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WINTERING WARBLERS IN JAMAICA

DAVID LACK AND PETER LACK

Photographs by the authors

Ecological isolation in the breeding season has been shown for species in many families of birds, but few data are yet available for migrants in winter quarters (Lack, 1971). The warblers of the family Parulidae present a special challenge in this respect, since so many of them winter in the same area, and most of them are separated ecologically in summer in subtle ways (MacArthur, 1958). During our stay in Jamaica, from mid-October 1970 until well after the warblers left in the summer of 1971, we studied their habitats, feeding stations, and feeding methods, but not their actual food. Because, so far as we could see, no species in other families share ecological niches with the Parulidae, we limited our study to the members of this family.

Thirty-five passerine species breed in Jamaica; of these four are mainly or exclusively summer visitors. The 31 resident species, which include two parulid warblers, are joined in winter by 18 other parulids and two other passerine species from North America. Hence, visitors comprise two-fifths of the passerine species present in winter—and roughly one-quarter of the individuals of all passerine species that we saw. The parulid species concerned, with two measurements from Ridgway (1902), appear in Table 1 with the resident Jamaican species first.

Methods and Localities of Study

Methods

We made three types of counts (Table 2): (1) slow walks through the forest, (2) quick walks through the forest, and (3) fairly slow walks along trails at the forest edge.

On slow walks through the various habitats we stopped to record the manner of feeding when we saw it. Our walking speed was roughly 0.8 kilometer per hour, but we did not attempt to keep our speed uniform and it varied somewhat with the birds seen feeding and other conditions. We recorded only the individual birds seen. Such counts, while superior to a simple record of "common," "rare," etc., are difficult to relate to the density of birds per unit area for the following reasons.

First, because warblers are much more in evidence soon after dawn than later in the day, we made all our counts in early morning. But the decline in warbler activity later in the day is much greater in some habitats, notably the

TABLE 1
The Warblers in Jamaica

<i>Species</i>	<i>Mean wing* length (mm)</i>	<i>Mean culmen* length (mm)</i>
<i>Resident</i>		
Yellow Warbler, <i>Dendroica petechia</i>	65	10.6
Arrow-headed Warbler, <i>Dendroica pharetra</i>	63	11.3
<i>Wintering**</i>		
Black-and-white Warbler, <i>Mniotilla varia</i>	69	11.4
Swainson's Warbler, <i>Limnothlypis swainsonii</i>	70	15.0
Worm-eating Warbler, <i>Helmintheros vermivorus</i>	69	13.7
Tennessee Warbler, <i>Vermivora peregrina</i>	65	9.6
Parula Warbler, <i>Parula americana</i>	61	9.9
Magnolia Warbler, <i>Dendroica magnolia</i>	60	9.0
Cape May Warbler, <i>Dendroica tigrina</i>	66	9.8
Black-throated Blue Warbler, <i>Dendroica caerulescens</i>	65	9.4
Myrtle Warbler, <i>Dendroica coronata</i>	74	10.0
Black-throated Green Warbler, <i>Dendroica virens</i>	64	9.9
Yellow-throated Warbler, <i>Dendroica dominica</i>	67	13.8
Prairie Warbler, <i>Dendroica discolor</i>	58	9.4
Palm Warbler, <i>Dendroica palmarum</i>	65	9.9
Ovenbird, <i>Seiurus aurocapillus</i>	73	11.7
Northern Waterthrush, <i>Seiurus noveboracensis</i>	77	12.7
Louisiana Waterthrush, <i>Seiurus motacilla</i>	81	13.2
Common Yellowthroat, <i>Geothlypis trichas</i>	53	10.5
American Redstart, <i>Setophaga ruticilla</i>	64	8.5

*Measurements of adult males (Ridgway, 1902).

**Two regular wintering species, Tennessee Warbler (*Vermivora peregrina*) and Myrtle Warbler (*Dendroica coronata*), omitted from other tables and analyses because they are too scarce to warrant quantitative assessment.

arid lowland forest, than in others such as the montane forest. Second, since the vegetation in the Jamaican forest is dense and many slopes are too steep for walking, one can census carefully only along tracks, which vary in width. Wide tracks make visibility in the forest canopy easier; narrow tracks help the observation of birds on the ground. Further, some forests have tracks only along the edge, making it easy to see birds of the forest edge and difficult to see birds on the forest floor. Finally, a quick walk is better than a slow one for seeing the shy, ground-feeding species which usually spot a strolling observer farther away and slip off unnoticed.

We observed the Swainson's Warbler and Ovenbird, both ground-feeding species, more often on quick walks than slow ones, and the Common Yellowthroat, a herb-feeding species, most often along the forest edge. All the rest, the tree-feeding species, were equally common on all three types of counts

(Table 2). A comparison of the birds seen with those caught in mist nets, extending from the ground to a height of two meters, revealed similar differences (Table 3). Although a comparison of birds seen with those caught on Port Henderson Hill in the lowland arid region shows no pattern comparable to the patterns in other areas, this may be due to the extremely low canopy caused by forest clearance. In the three other areas, we netted a much higher proportion of ground and shrub-feeding species than we saw, and we saw a greater proportion of tree-feeding species than we netted. Table 3 shows this crudely. The difference is particularly marked in the ground-feeding Swainson's Warbler and Ovenbird, the low-feeding Worm-eating Warbler, and the tree-feeding Parula, Yellow-throated, and Prairie Warblers.

The number of observers may also affect the number of birds seen per unit of time. On slow walks through montane forest near Hardwar Gap with one, two, three, and four observers, the average number of warblers recorded

TABLE 2
Variation in Number of Warblers Seen in Jamaica under
Different Conditions*

Species**	Number of birds per 10 hours		
	Slow walks† through forest	Quick walks† through forest	Fairly slow walks on roadside edges of forest
<i>Resident</i>			
Arrow-headed	21	18	19
<i>Wintering</i>			
Black-and-white	13	11	12
Swainson's	3	6	0
Worm-eating	1	1	1
Black-throated Blue	7	7	8
Ovenbird	2	6	1
Common Yellowthroat	x††	2	11
American Redstart	1	0	2
Total warblers (including a few warblers not listed above)	50	53	61
Total passerines	138	120	265
Number of hours	32	9	12

*Montane forest, near Hardwar Gap, 1,200 meters elevation.

**Commonest warblers.

†Slow walks, about 0.8 km per hour; quick walks, about 3.2 km per hour. Difference on slow walks and quick walks between Swainson's Warbler and Ovenbird and all the rest, except the Common Yellowthroat, is statistically significant ($\chi^2 = 10.98$, $P < .01$).

††Present but less than 0.5 per 10 hours.

per hour was 5.6, 4.1, 6.4, and 6.9, respectively; these differences are not statistically significant. In thick forest, two observers only a few feet apart often see different individual birds, partly because each tends to watch in a somewhat different direction and partly because, even when looking in the same direction, each has a different view through the cover.

