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ABUNDANCE, FEEDING BEHAVIOR, AND BODY CONDITION OF NEARCTIC WARBLERS WINTERING IN VENEZUELAN MANGROVES

GAETAN LEFEBVRE,[1] BRIGITTE POULIN,[1] AND RAYMOND MCNEIL[1]

ABSTRACT.—We studied the winter ecology of the Northern Waterthrush (*Seiurus noveboracensis*), Prothonotary Warbler (*Protonotaria citrea*), and American Redstart (*Setophaga ruticilla*) in tropical mangroves of northeastern Venezuela. Data were collected by mist netting, direct observation, and forced regurgitation. These allowed evaluation of the seasonal variations in bird abundance, site attachment, body mass, molt activity, and the foraging behavior and diet of each species. The migrant populations consisted of floaters and site-attached individuals throughout the winter, although their abundance showed different seasonal patterns. Most birds used mangroves during only a fraction of the wintering period. Prothonotary Warbler and Northern Waterthrush abundance differed considerably between the spring and fall migration periods, suggesting that different migratory routes are used during both seasons. The temporal and spatial distribution of Prothonotary Warblers and American Redstarts differed according to sex and/or age classes. The mean body mass of Northern Waterthrushes and Prothonotary Warblers varied significantly throughout the winter. Molt activity was limited mainly to body feathers. Foraging in the flooded mangrove habitat was accompanied by modifications of the feeding behavior of each species. *Received 11 Oct. 1991, accepted 20 Jan. 1992.*

Nearctic migrant warblers spend two-thirds of their annual cycle in tropical or subtropical habitats (Keast 1980). For most species, the general distribution and habitat associations on their wintering grounds have been reasonably well documented (Holmes et al. 1989, Terborgh 1989). On the other hand, few studies have quantified the various components of the winter ecology of Nearctic warblers (Rappole et al. 1983, Greenberg 1986, Holmes et al. 1989, Terborgh 1989). This topic is, however, essential in ascertaining the role of these migrant species in Neotropical avian communities (Greenberg 1984) as well as in understanding the demographic variations observed at temperate latitudes (Holmes et al. 1989).

This paper describes feeding behavior and temporal fluctuations in abundance, site attachment, sex ratio, body mass, and molt activity of the Northern Waterthrush (*Seiurus noveboracensis*), the Prothonotary Warbler (*Protonotaria citrea*), and the American Redstart (*Setophaga ruticilla*), three abundant warblers wintering in the coastal mangroves of northeastern Venezuela (McNeil 1982). The warblers' spatial and social behaviors will be discussed in another paper. Our knowledge of the ecology of these species in the winter quarters is still limited to some fragmentary

[1] Dépt. de sciences biologiques, Univ. de Montréal, C.P. 6128, Succ. "A", Montréal H3C 3J7, Canada.

results (Schwartz 1964, Lack and Lack 1972, Diamond et al. 1977, Post 1978, Bennett 1980, Morton 1980, Rappole and Warner 1980, Holmes et al. 1989). Moreover, few studies were conducted in mangroves (Bennett 1980), a habitat highly threatened by tropical deforestation (Terborgh 1989), and one of the most widely used over the wintering period by the warbler species under study (Barruel 1968, Edwards 1972, Lack and Lack 1972, ffrench 1973, Meyer de Schauensee and Phelps 1978, Morton 1980, Hilty and Brown 1986). We attempted to answer the following questions: During which portion of the wintering period is the mangrove habitat exploited? Are the mangroves used consistently by floaters and site-attached individuals? For sexually dimorphic species, is there any difference in the migration pattern according to sex? What physiological constraints (fat accumulation, molt activity) affect the birds in winter? What is the diet of each species on the wintering grounds? Finally, in a flooded habitat such as the mangroves, is the feeding behavior similar to that reported from other tropical habitats?

