SEASONAL ABUNDANCE OF MIGRANT BIRDS AND FOOD RESOURCES IN PANAMANIAN MANGROVE FORESTS

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ABSTRACT.—We studied temporal variation in abundance of Nearctic-Neotropical migrants, particularly the Northern Waterthrush (*Seiurus noveboracensis*), Prothonotary Warbler (*Protonotaria citrea*), and American Redstart (*Setophaga ruticilla*) in two black mangrove sites of central Panama from September 1993 through May 1995. The two sites, on the Caribbean and the Pacific coasts, differ importantly in annual rainfall, tide amplitude, and seasonal invertebrate abundance. Most migrant species varied temporally in abundance with the opposite pattern at each site, suggesting mid-winter movements correlated with abundance of food resources. Because of their wide geographic distribution and their particular response to hydrographic factors, mangroves are likely to have a temporally complementary role in sustaining migrant populations throughout the Neotropics. However, variations in migrant numbers reported in other Neotropical habitats could also reflect large-scale movements by migrants. Occurrence of mid-winter (facultative) migration has been documented mostly for the Palearctic-African migratory system, and needs to be investigated in the Nearctic-Neotropical realm for proper conservation of migratory species. *Received 17 Nov. 1995, accepted 16 April 1996.*

During the non-breeding period, Nearctic-Neotropical migrants generally use a succession of habitats. Movements between habitats are known to occur during the autumn and spring migrations, but most migrant populations are presumed to be spatially stable between these two periods (Rappole et al. 1993). Nonetheless, large variations in migrant abundance suggest that these movements occur throughout the non-breeding period in several Neotropical habitats (Galindo et al. 1963; Morton 1980; Emlen 1980; Hilty 1980; Johnson 1980; Orejuela et al. 1980; Greenberg 1984, 1992a; Blake and Loiselle 1992; Lefebvre et al. 1992; Sherry and Holmes 1996; Wunderle 1995). Although movements by migratory landbirds during the nonbreeding period have never been investigated in detail, a few lines of evidence suggest that they could be related to food abundance (e.g., Terrill and Ohmart 1984, Greenberg 1992a, Lefebvre et al. 1994b).

Mangrove forests are known to support high numbers of insectivorous migrants in several Neotropical regions (Russell 1980, Lynch 1989, Wunderle and Waide 1993, Lefebvre et al. 1994b). In particular, the Northern Waterthrush (scientific names in Table 1), the Prothonotary Warbler, and the American Redstart have been observed in mangroves of Mexico (Hutto 1980, Lynch 1989), Panama (Morton 1980), Colombia (Russell 1980),

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TABLE 1

NUMBER OF OBSERVATIONS OF EACH MIGRANT SPECIES AT TWO MANGROVE SITES

Species	Galeta (Atlantic)	Juan Diaz (Pacific)
Prothonotary Warbler (*Protonotaria citrea*)	200	222
Northern Waterthrush (*Seiurus noveboracensis*)	190	181
American Redstart (*Setophaga ruticilla*)	8	20
Black-and-white Warbler (*Mnioltila varia*)	13	7
Red-eyed Vireo (*Vireo olivaceus*)	17	1
Yellow Warbler (*Dendroica petechia*)	4	11
Chestnut-sided Warbler (*D. pensylvanica*)	9	0
Summer Tanager (*Piranga rubra*)	8	0
Tennessee Warbler (*Vermivora peregrina*)	5	2
Eastern Wood-pewee (*Contopus virens*)	4	2
Acadian Flycatcher (*Empidonax virescens*)	3	0
Canada Warbler (*Wilsonia canadensis*)	0	3
Blackpoll Warbler (*D. striata*)	1	1
Northern Oriole (*Icterus galbula*)	2	0
Golden-winged Warbler (*Vermivora chrysoptera*)	0	1
Blackburnian Warbler (*D. fusca*)	1	0
Bay-breasted Warbler (*D. castanea*)	0	1
Cerulean Warbler (*D. cerulea*)	0	1
Worm-eating Warbler (*Helmitheros vermivorus*)	1	0

Venezuela (Lefebvre et al. 1994b), and the West Indies (Arendt 1992, Wunderle and Waide 1993). Variation in species abundance and the birds' short length of stay (Lefebvre et al. 1992, 1994a) suggest that at least some individuals of these species undertake large movements during the nonbreeding period.

