TEMPORAL DYNAMICS OF MANGROVE BIRD COMMUNITIES IN VENEZUELA WITH SPECIAL REFERENCE TO MIGRANT WARBLERS

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ABSTRACT.—We studied bird phenology and abundance patterns relative to rainfall, ground inundation, and food abundance in three mangrove sites of northeastern Venezuela over two complete annual cycles. Bird abundance, breeding and molting activities were assessed through mist-netting sessions scheduled twice monthly. At the same frequency, food abundance was evaluated through the percentage of trees bearing flowers, and by sweep-netting arthropods. The birds' breeding season occurred from the mid-dry to the mid-wet seasons and was linked to the abundance of some arthropod taxa including caterpillars. The higher abundance of arthropods and the presence of breeding activities during the dry season suggest that environmental factors are less limiting in mangroves than in adjacent arid habitats. The abundance of most birds, grouped according to their diet and frequency of mangrove use, varied significantly over time. Many species from other habitats exploited the mangroves in the late-wet and dry seasons to take advantage of a higher food abundance and to join mixedspecies flocks. Abundance of Nearctic migrants was correlated with the abundance of several arthropod taxa, and diet analyses suggest that these birds feed opportunistically on seasonal abundant arthropods during their stay in mangroves. Received 3 March 1993, accepted 17 November 1993.

ALTHOUGH MANGROVES are widely distributed along the littoral in tropical and subtropical zones (Chapman 1977), our knowledge of mangrove bird communities is still mainly limited to species lists (e.g. Cawkell 1964, Haverschmidt 1965, Nisbet 1968) that sometimes are supplemented with abundance indices (Tostain 1986, Altenburg and van Spanje 1989).

Several investigations have demonstrated that the seasonal pattern of rainfall in the tropics affects the periodicity of food resources, influencing thereafter bird phenology and abundance patterns (e.g. Karr 1976, Levey 1988, Poulin et al. 1992, 1993). Flooded habitats such as the mangroves may show a distinct seasonality in food abundance (Portillo and Ezcurra 1985, Altenburg and van Spanje 1989), but we still ignore the degree to which bird abundance and phenology in mangroves differ from those of the nearby vegetation.

Various studies in Africa (Cawkell 1964, Altenburg and van Spanje 1989), Asia (Nisbet 1968) and the Neotropics (Haverschmidt 1965, ffrench 1966, Esquivel et al. 1986) show that the mangrove avifauna is partially composed of migrant species from the temperate zone. The role of migrants among mangrove bird communities remains poorly known. For tropical habitats in general, many authors (Emlen 1980, Keast 1980, Rappole and Warner 1980, Stiles 1980, Fitzpatrick 1982, Rappole et al. 1983, Morton 1992) consider that the winter assemblages of migrants and residents represent fully integrated ecological communities, while resident species do not fill the available niche space after the migrants leave. In contrast, others (Morel and Bourlière 1962, Willis 1966, Blondel 1965, Leck 1972, Karr 1976, Post 1978, Hutto 1980) suggest that the lack of competition between migrants and residents results from the exploitation by migrants of food resources unexploited by residents due to their irregular temporal or spatial distributions. Finally, some authors concluded that migrants compete with residents by limiting their breeding season (Terborgh and Faaborg 1980) or by promoting population movements (Lack and Lack 1972, Terborgh and Faaborg 1980).

Our study reports on the temporal dynamics (breeding, molt, and abundance) of avian communities in three mangrove sites of northeastern Venezuela. This is the first study quantifying simultaneously bird phenology and abundance, food resources, and environmental factors on a year-round basis in tropical man-

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groves. Because mangrove sites are largely exploited by some Nearctic warblers (Lefebvre et al. 1992a), attention will be drawn to the role of migrants among avian communities. In particular, we will attempt to answer the following questions: Are food abundance pattern and bird phenology in mangroves similar to those of adjacent habitats? Which factors govern the reproductive activities? What is the effect of rainfall, ground inundation, and food-abundance periodicity on bird phenology and abundance? How integrated are migrant species among avian communities through the kind of food resources they exploit?