STUDY AREA AND METHODS

This study was carried out in three coastal mangroves in the state of Sucre, in northeastern Venezuela. The Chacopata site (10°41'N, 63°47'W) was located in a coastal lagoon while the sites of Chiguana (10°29'N, 63°45'W) and Muelle de Cariaco (10°29'N, 63°45'W) were situated on the north and south shores, respectively, of the Gulf of Cariaco. The climate is tropical, with mean monthly temperatures ranging from 19.5° to 32.3°C. Average annual rainfall is 915 mm, with a severe dry season from late November to mid-May. The mangroves were flooded daily by tides except during a three-week period in March when the ground dries out completely. Data were collected from December 1984 through December 1985 in Chacopata and Chiguana, and from September 1986 through August 1987 in Chiguana and Muelle de Cariaco, by mist-netting, direct observation, and forced regurgitation.

Mist-netting sessions were carried out at two-week intervals (each month in Chacopata) on a 4- to 5-ha plot of black mangrove (*Avicennia germinans*). Twelve to fourteen mist nets (3 × 14 m, 32-mm mesh) were set up 50 m apart on two transects in 1984–1985, while 23 mist-nets were erected 25 m apart in 1986–1987. Mist-nets were operated from sunrise to sunset, with a break in early afternoon, for two consecutive days in 1984–1985 and one day in 1986–1987. The trapping effort included 2016, 4704, and 4968 net-h in Chacopata, Chiguana, in 1984–1985 and 1986–1987, and Muelle de Cariaco, respectively.

During mist-netting sessions, all birds were marked with a numbered aluminium band, weighed with a Pesola balance to the nearest 0.25 g (in 1984–1985 only), and examined to determine their age (juvenile or adult), sex, and molt activity. The sex was not determined in Northern Waterthrushes, due to the absence of sexual dimorphism in the plumage coloration (Pyle et al. 1987). Prothonotary Warblers were classified in two categories, adult males and dull plumaged individuals (adult females and individuals in first-year plumage): males were distinguished from females and juveniles by the nape coloration contrasting with that of the back (Pyle et al. 1987). For the American Redstart, all individuals were sexed, and the age of males was also noted (adult or individual in first winter plumage): adult males had a plumage coloration quite different from females, while juvenile males were slightly different from adult females, the orange-yellow colored patches along the breast contrasting

with the yellow underwing coverts (Pyle et al. 1987). The primary molt was evaluated, using the numerical system developed by Ashmole (1962), and that of rectrices by means of the percent of tail feathers in molt. The body-feather molt was determined on a semi-quantitative scale from 0 to 2 (0 = no feather molting, 1 = few, 2 = many) for the wing coverts, back and abdominal regions, leading to a cumulative value ranging from 0 to 6.

A total of 576 h of observation, regularly scheduled, were carried out in the Chiguana site over both years. For each individual observed, we noted the general foraging methods, the foraging heights (0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8 and 8–10 m), and the foraging sites, divided into four categories: ground, water (water surface, pneumatophores and partially immersed fallen trees), vegetation (foliage and twigs), and air. All observations were made on randomly selected individuals within a period of two minutes to maximize the number of individuals observed.

Each month, birds were forced to regurgitate by administering potassium antimony tartrate (1.5% solution, administered at 0.8 ml per 100 g body mass) following Tomback's (1975) method. This part of the study was carried out 150 m from the Chiguana site to avoid any disruption of migrant populations. Food items (arthropods) regurgitated were counted and identified to order.

We evaluated the biweekly abundance of each warbler species, distinguishing "floaters" (individuals captured only once and never observed thereafter) from "stable" individuals (banded birds observed or recaptured at least once over the same wintering period). The latter were considered present for the entire period between the first and last date of their captures, and their seasonal variations in abundance corresponded to the fluctuations in the number of individuals "present." Only the sites sampled in 1986–1987 were used for that part of the study. The data from 1984–1985 covered two incomplete wintering periods, and it was thus impossible to evaluate accurately fluctuations in the abundance of stable individuals. To determine if bird abundance varied significantly throughout the winter, the biweekly evaluations of total abundance and of the number of floaters and stable individuals were compared to a uniform distribution (G-test for goodness of fit). When floaters and stable individuals showed significant temporal variations, both abundances were compared by a G-test.

