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SOCIAL AND FORAGING BEHAVIOR OF WARBLERS WINTERING IN PUERTO RICAN COASTAL SCRUB

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The foraging behavior and social relationships of the warblers (Parulidae) during the breeding season have been studied extensively by Morse (1967a, 1968, 1971, 1973). Parnell (1969) examined the foraging behavior of migrating warblers. Other than the studies of Eaton (1953) and Lack and Lack (1972) no work has aimed specifically at investigating the ecology of warblers wintering in the tropics. My objectives in the present study were to describe and quantify the social and foraging behavior of parulids wintering in Puerto Rican coastal scrub and where possible to compare their behavior with that reported from other regions. The Puerto Rican study sites were chosen because of the structural simplicity of the vegetation, and the relatively high density of warblers. In addition, the lack of significant predators prompted me to examine the question of what influence this might have on flocking behavior.

STUDY AREA AND METHODS

I conducted the study on El Guayacán Island (35 ha) and on La Cueva Island (20 ha) on the SW coast of Puerto Rico, 2 km SW of La Parguera. These "islands" are peninsular, connected to the mainland by a narrow mangrove forest no more than 100 m wide. Before 1960 both islands were grazed by goats. In 1962 the Puerto Rican government leased the islands to the Caribbean Primate Research Center, which uses them as sites for free-ranging rhesus macaque (*Macaca mulatta*) colonies. High populations of monkeys have been on the island since 1966, and foraging by monkeys has kept the vegetation stunted. Except for a few scattered trees, all vegetation is less than 3.5 m. In addition, the islands are in a severe dry zone. Rainfall is only 35 cm per year (12 yr average for La Cueva Island). Scrubby vegetation predominates: corcho (*Pisonia albida*), oxhorn bucida (*Bucida buceras*), and gumbo-limbo (*Bursera simaruba*) are the dominant trees. Shrubs or small trees are pigeon-berry (*Bourreria succulenta*), *Bumelia* spp., *Lantana involucrata*, dildo (*Cephalocereus royenii*), and pricklypear (*Opuntia rubescens*). This community type is described in detail by Gleason and Cook (1926) as the xerophytic forest of the Ponce limestone. The scrub zone is bordered by black mangrove (*Avicennia nitida*) and red mangrove (*Rhizophora mangle*).

I observed warblers between 20 December and 15 April of 1975–76. Observations were made between dawn and 09:30. I walked along narrow paths ("slow walk" of Lack and Lack 1972) and, upon encountering a warbler, noted (1) its foraging site, e.g. whether it was on a broad-leaved or narrow-leaved tree; (2) its height; (3) its position in the vertical vegetation strata, e.g. canopy or subcanopy; (4) its position in the horizontal vegetational strata—inner, middle, or outer. These parameters were recorded only once for each individual. Then, for the same bird I recorded 5 consecutive foraging tactics, e.g. leaf-gleaning, flycatching, or hovering. During the time the bird was in view, I also noted whether it engaged in hostile interactions, gave contact calls, and the nature of its social affiliation (alone, part of a cohesive flock, or part of a stationary flock). Total observation time was 47 h.

I conducted censuses at the same time that I made observations of foraging and social behavior. On different days than those on which I made observations, I operated mist nets (12 m long; 30 mm mesh) from dawn to 09:30, to correspond to census times. Five sites, with 5 nets at each, were used throughout the study period. Total net-hours were 153.

RESULTS AND DISCUSSION

Population composition.—Censuses and mist-netting gave the same estimates of population composition (Table 1). Only uncommon species such as Yellow-rumped Warbler and Bahama Yellowthroat were missed by either one or the other method. Differences may be explained by the fact that mist nets only cover a space from ground to 2 m. The census method is probably more accurate for conspicuous, usually canopy-feeding species such as the Cape May and Prairie warblers. The absence of Adelaide's Warbler from the mist-net sample is explained by the fact that it was territorial, and no nets were placed within its home range. By both methods, the most common species on the study sites was the Cape May Warbler, followed by the permanent resident Yellow Warbler.