METHODS

Study area.-This study was carried out in three mangrove sites on the Araya Peninsula, in the State of Sucre, northeastern Venezuela. The site of Chacopata (10°41'N, 63°47'W) is located in a coastal lagoon, whereas the sites of Chiguana (10°29'N, 63°45'W) and Muelle de Cariaco (10°29'N, 63°45'W) are situated, respectively, on the north and south shores of the Gulf of Cariaco. Each study site corresponds to a 4.5to 5.5-ha plot of monospecific black mangrove (Avicennia germinans). Mangroves are isolated from the nearby arid vegetation by a mudflat zone 100 to 400 m wide with a vegetation height increasing gradually from 1 to 10 m. Two distinct zones were observed: one consisting of sparsely distributed, low and stubby (0 to 3 m) trees and shrubs; and the other formed of denser and more stratified vegetation (3 to 10 m) with an extensive ground cover of pneumatophores. Data were collected from December 1984 through December 1985 at Chacopata and Chiguana, and from September 1986 through August 1987 at Chiguana and Muelle de Cariaco. Our results will be compared to those of Poulin et al. (1992, 1993) obtained over the same period in a thorn scrub, thorn woodland, thorn forest, and deciduous forest (i.e. the main plant formations in region; Sarmiento 1972).

Field methods.—Variation in bird abundance, breeding periodicity, and primary-molt activity were evaluated through mist-netting sessions carried out twice monthly (monthly in Chacopata) along two transects separated by 50 m in the denser and more stratified vegetation (3–10 m). From 12 to 14 mist nets (3×14 m, 32-mm mesh) were set 50 m apart in 1984–1985, while 23 mist nets were erected every 25 m 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. Such a methodology led to a total trapping effort of 2,016, 4,704, 4,968 and 4,968 net-hours at the sites of Chacopata in 1984–1985, Chiguana in 1984–1985 and 1986– 1987, and Muelle de Cariaco in 1986–1987, respectively. During mist-netting sessions, birds were marked with a numbered aluminum band, aged, and examined for the presence of primary molt and brood patch. Juveniles were identified by plumage character and by the presence of yellow tomial flanges. Juveniles of Bicolored Conebills (*Conirostrum bicolor*), with a plumage differing from that of adults during a complete annual cycle, were considered separately from other species. Primary wing molt was evaluated using the numerical classification developed by Ashmole (1962) where: (0) old feather; (1 to 4) growing feather; and (5) new full-length feather. Birds with scores of 1 to 49 (1 to 44 in the Emberizidae) were considered to be actively molting.

Social behavior of birds, particularly the presence of flocks, was evaluated during observation periods at Chiguana, at a frequency of six mornings per month, totalling 576 h of observation over both years. These flocks correspond to the aggregations described by Powell (1985) as groupings formed incidentally when individuals are drawn together by environmental factors such as resource patches.

The birds' diet was evaluated by forcing over 500 individuals from 33 species to regurgitate using potassium antimony tartrate (Poulin et al. 1994a). Regurgitation sessions were conducted monthly during both years in dense mangrove stands at 500 m from the mist-netting site of Chiguana to avoid any disruption in bird phenology and abundance patterns.

Rainfall data were obtained from the meteorological station of Cariaco, located at 10 km from the sites of Chiguana and Muelle de Cariaco, and 50 km from Chacopata. In 1986–1987, ground inundation was evaluated twice monthly in Chiguana and Muelle de Cariaco. Flood level, or the maximum height of tide, was noted using a permanently installed rule in the deeper zone of the mangrove.

Food abundance was evaluated twice monthly at the netting sites of Chiguana and Muelle de Cariaco from September 1986 through August 1987. Flower abundance of Avicennia germinans was evaluated through the approximate percentage (10% intervals) of individuals bearing flowers along mist net lanes. Fruit abundance was not assessed because Avicennia pods are not consumed by passerines (Cawkell 1964). Arthropod abundance was evaluated by sweep netting the first 3 m of vegetation during 10 min in late afternoon. Although this method does not evaluate absolute abundance of arthropods, it is quite useful to determine seasonal fluctuation in abundance of foliage-dwelling arthropods (Janzen 1973). Captured arthropods were identified to the taxonomic order, counted, and assigned to size classes (small, ≤ 5 mm; large, >5 mm). Larvae of each size class were grouped together: small larvae were represented by various taxa, whereas the larger ones were mainly composed of caterpillars. Sweep-netted arthropods should be a good estimate of the birds' prey abundance: relative abundance of the different arthropod taxa captured was significantly correlated ($r_s = 0.56$, n = 22, P < 0.01) with that found in emetic samples.

