.49$, $P = 0.012$, Wilcoxon's rank sum test).

Capture rates of new birds and total captures (captures and recaptures) decreased significantly during the course of the 1984–1985 field season, while recaptures increased significantly (Table 4, case A). Individuals of the wanderer class were captured throughout the winter season.

Vocalizations and agonistic encounters. Taped playbacks were less likely to elicit an aggressive response from presumed territory holders on rainy days (days associated with *nortes*) than on sunny and nonrainy days ($G = 6.47$, $0.25 > P$

> 0.01 ; G -test using Yates' correction [Sokal and Rohlf 1981]; Table 5). A separate analysis of vocalization data corroborated this apparent weather-related change in aggression. Vocalizations consisted of calls (breeding ground song was rarely heard in winter), and appeared to be given primarily during agonistic encounters with conspecifics (unpubl. data). Observed intraspecific interactions were always accompanied by vocalizations, and spontaneous vocalizations were confined mainly to periods of low light: usually dawn and dusk (unpubl. data). Only vocalizations believed to be given in agonistic intraspecific interactions were included in this analysis. Vocalization data for the 1984–1985 field season were analyzed by frequency under different

TABLE 4. Correlation coefficients (r) for Wood Thrush captures, recaptures, and totals (captures + recaptures) during (A) the entire course of the 1984–1985 field season, and (B) during a period after which all residents should have been captured.

Case	No. days	New captures	Recaptures	Totals
A	77	-0.52**	0.27*	-0.32*
B	56	-0.31*	0.27	-0.11

* $P < 0.01$,
** $P < 0.001$.

TABLE 5. Weather-related occurrences of aggressive responses to playback of recorded aggressive vocalizations in the Wood Thrush.

	Response	No response
Rainy days	0	10
Sunny and nonrainy days	23	30

($G = 6.47$, $0.25 > P > 0.01$; corrected G -test).

weather conditions (Tables 6, 7), showing that significantly fewer vocalizations were given on days when it rained (days associated with *nortes*) than on days when there was no rain.

In examining vocalization data, all low-light vocalizations that were not verified aggressive encounters with conspecifics were excluded. This weather-related difference in vocalization rates was not an artifact of reduced hearing ability during rain; during heavy rain we were usually not at the study site (such days were excluded from the analysis), and the rain on those days that vocalizations were noted was usually restricted to a light, steady drip, or to brief showers, neither of which affected our ability to hear other vocalizing forest residents. Hearing was noticeably reduced only during 1–3 day periods of strong southerly winds (*suradas*), which were included in the “sunny” days sample. With spontaneous vocalizations removed from the sample we believe these vocalization data are a good index of intraspecific agonistic encounters.

These analyses suggest that during *nortes* there is a decline both in the likelihood of an aggressive response to a conspecific stimulus and in actual aggressive encounters. This is opposite to what might be expected, given that intrusion rates were higher at these times.

TABLE 6. Number of Wood Thrush vocalizations heard per day under different weather conditions (1984–1985). On 15 rainy days no calls were heard, while on 5 sunny days two calls were heard, etc.

Vocalizations/day	Rainy days	Sunny days	Cloudy days
0	15	6	3
1	7	12	10
2	1	5	2
3	0	0	2
4	0	1	1
6	0	1	1
Total vocalizations	9	32	30

TABLE 7. Wilcoxon's rank sum test results of Wood Thrush vocalizations per day under different weather conditions.

Comparison	z	P
Rainy vs. sunny	-19.48	<0.001
Sunny vs. cloudy	-1.40	0.082
Rainy vs. cloudy	-5.66	<0.001
Rainy vs. all others	-5.06	<0.001

DISCUSSION

Our two categories, sedentary and wanderer, fit a general conception of “territorial” and “float-er”; however, in keeping with the caution urged by authors such as Burt (1943) and Emlen (1956) we refrain from using those particular labels in describing individuals. Although many individuals in this Wood Thrush population were territorial, the descriptor “territorial” cannot be confidently attached to *all* sedentary individuals given a lack of corroborant behavioral data (i.e., aggressive behavior), which were collected only incidentally. Nevertheless, the preceding results are considered in the context of a territorial system, reflecting our knowledge of the underlying social system, if not of the exact status of all individuals considered.