Although Lack and Lack (1972: Table 3) do not give comparative census and netting times for their Jamaica study sites, a comparison of the proportions of species seen and captured in Puerto Rico with proportions seen and captured in Jamaican lowland arid habitat shows differences. Overall they saw 34 and captured 55 individual warblers, and the numerically dominant species was Prairie Warbler (26% of those seen and 33% of those netted), followed by Ovenbird (15%, 13%), Common Yellowthroat (12%, 0), N. Parula (9%, 7%), and Palm (9%, 0). Interestingly, the ground feeding Palm Warbler and Common Yellowthroat were not represented in their net sample. The Cape May, although wintering in Jamaica, was not recorded in lowland arid habitat there.

The results of Lack and Lack's (1972: Table 4) censuses for all 9 lowland dry limestone forest localities in Jamaica reveal a greater number of species than for my 2 Puerto Rican sites: 19 species vs. 11, although the number of individuals recorded per 10 h was almost the same: 131 in Jamaica and 129 in Puerto Rico. The total number of species of North American warblers wintering in Jamaica and Puerto Rico is the same (18; Bond 1956), and the higher number of species recorded by the Lacks is presumably due to the greater number of sites they visited. My study areas are probably most similar to the Lacks' arid cut-over habitat, where they saw only 16 individuals of 7 warbler species per 10 h (Lack and Lack 1972: Table 5).

TABLE 1

NUMBER OF WARBLERS SEEN AND MIST-NETTED IN COASTAL SOUTHWESTERN PUERTO RICO

	El Guayacán and La Cueva study sites		Mainland opposite to study sites
Species	Number seen per 10 h	Number captured per 100 net h	Number seen per 10 party hours in dry forest[1]
Black-and-white Warbler (*Mniotilta varia*)	4.8 (3.7)[2]	3.9 (3.5)[2]	0.3 (0.4)[2]
Prothonotary Warbler (*Protonotaria citrea*)	1.3 (1.0)	2.6 (2.3)	0.1 (0.1)
N. Parula (*Parula americana*)	17.6 (13.7)	16.4 (14.8)	12.1 (16.5)
Yellow Warbler (*Dendroica petechia*)	18.9 (14.7)	19.6 (17.7)	26.2 (35.8)
Cape May Warbler (*D. tigrina*)	41.0 (31.9)	26.2 (23.7)	2.1 (2.9)
Black-throated Blue Warbler (*D. caerulescens*)	0	0	0.1 (0.1)
Yellow-rumped Warbler (*D. coronata*)	1.9 (1.5)	0	3.2 (4.4)
Yellow-throated Warbler (*D. dominica*)	0	0	0.2 (0.3)
Adelaide's Warbler (*D. adelaidae*)	3.5 (2.7)	0	7.2 (9.8)
Blackpoll Warbler (*D. striata*)	0	0	0.4 (0.6)
Prairie Warbler (*D. discolor*)	16.0 (12.4)	11.8 (10.7)	2.6 (3.6)
Palm Warbler (*D. palmarum*)	0	2.0 (1.8)	3.9 (5.3)
Ovenbird (*Seiurus aurocapillus*)	0	1.3 (1.2)	0.1 (0.1)
N. Waterthrush (*S. noveboracensis*)	12.7 (9.9)	11.8 (10.7)	9.7 (13.3)
Louisiana Waterthrush (*S. motacilla*)	0	0	0.2 (0.3)
Bahaman Yellowthroat (*Geothlypis rostrata*)	1.0 (0.8)	0	1.3 (1.8)
Hooded Warbler (*Wilsonia citrina*)	0	0.7 (0.6)	0.1 (0.1)
American Redstart (*Setophaga ruticilla*)	9.9 (7.7)	14.4 (13.0)	3.4 (4.6)
Total	128.7 (100.0)[3]	110.7 (100.0)[3]	73.2 (100.0)

[1] Calculated from three Christmas bird counts, 1972–1974.

[2] Percentages in parentheses.

[3] No difference between census and mist-net estimates of the relative numbers of the 8 species that were recorded by both methods ($\chi^2 = 9.6$, d.f. $= 7$; $0.25 > P > .1$).