Data analysis.-To simplify among-site comparisons and reveal general trends, bird species were grouped according to feeding category and regularity and intensity of mangrove use. Insectivorous species were categorized into one of four groups: (1) resident insectivores (RI), species regularly captured over annual cycle; (2) migrant insectivores (MI), Nearctic migrants captured during winter only; (3) seasonal insectivores (SI), Neotropical species regularly captured during only fraction of annual cycle; and (4) occasional insectivores (OI), those captured sporadically over year (this group also may include resident species exploiting canopy). Species that potentially are consumers of nectar were divided in two groups: (1) trochilid nectarivores (TN); and coerebid nectarivores (CN; including only the Bananaquit, Coereba flaveola). The final three groups, represented by fewer individuals, correspond to granivores (G; Emberezinae, Columbidae), piscivores (P; Coraciidae), and nest parasites (NP; Shiny Cowbird, Molothrus bonariensis). None of the species recorded was defined as frugivorous (i.e. consuming fleshy fruits) in mangroves.

G-tests were used to compare variations in abundance of birds from the same group of species at different sites. A G-test for goodness of fit to a uniform distribution was used to evaluate if bird monthly abundance was significantly variable over time.

A canonical correspondence analysis (CCA; program CANOCO; ter Braak 1986) was used to evaluate the relationships between abiotic factors (rainfall, ground inundation), food abundance, reproductive activities, and the monthly abundance of the different groups of species over the year. The data from 1986-1987 (period during which all environmental variables were sampled) were used for this analysis. CCA is a multivariate technique that can be used to identify an environmental basis for community ordination by detecting the patterns of variation in species abundance that can be best explained by environmental variables. In the resulting ordination diagram, species and samples (dates in this case) are represented by points, and environmental variables are represented by arrows. For interpretation of the resulting diagram, only the direction and relative lengths of arrows convey information. Each arrow determines a direction or axis in the diagram, obtained by extending the arrow in both directions. From each point, one can drop a perpendicular to the axis to evaluate the relative influence of the environmental variables on bird abundance.

RESULTS

Mangrove phenology.—The study areas are located in a tropical semi-arid region with an average annual rainfall of 915 mm and a severe

-0-Precipitations during the study Mean precipitations (1967-1987) -0 Ground inundation 25 160 Rainfall (mm) 80 inundation 20 (Cm 10 40 5 . n 0 Flowers 80 Arthropods aroup 1 ____ Number 400 Arthropods group 2 flowers Arthropods group 3 ₫ 60 300 Percent of plants with sweep-netted arthropods 40 200 20 100 ٥ F N D Μ S J Α Μ Dry season -----> ₼

Fig. 1. Monthly variation in abiotic factors and food resource abundance for all sites combined. Arthropod groups refer to the cluster diagram in Figure 2.

dry season from late November to mid-May receiving 25% of the total precipitation (cumulative data 1967–1987). In 1984–1985 and 1986– 1987, annual rainfall was 992 and 857 mm, respectively, with a normal periodicity except for June which appeared drier than usual (Fig. 1). Ground inundation was quite seasonal, varying similarly to the rainfall pattern, with a season of low tides from January through April (Fig. 1).

Food abundance showed a marked periodicity over the year (Fig. 1). Flowers were observed during the dry season only (December to May), particularly in January and February. Arthropod taxa showing a similar temporal pattern in abundance were grouped using a completelinkage clustering (Legendre and Legendre 1984). Three groups resulted from the cluster analysis (Fig. 2): (1) mainly small arthropods (Coleoptera, Hymenoptera, Diptera, Orthoptera, Araneae and larvae), with maximal abundance from August to January, and minimal abundance from April to June (Fig. 1); (2) primarily large arthropods (Neuroptera, Homop-



Fig. 2. Cluster diagram between arthropod taxa sampled by sweep net in 1986–1987 based on their temporal variation in abundance. Groups indicated by bolder lines.

tera, Diptera and Araneae), abundant during dry season (December–March); (3) Lepidoptera adults, large Hymenoptera and large larvae (almost exclusively caterpillars), abundant in first half of wet season (June–August).

