SEASONAL FORAGING SPECIALIZATION IN THE WORM-EATING WARBLER[1]

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Abstract. The foraging behavior of Worm-eating Warblers (*Helmitheros vermivorus*) was studied in Maryland during the breeding season and in Jamaica, Dominican Republic, and Belize during the nonbreeding season. Over 75% of the foraging maneuvers recorded from May to early August in Maryland were directed towards live foliage, whereas over 75% of the maneuvers were directed towards dead curled leaves in the understory of tropical forest in the temperate zone winter. Sampling of the relative abundance of arthropods associated with dead and live foliage showed that although the ratio of total numbers in dead and live leaves was similar in the temperate and tropical sites, the overall ratio of estimated biomass was considerably greater in the tropical sites. This is because large arthropods commonly use dead curled leaves as daytime roosts in tropical forests. However, the largest temperate-zone arthropods are generally found on leaf surfaces during the day. The winter-foraging specialization on dead leaf arthropods apparently is the more demanding; the most specialized search and attack behaviors are associated with feeding at dead and live curled leaves. I revisited the Belize study sites in September, when Worm-eating Warblers were presumably arriving and found an intermediate use of dead and live leaves. Relative abundances of arthropods on dead and live leaves were similar to those found in the winter period at the same sites. This suggests a period of transition which is consistent with the trial and error learning hypothesis for the development of seasonal foraging specializations in this species.

Key words: Helmitheros; Parulinae; foraging behavior; insectivorous bird; specialization.

INTRODUCTION

Migratory birds often move between habitats that are very different, such as temperate woodlands and tropical forests. They, therefore, provide an excellent focus for studies on how birds make foraging decisions in changing environments (Baker and Baker 1973, Greenberg 1979, Bennett 1980, Rabenold 1980, Hutto 1981, Greenberg 1984). Although most migrant passerines forage in a similar manner throughout the year, a few species shift between distinct specializations. The study of such species may provide insight into how prey distribution differs between comparable habitats. Such insight may be of general interest, because despite recent interest in latitudinal gradients, few data are available comparing the abundance and distribution of tropical and temperate arthropods (but see Schoener and Janzen 1968).

The Worm-eating Warbler (*Helmitheros vermivorus*) has been reported in the nonbreeding season to be a specialist at searching for arthropods in the aerial leaf litter (Willis 1960, Lack

and Lack 1972, Rappole and Warner 1980), which consists of dead curled leaves suspended from forest understory plants. It shares this specialization with a number of resident species in Central and South America, particularly in *Philydor*, *Myrmotherula*, *Automolus*, and *Thryothorus* (Remsen and Parker 1983, Gradwohl and Greenberg 1984). Because the Worm-eating Warbler moves between temperate and tropical habitats, its study may provide insight into the factors that promote dead leaf specialization in tropical birds. In this paper I describe the seasonal change in foraging site selection between temperate and tropical areas and differences in prey abundance in live versus dead foliage on the breeding and wintering range.

The Worm-eating Warbler breeds throughout a large portion of eastern United States (AOU 1983), occurring primarily in broad-leafed forests on hill slopes or ravines; in such areas they can be quite common (Bent 1953, Stewart and Robbins 1958, Griscom and Sprunt 1957, Mengel 1965, Hall 1983). During the temperate-zone winter they have been reported from moist tropical forest of Central America and the West Indies (Russell 1964, Lack and Lack 1972, Ter-

borgh and Faaborg 1980, Rappole and Warner 1980).

For a species so widespread in North America, the behavior of the Worm-eating Warbler is poorly understood. Dating from Brewster (1875) and Burns (1905) most authors have reported that Worm-eating Warblers are largely terrestrial and *walk* on the forest leaf litter (Forbush 1928, Griscom and Sprunt 1957, and many others). Bennett's (1980) study, however, was probably the first to record that Worm-eating Warblers were primarily arboreal live-foliage gleaners on the breeding grounds. Several authors have observed that this species occasionally switches back and forth along limbs in a manner reminiscent of the Black-and-white Warbler (*Mniotilta varia*) (Brewster 1875).