RESULTS

Seasonal variations in abundance.—The Northern Waterthrush was the most abundant warbler in the study area, followed by the Prothonotary Warbler and the American Redstart. Each species represented 75%, 20% and 5% of the captures, respectively (Table 1).

Northern Waterthrushes were present in the mangrove sites from early September through early May (Fig. 1), with their abundance varying significantly over that period ($G = 421.3$, df = 16, $P < 0.01$). The number of individuals increased rapidly during September, reached maximum values from mid-October to early February, then gradually decreased until the departure in May. The abundance of stable individuals followed the same general pattern, but they arrived a month later (early October) and were not numerous until early November. Seasonal variations of floaters differed significantly from those of stable individuals ($G = 111.6$, df = 16, $P < 0.01$); floaters were present throughout the winter but slightly more abundant from October to February.

Prothonotary Warblers were captured from early September through

TABLE 1
ABUNDANCE, BODY MASS, AND FORAGING SITE FOR EACH WARBLER SPECIES

	Northern Waterthrush	Prothonotary Warbler	American Redstart
Abundance (number of individuals captured)			
Chacopata	80	12	2
Chiguana (1984–1985)	191	63	13
Chiguana (1986–1987)	121	34	6
Muelle de Cariaco	329	122	39
Body mass			
Number of individuals weighed	391	135	15
Mean body mass (g)	15.86	13.06	8.05
Confidence interval ($P < 0.05$)	0.14	0.17	0.74
Foraging site			
Number (%) of observations for each category			
Vegetation	52 (17)	179 (99)	243 (51)
Ground	117 (38)	1 (1)	0
Water	136 (45)	0	0
Air	0	0	229 (49)
Number of individuals observed	129	32	49

mid-March (Fig. 1), and their abundance varied significantly over that period ($G = 86.6$, df = 12, $P < 0.01$). The number of individuals increased rapidly from early September through October, decreased markedly from November to December, then remained constant until early February, and quickly dropped off thereafter. Both floaters and stable individuals were present during most of the winter but showed different temporal variations in abundance ($G = 26.9$, df = 13, $P < 0.01$). Abundance of stable individuals was high and regular from early October through early February, while floater abundance was much more variable, the disappearance of a high proportion of these individuals being responsible for the drop observed in the middle of the wintering period.

American Redstarts, present from mid-September through mid-April (Fig. 1), were also characterized by significant temporal variations in abundance ($G = 32.9$, df = 13, $P < 0.01$). Their abundance increased gradually until mid-December, then slowly decreased until early April. Floaters were the primary cause of these temporal variations, as the biweekly abundance of stable individuals did not differ significantly from a uniform distribution ($G = 20.3$, df = 13, $P > 0.05$).

Age/sex ratios.—In American Redstarts, females comprised about 85% of all individuals, while two-thirds (6/9) of the males observed were in

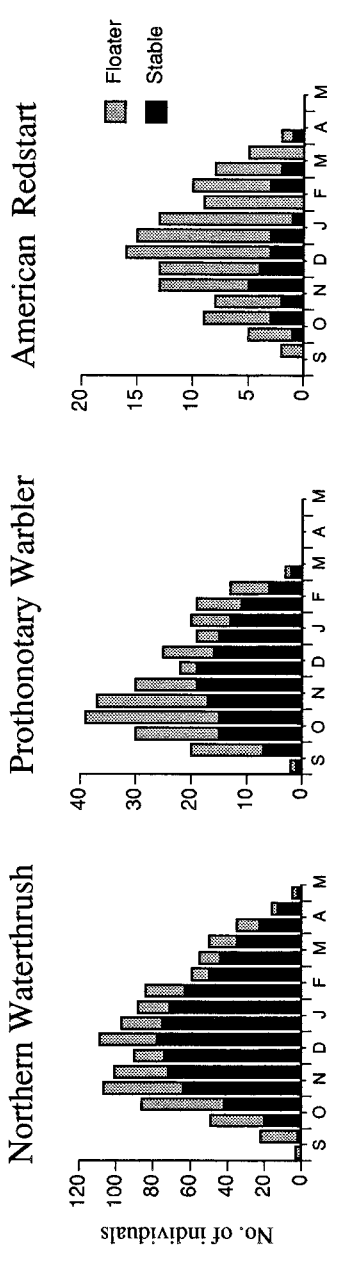

FIG. 1. Seasonal variations in the abundance of floaters and stable individuals of Northern Waterthrushes, Prothonotary Warblers, and American Redstarts in 1986–1987.