Among bird communities, breeding activity of all resident species occurred from the middry to the mid-wet season. Adults with a brood patch were observed from January through August, but primarily at the end of the dry season (May) and at the beginning of the wet season (July) (Fig. 3). Juveniles (excluding Bicolored Conebills) were abundant in June and August (i.e. a month after each main period of broodpatch observations; Fig. 3). This one-month shift agrees with the length of the incubation and nestling periods observed in various species from semi-arid habitats of Ecuador (Marchant 1960) and from flooded savanna of Venezuela (Cruz and Andrews 1989), suggesting that juveniles really came from the study sites. Primary molt was observed year-round in at least 5% of individuals, but predominantly during the first months of the wet season from June through September (Fig. 3).

Juvenile Bicolored Conebills were more abundant in the dry season (December-April), when they sometimes represented 15% of all captures (Fig. 3). They were frequently observed as members of unstable mixed-species flocks among which were seen 27 of the 70 species captured at Chiguana. During the period of maximal abundance of juvenile Bicolored Conebills, flocking species accounted for nearly 40% of all birds observed, compared to 24% for the rest of the year. During the breeding season, the abundance of those juveniles remained stable, while birds molting to an adult plumage were gradually replaced by new juveniles.

Bird-abundance variation.—A list of all species captured and their group membership are presented in the Appendix. The Yellow Warbler (Dendroica petechia), represented in the study areas by both Nearctic migrants and Neotropical residents, was considered as a Neotropical resident due to the difficulty of defining the subspecies in females (Wiedenfield 1992) and the low number of migrant males. Monthly abundance variation of the different groups of species, calculated based on 150 net-hours (nearly the monthly trapping effort at Chacopata), are presented in Figure 4. Temporal variation in abundance of all groups were found to be similar among years and sites (SI, $G_{33} = 45.9$; OI, $G_{33} = 29.7$; MI, $G_{33} = 6.4$; TN, $G_{33} = 41.5$; G, G_{33} = 22.1; CN, $G_{22} = 23.7$; P, $G_{22} = 9.7$; all ns), except for resident insectivores ($G_{33} = 115.8$, P < 0.05). The resident insectivores showed no significant temporal variation at Chiguana in 1986-1987 $(G_{11} = 11.5, \text{ ns})$, but overall peaked twice due to significant increases from December through February at Chacopata ($G_{11} = 53.8, P < 0.05$), and from July through September at Muelle de Cariaco ($G_{11} = 72.0, P < 0.05$). The abundance of seasonal insectivores varied significantly over time ($G_{11} = 62.7, P < 0.05$), with a low from May through November (wet season), and a high from December through April (dry season). Occasional insectivores showed a regular abundance over the year ($G_{11} = 5.8$, ns). Abundance of migrant insectivores, nectarivores and granivores varied significantly over time (MI, $G_{11} =$ 569.7; NC, $G_{11} = 36.0$; NT, $G_{11} = 33.2$; G, $G_{11} =$ 31.8; all P < 0.05). Migrant insectivores increased rapidly in September to reach a high in October, and decreased more or less gradually until their disappearance in June. Among nectarivores, coerebids were abundant from November through March (dry season), whereas trochilids were abundant from April through November (wet season). Granivores were abundant during the wet season (June–November) only. The few nest parasites were almost exclusively present from May through July. Piscivores showed no significant variation in abundance over time ($G_{11} = 14.7$, ns), but were less abundant when ground inundation was minimal (January–April).

Bird abundance in relation to rainfall, ground inundation, food abundance, and breeding.—We selected 9 variables for CCA: monthly rainfall, ground inundation, flower abundance, arthropod abundance (all three groups), abundance of birds with a brood patch, abundance of juveniles of Bicolored Conebills, and abundance of juveniles of other species. Bird data correspond to the monthly abundance of each group of species at each of both sites sampled in 1986-1987 (granivores, piscivores, and nest parasites from both sites were combined given the low numbers). The CCA explained 93% of the variance of the data set, 81% of which was accounted for by the first two axes.

The orientation of environmental variables and their relationships with date positions on the diagram reflect well the mangrove phenology (Fig. 5). Flowering activity coincides with a period of low rainfall. Adult birds with a brood patch and juveniles are linked to the May-to-September period. Arthropods from group 1 are linked to the late wet season (October-November). Two groups of arthropods were totally opposed: group 2 is associated with a period of low rainfall (December-March), while group 3 is linked to the early wet season (June-August). Abundance of juvenile Bicolored Conebills differed greatly from that of other juveniles and is linked to the February-May period.