Differences, occasionally large, occur in the number of warblers seen on different days in the same place, between the same times, and by the same observers. We noted the biggest difference along a narrow road in a good secondary forest at Ferry River where the same three observers counted from 08:00 until 10:30 on 15 and 27 January. On the first walk, they saw 24 parulids and 44 individuals of other passerine species; on the second, 48 parulids and 17 individuals of other passerines. We believe that a wind on the second walk may have depressed the activities of the other passerines, but we cannot explain the increase in the number of parulids. Thus, one must exercise great caution in interpreting the differences in the numbers of birds observed.

We recorded feeding height only once for each individual — at the time when we first saw it feeding; we noted its manner of feeding for up to five successive times when we could follow it. After the fifth observation we turned to another individual. Because some types of feeding are far more conspicuous than others — a warbler snatching insects in the air is far easier to see than a warbler gleaning insects from a leaf — the recorded proportions of each type of feeding may be somewhat biased.

Habitats

The vegetation of Jamaica includes four main types of natural forest and woodland — mangroves, lowland dry limestone forest, midlevel wet limestone forest, and montane shale forest (Asprey and Robbins, 1953). Mangroves, which are not extensive except in Kingston Harbour, usually form a relatively narrow strip. We made censuses in mangroves along the south coast near Morant Point, Morant Bay, Kingston Harbour, and the edges of the Hellshire Hills and Portland Ridge.

Lowland dry limestone forest is variable. We censused at sea level at Morant Point and Negril. There has been a great deal of clearing in both areas which were apt to be flooded. We often counted in the extremely arid scrub forest, still in its natural state except for a few trails, in the Hellshire Hills (Figure 1) and on Portland Ridge and in similar but heavily cut-over forest on Port Henderson Hill. Less arid, cut-over scrub forest covers much of the southern lowland hills, where we censused on Long Mountain near Mona. We worked frequently in the relatively rich secondary woods at an altitude of 60 to 120 meters above Ferry (Fresh) River, west of Kingston, and in secondary riverine woodland with taller trees along the Ferry River and beside the stream from Mona Reservoir. We worked in a tall natural riverine forest in Fern Gully in the north.

We counted in midlevel forest mainly on Mount Diablo above Worthy Park where we had to observe mostly from grassy pastures at the edge and thus saw very few ground-feeding warblers. We also made a few counts in the natural forest of the Cockpit Country (Figure 2) and at Dolphin Head. We counted in montane forest mainly between Catherine's Peak and Middleton Mount, near Hardwar Gap, between 1,200 and 1,500 meters above sea level, and several times along the higher trail from St. Helen's to Morce's Gap (Figure 3).

TABLE 3
Comparison of Warblers Seen and Mist-netted in the
Same or Similar Areas in Jamaica

Species	Percentages of birds recorded*						
	Lowland** arid	Lowland*** riverine	Middle† elevation	Montane††			
<i>Residents</i>							
Yellow	12	—	—	—	—	—	—
Arrow-headed	—	—	—	—	8	21	28
<i>Wintering</i>							
Black-and-white	18	38	21	10	21	18	16
Swainson's	—	—	1	5	—	2	—
Worm-eating	—	—	x‡	7	—	11	1
Tennessee	—	—	2	2	—	—	1
Parula	9	7	10	5	4	2	2
Magnolia	—	—	4	2	—	—	1
Cape May	—	—	2	—	12	10	—
Black-throated Blue	—	—	7	7	25	11	17
Myrtle	—	—	—	—	—	—	—
Black-throated Green	—	—	4	1	7	6	8
Yellow-throated	—	—	—	—	5	1	2
Prairie	26	33	14	3	9	4	1
Palm	9	—	—	—	1	3	3
Ovenbird	15	13	3	12	3	7	1
Northern Waterthrush	—	—	5	7	—	—	—
Louisiana Waterthrush	—	—	—	—	—	—	3
Common Yellowthroat	12	—	15	33	3	1	12
American Redstart	—	9	12	5	2	2	3
Total warblers	34	55	248	136	126	90	138
							39

*First figure is percentage of birds seen only; second figure is percentage of birds netted. Of the 6 ground-feeding and low feeding species, 47 individuals were seen, 123 netted. Of the 11 tree-feeding species, 248 individuals were seen, 172 netted.

**Port Henderson Hill: Extremely arid area of abnormally low natural scrub forest; totals not included in main counts for lowland limestone forest in Table 4 because of heavy cutting by charcoal burners.

***Near Mona Reservoir: 150 meters elevation with stream and mimosaceous trees; somewhat disturbed by cutting.

†Irish Town: Netting in wild garden with adjoining woodland and cultivated land at 600 meters elevation; census at Guava Ridge, many more conifers, 1,200 meters elevation.

††Green Hills: Netting at field station of Institute of Jamaica, overgrown wild garden adjoining montane forest; census through garden, forest, and at Hardwar Gap, 1,100 to 1,200 meters elevation.

‡Seen outside counts.



Figure 1. Lowland dry limestone forest (xeric scrub forest) in the Hellshire Hills, Jamaica.

We counted in all the main natural habitats except river swamps with sedges, where Northern Waterthrushes and Common Yellowthroats are the only common warblers. We also censused five wooded habitats much modified by man: the Royal Botanical Garden in Kingston, the midlevel woods around the Hermitage Reservoir at 500 to 600 meters elevation, Guava Ridge at about 1,200 meters, Holywell Picnic Site at Hardwar Gap, and Cinchona Botanic Garden at 1,400 meters. Although these five places have many wintering warblers, artificial habitats occupy such a small part of Jamaica that the majority of the wintering warblers live in natural, though often partly cleared, forest. We did not census agricultural areas of sugar cane, coconuts, bananas, or citrus fruits where warblers are scarce. Nor did we census in grassy pastures where the only parulid is the Palm Warbler, usually found near trees and bushes.

The summary of our censuses in Table 4 shows that most of the wintering warblers occur in both lowland and montane forest, and that habitat separates hardly any. Two exceptions are the waterthrushes and two resident species: the Northern Waterthrush occurs in the lowlands and the Louisiana Waterthrush mainly at midlevels and in the mountains; and the resident Yellow Warbler in the lowlands and the resident Arrow-headed Warbler at midlevels and in the mountains. A few other parulids — the Parula and Prairie Warblers and American Redstart — are much commoner in lowland than montane forest. The subdivision of the main types of lowland forest in Table 5 again shows no species separated by habitat though some are more common in the wetter, richer forests and others in the more arid types of lowland forest. This is due to their preference for feeding in trees with particular types of leaves. We classified differences of this sort as contrasts in feeding stations, not habitat.

Annotated List

We first consider four specialized species, each of which has an obviously different ecological niche from any other, then five ground-feeding species,

and finally 11 leaf-gleaning species that obtain most of their food off leaves by reaching from a perch. Only in the last group is there any difficulty in understanding how the various species might be separated ecologically from each other. The North American range and habitat are from Chapman (1917), Bent (1953), and Robbins *et al.* (1966); Tables 3 and 4 summarize the habitats in Jamaica; Tables 6 through 10 give the feeding stations and feeding methods. The totals differ somewhat in different tables partly because, at first, we did not always obtain pertinent information on the feeding.