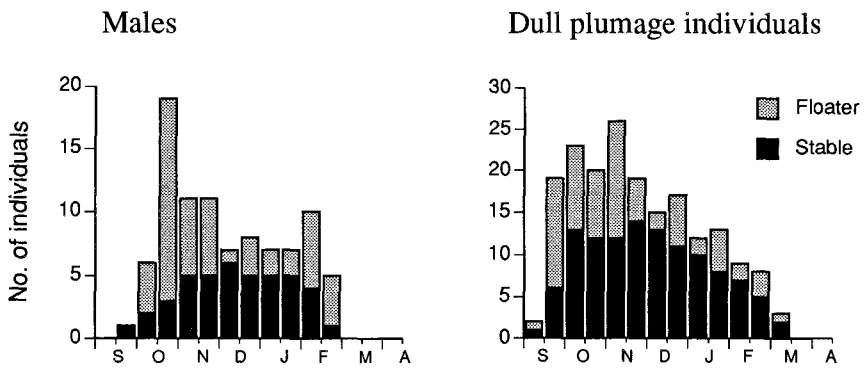

FIG. 2. Seasonal variations in the abundance of floaters and stable individuals among males and dull plumaged individual Prothonotary Warblers (females and juveniles) in 1986–1987.

first-year plumage. In Prothonotary Warblers, 61% of the population was composed of dull plumage individuals, i.e., females and juveniles. The abundance of both types of individuals differed significantly over time ($G = 30.5$, df = 13, $P < 0.01$). Indeed, dull plumage individuals began arriving in early September and were already abundant by mid-September, while adult males arrived in mid-September, with a distinct peak occurring in mid-October (Fig. 2).

Variations in body mass.—We evaluated the mean body mass of each species, using all captured and recaptured birds (Table 1). Temporal variations in body mass were determined only for the Northern Waterthrush and the Prothonotary Warbler (Fig. 3), as few data were available for the

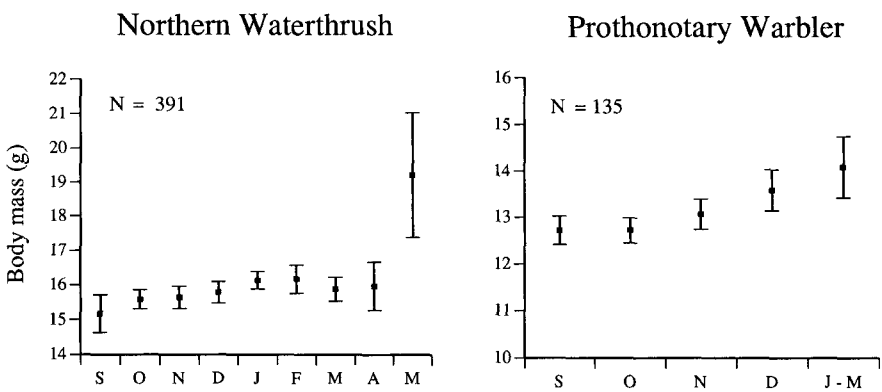

FIG. 3. Mean body mass and confidence interval ($P < 0.05$) of Northern Waterthrushes and Prothonotary Warblers over the wintering period in 1984–1985 (J–M = January through March).