The diagram shows that the temporal variations in abundance of most groups of birds are strongly influenced by specific variables (Fig. 5). Migrant insectivores (MI) from both sites are linked to the first two groups of arthropods. Seasonal insectivores (SI) from both sites are associated with a period of low rainfall, and also with arthropods from group 2 and juveniles of Bicolored Conebills. The resident insectivores (RI), occasional insectivores (OI), and piscivores (P) are located near the center of the diagram, suggesting that their abundance is poorly influenced by environmental variables. For nectarivores-insectivores, coerebids (CN) are linked to flowering activity, whereas trochilids (TN)



Fig. 3. Monthly variation for all sites combined in percentage of birds with primary molt, adults with a brood patch, and juveniles.

from Chiguana are associated with arthropods from group 1. Trochilids from Muelle de Cariaco apparently are not influenced by any factor, but this group was poorly represented at this site (Fig. 4). Granivores (G) are linked to rainfall and arthropods from group 3. Nest parasites (NP) are associated with the two avian breeding parameters (brood patches and juveniles).

DISCUSSION

Mangroves from northeastern Venezuela showed a marked temporal dynamic in abiotic factors and abundance of food resources. The rainfall pattern and ground inundation varied similarly, while the dry season coincided with the period of low tides. Flowering activity occurred in the dry season and, probably due to the monospecific character of mangroves, flower production was limited almost exclusively to a few months of the year. Flowering activity during the dry season characterizes various tropical habitats (Janzen 1967, Fodgen 1972, Medway 1972, Ewusie 1980, Opler et al. 1980). However, in tropical regions experiencing an



Fig. 4. Monthly variation in abundance of birds from each group of species at each site.



Fig. 5. Ordination diagram of first two axes of canonical correspondence analysis (CCA). Dates represented by asterisks numbered from 1 to 12 for months of January to December. Bird abundance data from Chiguana (filled squares), Muelle de Cariaco (open squares), or both sites (mid-filled squares). Species group are: (RI) resident insectivores; (SI) seasonal insectivores; (OI) occasional insectivores; (MI) migrant insectivores; (CN) coerebid nectarivores; (TN) trochilid nectarivores; (G) granivores; (P) piscivores; and (NP) nest parasites.

annual rainfall similar to that of the study area (Opler et al. 1980, Lieberman 1982), including the arid habitats adjacent to the study sites (Guevara de Lampe et al. 1992, Poulin et al. 1992), flower abundance generally is minimal during the dry season. A lower arthropod abundance during the dry season also is a common trend in various tropical seasonal habitats (Janzen and Schoener 1968, Fodgen 1972, Janzen 1973, Buskirk and Buskirk 1976), including the nearby vegetation (Poulin et al. 1992). This tendency was observed in several arthropod taxa and especially those from groups 1 and 3. However, in contrast to other habitats, arthropod abundance dropped only at the end of the drought period; in fact, some large arthropods (group 2) were most abundant when precipitation was lowest. Consequently, during the major part of the dry season, mangroves would be similar to

the more humid tropical habitats described by Janzen (1973) as refuges for insects.

The birds' breeding season occurred from the mid-dry to the mid-wet season, and the primary molt in the first half of the wet season. These results differ considerably from those obtained in the thorn scrub, thorn woodland, thorn forest, and deciduous forest of the same region (Poulin et al. 1992), where breeding was limited to the wet season and molt activity (more synchronized among individuals) was almost totally absent in the dry season. Such differences suggest that the severity of the dry season is less limiting in mangroves than in adjacent habitats.

Food abundance, particularly during the dispersion of juveniles, is widely recognized as the main factor governing the timing of the birds' breeding season (Immelmann 1971). Because arthropod abundance was minimal in the mangroves at the onset of the breeding season, reproductive activities are apparently influenced by the abundance of some specific arthropod taxa only, such as Lepidoptera adults, large Hymenoptera, and caterpillars. Monthly abundance of juveniles was further correlated ($r_s =$ 0.64, n = 12, P < 0.05) with caterpillar abundance, a food resource widely exploited for feeding of the young (Busby and Sealy 1979, Poulin et al. 1994b). Accordingly, caterpillar abundance is probably more important than competition with migrants for limiting breeding activity of resident birds. Primary-molt activity took place immediately after breeding, a general trend in the temperate (Payne 1972) and tropical (Snow and Snow 1964, Keast 1968, Diamond 1974, Britton 1978, Prys-Jones 1982) zones.