Four Specialists

Black-and-white Warbler (*Mniotilla varia*): Breeds in most of North America, preferring open and secondary growth in broad-leaved deciduous woods. Common in Jamaica in all types of natural forest, both open and closed, from mangroves and the most arid lowland forest to the wettest and highest montane forest and also in cultivated forest, including introduced pines. It is the only species which feeds primarily by creeping up and along trunks, branches, and twigs of all sizes, taking insects off bark or probing for them in crevices, and, occasionally, by following termite trails or climbing damp rocks or vertical banks with short vegetation. Rarely, it takes an insect off a leaf or catches in the air one that it has disturbed.

Worm-eating Warbler (*Helmitheros vermivorus*): Breeds in eastern United States on wooded hillsides with broad-leaved deciduous trees and saplings. Occurs in Jamaica in all types of natural forest, except mangroves, and in cultivated forest with rather thick cover. Generally, we found it low in trees but not on the ground. Although we did not see many, it was the fifth commonest species captured in our mist nets (Table 3), suggesting that



Figure 2. Midlevel wet limestone forest in a new clearing in the Cockpit Country, Jamaica.



Figure 3. Montane cloud forest in the Blue Mountains, Jamaica.

it keeps low. It is the only warbler in Jamaica which feeds primarily by probing among clusters of hanging dead leaves or pulling bark from dead twigs. Often it feeds in the only cluster of dead leaves among many green ones.

Common Yellowthroat (*Geothlypis trichas*): Widespread in North America in tangled low vegetation at the edges of woods and swamps. Common in Jamaica in the lush herb layer, usually between 1.0 and 1.5 meters high, at the edges of swamps and some forests including montane forest. In the lowlands, it occurs at times in damp woodland, where there is no lush herb layer, and feeds up to 10 meters above the ground in thick bushes or low trees. It is the only warbler in Jamaica that feeds in thick herbage.

American Redstart (*Setophaga ruticilla*): Widespread in North America in broad-leaved deciduous forests with a rich understory. Found in Jamaica in all types of natural woodland, particularly mangroves, sea-level forest, and lowland riverine forest; scarce in the mountains. It is the only warbler in Jamaica which catches almost all of its prey in the air; the Magnolia Warbler feeds in this way some of the time and other species do so occasionally. Flashing its tail and darting out to take insects at any height — often just under the canopy, sometimes lower, and even on the ground — it takes quick, short flights never far from the vegetation where it hops among the twigs, especially the leafy twigs.

TABLE 4

Number of Warblers Seen per Ten Hours of Slow Walking in Jamaica

Species	Natural forest			Gardens, parkland			
	Mangroves*	Lowland	Mid-level	Montane	Lowland	Mid-level	Montane
<i>Resident</i>							
Yellow	62	1	—	—	—	—	—
Arrow-headed	—	2	11	18	—	5	10
<i>Wintering</i>							
Black-and-white	24	22	12	12	16	13	10
Swainson's	—	2	x**	2	—	—	—
Worm-eating	—	2	2	1	1	4	1
Tennessee	—	1	—	1	1	—	1
Parula	3	17	5	x	10	—	1
Magnolia	—	5	x	x	5	3	x†
Cape May	—	5	—	—	16	1	4
Black-throated Blue	—	10	13	6	4	25	14
Myrtle	—	x	—	x	7	—	x
Black-throated Green	—	3	2	1	3	—	7
Yellow-throated	—	—	—	—	2	—	3
Prairie	5	19	4	x	4	10	3
Palm	5	3	x	x	3	3	1
Ovenbird	6	7	2	2	3	3	2
Northern Waterthrush	35	2	—	—	5	x	—
Louisiana Waterthrush	—	x	—	1	x	10	x
Common Yellowthroat	6	14	3	3	7	15	3
American Redstart	29	17	7	1	3	28	1
Total warblers	174	131	61	49	90	121	60
Total passerines	230	396	392	180	676	401	319
Number of hours	9	86	30	65	10	8	40

*Mangroves censused much less often than other natural forests.

**x means recorded, but less than 0.5 birds per 10 hours.

†Seen in habitat, but only outside counts.

TABLE 5
Number of Warblers Seen per Ten Hours in Lowland Dry Limestone Forest in Jamaica

Species	Forest type					
	Sea-level*	Arid** natural	Arid*** cut-over	Typical† cut-over	Good‡‡ secondary	Riverine‡
<i>Resident</i>						
Yellow	8	—	2	—	—	—
Arrow-headed	—	—	—	—	8	—
<i>Wintering</i>						
Black-and-white	22	14	3	25	16	35
Swainson's	3	—	—	3	1	2
Worm-eating	5	1	—	2	3	1
Tennessee	—	—	—	—	—	3
Parula	19	4	1	19	22	22
Magnolia	6	—	—	9	4	9
Cape May	6	1	—	10	4	4
Black-throated Blue	19	1	—	2	17	14
Myrtle	—	—	—	1	—	—
Black-throated Green	—	1	—	9	2	5
Prairie	29	11	4	30	7	22
Palm	3	—	1	12	—	1
Ovenbird	2	9	2	12	4	6
Northern Waterthrush	—	—	—	2	—	8
Common Yellowthroat	27	—	2	19	2	31
American Redstart	29	6	—	9	14	30
Total warblers	179	49	16	163	103	196
Total passerines	552	234	264	389	300	599
Number of hours	11	20	21	17	20	18

*Morant Point and Negril: parts liable to flooding, parts cut over.

**Hellshire Hills and Portland.

***Port Henderson Hill in Hellshires.

†Long Mountain beside University campus at Mona: much cut over.

‡‡Valley up from Ferry (Fresh) River.

‡Along Ferry River and in woods beside Mona Reservoir.

Ground-feeding Species (Table 8)

Swainson's Warbler (*Limnothlypis swainsonii*): Breeds in southeastern North America, mainly in flood-plain forest with thick undergrowth and also in forested mountain ravines. Commoner everywhere in Jamaica than our slow-walk counts suggest (Tables 2 and 3). Its apparent scarcity in the mid-level forest is probably due to our censusing at the forest edges, disturbing the bird, and causing it to fly into thick bushes before we saw it. It always feeds on the forest floor where it rummages and probes in leaf litter, sometimes tossing leaves aside just as it does in North America (Meanley, 1966). The only other parulid feeding on the forest floor in Jamaica is the Ovenbird, which picks up insects in its much shorter beak but does not probe.

Palm Warbler (*Dendroica palmarum*): Breeds in central and eastern Canada in swamps and bogs. Occurs in Jamaica mainly in the man-modified habitat of grassland with scattered trees and at the forest edge, chiefly in the lowlands though we saw one on the grassy top of Blue Mountain Peak. It is the only warbler in Jamaica which feeds primarily on grassy ground in the open. Occasionally, it snatches an insect from the vegetation or in the air, but the high number of such records in Table 7 is misleading because we failed to record all the normal feedings that we observed on the ground.