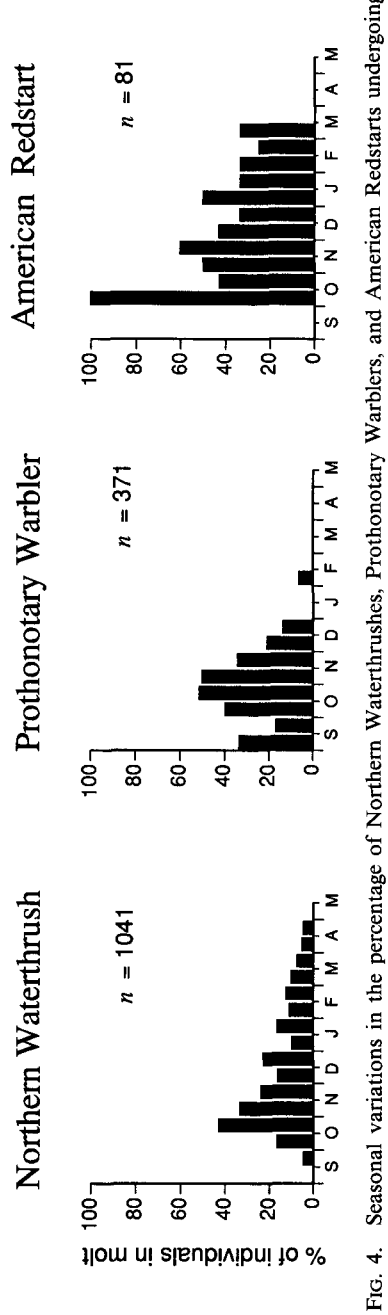

FIG. 4. Seasonal variations in the percentage of Northern Waterthrushes, Prothonotary Warblers, and American Redstarts undergoing body-feather molt.

American Redstart. In Northern Waterthrushes, the mean monthly body mass did not vary significantly from October through April ($F = 2.07$, df = 6,292, $P = 0.056$). Over that period, individuals were significantly heavier than in September ($t = 2.58$, df = 381, $P < 0.05$) and significantly lighter than in May ($t = 6.07$, df = 361, $P < 0.01$). In Prothonotary Warblers, the mean monthly body mass remained constant from September though November ($F = 1.88$, df = 2,100, $P = 0.157$) and from December through March ($t = 1.31$, df = 31, $P = 0.200$, between December and the January–March period), being significantly lower over the first period ($t = 4.65$, df = 134, $P < 0.01$). Although the proportion of floaters was greater during the period of lower body mass in both species, these individuals were not responsible for declining weights. No significant difference was found between the mean body mass of floaters and stable individuals (Northern Waterthrush: $t = 0.470$, df = 296, $P = 0.478$; Prothonotary warbler: $t = 0.712$, df = 115, $P = 0.639$).

Molt.—Primary molt was observed in four warblers only (less than 0.5 % of individuals) and was probably related to the replacement of accidentally lost feathers. Rectrice molt was occasionally observed (in 4% to 7% of individuals). The body-feather molt was, however, regularly noted in many individuals, although each species showed a slightly distinct molt pattern (Fig. 4). In Northern Waterthrushes, the body-feather molt was observed in 19% of individuals and occurred throughout the winter but primarily from mid-October through late December. In Prothonotary Warblers, the body-feather molt occurred mainly from early September to late December and was noted in 29% of individuals. In American Redstarts, the body-feather molt occurred over most of the wintering period and was noted in 38% of the birds. Although body-feather molt was observed over several months in all three species, molt intensity remained low, with nearly 70% of molting individuals having only a few body feathers molting in a single body region.

Diet and feeding behavior.—The three warbler species varied greatly with respect to their diets (Table 2), foraging heights (Fig. 5) and foraging sites (Table 1). The diet of the Northern Waterthrush consisted mainly of Coleoptera, insect larvae, and Hymenoptera (ants), found mostly (85%) from 0 to 1 m above the ground. Some eight insect taxa were occasionally taken, in addition to Araneae, Gasteropoda and Decapoda. The Northern Waterthrush foraged predominantly in aquatic sites, perching on fallen trees (49%) or pneumatophores (51%), and picking up prey either on these substrates or near the water surface. Ground and foliage were less frequently used as foraging sites.