WEATHER-RELATED BEHAVIOR

Wanderers. During *nortes*, our lowland study site became host to large numbers of newly arrived, unbanded birds of many species (unpubl. data, Ramos 1983). Ramos (1983, part 2, p. 4) found a significant difference in capture rates between rainy and “sunny” days for many species in this region, as well as for overall (all species) capture rates. Our netting results show that these temporarily resident individuals and species departed either immediately or soon after the *norte*. Telemetry data revealed that the movements of transient Wood Thrushes during *nortes* usually encompassed an area much larger than the La Peninsula site. Unbanded birds, presumably transients, were often seen during *nortes* foraging along trails and small, dry streambeds, either individually or in loose aggregations of two to three individuals.

Because birds resident on the site usually do not depart, new captures during *nortes* presumably came from habitats other than the lowland types in which we were netting. Rappole and Warner (1980) and Ramos (1983, p. 9) conclud-

ed that since these new birds were accompanied by species normally associated with the local highlands (e.g., *Myioborus miniatus*, *Catharus mexicanus*), the newcomers came from higher elevations. Reduced food availability in the highlands was hypothesized as the reason for these movements.

Although we have no measurements of food availability, our observations seem to support this hypothesis. The highlands are exposed to stronger winds, heavier rains (see also Goldman 1951, p. 283), and cooler temperatures than the lowlands (unpubl. data), suggesting that insect food might be depleted (Buskirk and Buskirk 1976), and that foraging efficiency may be reduced. We have observed feeding arboreal insectivorous birds slowly descend steep valley walls on Volcan Santa Martha as the cloud cover of a mild *norte* descended (16 March 1985). The movements of the single Wood Thrush captured and followed on the slopes of Volcan Santa Martha also suggest that *norte* conditions in the highlands might be the cause of lowland influxes. The mover category of wanderer included individuals which fit Ramos' (1983) hypothesis of temporary visitors from the highlands during inclement weather (e.g., nos. 555, 1773, 1779, and 1780). Number 1773 (Fig. 3) was captured during a *norte*, and its final disappearance upriver corresponded with another *norte*. Although this general movement pattern supports Ramos' "lowland retreat" hypothesis, it should be recalled that there was almost no forest further downriver (i.e., at lower elevations) for these birds to use.

Weather-related altitudinal movements by birds in the tropics have been reported by Wetmore (1926), and "hard-weather movements" were noted by Lack (1968) and summarized for palearctic thrushes by Simms (1978).

The reason *norte*-resident transients leave following the *nortes* that brought them in is a mystery. Perhaps it is a combination of the "return" of suitable habitat elsewhere (a place to go) and an increase in aggression on the part of the local territorial birds. An increase in aggression during a *norte* could have little effect if there is nowhere for expelled intruders to go; with such a "sink" available after a *norte*, however, a resurgence of aggression might effectively lower densities (see also Lack 1968).

The large, weather-related shifts in movement patterns evident through telemetry (wanderers) and netting (*norte*-resident transients) imply that

some habitats outside of our lowland study site undergo intolerable fluctuations in suitability, making lowland selva a desirable temporary refuge. A large portion of the Wood Thrush population (ca. 50%) appears to be subjected directly to these fluctuations.

Sedentaries. Through the presence of higher numbers of conspecifics during *nortes*, sedentaries seem to be indirectly affected by suitability fluctuations in habitat(s) outside the lowland selva in which they reside. Whereas most sedentary birds remained during *nortes*, two left the area, later returning to their home ranges. These two departures (nos. 1645, 1778) suggest that the suitability of the La Peninsula site underwent fluctuations that were intolerable to at least some residents. Although it is probable that the ultimate cause of these two temporary departures was weather, the proximate cause may have been intruder pressure, lowered resource availability, or both.