Ovenbird (*Seiurus aurocapillus*): Breeds in the eastern half of North America, mainly in broad-leaved forests with thick undergrowth. Common in Jamaica on the floor in all types of natural forest from the lowlands to the mountains, but uncommon in cultivated woods because it prefers thick tree cover. In the lowlands, we found the Ovenbird on dry ground and the Northern Waterthrush on muddy ground; in the wet, montane forest, we found the Ovenbird throughout but no Northern Waterthrushes. The Ovenbird picks insects off the leaf litter on the ground, usually under trees but also, unlike the Swainson's Warbler, on the forest paths and trails.

Northern Waterthrush (*Seiurus noveboracensis*): Breeds across Canada and northern conterminous United States, near standing water in forests and bogs. Abundant in Jamaica in mangroves. It is a regular, but sparse, inhabitant in lowland woods and cultivated woods on muddy ground, especially near standing water or muddy streams. We recorded it as high as 240 meters on trails through cultivated woods in the very wet limestone forest of the John Crow Mountains. It picks small invertebrates off mud or extremely shallow water. In the Kingston Botanic Garden, it walks on, and finds food on, the large leaves of an introduced water lily (*Victoria regia*).

Louisiana Waterthrush (*Seiurus motacilla*): Breeds in east-central United States, mainly south of the range of the Northern Waterthrush, usually beside rocky streams, but also in swamps. Occurs in Jamaica regularly in rather small numbers along rocky forest streams and, at times, along wider rocky rivers, chiefly at middle elevations and in the mountains, but also in the lowlands. It is the only warbler which feeds primarily from rocks beside or in the water. In the lowlands, it limits its feeding to rocks beside or in water, but at 500 meters elevation, near the Hermitage Reservoir where the Northern Waterthrush is absent, the Louisiana Waterthrush hunts regularly on mud and beside very shallow standing water — like the Northern Waterthrush in the lowlands. One individual fed again and again on a wet tarmac road through montane forest, and another on the stonework beside a pond in the Kingston Botanic Garden.

Summary of Ground-feeders

Four of the five ground-feeding species hunt on different substrates, and the Swainson's Warbler and Ovenbird that share the forest floor feed differently. The Swainson's Warbler probes and the Ovenbird pecks (Table 8). In a lowland wood we once saw a Louisiana Waterthrush on a rock in mid-stream, a Northern Waterthrush two meters away at the muddy edge of the stream, and an Ovenbird six meters away on dry ground under trees. Since all three were on the ground in the same lowland wood, it is hard to decide whether they differed in habitat or choice of feeding station.

In Trinidad, 1,600 km southeast of Jamaica, where the Northern Waterthrush is the only species of *Seiurus* present, David Lack found it not only on mud in the mangroves, as in Jamaica, but also on the dry forest floor in the lowlands, like the Ovenbird in Jamaica. Mr. A. Lill (pers. commun.) also found it regularly beside rocky streams in the mountains, like the Louisiana Waterthrush in Jamaica.

TABLE 6
Food of Warblers in Jamaica*

Species	Number of feedings seen	Percentage of major food types		
		Insect	Fruit	Nectar
<i>Resident</i>				
Yellow	67	100	—	—
Arrow-headed	392	96	3	1
<i>Wintering</i>				
Black-and-white**	256	96	4	—
Swainson's	32	100	—	—
Worm-eating	60	100	—	—
Parula	503	92	6	2
Magnolia	177	100	—	—
Cape May	277	71	14	15†
Black-throated Blue	372	94	2	4
Black-throated Green	374	95	5	—
Yellow-throated	61	100	—	—
Prairie	312	98	2	—
Palm**	81	100	—	—
Ovenbird**	106	100	—	—
Northern Waterthrush**	55	100	—	—
Louisiana Waterthrush**	45	100	—	—
Common Yellowthroat	97	99	1	—
American Redstart	322	100	—	—

*From mid-October to 15 April; resident species included for comparison.

**Observations include searchings as well as feedings; observations for other species include only actual feedings.

†Includes individuals taking sap from holes drilled by Yellow-bellied Sapsucker.

Resident Leaf-gleaning Species

(Tables 6, 7, 9, 10, and 11)

Yellow Warbler (*Dendroica petechia*): Resident in Jamaica; almost confined in winter to the mangroves and woodland close to shore; occurs sparsely in the immediately adjoining forest. In April, when the wintering warblers leave, it broadens its habitats by moving into marsh forest and riverine woodland, including that along the Black, Ferry, and Sweet Rivers, up to at least eight kilometers from the sea. It is the only common leaf-gleaning warbler in the mangroves. Since we concentrated on other warblers in the mangroves and tended to record only the unusual feedings of the Yellow Warbler, the percentages of feedings from the air and on the ground, in Table 7, are misleadingly high.

Arrow-headed Warbler (*Dendroica pharetra*): Resident and endemic in Jamaica; breeds commonly in montane forest and regularly in mid-elevation forest. Many stay in mountains in winter; but there is an increase in numbers in the mid-elevation forest and rich lowland forest, as in Fern Gully and above the Ferry River where we saw one or two at 100 meters elevation in summer but did not find a nest. The Arrow-headed Warbler feeds primarily on insects from the fairly thick evergreen leaves of forest trees, usually fairly high above the ground, both in the canopy and below it; at times, it feeds off twigs, branches, or tree ferns. The montane habitat of the Arrow-headed Warbler separates it from all wintering warblers except, in part, the Black-throated Blue, which is also common in some types of lowland forest (Tables 4 and 5). The Arrow-headed Warbler uses a different niche in that it takes almost all its food from leaves, typically spending much more time on one twig, peering about, and stretching farther from its perch to take an insect than does the Black-throated Blue Warbler, which gathers over half its food from twigs, ground, or air (Table 7), and tends to feed lower in the trees (Table 10), to change its perch much more often, and to move faster through the trees.

Wintering Leaf-gleaning Species

(Tables 6, 7, 9, 10, and 11)

Tennessee Warbler (*Vermivora peregrina*): Breeds across Canada in spruce and aspen forest. Occurs regularly in Jamaica in very small numbers in both lowland secondary riverine woodland and montane forest; we found one in the Kingston Botanic Garden. It takes insects off both large and small leaves, but since we saw this species too infrequently for quantitative assessment, we have omitted it from the main tables. Its small numbers are too few to compete seriously with the other warblers.