The abundance of most groups of bird species varied significantly and similarly over time at all three sites. Only resident insectivores showed a distinct pattern between sites, resulting probably from the irregular passage of flocks of Bicolored Conebills; when resident insectivore abundance was higher than average, juvenile Bicolored Conebills represented 51% of the captures, compared to 32% for the rest of the year. Seasonal insectivores were particularly abundant during the dry season when large arthropods and juvenile Bicolored Conebills also were quite abundant. Because 86% of the seasonal insectivore species were also captured in adjacent arid habitats (Poulin unpubl. data), and that 64% of them were observed among mixedspecies flocks, the temporal dynamic of seasonal insectivores is strongly linked to species coming from other habitats to take advantage of a higher arthropod abundance and flocking behavior in mangroves. The abundance of occasional insectivores was uniform and, apparently, was not influenced by cyclical phenomena. Migrant insectivores, almost absent from adjacent habitats (Poulin et al. 1993), were abundant during the wintering period, primarily from October through January. Their abundance followed that of several arthropod taxa (groups 1 and 2), suggesting that Nearctic migrants adjust their abundance to that of their primary food (these arthropods represented 93% of the migrants' diet). During the wintering period, food exploitation by resident (Bicolored Conebill; Pied Water-Tyrant, Fluvicola pica; Yellowthroated Spinetail, Certhiaxis cinnamomea) and

migrant (Northern Waterthrush, Seiurus noveboracensis; Prothonotary Warbler, Protonotaria citrea; American Redstart, Setophaga ruticilla) gleaning insectivores was similar (based on distribution of food items among 16 different arthropod taxa taken; $G_{w15} = 23.7$, ns), suggesting that migrants depend on seasonal abundant arthropods exploited by resident species as well.

Both groups of nectarivores frequented the mangroves at different periods of the year. Coerebids were abundant during the dry season when flowers were plentiful. Because this resource is minimal during the dry season in adjacent habitats (Guevara de Lampe et al. 1992, Poulin et al. 1992), where the Bananaquit is the most abundant species (Poulin et al. 1993), coerebids probably leave the xeric vegetation to take advantage of a high food abundance in mangroves at this period. In contrast to coerebids, trochilids were rare during the flowering period in mangroves and, in Chiguana, their abundance was linked to that of small arthropods. Emetic samples further suggest that hummingbirds fed mainly on arthropods in mangroves. Among 21 samples, many contained several small arthropods (for total of 196), whereas only three of them had pollen grains.

Various authors (Cawkell 1964, Macnae 1968, Haverschmidt 1965, ffrench 1966, Field 1968, Tostain 1986, Altenburg and van Spanje 1989) have noted the presence of granivorous species in mangroves. It is generally assumed that these birds feed in adjacent habitats, exploiting the mangroves primarily for nesting (Cawkell 1964, Macnae 1968, Altenburg and van Spanje 1989). On our study sites, granivores were present during the wet season only, from June through December, a period during which a nest of the White-tipped Dove (Leptotila verreauxi) was observed. In adjacent habitats, this period corresponds to the breeding season (June-August) and juvenile dispersal (August-December) of granivores (Poulin et al. 1992). Thus, although granivores probably fed on arthropods in mangroves, their abundance pattern coincided with their breeding period in adjacent habitats, suggesting that they also exploit mangroves for nesting.

Finally, the high abundance of the parasitic Shiny Cowbirds from May to July coincided precisely with the breeding season of the Pied Water-Tyrant (Lefebvre et al. 1992b), recognized as one of its preferred hosts in flooded savanna of Venezuela (Cruz and Andrews 1989).

Our results suggest that mangroves from northeastern Venezuela represent a refuge temporarily exploited by various species and this is how these habitats should be considered for conservation purposes (Terborgh 1989). In addition to permanent residents, several bird species exploit the mangroves for breeding or to benefit from periods of high food abundance. Because mangrove phenology differs from that of the nearby vegetation, those exceeding food resources can be exploited by several species from other habitats. Nearctic migrants differ from other seasonal users only by their very high abundance in both the late wet and early dry seasons, a period when the abundance of several arthropod taxa was maximal. The role of Nearctic migrants in mangrove bird communities of northeastern Venezuela, thus, would be similar to that of Neotropical residents that exploit seasonally abundant food.