There are few documented cases of wintering territorial birds being forced by climatological changes to leave their areas. Schwartz (1964) noted that in the Northern Waterthrush (*Seiurus noveboracensis*) in Venezuela, individuals occupying territories on higher ridges abandoned these sites as the winter progressed and these areas became dry. Snow (1956) described territorial Eurasian Blackbirds (*Turdus merula*) in Britain leaving their winter territories during severe weather due to reduced food availability and returning to their territories when conditions improved. These Eurasian Blackbird territories were defended for breeding season purposes, however, and not strictly as winter feeding territories. Davies and Houston (1981) noted that territorial Pied Wagtails (*Motacilla alba*) frequently left their territories to feed on superabundant food sources, but it appeared that the territories were being defended as insurance against the time that the concentrated sources were not available. Myers et al. (1979) found that individual Sanderlings (*Calidris alba*) alternated between territorial and nonterritorial behavior, presumably due to fluctuations in prey density.

Vocalizations and agonistic encounters. The decrease in vocalizations during *nortes* implies that fewer aggressive interactions between Wood Thrushes occurred during these weather systems. Given that this change in behavior occurs when population densities are at their highest, we postulate that territorial defense becomes uneco-

nomical for most of the La Peninsula residents during *nortes*, due to increased costs associated with foul weather and increased intruder pressure. Recher and Recher (1969, p. 146) described decreased levels of aggression at high population levels among some shorebird species, but they hypothesized that these aggregations were formed because of locally abundant food organisms, and that this, in combination with high population density, caused the reduced frequency of aggressive interactions observed. Myers et al. (1979) described curtailed aggression when the non-breeding territories of individual Sanderlings were suddenly invaded by nonterritorial flocks of conspecifics. Given a sufficient number of intruders, a similar response might occur within an entire local population. However, there are two potential costs to territorial Wood Thrushes during *nortes*—increased intruder pressure and bad weather.

DIFFERENCES BETWEEN SEDENTARIES AND WANDERERS

Three hypotheses could explain the existence of two behavioral classes among wintering Wood Thrushes. (1) A genetic polymorphism exists in the population, causing some individuals to wander and others to be sedentary. (2) The two strategies exist in an evolutionary stable mixture, each having equal fitness (Davies 1980, p. 72). (3) Territorial aggression by sedentary individuals prevents some individuals from settling. If either of the first two hypotheses applied to the Wood Thrush in Los Tuxtlas, we would expect to see no differential mortality between sedentaries and wanderers (because both hypotheses imply equal fitness). Also, in regard to the first hypotheses, we would expect little or no behavior switching (e.g., Rappole et al. 1989, p. 407, 408). Although we did not examine interactions between sedentaries and wanderers, aggressive reaction to conspecifics was demonstrated through playback experiments, suggesting that the latter hypothesis merits consideration. Removal experiments needed to test this hypothesis were not performed, however (discussed below). We have only one observation to suggest that wanderers might be prevented from settling because of aggression from sedentary conspecifics (unpubl. data). As Greenberg (1986) noted, these interactions are difficult to observe in dense tropical vegetation.

Differential mortality. Rappole et al. (1989) found that nine birds were killed by predators

during 6 years of study: seven killed were of a group of 27 wanderers (moved >150 m from point of capture); two killed were of a group of 34 sedentary birds (moved 150 m or less from initial capture point). These two proportions are significantly different (chi-square test, $P < 0.05$), and these data suggest that wandering birds experience a higher mortality rate than sedentary individuals. Mortality rates in birds per tracking day were estimated as 0.026 for wanderers and 0.004 for sedentary individuals (Rappole et al. 1989). Note that the criteria for categorization in Rappole et al. (1989) are simpler than those used here, causing some incongruity in the categorization of individuals between these papers. This difference has no effect upon the outcome of this comparison, however.

Although avian evidence for differential mortality between sedentary individuals and wanderers is scarce (but see Tompa 1962; Carrick 1963; Jenkins et al. 1963, 1964, 1967; cf. Catterall et al. 1989), mammalian nomads are known to suffer high mortality (see Errington 1943, 1963; Beer and Meyer 1951; Hawkins et al. 1971; Gaines and McClenaghan 1980, p. 184–185; Packard and Mech 1980, Andelt 1985). Nomadic individuals lack intimate knowledge of an area, a fact that may be disadvantageous (Brown 1963). In addition to lacking stable food resources, nomads can also be more vulnerable to predation. In experimental studies, Metzgar (1967) and Ambrose (1972) found that in rodents similar otherwise, those unfamiliar with their environment (experimentally induced transients) sustained higher predation rates by owls than sedentary individuals. Physically degraded transients might show a higher mortality rate than sedentary conspecifics in good condition (Gaines and McClenaghan 1980, p. 185), but this is not the only reason for observed differential mortality; nomads are not always physically inferior to sedentary individuals (Metzgar 1967, Ambrose 1972). Environmental unfamiliarity may have been the reason for the different flushing behaviors observed when tracking Wood Thrushes. The benefits of familiar surroundings may be a factor in the season-to-season site fidelity often seen in sedentary (in many cases territorial) birds, both on the breeding and wintering grounds.