Parula Warbler (*Parula americana*): Breeds in eastern North America, most commonly in the southeast, in broad-leaved forest, swamp forest, and on the edges of coniferous forest. In Jamaica, one of the two commonest leaf-gleaners in dry, limestone lowland forest; the other is the Prairie Warbler. Small numbers of both species inhabit mid-elevation forests and both occur rarely in the mountains where they are almost restricted to introduced trees. In the lowlands, we found the Parula Warbler most common in richer, damper woodland, all secondary at the present time, and the Prairie Warbler in both natural and cut-over arid forest. This partial difference in habitat is due to

TABLE 7
Feeding Sites of Warblers in Jamaica

Species	Number of feedings observed	Insect-feeding sites*						
		Broad leaves	Conifer needles	Bromeliads	Air	Ground	Twigs	Flowers or fruit
<i>Resident</i>								
Yellow**	67	76	—	—	9	7	—	7
Arrow-headed	377	92	—	3	3	—	3	—
<i>Wintering</i>								
Black-and-white†	246	11	2	2	7	6	70	3
Swainson's	26	4	—	—	—	96	—	—
Worm-eating††	60	69	—	3	—	—	20	8
Parula	461	87	—	—	2	—	7	5
Magnolia	178	73	—	—	11	—	11	6
Cape May	198	81	—	1	11	—	4	4
Black-throated Blue	350	46	2	—	17	15	13	8
Black-throated Green	354	61	26	—	5	—	6	3
Yellow-throated	61	—	72	8	—	—	11	8
Prairie	305	84	2	—	5	1	7	2
Palm	81	9	—	—	15	77	—	—
Ovenbird	106	1	—	—	—	94	5	—
Northern Waterthrush	55	2	—	—	—	98	—	—
Louisiana Waterthrush	53	—	—	—	—	100	—	—
Common Yellowthroat	96	65	—	—	—	11	19	5
American Redstart	322	28	—	—	64	x	8	—

*Figures indicate percentages of insects taken at given site.

**Five "ground feedings" were actually from the surface of water.

†Of 27 feedings on broad leaves, 70 per cent were on living leaves and 30 per cent on dead leaves.

††Of 60 feedings, 75 per cent were on dead leaves, 18 per cent on living vegetation, and 7 per cent not recorded.

the tendency of the Parula to feed in trees with broad thin leaves and the Prairie to feed in mimosaceous trees and others with very small leaves. No doubt the two species are separated in their feeding, but we discovered the difference in their choice of leaves too late for quantitative records of the critical points. In addition to the preference for different leaf types, the Parula prefers taller and denser trees and usually feeds in the upper levels, at times near the trunk and on creepers, moving rather slowly through the vegetation. It rarely feeds in flight. The Prairie Warbler moves rapidly through low, scrubby and rather open trees, typically feeding among the leaves at the ends

TABLE 8
Feeding Sites of Ground-feeding Warblers in Jamaica*

<i>Species</i>	<i>Forest floor</i>	<i>Ground at forest edge</i>	<i>Mud in shallow water or beside it</i>	<i> Rocks by water</i>	<i>Short grass and trees</i>	<i>Any ground</i>	<i>Herbage</i>	<i>Air</i>
Swainson's	77	—	—	—	—	20	4	—
Palm	2	11	—	—	48	15	9	15
Ovenbird	30	20	2	5	8	28	7	—
Northern Waterthrush	—	—	89**	—	—	—	2	—
Louisiana Waterthrush	—	9	38	53	—	—	—	—

*Figures indicate percentages of feedings observed at a given site.

**Nine per cent on leaves of water lily (*Victoria regia*) in Kingston Botanic Garden.

of branches and in the crowns of low open trees and, while it often feeds from a perch, it also picks many insects off leaves and branches while hovering. One other species, the Magnolia Warbler, prefers the same type of tree as the Parula. In North America, in summer, the Parula may feed more from the tips of branches, at least in conifers, than it does in Jamaica (Morse, 1967, 1971). On spring passage to North America, it frequents taller trees than the Prairie Warbler (Parnell, 1969).

Magnolia Warbler (*Dendroica magnolia*): Breeds in Canada and northeastern United States, primarily in spruce and hemlock forests, especially thickets. In Jamaica, rather scarce, encountered mostly in rich lowland forest, less frequently at mid-elevations and in the mountains where it is found almost always in and at the edges of introduced trees, and absent from the arid lowlands. In the lowland forest, we found the Magnolia Warbler feeding in trees with broad thin leaves, like the longer-billed Parula Warbler, but it prefers the lower half of somewhat taller trees, whereas the Parula Warbler forages in the upper half (Table 10). Furthermore, the Magnolia Warbler moves much more rapidly through the vegetation than the Parula Warbler and takes a higher percentage of its insects off twigs and from the air. In its aerial feeding, it resembles the American Redstart. In summer in Maine, the Magnolia likewise feeds lower in the trees than the Parula (Morse, 1967, 1971).

Cape May Warbler (*Dendroica tigrina*): Breeds in spruce and fir forests of Canada and northern conterminous United States, especially in park-like areas. In Jamaica, occurs mainly in parkland and at the edges of woodland. Although the data in Table 4 suggest that it occurs mainly in the lowlands, we saw it rather often outside the census areas in open woods and partly cultivated areas at mid-elevations and in the mountains. It usually feeds in the upper levels of deciduous, not coniferous, trees with small leaves, preferring much higher trees than the Prairie Warbler. The Cape May Warbler travels

rather slowly through the trees and, unlike other warblers, may peck repeatedly — as many as 20 times — at the same leaf, suggesting that it takes extremely small, plentiful insects, such as aphids. Frequently, it takes insects in the air (Table 7) or from leaves by hovering (Table 9), and it eats more small fruits and nectar than the other parulids (Table 6), sucks sap from holes drilled in eucalyptus by the Yellow-bellied Sapsucker (*Sphyrapicus varius*), as in other kinds of trees in North America (Foster and Tate, 1966), and visits hummingbird feeders in gardens.

Myrtle Warbler (*Dendroica coronata*): Breeds in Canada and northern conterminous United States in spruce-fir forests. Arrives in Jamaica much later than the other species — we first saw it on 10 January — and although in some years it is a common transient, so few stay for the winter that we did not observe enough feeding to include it in the tables. We saw four Myrtle Warblers in mimosaceous trees in cultivated woodland near Kingston, two in introduced pines, and one in mountainous sclerophyllous forest — forest characterized by trees with small, narrow leaves. The preferred types of trees suggest potential competition with the Cape May or Black-throated Green Warblers, but the Myrtle Warbler is larger than either of them, and we did not see it feeding in the terminal twigs of the canopy or side branches, as they do, a difference that continues through the summer (MacArthur, 1958).

Black-throated Green Warbler (*Dendroica virens*): Breeds in coniferous and mixed forests in Canada and northern conterminous United States. In Jamaica, occurs regularly in woodland at all altitudes. We saw it most frequently in secondary woodland in the lowlands near Mona, and in junipers and introduced pines in the mountains, and sometimes also in natural montane forest where it usually foraged for fruits. In the lowlands, it usually feeds in small-leaved, mimosaceous trees. In this way, its niche resembles that of the Prairie Warbler, except that the Black-throated Green Warbler feeds to a greater extent in taller trees of this type, usually at the top or on the tips of the branches. More importantly, the Black-throated Green is almost absent from the lowland forest where the Prairie Warbler is common, and widespread in the mountains where the Prairie Warbler is absent. In the mountains, only the Black-throated Green feeds commonly among juniper needles and only one other leaf-gleaner, the Yellow-throated Warbler, is common in the introduced pines. While the Yellow-throated Warbler probes for food, the Black-throated Green picks insects off the needles, especially the needles at the tips of the canopy and side branches, usually when perched, but often when hovering. It does the same in summer (MacArthur, 1958; Morse, 1967).