TABLE 2

SOCIAL AFFILIATIONS OF INDIVIDUAL WARBLERS OBSERVED IN PUERTO RICAN COASTAL SCRUB

Species	Bird alone	Individuals in stationary flock[1]	Individuals in cohesive flock[1]	Total individuals in flocks[2]
Black-and-white Warbler	8	5	2	9
Prothonotary Warbler	2	6	0	9
N. Parula	15	55	5	76
Yellow Warbler	20	22	0	23
Cape May Warbler	41	78	19	145
Prairie Warbler	27	32	5	46
N. Waterthrush	24	3	0	3
American Redstart	13	19	0	29
Total	150	220	31	340

[1] All flocks were composed of more than 1 species.
[2] Includes birds that were not classified as to whether they were in stationary or cohesive flocks.

In comparison to the Christmas bird count censuses of warblers on the adjacent Puerto Rican mainland (Table 1), the results obtained on my study sites differed mainly in the higher proportion of Cape May and Prairie Warblers and lower proportion of Yellow Warblers that I recorded. Although data are lacking, these differences are presumably due to vegetational differences between the islands and adjacent mainland.

Social behavior.—Warblers wintering on the study sites were often members of flocks (Table 2), but these flocks were stationary aggregations, usually organized around concentrations of insects. Such flocks correspond to the "collections" of Lack and Lack (1972). The behavior of the Puerto Rican flocks was similar to that described for the Jamaican flocks: birds were often within a few meters of each other but moved about independently. The Lacks' stationary flocks had up to 8 individuals and usually no more than 2 of 1 species. I found stationary flocks of up to 25 individuals and some species, notably Cape May and Yellow warblers, were represented by up to 7 individuals.

Few warblers, only 7.7% (31 out of 401: Table 2) were organized into cohesive flocks, i.e., flocks that maintained their integrity as they moved through the scrub. Such cohesive flocks were easily identified because their members consistently followed each other, rarely remaining at one position long.

Morse (1970) defined a flock as 2 or more birds in a group, formation of which depended upon positive responses by these individuals towards one another. Groups that form due to common responses of individuals to an extrinsic factor such as localized water or food Morse termed aggregations.

Several workers have studied stationary flocks or aggregations that gather at fruiting trees. For example, Leck (1972) described the behavior of warblers and other species aggregating at *Cecropia* trees in Puerto Rico. In the tropics warblers and other species often gather to forage on insects flushed by army ant swarms (Willis 1966 a,b). Flocking behavior may be viewed as an adaptation to enhance foraging efficiency (Cody 1971, Krebs et al. 1972), a means of improved protection against predators (Moynihan 1962, Powell 1974), and a means of reducing intraspecific aggression (Barash 1974). The relative importance of these factors probably varies with species and habitat. In this study I was particularly interested in flocking behavior because of the few aerial predators in the study areas. Willis (1973) correlated a widespread absence of cohesive flocks in Puerto Rico with paucity of accipiter species. The one locality where Willis found cohesive flocks, Maricao, also has Sharp-shinned Hawks (*Accipiter striatus*).

At the La Parguera study sites, I found 2 species of avian predators, American Kestrels (*Falco sparverius*) and Short-eared Owls (*Asio flammeus*). A pair of Kestrels lived on La Cueva in 1972–1973. In 1974 they moved to El Guayacán, probably in response to new feeding habitat created by the clearing of land. Direct observations suggested that this pair specialized on house mice (*Mus musculus*) and rats (*Rattus norvegicus*) that were abundant around monkey enclosures. Although the Kestrels flew over groups of warblers I was watching, the warblers did not appear to respond. A single Short-eared Owl appeared sporadically on El Guayacán, and it may occasionally have taken small birds, although I saw it foraging only at twilight around the monkey enclosures. On 19 February 1975 I flushed it from some dense grass, and it perched on an exposed stub, whereupon it was mobbed by a Black-and-white, a Northern Parula, a Cape May Warbler, and a Northern Waterthrush, all of which approached within 5 m of the owl. After about 3 min, the warblers resumed foraging within view of the perched owl. Cats, mongooses (*Herpestes javanicus*), and monkeys, all common on the study sites, did not seem to influence the behavior of foraging warblers. Twice I saw a mongoose move under foraging Northern Parulas and American Redstarts, none of which altered their behavior. Cats were active during crepuscular periods; rhesus monkeys seemed to ignore free-flying birds.