During the winter Worm-eating Warblers are consistently reported to probe into dead leaves (Lack and Lack 1972; Willis 1960, 1980; Rappole and Warner 1980) and to a lesser extent glean twigs, branches, and vines (Gosse 1847, Rappole and Warner 1980). Still, most observers have suggested that they are either terrestrial or restricted to shrubbery near the ground (Skutch 1957, Lack and Lack 1972, Terborgh and Faaborg 1980; but see Rappole and Warner 1980). There are few quantitative data on the foraging behavior of Worm-eating Warblers (but see Lack and Lack 1972).

STUDY SITES

I studied the foraging ecology of the Worm-eating Warbler from May to August 1983 and 1984 at Sugarloaf Mountain (elevation 350 m), 10 km southeast of Frederick, Maryland. Worm-eating Warblers occurred in densities of 100 to 150 pairs/100 ha mainly in the Chestnut Oak (*Quercus prinus*) dominated woods that covered the south-facing slopes.

For the nonbreeding season I was particularly interested in generalizing about the feeding behavior of the Worm-eating Warbler as a species, and so I worked in several widely separated areas. In particular I wanted adequate representation for both West Indian and Central American sites. All of the following sites were visited in January and February 1984. In addition, I returned to the Belize sites in September 1984 during the period of arrival of Worm-eating Warblers.

Monte Bonito, Los Haitises National Park approximately 10 km north of Trepada Alta and 15 km southwest of La Sabana, Dominican Republic (elevation 100 to 200 m): 20 January to 5 February 1984. This was an area of moist forest on low limestone hills and valleys with an annual rainfall averaging approximately 2,000 mm (Dominican Parks Office).

Windsor Caves, Trelawny Parish, Jamaica (elevation 100 to 300 m): 10 to 20 January 1984. This location is 32 km southeast of Montego Bay at the southern edge of the "cockpit country," an area of hilly karst topography covered by mature moist limestone forest (2,000 to 3,000 mm annual rainfall, Lack 1976).

Hardwar Gap, St. Andrews Parish, Jamaica (elevation 1,000 to 1,500 m): 5 to 10 January 1984. I searched the moist montane forest of the forest reserve on Catherine's Peak. This forest, which receives over 2,000 mm of rainfall each year (Cruz 1976), is of low stature (10 to 15 m) with a dense understory of ferns including tree ferns (*Cyathea*) and moss and epiphyte-covered logs.

Hummingbird Highway, Cayo District, Belize (elevation 100 to 300 m): 10 to 25 February; 25 September to 10 October 1984. This area consists of heavily disturbed moist limestone forest on rolling hills adjacent to the first 19 km of highway between Belmopan and Dangriga, Belize. Although the forest has remained uncut (until very recently), two hurricanes in the early 1960s levelled most of the large trees, and the regrowth was low in stature (15 to 25 m) and heavily dominated by palms at the time of the study.

Salamanca, 8 km northwest of San Antonio de Viejo, Toledo District, Belize (elevation 100 to 300 m): 17 to 25 February and 29 September to 10 October 1984). I worked along two trail systems: the first traversed old growth forest connecting Salamanca with Esperanza Camp in the foothills of the Maya Mountains. The forest was very wet (3,000 to 4,000 mm annual rainfall, D. Wyer, pers. comm.), undisturbed, and had an impressively tall canopy (30 to 40 m) and a relatively open understory (except for tree fall gaps and clearing edges). The second trail system passed through second-growth forest with 25 to 30 m canopy and a relatively thick understory.

METHODS

FORAGING BEHAVIOR

Observations during the breeding season were taken mostly in the course of searching for nests. To reduce noise, I recorded my data in field note-

books rather than on an audio-cassette recorder. Each field day I traversed a number of territories (from a total population of 20 pairs) searching for adults of both sexes. Upon locating a warbler I recorded its foraging height and the type and substrate of each foraging maneuver. A maneuver consisted of any lunge or peck at a substrate. Such actions are common and easily discerned in Worm-eating Warblers because they usually peck or probe at surfaces in the course of searching for prey. Because long sequences of maneuvers ($\bar{x} = 10$, range 1–40) were taken from some individuals, I made an effort to locate many different birds each day to increase the independence of the observations. In addition, I generally used the individual sighting rather than each foraging maneuver as an observation for statistical testing.

At each of the nonbreeding study sites I walked several kilometers of trail each day to locate different warblers. I recorded continuous observations of foraging behavior on a cassette recorder so that foraging events could be timed.