Prothonotary Warblers fed mostly on Coleoptera, Lepidoptera, insect larvae, Hymenoptera (ants), and Araneae, found primarily (60%) from 1

TABLE 2
DIET OF EACH WARBLER SPECIES

Arthropod taxa	Number (%) of food items taken[a]		
	Northern Waterthrush	Prothonotary Warbler	American Redstart
Odonata	2 (0.3)	0	1 (1.8)
Orthoptera	16 (2.1)	1 (1.0)	3 (5.3)
Isoptera	3 (0.4)	0	0
Heteroptera	29 (3.9)	0	2 (3.5)
Homoptera	23 (3.1)	7 (7.1)	17 (29.8)
Neuroptera	2 (0.3)	0	0
Coleoptera	287 (38.2)	42 (42.4)	21 (36.8)
Lepidoptera	5 (0.7)	16 (16.2)	2 (3.5)
Diptera	10 (1.3)	2 (2.0)	5 (8.8)
Hymenoptera	105 (14.0)	10 (10.1)	1 (1.8)
Insect larvae	182 (24.2)	12 (12.1)	3 (5.3)
Araneae	38 (5.1)	9 (9.1)	2 (3.5)
Gasteropoda	35 (4.7)	0	0
Decapoda (*Uca thayeri*)	14 (1.9)	0	0

[a] Number of emetic samples: Northern Waterthrush, 113; Prothonotary Warbler, 39; American Redstart, 15.

to 3 m above the ground. This species foraged in vegetation, using short hops, and captured prey by gleaning almost exclusively on foliage and twig substrates.

The diet of the American Redstart differed from that of the other species by the regular occurrence in its diet of Homoptera and Diptera in addition to Coleoptera. More than 70% of individuals foraged higher than 3 m above the ground. This species fed by gleaning in vegetation as well as by aerial hawking.

DISCUSSION

The Northern Waterthrush inhabits the mangroves throughout the winter, with a higher abundance from October to February. In September, only a few floaters are present. The lower mean body mass observed at this period is similar to that reported in Panama (Rogers and Odum 1966) and in Belize (Mills and Rogers 1990) for postmigrant individuals. From early October, the species abundance rapidly increases, and subsequently the migrant population consists of many site-attached individuals and a few floaters. For most birds, the mangrove study area did not represent the only winter quarters as, in early February (i.e., two months before the onset of the spring migration period in Venezuela, Schwartz 1964), many individuals left the study area without apparent fat accumulation, the mean body mass remaining constant over that period. Neither were the

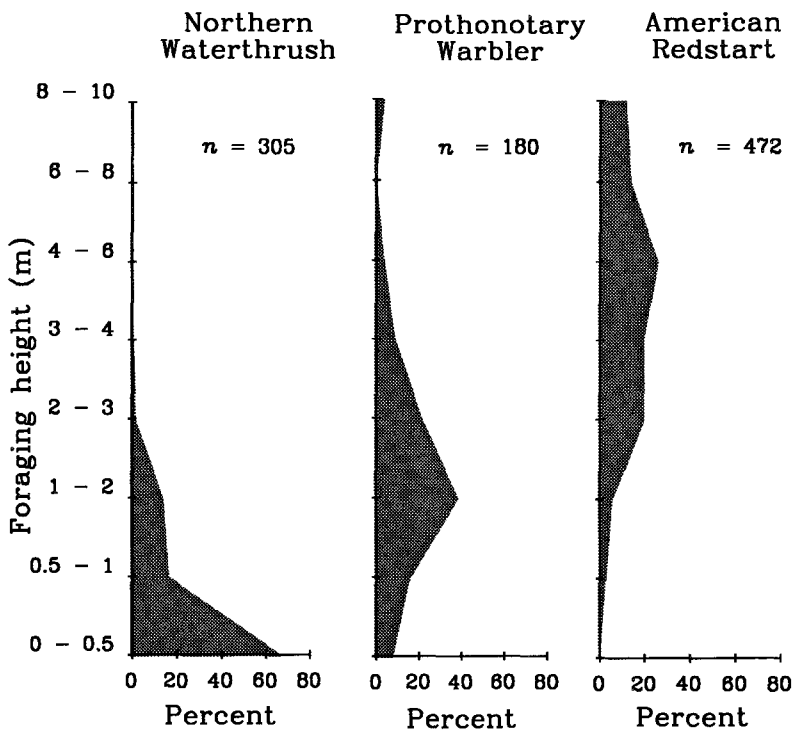

FIG. 5. Percent of Northern Waterthrushes, Prothonotary Warblers and American Redstarts at each foraging height.