Mangroves are widely distributed in the Neotropics and often support more migrants than nearby terrestrial habitats (Hutto 1980, Lynch 1989, Wunderle and Waide 1993, Poulin et al. 1994). One possible explanation is that flooded habitats such as mangroves are buffered from the effect of rainfall seasonality and the resulting marked fluctuations in arthropod availability (Morton 1980, Lefebvre et al. 1994b, Sherry and Holmes 1996). Food available in mangroves is, however, likely to vary geographically and with latitude through the differing salinity and inundation patterns at each locality (Duke 1990, Lefebvre and Poulin, in press). Therefore, migrant species that use mangroves extensively as a wintering habitat could move between mangrove forests to take advantage of these temporal variations in food resource.

In this paper we compare the seasonal abundance of Nearctic-Neotropical migrants from two Panamanian black mangrove forests experiencing

different hydrographic conditions. In particular, we attempt to answer the following questions: Do migrant populations show large variation in abundance during the nonbreeding season? Are the two mangrove sites used differentially through time by migrants? Is variation in migrant abundance related to the abundance of food resources at each site?

STUDY AREAS AND METHODS

Study areas.—We carried out this study in two coastal mangrove forests 65 km apart in central Panama from September 1993 to May 1995. These were Juan Diaz (9°00'N, 79°04'W) on the Pacific coast and Galeta (9°20'N, 79°09'W) on the Caribbean coast. Each study site was 4.5 ha of black mangrove (*Avicennia germinans* L.) with red (*Rhizophora mangle* L.) and white (*Laguncularia racemosa* L.) mangroves comprising around 30%. Annual rainfall in Galeta (3244 mm) averages nearly twice that in Juan Diaz (1786 mm). The two sites also differ importantly regarding mean tidal range, with a value of 24 cm for Galeta and 395 cm for Juan Diaz. Both sites, however, experience a dry season of similar intensity from January to April which coincides with the period of lowest high tides (Lefebvre and Poulin, in press).

Bird abundance.—Migrant abundance was evaluated during observation sessions twice monthly from September 1993 through May 1994. To eliminate any short-term temporal bias, the two sites were sampled on two consecutive days. At each site, observations were carried out at 18 spot counts located 50 m apart along two transects. Starting at sunrise, we surveyed each spot for 10 min, and noted every new bird seen within 25 m.

Invertebrate abundance.—Abundance of invertebrates, the main food resource available to passerines in mangroves (Lefebvre et al. 1994b), was estimated during each observation session. The first 2 m of vegetation were swept with a standard insect net in late morning during 15 min. Sweep-netted invertebrates were preserved in 70% ethanol and sorted using a dissecting scope. Each invertebrate was identified to order or family and categorized as small (≤0.5 mm) or large (>0.5 mm). Sub-adult forms of insects were assigned either to eggs or larvae without taxonomic distinction.

Bird diet.—We determined diets of migrants through regurgitation sessions during two non-breeding seasons. We sampled sites alternately twice monthly so that regurgitations were collected during each calendar month at each site. Twelve mist-nests (10 m × 3 m, 32-mm mesh) were operated from dawn until early afternoon. Some 452 migrants from 14 species were captured and administered tartar emetic following the method of Poulin and Lefebvre (1995). Diet samples were preserved and sorted using the same methodology as for sweep-net samples.

Food abundance.—Using data from sweep-net and emetic samples, a monthly index of food abundance was calculated as follows:

$$\text{Index of food abundance} = \sum p_i \frac{x_i}{n_i}$$

where p_i is the proportion of a specific arthropod group (taxa/size) in migrants' diet, x_i is the number of arthropods from that group sampled with sweep net during a specific date, and n_i is the total number of arthropods from that group sampled with sweep net. Accordingly, this index reaches a maximal value when several arthropod groups extensively taken by the birds simultaneously show a high abundance.

Statistical analyses.—We used Spearman's correlation rank coefficient to compare temporal abundance in migrants between the two sites. We compared abundance of each ar-

thropod group (taxa/size) between the two sites with contingency tables using *G*-tests. All 18 sweep-net samples collected at each site were combined since they were independent samples without replicate. To determine whether changes in bird abundance between sites were correlated with changes in food abundance between sites, we subtracted bird and food abundances at one site (Juan Diaz) from the other (Galeta) for each sampling date throughout the nonbreeding period and calculated Spearman correlations between the two data sets. Most data were pooled by month in presentation of figures, but all analyses were run on data collected twice each month.