Maneuver types included: *glean*, reaching, pecking or probing from a normal perching bird posture; *sally*, consists of upward flight or strike; *hang-down*, grasp perch or leaf and extend body downwards; *hang-side*, grasping on side or undersurface of leaf with head pointed horizontally; *hang-up*, grasping side of leaf with head pointed upward; *lean*, leaning over the side of a leaf or branch with no extension of legs (often involved in alternate motions or "switching" back and forth); *crane*, extension of legs and neck upward from perch. In addition, I recorded whether the bird grabbed a leaf or twig in its bill and manipulated it with its feet.

Foraging substrate included: *live leaf* (adding species for temperate localities and size and shape for tropical localities), *dead leaf* (adding species for temperate location, estimated length and some distinct types such as *Cecropia* and palms for tropical localities, also single or clustered), *vine*, *twig* (<1 cm diameter), *branch* (>1 cm diameter), *flower cluster*, *fruit cluster*, *epiphyte*, and *fern frond*.

ARTHROPOD ABUNDANCE

I used census techniques previously developed for estimating the abundance of arthropods in dead and on live leaves in tropical forests (Greenberg and Gradwohl 1980; Gradwohl and Greenberg 1982, 1984; Greenberg 1984). Each census

of live leaves was conducted between 10:00 and 15:00 hr along routes parallel to trail sections distributed through the study site. I sampled the closest 50 leaves (or fraction thereof) from each plant within arm's length as I walked within 2 m of the trail. A total census generally consisted of 50 shrubs or saplings totalling 2,500 leaves; at most study sites I conducted four censuses totalling 10,000 leaves. I censused during several periods of the breeding season: May 1984, early June 1983 and 1984, early July 1983 and 1984. Because thickets of Mountain Laurel cover approximately 40% of the forest floor at the breeding sites, I stratified the sampling during that season so that during each census I examined 1,000 laurel leaves and 1,500 leaves of other shrubs and saplings.

On each census I recorded the number, size (length in mm, excluding wings), general color, and gross taxonomy (orders or families) of arthropods on leaf surfaces.

Along nearby transects I collected dead curled leaves from 1 to 2 m height in the understory. These comprised mainly fallen leaves lodged in understory shrubs. I collected the first 100 leaves within arm's length of the straightline transect through the forest, with the dual restriction that no more than five leaves were collected from the same shrub or tree and palm leaves were avoided (the collecting method made it impractical to sample arthropods of large palm fronds). Leaves from each sample were placed into one large plastic bag, which was then either injected with ethyl acetate or placed in a freezer to kill or slow the arthropods.

For live and dead leaf censuses I compared the numbers of arthropods (excluding ants and large wasps) per sample. I then converted arthropod numbers to crude live biomass based on length-weight regressions for forest arthropods (Zug and Zug 1979) and compared these estimates between live and dead leaf samples.

SIZE DISTRIBUTION OF DEAD LEAVES

At each study site I measured the dead curled leaves collected in the arthropod censuses to estimate the size distribution of available dead leaves. These estimated distributions represent my best estimate of the relative abundance of different leaf types in the aerial leaf litter but have two potential biases: (1) only low understory leaves were collected, and (2) large clumps of one leaf type were under-represented because I only

TABLE 1. Mean proportion of visits to various microhabitats in the major study sites (standard error in parentheses).

Site	n	Typical DL	"Tropical"[a] DL	Total DL	Vine	Twig	Branch	Dead twig	Live leaves	Other[d]
Monte Bonito, DR	30/402[b]	63 (5)	17 (6)	81 (4)	8 (2)	6 (2)	3 (1)	+[c]	2 (1)	0
Windsor, Jmca	39/390	67 (5)	3 (1)	70 (3)	8 (2)	10 (3)	0	4 (2)	11 (4)	0
Belize winter	28/320	47 (6)	37 (6)	84 (5)	10 (3)	3 (2)	0	0	+	0
Belize fall	25/310	40 (7)	18 (6)	58 (6)	7 (2)	+	2 (1)	0	31 (3)	0
Maryland 1983	105/1,027	7 (+)	0	7 (+)	0	1 (+)	2 (+)	0	85 (3)	4 (1)
1984	79/845	15 (3)	0	15 (3)	0	+	7 (2)	0	72 (3)	6 (1)
Mean	184/1,870	11 (2)	0	11 (2)	0	+	4 (1)	0	78 (3)	5 (1)