mangroves used as transitory migration site in spring, as only a few individuals then were present and undertook the spring migration with a high mean body mass. These results differ greatly from those of Schwartz (1964) for an urban park in Caracas, Venezuela, where most floaters were observed in early winter, and where most site-attached individuals left the area after mid-April. These differences are probably linked to artificial irrigation in those parts of the park where Northern Waterthrushes concentrated from January through the end of the wintering period (Schwartz 1964).

In mangroves, the Northern Waterthrush feeds mostly on Coleoptera, insect larvae, and ants found at the water surface, on the ground, on pneumatophores, on fallen tress, or occasionally in foliage at lower elevations. Thus, a high variety of foraging sites and substrates were used by this species. These results differ from those reported in other tropical habitats (Schwartz 1964, Willis 1966, Post 1978, Rappole and Warner 1980) where the Northern Waterthrush foraged almost exclusively on the

ground. The body-feather molt occurs throughout the winter, but predominantly from October through December.

Some Prothonotary Warblers were present throughout the winter while others used the mangroves during the first half of the wintering period only. Most adult males arrive one month after dull plumage individuals, suggesting some sex and/or age class differences in the fall migration pattern. Many floaters and stable individuals inhabit the mangroves in early winter, a period during which birds undergo body-feather molt and have a significantly lower mean body mass. After the disappearance of a high proportion of floaters in mid-November, the species abundance remains constant until the synchronous departure of all birds in mid-February. These seasonal variations seem contrary to those observed in Colombia (Orejuela et al. 1980, Russell 1980) where the Prothonotary Warbler is present from November through March (Orejuela et al. 1980), with a higher abundance at the end of this period (Russell 1980). Consequently, some individuals wintering in Colombia could have previously passed through Venezuela.

In the mangroves, the Prothonotary Warbler feeds on a great variety of insects, mostly Coleoptera, captured on foliage and twig substrates at low and mid-elevations. The feeding behavior noted in this study (types of prey taken, foraging site and method) are similar to those reported from xeric habitats in Puerto Rico (Post 1978). Only the exploitation intensity of some vertical strata differed: in comparison with Post's (1978) results, the 0 to 1 m stratum was less frequently used in mangroves (24 vs 38%), while the 2 to 3 m stratum was more regularly exploited (21 vs 8%).

For the American Redstart, the coastal mangroves of Venezuela represent a transitory site, primarily used in the middle of the wintering period by a low number of females. The few individuals present in early and late winter suggest that other wintering sites are used then. These could include xeric habitats of western Venezuela, where the American Redstart is present predominantly during the first half of the wintering period (Bosque and Lentino 1987).

In the mangroves, as well as in xeric habitats of Puerto Rico (Faaborg 1984), the proportion of females among the American Redstart population is very high. This suggests a segregation of sexes on the wintering grounds through geographic distribution or habitat association. Nevertheless, the mangrove habitat is not always occupied predominantly by females; mangroves in Jamaica are frequented equally by both sexes (Holmes et al. 1989).

Over the wintering period, the American Redstart undertakes a partial body-feather molt and feeds mostly on Coleoptera, Homoptera, and Dip-

tera captured in the foliage and in the air at high elevations. The foraging height noted in this study differs from those reported by Post (1978) and Bennett (1980) for various Neotropical habitats, including black mangroves. These variations are probably due to the differing foliage height profiles as, in all cases, the American Redstart primarily exploits the subcanopy strata. The foraging methods observed in this study (gleaning and aerial hawking) correspond to those previously reported for this species on the wintering grounds (Post 1978, Bennett 1980).