A legitimate question, given this apparent mortality imbalance, is whether wanderers declined over the season. If we suppose that all residents (i.e., sedentaries) should be captured after 21 days of netting (an arbitrary figure) and

that new captures after that are mostly nonterritorial, or wanderers, it appears that this category continues to decline significantly (Table 4, case B). What this means is uncertain. It could mean: (1) that wanderers are dying; (2) that wanderers are leaving the area (facultative migration, *sensu* Terrill and Ohmart 1984); (3) wanderers are finding suitable vacant space and are becoming sedentary, or (4) that *nortes* are not as severe later in the season, causing fewer birds to seek refuge in the lowlands. None of these possibilities need be occurring exclusively. Although wandering Wood Thrushes appear to be disadvantaged, practicing this strategy is not immediately detrimental: three were tracked for 2 weeks, and individuals assignable to the wanderer class were present throughout the season.

Subcutaneous lipids. The physical status of wandering Wood Thrushes seemed very similar to that of sedentary birds. In fact, wanderers had higher subcutaneous fat deposits than sedentaries, which is commonly regarded as a "superior" condition (Rappole and Warner 1976, Real and Caraco 1986). We hypothesize that the ultimate reason for the larger fat deposits of wanderers was their uncertain food supply. Survival when dependent upon an insecure food source probably necessitates the practice of storing energy when food is available. A similar reasoning was followed by Rappole and Warner (1980, p. 380-384) in comparing the fat deposits of a variety of species to the social systems of those species. They saw fat deposition as an adaptation to anticipate energy stress. They made the prediction and presented evidence that fat levels should be higher in species subsisting on resources clumped in space and time than in species whose resources are evenly distributed. The Wood Thrush data suggest that this prediction also holds within a single population.

THE FUNCTION OF WINTER TERRITORIALITY

Unlike territories held for breeding purposes, where reproduction is the primary concern, the wintering territories of nearctic migrant passerines are probably held for survival value. Holding a suitable nonbreeding territory has in some cases been demonstrated to confer a survival advantage (e.g., Jenkins et al. 1964, Dhondt 1971). In the territorial systems of wintering migrants it appears that the resource being defended is food, but familiarity with an area might also increase the probability of survival.

Migrants defending territories on their wintering grounds have been considered under the light cast by territorial theory developed primarily from temperate breeding ground research (e.g., Rappole and Warner 1980, Price 1981). Although studies of true nonbreeding territorial systems are few (as opposed to systems in which territories are held during the nonbreeding season on the breeding grounds), evidence suggests that territorial theory has wide applicability in nonbreeding systems (e.g., Schwartz 1964; Rappole and Warner 1976, 1980; Kodric-Brown and Brown 1978; Myers et al. 1979; Davies and Houston 1981; Price 1981; Morton et al. 1987). Basic similarities probably exist among populations in which individuals defend resources and the space these resources occupy (e.g., the unifying concept of economic defendability; Brown 1964). These similarities apparently constitute a sufficient basis for considering nonbreeding territorial systems under the rubric of a general body of territorial theory.

Brown (1969, p. 294) proposed that populations on their breeding grounds could be classified into three critical density levels, based on how territoriality affects individual distribution. As population size increases, individuals are forced to utilize less suitable habitats, until, at level 3, all habitats suitable for breeding are taken by territorial individuals, and a nonbreeding surplus is left over for which space is unavailable (breeding-ground floaters). Brown's (1969) critical density model, together with the more rigorous but similar Fretwell-Lucas ideal despotic model (Fretwell and Lucas 1970, Fretwell 1972), seems applicable to populations that are territorial during the nonbreeding season. Both of these models predict that habitats of lower suitability will be occupied when population demands exceed the amount of available space/resources in preferred habitats. Further, Brown (1969) predicts the occurrence of a nonterritorial class at peak, or level 3 densities.