Sweep samples made at different warbler foraging sites (Table 3) revealed that insects were locally concentrated. Shrubs such as *Bumelia* supported abundant populations of homopterans, while neighboring patches of vegetation such as *Lantana* had few insects. Similarly, black mangrove stands were infested with homopterans, while adjacent red mangroves were relatively insect free. Such a patchy distribution of insects facilitated concentrations of warblers. Homopterans were so abundant that birds foraging on *Bu-*

TABLE 3

NUMBERS OF ARTHROPODS COLLECTED IN FEBRUARY IN DIFFERENT TYPES OF VEGETATION IN PUERTO RICAN COASTAL SCRUB AND EDGE[1]

	Vegetation type					
Group	*Lantana*	*Lantana* and grass	Grass (*Uniola* and *Chloris*)	*Bumelia*	*Avicennia*	*Avicennia*: 90% *Rhizophora*: 10%
Odonata	—	—	1	—	—	—
Orthoptera	—	7	6	—	—	—
Hemiptera and Homoptera	52	20	435	1786[2]	609[3]	851
Neuroptera	—	2	38	1	—	4
Coleoptera	—	5	—	—	1	1
Lepidoptera	—	3	3	12	3	6
Diptera	—	2	4	1	2	—
Hymenoptera	9	23	5	—	9	8
Spiders	—	35	44	—	1	7

[1] Each sample consisted of 40 sweeps made with 35 cm net through 180° arc from ground to 3 m high. All collections made at same time of day on El Guayacán.

[2] Out of 1786 homopterans, 1740 were 1 species (*Petrusa epilepsis*).

[3] 570 were *P. epilepsis*.

melia often flushed 5–10 insects with each move. I commonly observed flocks of up to 25 warblers foraging in a dense area of *Bumelia* about 100 m^2. Although the study was conducted during the dry season (December–April), and the coastal scrub habitat has the superficial appearance of being barren, insects such as Homoptera, which can puncture plant tissue to reach phloem tissue, are abundant. Janzen (1973) commented upon the disproportionate abundance of Homoptera on Caribbean islands, and he considered the numbers of Homoptera that he collected on Icacos Island, Puerto Rico (vegetationally similar to the La Parguera study sites), to be "phenomenal." Other than birds I saw few insect predators on the study sites. *Ameiva* and *Anolis* lizards were uncommon on the study sites, although common on the adjacent mainland, and their numbers are probably reduced by cats and mongooses. I captured relatively few spiders in my sweep net samples (Table 3).

All warbler species were found most often in stationary flocks, and several were found only in stationary flocks or alone (Yellow Warbler, American Redstart, and N. Waterthrush, Table 2). The American Redstart and Northern Waterthrush, because of their foraging tactics (see below), may be predisposed to forage in one position for long periods, making them even more likely members of stationary flocks. Northern Waterthrushes occupied winter territories, as probably did Yellow Warblers, but both species apparently left them to visit insect concentrations. From the point of view of motivation, being alone or in a stationary flock may be the same, since these flocks are apparently passive assemblages. The determinants of social affiliation in these assemblages thus appeared to be food distribution and the foraging tactics of the birds.

As suggested by Cody (1971), cohesive flocking may be adaptive under conditions of low food availability. Kepler and Kepler (1970) observed that mountainous areas of Puerto Rico have fewer bird species than the lowlands and related this to the reduced number of flying insects in the mountains, perhaps due to heavy rainfall. It is significant that the only area where Willis (1973) found cohesive flocks was in the mountains, around Maricao. Willis commented upon the low productivity of Maricao, relating it to the area's poor soil characteristics. He suggested that under the conditions of low food availability there, birds may have large home ranges, facilitating the formation of cohesive flocks. Morse (1970) demonstrated that flock-joining species showed the greatest tendency to group when overall population density was lowest, and he viewed cohesive flocking as an adaptation to improve foraging. Conversely, Morse (1967b) found that when food was abundant, Brown-headed Nuthatches (*Sitta pusilla*) dropped out of mixed-species flocks (of which they were usual members) to forage alone.