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APPENDIX. Number of captures and group membership of each bird species sampled at the three mangrove sites. Species name^a followed by number of birds and group membership for: (1) Chacopata, 1984–1985; (2) Chiguana, 1984–1985; (3) Chiguana, 1986–1987; (4) Muelle de Cariaco, 1986–1987.

Common Ground-Dove (Columbina passerina), 7G, 11G, 0, 0; Plain-breasted Ground-Dove (C. minuta), 0, 1G, 0, 0; Whitetipped Dove (Leptotila verreauxi), 0, 1G, 0, 0; Dark-billed Cuckoo (Coccyzus melacoryphus), 0, 0, 0, 0, 3SI; White-tailed Nightjar (Caprimulgus cayennensis), 0, 10I, 0, 10I; Spot-tailed Nightjar (C. maculicaudus), 0, 0, 0, 10I; Rufous-breasted Hermit (Glaucis hirsuta), 0, 2TN, 9TN, 1TN; Buff-breasted Sabrewing (Campylopterus duidae), 0, 1TN, 0, 0; Green-breasted Mango (Anthracothorax prevostii), 6TN, 0, 0, 0; Black-throated Mango (A. nigricollis), 0, 0, 1TN, 1TN; Ruby-topaz Hummingbird (Chrysolampis mosquitus), 0, 1TN, 0, 0; Blue-chinned Sapphire (Chlorestes notatus), 0, 1TN, 0, 0; Blue-tailed Emerald (Chlorostilbon mellisugus), 0, 3TN, 7TN, 2TN; Fork-tailed Woodnymph (Thalurania furcata), 0, 1TN, 1TN, 0; Buffy Hummingbird (Leucippus fallax), 73TN, 36TN, 10TN, 6TN; White-chested Emerald (Amazilia chionopectus), 0, 3TN, 0, 0; Copper-rumped Hummingbird (A. tobaci), 1TN, 60TN, 18TN, 18TN; Speckled Hummingbird (Adelomyia melanogenys), 0, 1TN, 0, 0; Amazon Kingfisher (Chloroceryle amazona), 0, 1P, 0, 1P; Green Kingfisher (C. americana), 0, 25P, 23P, 0; American Pygmy Kingfisher (C. aenea), 0, 8P, 16P, 13P; Russet-throated Puffbird (Hypnelus ruficollis), 0, 501, 601, 201; Rufous-tailed Jacamar (Galbula ruficauda), 0, 0, 101, 101; Red-crowned Woodpecker (Melanerpes rubricapillus), 0, 40I, 40I, 0; Spot-breasted Woodpecker (Colaptes punctigula), 0, 0, 0, 10I; Lineated Woodpecker (Dryocopus lineatus), 0, 201, 201, 0; Yellow-throated Spinetail (Certhiaxis cinnamomea), 0, 49RI, 43RI, 10I; Straight-billed Woodcreeper (Xyphorhynchus picus), 0, 601, 801, 1001; Streak-headed Woodcreeper (Lepidocolaptes souleyetii), 0, 38RI, 30RI, 7SI; Redbilled Scythebill (Campylorhamphus trochilirostris), 0, 10I, 0, 0; Black-crested Antshrike (Sakesphorus canadensis), 0, 0, 0, 5SI; Barred Antshrike (Thamnophilus doliatus), 0, 0, 0, 101; Golden-faced Tyrannulet (Tyranniscus viridiflavus), 0, 101, 0, 0; Southern Beardless-Tyrannulet (Camptostoma obsoletum), 0, 12SI, 2OI, 2OI; Mouse-colored Tyrannulet (Phaeomyias murina), 0, 22SI, 5SI, 285I; Scrub Flycatcher (Sublegatus modestus), 0, 10I, 0, 10I; Forest Elaenia (Myiopagis gaimardii), 0, 0, 10I, 30I; Yellow-bellied Elaenia (Elaenia flavogaster), 0, 101, 0, 101; Small-billed Elaenia (E. parvirostris), 0, 101, 0, 301; Ochre-bellied Flycatcher (Mionectes oleggineus), 0, 