[a] "Tropical" dead leaves include palms, epiphytes, and tree ferns.
[b] Individuals/maneuver.
[c] Less than 1%.
[d] Laurel blossoms and ground.

collected a maximum of five leaves from one plant. I have no reason to suspect that either of these biases should systematically influence the results. Because I specifically excluded palm leaves from the collections, I cannot estimate their relative abundance in the aerial leaf litter. When I compared the types of leaves that the Worm-eating Warblers use with their proportion in the aerial leaf litter, I have excluded the number of palms from both the foraging and availability data.

RELATIVE ABUNDANCE OF DEAD CURLED LEAVES

I conducted a number of censuses at the Belize and Maryland study sites to determine if there were gross differences in the dead leaf : live leaf ratio, at least in the low understory. At each site I walked transects parallel to haphazardly selected sections of trail. At each shrub or vine encountered I encircled the closest 50 live leaves (or fraction thereof) and counted the number of dead leaves enscribed by this volume. For this census of total available dead leaves, I included dead palm leaves. I conducted a total of 10 such transects in September at the Belize study sites and 10 in July at the Maryland study site.

RESULTS

FORAGING MICROHABITAT

Worm-eating Warblers foraged primarily at dead curled leaves in the forest understory at all three major nonbreeding study sites (Table 1). In midwinter an average of approximately 75% of the maneuvers recorded from 107 individuals were directed towards dead leaves. A similar value (79%) was obtained by summing the number of seconds spent on dead leaves as opposed to other

substrates ($n = 14,682$ sec). The use of dead leaves was followed by searching of various types of bark or rotting wood; live leaf maneuvers were decidedly rare comprising only 10 of the 1,112 maneuvers during the mid-winter period (nine of these observations were for visits to noticeably damaged leaves). Some variation was observed among the tropical sites: the two major Antillean sites (Dominican Republic and Windsor Caves, Jamaica) had small, but significantly lower mean proportions of dead leaf maneuvers than the Belizean site (72% versus 84%, Mann-Whitney $U = 243$, $n = 107$, $P < 0.01$). The higher use of dead leaves in Belize is mostly due to a high rate of visitation to palm leaves. If only "typical" broad leaves (excluding palms, epiphytes, and ferns) are considered, then their use by the West Indian birds surpasses that of the Belizean birds 65% to 50% ($U = 270$, $n = 107$, $P < 0.01$). The small amounts of data from the montane forest at Hardwar Gap indicate that use of vines, branches, and tree fern shoots surpasses visitations to dead leaves (65% versus 35% respectively, $n = 10$ individuals and 55 maneuvers), but no live leaf foraging was observed.

During the fall period at the Belize study sites, I found dead leaf foraging to be less common ($\bar{x} = 55\%$) and live leaf foraging to be more common than during the mid-winter. Both the reduced use of dead leaves and the increased use of live leaves were significantly different from the mid-winter data at the same sites (live leaves $U = 334$, $n = 25$, 28 individuals, $P < 0.001$; dead leaves $U = 310$, $P < 0.001$).

During the breeding season I observed Worm-eating Warblers to forage primarily off live foliage ($\bar{x} = 78\%$). Dead leaf maneuvers were uncommon: comprising only 11% of all maneuvers

TABLE 2.   Availability and use of large and "tropical" dead leaf types by Worm-eating Warblers at the major study sites.

Site	% Unusual used[a]	% Available	χ^2	% Large[b] used	% Available	χ^2
Dominican Republic	8 (18)	3	$P < 0.001$	21	8	$P < 0.001$
Windsor, Jmca	10 (10)	3	$P < 0.01$	12	5	$P < 0.01$
Belize	0 (37)	3	ns	31	14	$P < 0.001$
Maryland	0	0	ns	0	0	ns

[a] Number in parentheses includes use of dead palm leaves. Since palm leaves were not collected on arthropod censuses no expected value could be calculated for use of unusual leaves including palm leaves. Includes palms, ferns, and epiphytes.
[b] >20.5 cm long.

over both seasons. This is significantly lower than the pooled data from the three major tropical sites at mid-winter (U = 6,676, n = 270, $P <$ 0.0001).