A possible further explanation for the lack of cohesive flocking in the warblers I studied is the lack of nuclear species. Moynihan (1962) observed that migrants or winter visitors are joiners or followers of mixed flocks of permanent residents such as tanagers or honey creepers, which by their gregarious and conspicuous behavior act as focal points of flock integration. On my study sites no residents acted as nuclear species. Puerto Rican Todies (*Todus mexicanus*), although noisy, tended to remain in one area for long periods. Bananaquits (*Coereba flaveola*) concentrated their activities around flowers. Stolid Flycatchers (*Myiarchus stolidus*) foraged near groups of warblers, but their foraging method probably precluded their membership in cohesive flocks. The greater proportion of migrants which compose the avifauna of islands, e.g. 44% for Puerto Rico vs. 26% for the Canal Zone (Leck 1972) may influence the frequency of cohesive flocking, due to the relative rarity of potential nuclear species on islands.

Calling behavior.—I made 216 observations of the frequency that warblers gave contact calls, the sibilant *tseep* or *tsip* notes often heard during migration. On 99 occasions (45.8%) warblers uttered contact calls (Table 4). The occurrence of these calls was related to the social situation of the warblers. Birds in flocks gave the calls significantly more often than did those alone ($\chi^2 = 7.3$; $P < .01$), and birds in cohesive flocks called more often than those in stationary flocks ($\chi^2 = 19.6$; $P < .005$). However, birds alone and in stationary flocks called with the same frequency ($\chi^2 = 1.6$; N.S.). This latter result is further evidence of the similarity between foraging in stationary flocks and solitary foraging.

Although the data are few, some species differences in calling behavior are evident (Table 4). Cape May Warblers called proportionally more often than other species, whether alone or in flocks. At least in flocks, this could be due to the numerical dominance of this species: contact calls may be responded to more often by conspecifics. In contrast to other species, Prairie Warblers seldom called, whether in or out of flocks.

Aggressive interactions.—I recorded hostile interactions between warblers, which included chases, supplants, and fights. As found by Morse (1970), most aggressive encounters were intraspecific (Table 5). This is due to the fact that a bird is more likely to encounter a member of its own than another species in its preferred foraging space. In addition, members of the same species may be attracted by each others' morphological and behavioral characteristics (Moynihan 1962). For example, on several occasions, I saw dull-plumaged Cape Mays, presumably juveniles, following adult male Cape Mays as they foraged. Warblers that captured a large food item such as a caterpillar were often chased by conspecifics.

If we assume that each species has an equal probability of encountering another, then we may calculate the expected number of hostile interactions

TABLE 4

SUMMARY OF WHETHER CONTACT CALLS WERE GIVEN OR NOT GIVEN IN DIFFERENT SOCIAL SITUATIONS

Species	Bird alone		Individuals in stationary flocks		Individuals in cohesive flocks		Total individuals in flocks[1]	
	Call given	No call given	Call given	No call given	Call given	No call given	Call given	No call given
N. Parula	0	6	10	19	3	0	16	19
Yellow Warbler	1	2	1	10	—	—	1	10
Cape May Warbler	13	14	36	18	16	3	59	21
Prairie Warbler	0	11	3	17	3	0	8	18
American Redstart	1	3	0	12	—	—	0	13
Total	15	36	50	76	22	3	84	81

[1] Includes birds that were not classified as to whether they were in stationary or cohesive flocks.