Black-throated Blue Warbler (*Dendroica caerulescens*): Breeds in southeastern Canada and northeastern United States. In Jamaica, recorded commonly in rich lowland forest, mid-elevation and montane forest, and in cultivated woodland; absent from the arid lowland forest. It differs from the other leaf-gleaners in that it feeds much more often on the ground, in the air (Table 7), and off twigs. When feeding off leaves, it tends to be close to the ground (Table 10). Furthermore, it differs from all the other species, except the Arrow-headed Warbler, in preferring to feed in trees with broad, rather thick leaves.

Yellow-throated Warbler (*Dendroica dominica*): Breeds in southeastern North America in open pine woods and in broad-leaved trees covered with Spanish moss (*Tillandsia* sp.). In Jamaica, found regularly in small numbers in introduced pines in both lowlands and mountains; also occurs in the King-

ston Botanic Garden. When foraging, it probes its relatively long bill into the bases of pine needles or the small narrow leaves of the xerophytic species of *Tillandsia*. Ficken *et al.* (1968) and Morse (1968) described its summer feeding habits.

Prairie Warbler (*Dendroica discolor*): Breeds in eastern North America in scrubby, broad-leaved and coniferous forests and at the forest edge. In Jamaica, the commonest leaf-gleaner in all types of lowland forest except good secondary forest; occurs especially in the more open areas and places where scrubby mimosaceous trees predominate. It is sparse at mid-elevations and rare in the mountains where we found it only at the forest edge and in cultivated woodland. It takes insects off leaves at the ends of side branches and in the canopy, usually from a perch, but often by hovering. Its preference for low mimosaceous trees separates it from most other species. We described the ways in which it differs from the Parula, Cape May, and Black-throated Green Warblers in the discussions of those species.

Summary of Leaf-gleaners

Table 11 indicates the probable ways by which the nine common leaf-gleaners are isolated ecologically from each other. The two resident species,

TABLE 9

Behavior of Warblers Feeding on Insects in Trees or Herbage in Jamaica

Species	Activity of bird*				Total** of insects feedings
	Perched	Flying	Hovering	Fluttering from perch	
<i>Resident</i>					
Yellow	81	16	3	—	67
Arrow-headed	96	3	x†	—	377
<i>Wintering</i>					
Black-and-white	93	6	1	x	246
Worm-eating	100	—	—	—	60
Parula	95	3	2	x	461
Magnolia	79	12	6	3	178
Cape May	75	11	14	—	198
Black-throated Blue	72	18	8	2	350
Black-throated Green	78	5	14	3	354
Yellow-throated	98	—	2	—	61
Prairie	82	5	11	2	305
Common Yellowthroat	99	1	—	—	96
American Redstart	15	81	3	1	322

*Figures indicate percentages of insects captured by each method.

**From Table 7.

†x indicates less than one per cent.

TABLE 10

Height at Which Leaf-gleaning Warblers Feed in Jamaica

Species	Feedings at all heights			Feedings at three meters and higher				
	Number of* observations	Mean** height	Standard** deviation	Number of* observations	Percentage in			
					Lowest quarter	Second quarter	Third quarter	Top quarter
<i>Resident</i>								
Yellow	17	5.6	4.5	13	0	31	23	46
Arrow-headed	107	6.8	4.1	76	4	28	30	38
<i>Wintering</i>								
Parula	131	6.4	3.6	105	4	28	31	38
Magnolia	49	6.3	3.3	46	7	50	22	22
Cape May	39	7.6	3.5	38	0	18	34	48
Black-throated Blue	152	4.5	4.0	67	6	36	30	28
Black-throated Green	81	7.8	4.0	72	1	24	32	43
Yellow-throated	11	8.6	4.7	11	0	36	36	27
Prairie	93	5.3	4.0	59	3	34	21	42

*Each observation represents a different bird.

**Meters.

the Arrow-headed and Yellow Warblers, maintain their separation through their preference for different habitats. The wintering species differ markedly from each other in the type of leaves preferred for feeding, their feeding stations, or feeding methods. These differences might well suffice for full ecological isolation although more detailed study is necessary. We may add that no ecological separation was obvious to us when we first observed this diversity of similar-sized species in the Jamaican forests in October 1970.

Discussion

Comparison of Summer and Winter Ecology

Of the 18 species of parulid warblers wintering in Jamaica, four—the Black-and-white Warbler, Ovenbird, Common Yellowthroat, and American Redstart—occur widely in summer in eastern North America from Canada to the southern United States. The summer range of a fifth, the Parula Warbler, overlaps these four except in the north. Seven others—the Tennessee, Magnolia, Cape May, Myrtle, Black-throated Green, and Palm Warblers and the Northern Waterthrush—breed mainly in the coniferous forests of Canada and northeastern United States. The Black-throated Blue Warbler

TABLE 11

Major Mechanisms of Ecological Separation in Leaf-gleaning
Warblers in Jamaica

Yellow								
Arrow-headed	H	Arrow-headed						
Parula	H	H	Parula					
Magnolia	H	H	PS	Magnolia				
Cape May	H	H	LPS	LSN	Cape May			
Black-throated Blue	H	(H)S	(H)LS	(H)LS	LSN	Black-throated Blue		
Black-throated Green	H	(H)L	LPS	LPS	LSN	LPS	Black-throated Green	
Yellow-throated	H	H	HLP	LS	LSN	LPS	LS(N)	Yellow-throated
Prairie	H	H	LP	LS	HSN	(H)LPS	H(P)?	HL

The symbols indicate the following means of separation:

H By habitat: mangroves, lowland dry forest, mid-elevation forest, montane forest, or parkland.

L By leaf-type feeding: mainly on narrow mimosaceous leaves, broad thin leaves, pine needles, or juniper needles.

P By feeding on given part of tree: mainly in upper or lower section, near trunk, or on terminal twigs.

S By feeding station on insects: off leaves from perch, in the air, from twigs, on the ground, or for those in conifers whether or not taken from base of needles by probing.

N By type of food besides insects, mainly fruit or nectar.

A single H indicates clear-cut separation by habitat even though there may be other important differences in feeding.

An H, followed by another letter, indicates partial separation by habitat and the rest by other factors.

A letter in parentheses means that that particular difference is of less importance.

Tennessee and Myrtle Warblers omitted because of scarcity; Myrtle separated from others mainly by size and somewhat by feeding station.

breeds farther south and not as far north as these seven, and lives in broad-leaved forest instead of coniferous forest. The remaining five—the Swainson's, Worm-eating, Yellow-throated, and Prairie Warblers and the Louisiana Waterthrush—breed in eastern North America, except in the extreme northeast, and hardly come in contact with the seven northern species until they meet in Jamaica during the winter.