In the early breeding season (May) maneuvers directed to oaks (*Quercus prinus*) comprised 80% (SD = 8.9%) of all foraging, but this proportion declined rapidly to 13.7% (SD = 27) after the first of June. The seasonal difference is significant (U = 3,234, n = 164, $P <$ 0.001). In contrast, early season use of understory shrubs, particularly mountain laurel is negligible but increases dramatically during June and July (2.1 to 48%, U = 1,724, n = 164, $P <$ 0.001). This shift corresponds to the timing of new leaf and flower production, which occurs in early to mid-May in oaks and in late May to mid-June in mountain laurels. In addition, Worm-eating Warblers travel with their fledged young into thickets denser than those in which they place their nest.

Despite the fact that Worm-eating Warblers move into the understory as the summer progresses, dead leaf visitation showed no strong seasonal pattern during the breeding season. The average proportion of dead leaf maneuvers was 11% for the early (May to mid-June) and 7% for the late season (June to July) (U = 217, n = 180, n.s.). There were some indications that foraging substrate preference was adjusted in response to temporary conditions. In early May of 1984, severe cold and windy conditions seemed to depress bird activity in the emerging oak canopy and most Worm-eating Warblers foraging in the understory visited dead curled leaves. In the period 1 to 4 May (good weather) the average percent maneuvers to dead leaves was 2.5% (10 individuals, 89 maneuvers); the average percent from 5 to 10 May (poor weather) was 50% (10 individuals, 141 maneuvers); and for 11 to 13 May (good weather) the percent visitation was 4% (n = 13, 123 maneuvers). The variation in

the visits to dead leaves/individual across time periods was significant (Kruskall-Wallis χ^2 = 88.4, df = 2, n = 33, $P <$ 0.001).

TYPES OF DEAD LEAVES VISITED

Worm-eating Warblers are rather catholic in their use of dead leaf types in the field (Table 2). Foraging observations from all of the nonbreeding sites include relatively large percentages for tropical leaf morphotypes (palm, epiphyte, and tree fern) as well as very large leaves (>20.5 cm long). Visits to large leaves comprised 5 to 22% of the total leaf visits and 17 to 22% of the total foraging time (excluding travel time); visits to tropical morphotypes comprised 2 to 42% of the total visits. No visits to large or unusual leaves were recorded from the Maryland breeding site. This difference is largely a result of the lack of such unusual leaves in the temperate zone aerial leaf litter. In addition, Worm-eating Warblers tend to visit large and unusual leaves out of proportion to their abundance in the leaf litter as sampled (Table 2).

FORAGING MANEUVERS

During the breeding season Worm-eating Warblers used the glean maneuver almost exclusively (Table 3). Upward-strike, hanging, and leaning comprised less than 10% of the maneuvers. In contrast, Worm-eating Warblers commonly used various types of hanging maneuvers on the wintering sites (28 to 40%). The difference between the pooled nonbreeding data and the breeding data is significant (χ^2 = 363, df = 3, $P <$ 0.0001). During the breeding season, when hanging was rare, such maneuvers were significantly associated with foraging at live leaf curls or dead leaves; 73% of the hanging maneuvers observed were at such leaves yet visits to curled leaves comprised only 15% of the total leaf forages (χ^2 = 198, df = 2, n = 109, 1500, $P <$ 0.001). Other foraging

TABLE 3.   Percentage of foraging maneuver types found in Worm-eating Warblers from the major study sites.

Location	n	Perch-glean	Hang-down	Hang-side	Hang-up	Lean	Hover	Grab
Monte Bonito	402	62	30	4	1	2	+[a]	4
Windsor, Jmca	390	60	32	7	+	+	0	2
Belize	320	72	19	5	2	3	0	2
Maryland	1,870	90	7	0	+	+	2	+

[a] Less than 1%.

specializations that are associated with foraging in dead leaves or leaf curls include gaping, in which the bill is inserted into a crevice or hole and opened, and grabbing which occurred in 3 to 5% of all dead leaf forages.