0, 10I, 10I; Gray-crowned Flycatcher (Tolmomyias poliocephalus), 0, 0, 20I, 0; Yellow-breasted Flycatcher (T. flaviventris), 0, 15SI, 19SI, 3OI; Fuscous Flycatcher (Cnemotriccus fuscatus), 0, 2OI, 0, 0; Bran-colored Flycatcher (Myiophobus fasciatus), 0, 0, 0, 10I; Tropical Pewee (Contopus cinereus), 0, 0, 0, 10I; Pied Water-Tyrant (Fluvicola pica), 0, 81RI, 62RI, 14SI; Brown-crested Flycatcher (Myiarchus tyrannulus), 10I, 13SI, 11SI, 40I; Great Kiskadee (Pitangus sulphuratus), 0, 40I, 70I, 60I; Social Flycatcher (Myiozetetes similis), 0, 101, 0, 201; Streaked Flycatcher (Myiodynastes maculatus), 0, 6SI, 4SI, 0; Variegated Flycatcher (Empidonomus varius), 10I, 0, 0, 0; Fork-tailed Flycatcher (Tyrannus savana), 10I, 30I, 20I, 20I; Tropical Kingbird (T. melancholicus), 6OI, 1OI, 0, 3OI; Gray Kingbird (T. dominicensis), 21SI, 0, 0, 0; White-winged Becard (Pachyramphus polychopterus), 0, 301, 0, 401; Lance-tailed Manakin (Chiroxiphia lanceolata), 0, 101, 0, 201; Southern Rough-winged Swallow (Stelgidopteryx ruficollis), 0, 1OI, 0, 45SI; Bicolored Wren (Campylorhynchus griseus), 0, 0, 0, 3OI; House Wren (Troglodytes aedon), 101, 801, 1601, 1101; Tropical Gnatcatcher (Polioptila plumbea), 0, 0, 101, 3SI; Bare-eyed Thrush (Turdus nudigenis), 0, 101, 0, 201; Red-eyed Vireo (Vireo olivaceus), 101, 101, 0, 751; Scrub Greenlet (Hylophilus flavipes), 0, 101, 201, 201; Golden-fronted Greenlet (H. aurantiifrons), 301, 101, 0, 0; Tropical Parula (Parula pitiayumi), 0, 0, 101, 0; Yellow Warbler (Dendroica petechia), 19SI, 17RI, 10SI, 13SI; Bay-breasted Warbler (D. castanea), 0, 1MI, 0, 0; Blackpoll Warbler (D. striata), 1MI, 5MI, 3MI, 1MI; American Redstart (Setophaga ruticilla), 2MI, 13MI, 7MI, 61MI; Prothonotary Warbler (Protonotaria citrea), 15MI, 117MI, 45MI, 67MI; Northern Waterthrush (Seiurus noveboracensis), 97MI, 278MI, 187MI, 473MI; Bananaquit (Coereba flaveola), 0, 60CN, 53CN, 5CN: Bicolored Conebill (Conirostrum bicolor), 530RI, 209RI, 137RI, 659RI; Trinidad Euphonia (Euphonia trinitatis), 0, 0, 0, 10I; Glaucous Tanager (Thraupis glaucocolpa), 0, 10I, 10I, 40I; Streaked Saltator (Saltator albicollis), 0, 0, 0, 30I; Gravish Saltator (S. coerulescens), 0, 10I, 0, 10I; Blue-black Grassquit (Volatina jacarina), 0, 2G, 0, 3G; Lined Seedeater (Sporophila lineola), 0, 9G, 10G, 45G; Ruddy-breasted Seedeater (S. minuta), 0, 0, 0, 1G; Black-faced Grassquit (Tiaris bicolor), 0, 2G, 0, 0; Grassland Yellow-Finch (Sicalis Iuteola), 0, 0, 0, 1G; Yellow-hooded Blackbird (Agelaius icterocephalus), 0, 0, 201, 0; Carib Grackle (Quiscalus lugubris), 101, 0, 0, 0; Shiny Cowbird (Molothrus bonariensis) 1NP, 8NP, 1NP, 6NP; Yellow Oriole (Icterus nigrogularis), 0, 601, 701, 301.

^a Nomenclature following AOU (1983) and Phelps and Meyer de Schauensee (1979).