TABLE 5

HOSTILE INTERACTIONS OF WARBLERS WINTERING IN PUERTO RICAN COASTAL SCRUB

	Species attacked								
Species attacking	Prothonotary Warbler	N. Parula	Yellow Warbler	Cape May Warbler	Prairie Warbler	N. Waterthrush	American Redstart	Unidentified Warbler	Total
Prothonotary Warbler (14.1;12.7–15.5)[1]	—	—	1	1	—	—	—	—	2
N. Parula (7.5 ± 0.3)[2]	—(0)[3]	3(1)	—(1)	1(3)	1(1)	—(1)	—(1)	3	8
Yellow Warbler (11.3 ± 0.5)	—(0)	—(2)	2(2)	6(4)	—(1)	1(1)	1(1)	1	11
Cape May Warbler (10.1 ± 0.2)	—(1)	13(9)	—(10)	44(22)	2(8)	—(6)	—(5)	1	60
Prairie Warbler (6.9 ± 0.2)	—(0)	1(1)	—(1)	—(2)	4(1)	—(1)	—(0)	—	5
N. Waterthrush (15.1 ± 0.6)	—	—	—	—	—	—	1	—	1
American Redstart (7.4 ± 0.3)	1	—	—	—	—	—	2	—	3
Unidentified Warbler	—	—	—	1	—	—	—	6	7
Total	1	17	3	53	7	1	4	11	97

[1] Mean weight (g) followed by range (N = 5).

[2] Mean weight (g) followed by 95% confidence interval (sample size >10) for species other than Prothonotary Warbler.

[3] Expected number of aggressive encounters, correcting for relative abundance (Table 1) and assuming all species are equally likely to encounter each other (for species which gave 5 or more attacks to identified species).

per species pair (Table 5: values in parentheses). A comparison of observed and expected values shows that birds did attack members of their own species more often than expected. The Cape May, which comprised 32% of the warbler population (Table 1) gave 62% of the attacks (Table 5), and 73% of these were to conspecifics. Species which were similar in foraging behavior were also attacked more frequently than expected; for example Cape Mays vs. Parulas. The 4 species for which I have sufficient data may be ordered into a linear hierarchy with Yellow Warblers dominating Cape Mays, fol-

Table 6

Foraging Heights of Warblers in Puerto Rican Coastal Scrub

Species	Foraging height (m above ground)			Distribution of birds at different heights (m above ground)								Distribution of birds in vertical structural units of vegetation				
	Number of observations	Mean	95% Confidence interval	Number of observations	Percentage at:							Number of observations	Percentage in:			
					0–1	1–2	2–3	3–4	4–5	5–6	6–7		Canopy	Sub-canopy	Herb layer	Ground
Black-and-white Warbler	22	1.39	±0.25	22	22.7	68.2	9.1	-	-	-	-	22	4.5	95.5	-	-
Prothonotary Warbler	—	—	—	13	38.5	30.8	7.7	7.7	15.4	-	-	12	8.3	75.0	16.7	-
N. Parula	101	2.47	±0.30	107	7.5	20.6	42.1	10.3	11.2	8.4	-	107	43.9	52.3	3.8	-
Yellow Warbler	51	1.89	±0.32	53	11.3	37.7	30.2	7.6	11.3	1.9	-	55	20.0	80.0	-	-
Cape May Warbler	183	2.82	±0.30	230	15.2	23.0	25.7	16.1	10.0	5.2	3.0	220	45.5	43.6	9.5	1.4
Prairie Warbler	84	2.12	±0.26	87	17.2	36.8	19.5	12.6	8.1	2.3	-	87	34.5	50.6	13.8	1.1
N. Waterthrush	—	—	—	28	96.4	3.6	-	-	-	-	-	32	-	12.5	6.2	81.3
American Redstart	44	1.57	±0.20	48	29.2	39.6	27.1	2.1	2.1	-	-	46	4.3	95.7	-	-

TABLE 7

FORAGING SITES OF WARBLERS IN PUERTO RICAN COASTAL SCRUB

Species	Number of observations	Percentage of foraging sites that were on:					
		Broad-leaved vegetation	Dead vegetation	Narrow-leaved vegetation	Herbs and succulents	Vines	Ground
Black-and-white Warbler	22	86.4	13.6	–	–	–	–
Prothonotary Warbler	12	58.3	–	16.7	25.0	–	–
N. Parula	105	81.0	5.7	5.7	6.7	0.9	–
Yellow Warbler	56	73.2	7.1	14.3	3.6	1.8	–
Cape May Warbler	216	62.0	13.0	11.6	10.6	2.8	–
Prairie Warbler	89	56.2	9.0	18.0	12.3	3.4	1.1
N. Waterthrush	31	16.1	–	–	6.5	–	77.4
American Redstart	45	88.9	–	11.1	–	–	–