RESULTS

Bird abundance.—Overall, 466 and 453 migrants from 15 and 13 species were observed at Galeta and Juan Diaz, respectively (Table 1). Nine species representing over 95% of all observations were sampled at the two sites. Both migrant communities were dominated by the Prothonotary Warbler and the Northern Waterthrush (Table 1). Most species showed large variations in abundance with a different temporal trend at each site (Fig. 1). Abundances of the Northern Waterthrush at Galeta and Juan Diaz were inversely correlated from October through March (r_s = −0.713, df = 10, P < 0.01), with higher numbers on the Pacific coast in early winter and on the Caribbean coast in late winter. The Prothonotary Warbler was abundant at both sites from September through January only. In Galeta, its abundance was high in September and gradually decreased during winter, whereas in Juan Diaz it was high and stable from October through January. Abundances of the American Redstart at Galeta and Juan Diaz were negatively correlated from November through March (r_s = −0.792, df = 9, P < 0.05), showing an inverse pattern to the one of the Northern Waterthrush. The remaining 16 migrant species were sampled only occasionally and were clumped in "other" migrant species (Table 1). Their abundances at Juan Diaz and Galeta were inversely correlated from September through May (r_s = −0.566, df = 13, P < 0.05). These migrants were sampled mostly during autumn migration at Juan Diaz and at the end of the wintering period at Galeta (Fig. 1).

Estimation of food resources.—Over 400 diet samples were collected (218 from Juan Diaz and 196 from Galeta), from which 3689 items were identified and assigned to one of 34 invertebrate groups (taxa/size) (Table 2). Over 98% of the invertebrates taken by migrants were from taxa also sampled by sweep net. Some 78% of these invertebrates were present in at least half of the 36 sweep-net samples. In Galeta, migrants fed mostly on small beetles, small ants, large insect larvae, and small spiders, whereas in Juan Diaz small snails, beetles, and ants were the most common invertebrates in migrants' diet (Table 2).

Abundance of food resources.—Between-site comparisons in the index of food abundance show that food resources were more abundant in Juan
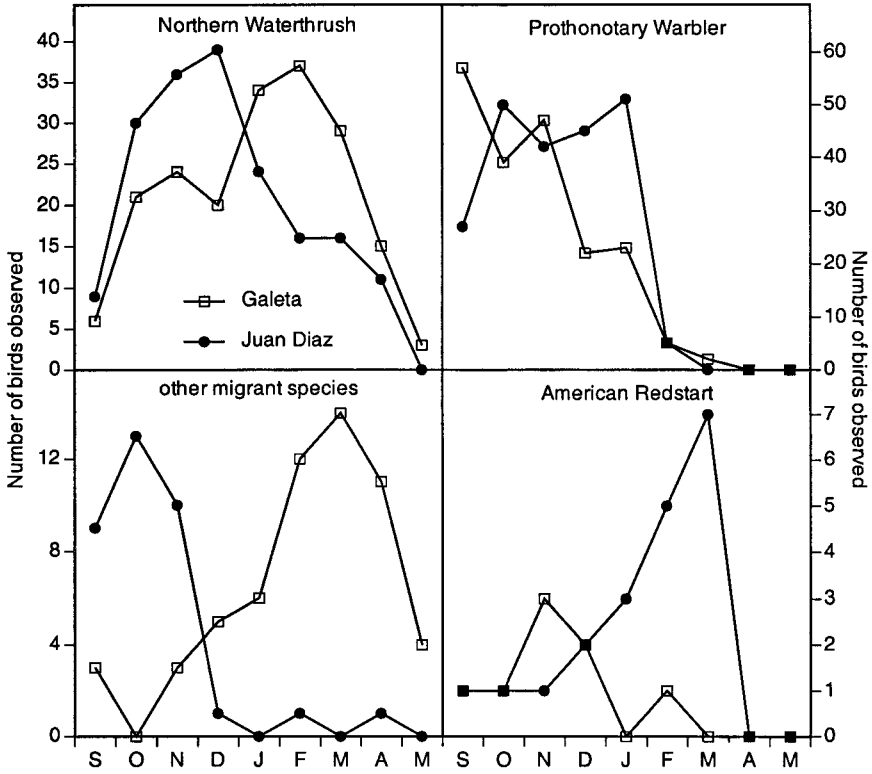
FIG. 1.   Monthly abundance of migrant species at the two study sites.