The Northern Waterthrush, Prothonotary Warbler, and American Redstart differed considerably in their winter ecology. For all three species, the coastal mangroves of Venezuela probably represent a crucial overwintering habitat. Although most birds used the mangroves during only a fraction of the wintering period, they showed some adaptability to mangrove features. Complementary studies of the winter ecology of these warblers on a larger geographic scale and habitat range would be necessary for ascertaining migrant population dynamics and behavioral plasticity of warblers on wintering grounds.

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LITERATURE CITED

ASHMOLE, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. Ibis 103:235–273.

BARRUEL, P. 1968. Birds of Surinam. Oliver and Boyd, Edinburgh, United Kingdom.

BENNETT, S. E. 1980. Interspecific competition and the niche of the American Redstart (*Setophaga ruticilla*) in wintering and breeding communities. Pp. 319–335 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Inst. Press, Washington, D.C.

BOSQUE, C. AND M. LENTINO. 1987. The passage of North American migratory land birds through xerophytic habitats on the western coast of Venezuela. Biotropica 19:267–173.

DIAMOND, A. W., P. LACK, AND R. W. SMITH. 1977. Weights and fat condition of some migrant warblers in Jamaica. Wilson Bull. 89:456–465.

EDWARDS, E. P. 1972. A field guide to the birds of Mexico. E. P. Edwards, Sweet Briar, Virginia.

FAABORG, J. 1984. Population size and philopatry of winter resident warblers in Puerto Rico. J. Field Ornithol. 55:376–378.

FFRENCH, R. 1973. A guide to the birds of Trinidad and Tobago. Livingston Publishing Company, Wynnewood, Pennsylvania.

GREENBERG, R. 1984. The winter exploitation systems of Bay-breasted and Chestnut-sided warblers in Panama. Univ. California Publ. Zool. 116:1–107.

———. 1986. Competition in migrant birds in the nonbreeding season. Pp. 281–307 *in* Current ornithology; Vol. 3 (R. J. Johnston, ed.). Plenum Press, New York, New York.

HILTY, S. L. AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.

HOLMES, R. T., T. W. SHERRY, AND L. REITSMA. 1989. Population structure, territoriality and overwintering survival of two migrant warbler species in Jamaica. Condor 91:545–561.

KEAST, A. 1980. Migratory Parulidae: what can species co-occurrence in the North reveal about ecological plasticity and wintering patterns. Pp. 457–479 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D. C.

LACK, D. AND P. LACK. 1972. Wintering warblers in Jamaica. Living Bird 11:129–154.

MCNEIL, R. 1982. Winter resident repeats and returns of austral and boreal migrant birds banded in Venezuela. J. Field Ornithol. 53:125–132.

MEYER DE SCHAUENSEE, R. AND W. H. PHELPS. 1978. A guide to the birds of Venezuela. Princeton Univ. Press, Princeton, New Jersey.

MILLS, E. D. AND D. T. ROGERS, JR. 1990. Nearctic passerine fall migration in central Belize. Wilson Bull. 102:146–150.

MORTON, E. S. 1980. Adaptations to seasonal changes by migrant land birds in Panama Canal Zone. Pp. 437–453 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.

OREJUELA, J. E., R. J. RAIT, AND A. HUMBERTO. 1980. Differential use by North American migrants of three types of Colombian forest. Pp. 253–264 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Inst. Press, Washington, D.C.

POST, W. 1978. Social and foraging behavior of warblers wintering in Puerto Rican coastal scrub. Wilson Bull. 90:197–214.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY, AND J. L. RUOS. 1983. Nearctic avian migrants in the Neotropics. U.S. Dept. of the Interior, Fish and Wildlife Service, Washington, D.C.

——— AND D. W. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353–392 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.

ROGERS, D. T., JR. AND E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. Wilson Bull. 78:415–433.

RUSSELL, S. M. 1980. Distribution and abundance of North American migrants in lowlands of northern Colombia. Pp. 249–252 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Inst. Press, Washington, D.C.

SCHWARTZ, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:169–184.

TERBORGH, J. 1989. Where have all the birds gone? Princeton Univ. Press, Princeton, New Jersey.

TOMBACK, D. F. 1975. An emetic technique to investigate food preferences. Auk 92:581–583.

WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187–231.