Because many Wood Thrushes appear to (1) use habitats that undergo intolerable fluctuations in suitability, and (2) often use a nonterritorial strategy, we accept these models as a valid conceptual paradigm in which to consider this nonbreeding territorial population. In addition, we tentatively accept Brown's (1969) critical density level 3 as a valid descriptor of wintering Wood Thrush densities in Los Tuxtlas.

Nomadic individuals in this population appear to be at a disadvantage when compared to

sedentary conspecifics. Our data (cf. Rappole et al. 1989) are among the first for territorial systems of nonbreeding migrants, and further research is needed to ascertain the degree of this disadvantage. If further work supports the application of the above models to nonbreeding migrants, however, our data imply a mechanism for winter population regulation in territorial nonbreeding migrants. It is clear that further examination of the applicability of these models to populations of territorial wintering migrants is necessary. In particular, it must be demonstrated that nonterritorials adopt the wandering strategy as a forced choice due to the presence of territorial conspecifics. Removal experiments will be crucial to this demonstration.

Through removals of territorial individuals, presumable nonterritorials have been shown to occupy vacancies rapidly and become territorial. Numerous studies have demonstrated the presence of these nonterritorials (critical density level 3) on the breeding grounds (reviewed by Klomp 1972, Stutchbury and Robertson 1985). Thus far, however, comparable evidence from the wintering grounds of migrants is scarce. Rappole and Warner (1980) reported seven removal experiments in four species resulting in the occupancy of the vacated area by presumed floaters. Morton et al. (1987) performed removal experiments in wintering Hooded Warblers (*Wilsonia citrina*), but were uncertain of the behavioral status of territorial replacements. We found (unpubl. data) three similar instances in the Wood Thrush after accidental removal (death) of territory holders (only one of these birds, no. 1778, had a transmitter; the other two were deemed territorial based upon capture, recapture, and/or resighting records). In each case, the vacancy was occupied, but it was uncertain whether the occupants were neighbors expanding their home ranges or former wanderers.

Winter population regulation? It is apparent from this study that two wintering strategies exist in the wintering population of Wood Thrushes that we studied: sedentary (most of which are probably territorial) and wanderer (most of which are probably not territorial). The wanderer class may be disadvantaged through a higher rate of predation, but this study has demonstrated neither the degree of this disadvantage nor the factor(s) causing wanderers to adopt this strategy. In addition, although these data, together with those presented in Rappole et al. (1989), appear

to provide a mechanism for winter population regulation, we have not shown that this mechanism occurs as a result of territorial spacing, only that it occurs in a territorial system. Proximately, it seems that this mechanism is not starvation, as Price (1981) implied it should be in a system in which food is defended, but predation. Individual strategies of resource exploitation frequently reflect predation factors, however (Pulliam and Caraco 1984). Ekman (1984) found that although the proximate factor contributing to wintering Willow Tit (*Parus montanus*) mortality was predation, this predation was ultimately a consequence of intense competition for food.

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APPENDIX. Data from 85 specimens collected as winter residents in Los Tuxtlas during 1973-1974 and 1974-1975. Skins are housed in the Bell Museum of Natural History, Minneapolis, Minnesota. Numbers in parentheses are the number of specimens for which data were available.

Presence (P) or absence (A) of wing bars (70):					
HY			AHY		
P	?	A	P	?	A
11	8	5	6	8	32
Age*:					
			HY	AHY	
All winter (70):			24 (34%)	46 (66%)	
Pre-25 February (57):			23 (40%)	34 (60%)	
Sex (82):					
Male		Female			
59 (72%)		23 (28%)			
Stomach contents (26):					
Seeds ^b		Fruit	Arthropods		
11 (42%)		5 (19%)	16 (62%)		

* Due to progressing ossification, a more reliable age ratio is obtained by using the 57 specimens collected before 25 February.
^b Probably fruit seeds.