Diaz from September to December (wet season) and more abundant in Galeta from January to April (dry season) (Fig. 2). Actually, several invertebrate groups (taxa/size) showed a significantly different abundance between the wet and the dry seasons, with an opposite trend at each site (Table 2). In Juan Diaz, nine invertebrate groups representing 53% of all invertebrates sampled were significantly more abundant during the wet season. In Galeta, 13 invertebrate groups representing 63% of all invertebrates sampled were significantly more abundant during the dry season.

Relationships between migrant and food abundance.—Concurrent changes in numbers of Northern Waterthrushes and in the index of food abundance were positively correlated between the two sites (r_s = 0.5772, df = 15, P < 0.05). No such relation was found for the Prothonotary Warbler (r_s = −0.1545, df = 11, P = 0.94) or the American Redstart (r_s = −0.0168, df = 11, P = 0.96). Between-site variations in abundance of

TABLE 2
SEASONAL VARIATION IN SWEEP-NET SAMPLES AND PROPORTION OF EACH INVERTEBRATE-
PREY GROUP IN THE MIGRANT'S DIET

Taxa	Size	Sweep net WS vs DS[a] Galeta	Juan Diaz	Number of items in migrants' regurgitations (%) Galeta	Juan Diaz
Gastropoda (snails)	Small	***	=	65 (4.3)	1089 (49.8)
Gastropoda (snails)	Large	+	++	1 (0.1)	
Pseudoscorpionida	Small	=	=	10 (0.7)	5 (0.2)
Araneida (spiders)	Small	+++	**	127 (8.4)	41 (1.9)
Araneida (spiders)	Large	**	=	53 (3.5)	9 (0.4)
Isopoda	Small	=	*	1 (0.1)	13 (0.6)
Decapoda (crabs, shrimps)	Small	?	?	5 (0.3)	2 (0.1)
Decapoda (crabs, shrimps)	Large	?	?	3 (0.2)	4 (0.2)
Chilopoda (centipedes)	Large	=	?		1 (0.0)
Thysanura (bristletails)	Large	?	?		1 (0.0)
Odonata	Large	=	=	7 (0.5)	
Orthoptera	Small	=	***	5 (0.3)	4 (0.2)
Orthoptera	Large	+++	***	14 (0.9)	7 (0.3)
Dermaptera (earwigs)	Large	?	?		1 (0.0)
Heteroptera (true bugs)	Small	+++	=	15 (1.0)	9 (0.4)
Heteroptera (true bugs)	Large	=	***	8 (0.5)	1 (0.0)
Homoptera (plant bugs)	Small	+++	=	4 (0.3)	88 (4.0)
Homoptera (plant bugs)	Large	+	=	2 (0.1)	4 (0.2)
Coleoptera (beetles)	Small	+++	**	351 (23.4)	385 (17.6)
Coleoptera (beetles)	Large	=	***	13 (0.9)	9 (0.4)
Lepidoptera	Small	+++	=		1 (0.0)
Diptera (flies)	Small	**	**	12 (0.8)	15 (0.7)
Diptera (flies)	Large	=	=	1 (0.1)	2 (0.1)
Hymenoptera (ants)	Small	+++	=	294 (19.6)	321 (14.7)
Hymenoptera (ants)	Large	+++	+++	19 (1.3)	17 (0.8)
Hymenoptera (wasps)	Small	+++	=	87 (5.8)	76 (3.5)
Hymenoptera (wasps)	Large	+++	**	18 (1.2)	2 (0.1)
Insect eggs	Small	+++	+++	72 (4.8)	59 (2.7)
Insect eggs	Large	=	=	2 (0.1)	
Insect larvae	Small	+++	+++	42 (2.8)	13 (0.6)
Insect larvae	Large	=	=	266 (17.7)	7 (0.3)
Fishes	Large	?	?	5 (0.3)	
Frogs	Large	?	?		1 (0.0)
Lizards	Large	?	?	1 (0.1)	