TABLE 8

STRUCTURAL UNITS OF VEGETATION USED FOR FORAGING BY WARBLERS IN PUERTO RICAN COASTAL SCRUB

Species	Number of observations	Percentage of observations in:					
		Canopy			Subcanopy		
		Inner	Middle	Outer	Inner	Middle	Outer
N. Parula	60	1.7	5.0	31.7	15.0	13.3	33.3
Yellow Warbler	24	–	–	4.1	25.0	41.7	33.3
Cape May Warbler	103	1.0	5.8	40.8	9.7	16.5	26.2
Prairie Warbler	48	–	8.3	25.0	14.6	14.6	37.5
American Redstart	31	–	–	–	64.5	12.9	22.6

lowed by Northern Parulas, then Prairies. This is also the order of decreasing weight (Table 5).

Foraging behavior.—My observations indicate that warblers wintering in Puerto Rican coastal scrub often used similar foraging spaces and feeding tactics (Table 6–9). Two species, the Black-and-white Warbler, a trunk and branch gleaner, and the Northern Waterthrush, a ground feeder, are clearly separated from the other species. Of the others, all of which concentrated their foraging activities in above-ground foliage, the American Redstart is a specialist of the inner subcanopy (Table 8), and it obtained most of its prey on the wing (Table 9). The remaining 4 species, the Northern Parula, Yellow, Cape May, and Prairie warblers were not clearly separated in their foraging behavior: The similarities among these species may be quantified by using the index of overlap (Table 10) developed by Horn (1966):

$$R_0 = \frac{\sum (\chi_i + y_i) \log (\chi_i + y_i) - \sum \chi_i \log \chi_i - \sum y_i \log y_i}{(X+Y) \log (X+Y) - X \log X - Y \log Y},$$

where X and Y equal the number of observations in samples of foraging of the two species being compared; χ_i and y_i equal the proportion of observations in the i^{th} foraging category of the samples.

The data show broad overlap in many categories of foraging behavior, particularly in foraging site use and in foraging tactics. Less overlap was shown among use of structural units. Northern Parulas were very similar to Cape Mays in the 3 parameters considered. Parulas were also somewhat close to Prairies but quite dissimilar to American Redstarts. The Cape May overlapped broadly in at least 2 categories with each of the other 4 species and, after the N. Parula, was most similar to the Prairie. The Yellow Warbler was closest to the Prairie Warbler.

TABLE 9

FORAGING TACTICS OF WARBLERS IN PUERTO RICAN COASTAL SCRUB

		Percentage of observations that were composed of:									
Species	Number of observations	Leaf gleaning	Trunk or branch gleaning	Twig gleaning[1]	Fly-catching	Hovering	Fruit eating	Chasing[2]	Web feeding[3]	Nectar feeding	Ground pecking
Black-and-white Warbler	85	11.8	75.3	5.9	4.7	2.4	–	–	–	–	–
Prothonotary Warbler	41	41.5	9.8	43.9	4.9	–	–	–	–	–	–
N. Parula	335	70.1	2.1	6.9	9.5	4.8	–	2.4	0.3	3.9	–
Yellow Warbler	114	57.0	4.4	15.8	10.5	7.9	–	3.5	0.9	–	–
Cape May Warbler	558	40.1	3.9	9.5	28.0	3.8	4.3	2.0	2.3	5.2	0.9
Adelaide's Warbler	18	50.0	11.1	–	22.2	16.7	–	–	–	–	–
Prairie Warbler	216	36.1	1.8	26.4	16.7	8.8	–	7.4	0.5	1.8	0.5
N. Waterthrush	18	–	–	5.6	5.6	5.6	–	22.2	–	–	61.1
American Redstart	158	8.2	0.6	3.2	45.6	29.8	–	11.4	0.6	–	0.6

[1] Structures less than 10 mm in diameter classified as twigs.

[2] A bird engaged in chasing when it fluttered or ran along a horizontal surface in pursuit of prey.

[3] Web-feeding birds reached out to take spiders or spiders' prey from web or thread.