The ecology of at least most of these species is similar in Jamaica in winter to that in North America in summer. This is true with respect to habitat, for instance, in the Northern and Louisiana Waterthrushes and Common Yellow-throat. The Black-throated Blue prefers broad and rather thick-leaved trees in Jamaica and nests in heavy broad-leaved forest. The Black-throated Green and Yellow-throated Warblers often frequent conifers in both regions. However, some others, including the Tennessee, Magnolia, and Cape May Warblers, which breed in conifers, do not normally frequent conifers in Jamaica. The feeding methods are similar for the Black-and-white and Swainson's Warblers, Ovenbird, and American Redstart in Jamaica and North America. A comparison with the studies of MacArthur (1958) and Morse (1967) shows that the Magnolia, Cape May, Myrtle, and Black-throated Green Warblers feed in the same sites and in the same ways in Jamaica and North America. For various other species we have no published quantitative observations, but the general descriptions are consistent with what we found in Jamaica, except possibly in the Parula and Yellow-throated Warblers (Morse, 1967, 1968; Ficken *et al.*, 1968).

Evolution of Ecological Isolation

At least most of the warblers in Jamaica appear to be isolated ecologically from each other (Tables 8 and 11).

The little evidence so far available (reviewed in Lack, 1971) suggests that a young passerine finds the habitat of its species partly through innate factors and partly through experience—what it sees when recently fledged and in the company of its parents. In contrast, the specific feeding stations and feeding methods seem mainly to be acquired through experience, the young passerine gradually discovering for itself which methods are the most rewarding, although it may also learn by watching others of its kind. The main factors responsible for success or failure in feeding are the bird's morphological, or physical, adaptations in bill, leg, musculature, and so on. This explains why species of the same genus that live in the same habitat often differ greatly in size of bill. Otherwise, they might seriously compete with each other for food. *Dendroica* warblers seem exceptional, both in the large number of coexisting species and in the small differences in the morphology of the different species. Nevertheless, differences exist and, though slight, might well be sufficient to promote ecological isolation.

A species that shares its mainland range with a congener may, on an island where the congener is absent, expand its ecological niche. Under these circumstances in the Southwest Pacific, frequent expansions occur in type of habitat, altitudinal zone, or a vertical feeding zone within a forest, but an expansion in foraging techniques or diet is rare without a marked morphological change in the island form concerned (Diamond, 1970).

The fact that at least 19 of the 20 wood warblers in Jamaica in winter differ in important ways from each other in ecology cannot be due to chance, and, presumably, means that competitive exclusion operates in the winter



Arrow-headed Warbler, *Dendroica pharetra*. Painting by John Henry Dick.

quarters. Jamaica, like other oceanic islands, has relatively few resident passerine species, and these few are characterized by relatively broad ecological niches. On the other hand, it has many wintering warblers with relatively narrow ecological niches, characteristic of passersines on continents. This contrast suggests that the warblers probably evolved the differences, on which their ecological isolation in Jamaica depends, on their continental breeding grounds. This view may need some modification since the wintering species from Canada do not meet those from southeastern United States when on the breeding ground. Furthermore, at least one species has modified its preferred habitat in the winter quarters. The Northern Waterthrush has a much broader habitat on Trinidad than in Jamaica.

In addition to the 18 regular wintering parulids, 12 North American warblers occur as transients in Jamaica: Prothonotary (*Protonotaria citrea*), Golden-winged (*Vermivora chrysoptera*), Blue-winged (*V. pinus*), Nashville (*V. ruficapilla*), Caerulean (*Dendroica cerulea*), Blackburnian (*D. fusca*), Chestnut-sided (*D. pensylvanica*), Bay-breasted (*D. castanea*), Blackpoll (*D. striata*), Pine (*D. pinus*), Kentucky (*Oporornis formosus*), and Hooded (*Wilsonia citrina*). Moreover, since there are few bird watchers in Jamaica, there may be still other species that occur there occasionally.

The transients would surely stay for the winter if they could live better there than elsewhere. Competition from the two resident species and 18 wintering species is probably the main reason for their moving on. Hence, even if the feeding adaptations of each species have evolved primarily in relation to the breeding grounds — which is not certain — these adaptations are critical in determining which of the warblers can survive the winter in Jamaica.

The nearest mainland to Jamaica is Honduras which, according to Monroe (1968), has about 242 breeding passerine species of which 14 are parulids; Jamaica has 35 breeding passersines with two parulids. Comparing Honduras and Jamaica, the number of breeding species in Jamaica is only 14 per cent of the number in Honduras; similarly, the number of breeding parulids in Jamaica is 14 per cent of the number in Honduras. Such figures are typical of the difference in numbers of species between a continental area and an oceanic island. In winter, the proportion changes: Honduras has 30 regular visiting parulids; Jamaica has 18 — 60 per cent of the number in Honduras. Of the 30 in Honduras, 13 are regular in winter in Jamaica and another six are transients. The Swainson's, Parula, Cape May, Black-throated Blue, and Prairie Warblers winter regularly in Jamaica but not in Honduras.

The traditional explanation for the small number of resident land birds on oceanic islands is the difficulty of dispersal from the mainland. We doubt this in general (Lack, 1969). Anyway, it does not hold for parulids in Jamaica. In addition to the two resident warblers, another 30 parulids have been recorded there, many of them regularly. What prevents at least some of these 30 from evolving breeding populations on Jamaica? That only two species breed on Jamaica conforms with the general proportion in numbers of terrestrial species compared to the nearest mainland; so whatever factors are responsible for fewer species breeding evidently operate on the warblers in summer. Why do these factors not operate in winter? Moreover, this high number of wintering species in Jamaica holds solely for parulids. Only two other North American passersines are regular in Jamaica in winter, the Catbird (*Dumetella carolinensis*), which is very sparse, and the Indigo Bunting (*Passerina cyanea*),

which appears locally, mainly after 21 December. The only other wintering land bird, the Yellow-bellied Sapsucker, occurs widely on the island.

The problem of bird species diversity with respect to winter visitors deserves further attention, and the parulids, with numerous species, afford an excellent opportunity for studying the problem. In particular, we need figures for other islands. Fewer parulid species winter in Puerto Rico (C. B. Kepler and A. K. Kepler, pers. commun.) than in Jamaica, and still fewer winter in the Lesser Antilles. In Jamaica, only the Yellow Warbler breeds in the lowlands — in mangroves and littoral and riverine woodland. Great areas of arid and semi-arid limestone forest are untenanted. Surprisingly, no other species of warbler summers in the lowlands — unless we consider the Bananaquit (*Coereba flaveola*) a parulid. We cannot comment further on this point without knowledge of the seasonal variations in the numbers of insects available to the warblers.

Foraging Parties

Insectivorous birds of diverse species characteristically form foraging parties in both tropical forest and north temperate woodland. Warblers join such parties in both winter and summer quarters (Eaton, 1953; Morse, 1970). In a typical party, the flock moves steadily through the forest, each individual keeping from one to a few meters from its nearest neighbors, maintaining contact by calls, and feeding in its specific fashion. In Jamaica, we observed no foraging parties.