[a] Comparison (*G*-tests) in numbers of sweep-netted invertebrates from the wet (WS; September through December) to the dry (DS; January through April) season. Increase: + (*P* < 0.05), ++ (*P* < 0.01), +++ (*P* < 0.001); no significant change: =; decrease: * (*P* < 0.05), ** (*P* < 0.01) *** (*P* < 0.001); ?: not sampled.
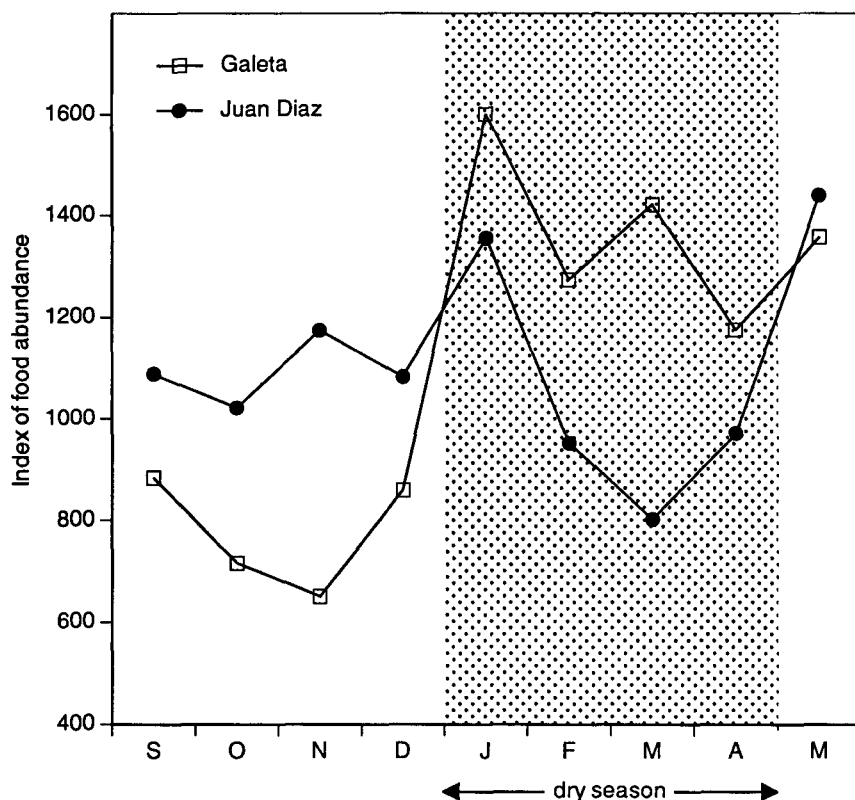
FIG. 2.   Monthly variation in the index of food abundance at the two study sites.

other migrant species was positively correlated with between-site varia-
tions in the index of food abundance (r_s = 0.7815, df = 15, P < 0.001).

DISCUSSION

The two mangrove sites were used by a similar number of migrant
birds. However, all species, with the exception of the Prothonotary War-
bler, showed an opposite abundance pattern at the two sites. We do not
pretend that these variations were related to bird movements from one
mangrove site to another (no bird was captured at both sites), but our
data suggest that the two mangrove sites have a temporally complemen-
tary role in sustaining migrant populations during their stay in central
Panama.

Because of the differing tide and inundation patterns, rainfall season-
ality affects differently the invertebrate fauna at the two mangrove sites

(Lefebvre and Poulin, in press). As a result, invertebrate abundance was higher in Pacific mangroves during the first part of the wintering period (wet season) and higher in Caribbean mangroves during the second part of the wintering period (dry season). This pattern was found in several groups of arthropods, including the ones frequently taken by the migrant species.

Between-site variations in abundance of Northern Waterthrushes were synchronised with between-site variations in food abundance. This species used extensively one mangrove only when food resources were proportionally more abundant than at the other, and its abundance at any site was low when food resources were proportionally less abundant.

Within and between site variations in abundance of Prothonotary Warblers were not correlated to abundance of food resources. This species was present only during the first part of the nonbreeding season when resources were relatively stable at both sites. However, the Prothonotary Warbler showed a different abundance pattern at the two sites, potentially reflecting differences in food abundance. In Juan Diaz, where resources were more abundant, the Prothonotary Warbler showed a high and uniform abundance. The departure of most individuals in February occurred when food abundance decreased sharply. In Galeta, where food resources were less abundant, abundance of Prothonotary Warblers decreased throughout the nonbreeding period.

The abundance pattern of the American Redstart suggests movements among mangrove patches, but these were not correlated with food abundance. This was especially notable at Juan Diaz, where bird abundance increased drastically during the dry season when resource abundance was low. The few regurgitation samples collected for this species show that the American Redstart, in contrast to other wood warblers, feeds extensively on small homopterans and insect eggs (76% of all food items taken). Small homopterans were more abundant in Juan Diaz than in Galeta (total in sweep-net samples: 422 vs 713, $G = 75.4$, df $= 1$, $P < 0.001$), even considering only the dry season when homopteran abundance increased in Galeta but remained stable in Juan Diaz (274 vs 377, $G = 16.4$, df $= 1$, $P < 0.001$). Small insect eggs were one of the few arthropod groups more abundant in the dry than the wet season at Juan Diaz.