TABLE 10

INDICES OF OVERLAP AMONG FORAGING WARBLERS

Species	Yellow Warbler			Cape May Warbler			Prairie Warbler			American Redstart		
	Foraging sites	Structural units	Foraging tactics	Foraging sites	Structural units	Foraging tactics	Foraging sites	Structural units	Foraging tactics	Foraging sites	Structural units	Foraging tactics
N. Parula	0.98	0.87	0.98	0.97	0.99	0.92	0.94	0.99	0.88	0.56	0.68	0.58
Yellow Warbler				0.98	0.79	0.89	0.99	0.86	0.95	0.93	0.87	0.66
Cape May Warbler							0.99	0.72	0.91	0.85	0.60	0.89
Prairie Warbler										0.84	0.70	0.75

Lack and Lack (1972) presented data on the foraging behavior of warblers wintering in Jamaica. Unfortunately, they lumped data from different habitats and localities, so it is not possible to quantify the overlap of feeding behavior with confidence. They stated that most of their flocks were collections, i.e., stationary flocks, perhaps attracted to locally abundant food, and this implies that within habitats there could have been much overlap among species. For example, 2 species in Jamaica that were not separated by habitat, Cape May and N. Parula, were said to be separated by feeding sites and foraging heights (Lack and Lack 1973: Table 11). These are roughly equivalent to my foraging sites (Table 7) and foraging heights (Table 6). The foraging site overlap value for these 2 species in Jamaica was 0.98 vs. my value of 0.97. In Jamaica the mean foraging height for these 2 did not differ significantly (N. Parula:6.4 m, 95% confidence interval ±0.6 m; Cape May:7.6 ± 1.1 m). Comparable heights in Puerto Rico were N. Parula:2.5 ± 0.3 m; Cape May:2.8 ± 0.3 m. In Jamaica, Prairie Warblers and N. Parula Warblers were also not separated by habitat, and their feeding site overlap is 0.99 (vs. 0.94 in Puerto Rico), while their feeding heights are not significantly different (N. Parula:6.4 ± 0.6 m; Prairie:5.3 ± 0.8 m vs. Puerto Rican figures of 2.5 ± 0.3 and 2.1 ± 0.3). My data indicate that there is less overlap among species in the structurally simple Puerto Rican habitat than in Jamaica. However, the Jamaican data are from several habitats and sites and thus may show more overlap due to the lumping of different data sets.

The patches of food visited by the stationary flocks that I studied were composed mainly of 1 species of insect (Table 3). Morse (1970) noted a convergence in the foraging behavior and use of feeding site of Brown-headed Nuthatches and Pine Warblers (*Dendroica pinus*) as they exploited heavy crops of pine seeds, even though this resulted in increased numbers of aggressive encounters.

When food is locally abundant and accessible, there may be little pressure for feeding specialization by members of mixed flocks. Food may be obtained by the simplest method, and if birds are using the same prey, convergence in their foraging patterns would be expected. North American warblers wintering in localities with high food concentrations appear to show few behavioral differences when foraging. As Willis (1966a) pointed out, superabundance of food may be frequent rather than exceptional due to the "irregularity principle": available food is often left by irregularities in time or space, since resource exploitation lags behind its appearance. In the tropics North American migrants, because of their mobility and opportunistic behavior, may often concentrate on irregularly distributed food that is not effectively used by resident populations.

SUMMARY

The population density of warblers wintering in arid coastal scrub in Puerto Rico was much higher than comparable sites in Jamaica. Warblers wintering in the coastal scrub usually foraged alone or in stationary (passive) flocks. Few were organized into cohesive (integrated) flocks. Warblers in stationary flocks gave contact calls with the same frequency as those alone, while warblers in cohesive flocks called more often. Aggressive behavior was common, and occurred most often between members of the same species or those with similar foraging behavior. The stationary flocks were usually composed of birds that gathered to harvest concentrations of insects whose distribution varied between vegetation patches. The few predators in the study sites apparently did not influence the flocking behavior of the warblers. Warblers showed considerable overlap in their feeding behavior, which may be due to convergence of foraging on the same abundant food source.

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