Instead of foraging parties, we saw what we called "collections." When we stopped to observe a bird feeding, we often spotted an individual of another species a few meters away, though rarely as close as two meters. A collection might include up to five or six, rarely as many as eight, birds with not more than two of the same species, feeding in an area of perhaps 40 meters square. Both ground-feeding and arboreal parulids are frequently a part of such a collection, and they may associate with virtually any of the resident forest birds — other passerines, woodpeckers, or doves. A collection differs from a typical foraging party in that only a small number of individuals are involved, the individuals are more widely spaced, there are no regular contact calls, and the birds do not travel together through the forest. Instead, each stays near where first seen for several minutes and then gradually drifts away, seeming to be independent of the others.

At first, we thought we might be seeing apparent collections because, when we saw a bird, we usually stopped to watch it feeding, and perhaps we were seeing more birds in the forest when standing still than walking. However, on random stops in the forest, we often saw no birds, and saw no more standing still than walking. We ruled out the possibility that the collections might be the result of a purely random distribution since they were so definite and so frequent. At the same time, we should not exaggerate their frequency; we saw the species concerned singly more often than in collections. Most collections occurred where both parulids and resident birds were sparse, in very arid lowland forest and in montane forest; this was probably because we noticed such collections more readily where the birds were sparse. Where birds were more numerous, a group of a few widely spaced individuals did not attract our attention. We have, of course, excluded here the instances in which several birds fed at a common food source — a fruiting tree or a swarm of insects. In a collection, each bird feeds on its own, each species often in a different

way from the rest; and while the collection includes mostly insectivorous birds, a seed-eater or fruit-eater sometimes joins the group.

Why are typical foraging parties absent from Jamaica? Such parties that include warblers occur on other islands of the Greater Antilles, including Cuba (Eaton, 1953), Hispaniola, and Puerto Rico (C. B. Kepler and A. K. Kepler, pers. commun.). The Jamaican forest has no avian predators on passerine birds; Cuba, Hispaniola, and Puerto Rico do have — accipitrine hawks. Although this fits with the theory that an advantage of feeding in mixed flocks is that several birds are more likely than one to notice an approaching predator (Lack, 1954), we are reluctant to believe that the absence of avian predators is the main factor responsible for the absence of foraging flocks in Jamaica.

Summary

At least 19 of the 20 parulid warblers found in Jamaica in winter have marked ecological differences from each other: One climbs branches and twigs; one feeds from hanging dead leaves and twigs; one lives in thick herbage; and one flycatches. There are also five ground-feeders — four separated by the type of terrain; two, inhabitants of the same terrain, are separated by feeding method — one probes and the other picks. Of the 11 leaf-gleaners, the two resident species are separated largely by habitat; the rest mainly by feeding methods, the parts of the tree in which they feed, or the type of leaf from which they take insects.

In Jamaica, where the Northern Waterthrush, Louisiana Waterthrush, and Ovenbird occur, the Northern Waterthrush confines its activities to mud in the lowlands; in Trinidad, where the Louisiana Waterthrush and Ovenbird do not occur, the Northern Waterthrush broadens its habitat to include the edges of rocky streams and dry forest.

Various warblers frequent riverine forest in Jamaica in winter; when the visitors leave in April, Yellow Warblers move into the riverine forest to breed. No warblers breed in the lowland, dry limestone forest.

The number of breeding passersines on Jamaica is 14 per cent of that in Honduras; the proportion of breeding parulids is the same. The small number of parulids breeding in Jamaica is not due to the failure of other parulid species to reach the island. Another 30 species have been recorded there.

Eighteen warblers regularly winter in Jamaica, 60 per cent of the number wintering in Honduras. Another 12 warblers occurring in Jamaica as transients are presumably excluded by competition with the winter residents. We do not know why the factors responsible for the low species diversity and broad niches of resident land birds on oceanic islands, including Jamaica, do not operate just as intensely in winter as in summer.

We did not see foraging parties of insectivorous birds in Jamaica, but we did see parulids and resident forest species sometimes feeding near each other in loose "collections" of from two to eight individuals. Foraging parties occur in Cuba, Hispaniola, and Puerto Rico, and so do accipitrine hawks. There are no accipitrine hawks in Jamaica.

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LITERATURE CITED

- ASPREY, G. F., and R. G. ROBBINS**
 1953 The vegetation of Jamaica. *Ecol. Monogr.*, 23:359-412.
- BENT, A. C.**
 1953 Life histories of North American wood warblers. *U. S. Natl. Mus. Bull.* 203.
- CHAPMAN, F. M.**
 1917 The warblers of North America. Third edition. D. Appleton and Company, New York.
- DIAMOND, J. M.**
 1970 Ecological consequences of island colonization by Southwest Pacific birds. I. Types of niche shifts. *Proc. Natl. Acad. Sci.*, 67:529-536.
- EATON, S. W.**
 1953 Wood warblers wintering in Cuba. *Wilson Bull.*, 65:169-174.
- FICKEN, R. W., M. S. FICKEN, and D. H. MORSE**
 1968 Competition and character displacement in two sympatric pine-dwelling warblers (*Dendroica*, Parulidae). *Evolution*, 22:307-314.
- FOSTER, W. L., and J. TATE, JR.**
 1966 The activities and coactions of animals at sapsucker trees. *Living Bird*, 5:87-113.
- LACK, D.**
 1954 The natural regulation of animal numbers. Oxford University Press, London.
 1969 The numbers of bird species on islands. *Bird Study*, 16:193-209.
 1971 Ecological isolation in birds. Oxford University Press, Cambridge.
- MACARTHUR, R. H.**
 1958 Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39:599-619.
- MEANLEY, B.**
 1966 Some observations on habitats of the Swainson's Warbler. *Living Bird*, 5:151-165.
- MONROE, B. L., JR.**
 1968 A distributional survey of the birds of Honduras. *Amer. Ornith. Union, Ornith. Monogr.* No. 7.
- MORSE, D. H.**
 1967 Competitive relationships between Parula Warblers and other species during the breeding season. *Auk*, 84:490-502.
 1968 A quantitative study of foraging of male and female spruce-woods warblers. *Ecology*, 49:779-784.
 1970 Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.*, 40:119-168.
 1971 The foraging of warblers isolated on small islands. *Ecology*, 52:216-228.
- PARNELL, J. F.**
 1969 Habitat relations of the Parulidae during spring migration. *Auk*, 86:505-521.
- RIDGWAY, R.**
 1902 The birds of North and Middle America. *U. S. Natl. Mus. Bull.* 50, pt. 2.
- ROBBINS, C. S., B. BRUUN, and H. S. ZIM**
 1966 Birds of North America: a guide to field identification. Golden Press, New York.
- SCHWARTZ, P.**
 1964 The Northern Waterthrush in Venezuela. *Living Bird*, 3:169-184.