The other migrant species showed large variations in abundance with an opposite pattern at each site. These species were predominantly found on the Pacific side during southward migration and on the Caribbean side during northward migration, which was positively correlated with variation in food resources at the two sites.

Large variations in migrant abundance occur in Panamanian man-

groves. Our data suggest that they are related to mid-winter movements associated with variation in food availability. The proximity of the Atlantic and Pacific coasts in Panama allowed the sampling of two mangrove sites experiencing different hydrographic conditions within a short range, but the variations observed in migrant abundance could conceal bird movements on a larger geographical scale. In coastal mangroves of Venezuela, the same warblers species exhibit large variations in abundance during the non-breeding period (Lefebvre et al. 1992). Because of their wide geographic distribution in the Neotropics and their particular response to hydrographic factors, mangroves are probably more likely to support large scale movements of migratory birds than other Neotropical habitats. However, and regardless of the fact that few studies have investigated seasonal variation in migrant abundance throughout the nonbreeding season, important changes in migrant numbers have been reported in grassland (Greenberg 1992a), pine forest (Emlen 1980), lowland second-growth forest (Blake and Loiselle 1992), lowland dry forest (Orejuela et al. 1980, Greenberg 1984, Sherry and Holmes 1996), lowland wet forest (Greenberg 1984), second-growth low mountain wet forest (Wunderle 1995), and low mountain wet forest (Johnson 1980) habitats. While these variations are often assumed to be associated with mortality or local habitat shifts, they could potentially reflect bird movements on a wide geographic distance. Nearctic-Neotropical migrants are more numerous and exploit a greater variety of winter habitats in the northern Neotropics (Terborgh and Faaborg 1980, Pashley and Martin 1988, Rappole et al. 1993) and are less numerous and more selective in their habitat choice farther south (Pearson 1980, Bosque and Lentino 1987, Wunderle and Waide 1993). Several studies carried out in the West Indies (Emlen 1980, Sherry and Holmes 1996, Wunderle 1995) and Central America (Galindo et al. 1963, Blake and Loiselle 1992, Greenberg 1992a) have reported a decrease in migrant abundance over the non-breeding season, whereas some habitats in South America support an increasing number of migrants throughout winter (Johnson 1980, Hilty 1980, this study). Considering the important changes occurring in food resources between the wet and the dry seasons in most Neotropical habitats (Poulin et al. 1992, Sherry and Holmes 1996), quality of the foraging microhabitat is likely to vary during the nonbreeding season. A migration in mid-winter could then represent an advantageous strategy for several migrant birds.

These migrations during the non-breeding period could correspond to facultative migrations which are directly in response to changes in environmental conditions and may or may not occur in any given year (Berthold 1975, Terrill 1990). Such migrations have been observed in long distance Palearctic insectivorous migrants (Gwinner et al. 1988, Wood

1979) and short distance Nearctic insectivorous migrants (Terrill and Ohmart 1984) experiencing an important decrease in food resources. Cage experiments have demonstrated that between fall and spring migrations, some insectivorous long distance migrants react to food shortage by night activity (*Zugunruhe*), similar to that observed during the obligatory migration phase (Terrill and Ohmart 1984, Gwinner et al. 1988). Actually, several lines of evidence suggest a much higher potential for extensive winter movement by migrants than has generally been considered to be the case (Curry-Lindahl 1981, Gwinner 1990, Terrill 1990).

Examples of winter site tenacity by migrants are numerous in the Neotropics (see Rappole and Warner 1980). However, the proportion of individuals exhibiting site tenacity within a species often varies among habitats (Greenberg 1984, Sherry and Holmes 1996, Wunderle 1995) and years (Emlen 1980, Greenberg 1992a, Wunderle 1995), potentially reflecting mid-winter migration by some individuals in response to a decrease in foraging microhabitat quality. Understanding seasonal changes in population and resource use is critical in providing efficient management policies for migratory birds (Greenberg 1992b, Sherry and Holmes 1995). Occurrence of multiple stage migrations has been documented, mostly for the Palearctic-African migratory system, and need to be investigated in the Nearctic-Neotropical realm for proper conservation of migrant species.

ACKNOWLEDGMENTS

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