ESTIMATED SUCCESS RATE AT DEAD AND CURLED LEAVES

Because Worm-eating Warblers examine each dead leaf and live curled leaf individually, it is possible to estimate rates of foraging success. When successful, warblers either extract the prey or immediately bill-wipe upon removal from leaf. Still, Worm-eating Warblers are often difficult to observe in dark viny vegetation and the success rates obtained are minimal estimates, particularly for the tropical sites. No differences in success rates were found between breeding and non-breeding season (breeding season 7% or 22/296 of the leaves checked; nonbreeding 5% or 50/1058). However, large items (> 1 cm) comprised 48% of the tropical and only 14% of the temperate foraging prey captures ($x^2 = 12$, df = 1, $n = 50, 22, P < 0.01$). Visits to curled live leaves were recorded almost exclusively for the early breeding season (May), when I observed 109 such maneuvers (only four during the nonbreeding

season). Worm-eating Warblers showed very high foraging success at this microhabitat (36%), where most prey items were large caterpillars (72%), which sew themselves in the leaves to make these curls. The success rate for Worm-eating Warblers at the Belize site in September was similar to the overall winter average and the average for the same sites for February (5.8% fall versus 5.9% winter).

THE RELATIVE ABUNDANCE OF POTENTIAL PREY IN DEAD AND LIVE LEAVES (TABLE 4)

To assess the *relative* availability of food in dead and live leaves, I have examined the ratios of arthropod abundance and estimated biomass. Although the ratios of the number of arthropods in dead versus live leaves were not greatly different between the temperate and tropical sites (18:1 for temperate and 35:1 for tropical mid-winter samples, data in Table 4), the ratios of estimated biomass were widely disparate (25:1 versus 153:1) because of the large difference in the distribution of arthropods greater than 5 mm in length which constitute most of the overall biomass.

A comparison of the relative arthropod abundance for the Belize study sites in the fall and

TABLE 4.   The mean number (and standard error) of arthropods in samples of 100 dead and 2,500 live leaves.

Location	n[a]	Dead leaf	Live leaf	DL/LL ratio[b]
Dominican Republic	10/4	19.8 (2.8)	17.8 (2.2)	28:1
Windsor Caves, Jamaica	7/4	13.4 (1.5)	8.8 (0.5)	39:1
Hardwar Gap, Jamaica	5/2	7.5 (2.7)	11.0 (1.3)	17:1
Salamanca, Belize (winter)	5/4	25.2 (2.2)	11.0 (0.8)	57:1
Hummingbird, Belize (winter)	7/4	13.2 (2.7)	9.3 (1.1)	35:1
Salamanca, Belize (Fall)	5/4	26.3 (3.3)	28.8 (2.3)	23:1
Hummingbird, Belize (Fall)	5/4	25.8 (0.9)	15.2 (2.7)	43:1
Maryland (June 1983)	5/4	19.4 (4.8)	10.0 (2.3)	49:1
(July 1983)	5/4	11.3 (1.9)	15.8 (1.6)	18:1
(May 1984)	5/4	7.2 (2.2)	9.3 (1.6)	19:1
(June 1984)	5/4	3.8 (1.5)	19.9 (6.9)	5:1
(July 1984)	5/4	9.3 (1.7)	19.1 (5.8)	12:1

[a] The number of samples, live leaf samples consisted of 2,500 and dead leaf samples of 500 leaves.
[b] The ratio in column 4 is based on a per leaf number.

TABLE 5. Mean (standard error) of estimated weights (g) of arthropods per 2,500 live leaves and 100 dead leaves (estimate based on substituting measured lengths in length weight regression).

Location	Dead leaves	Live leaves	Ratio
Monte Bonito, Dominican Republic	1.21 (0.28)	0.09 (0.02)	361:1
Windsor Caves, Jamaica	0.28 (0.06)	0.08 (0.04)	93:1
Hardwar Gap, Jamaica	0.20 (0.09)	0.05 (0.01)	100:1
Salamanca, Belize (winter)	2.88 (0.90)	0.82 (0.21)	90:1
Hummingbird, Belize (winter)	1.22 (0.21)	0.23 (0.19)	88:1
Salamanca, Belize (fall)	5.42 (1.50)	0.30 (0.09)	493:1
Hummingbird, Belize (fall)	1.62 (0.33)	0.48 (0.08)	93:1
Maryland (June 1983)	0.61 (0.10)	0.25 (0.13)	61:1
(July 1983)	0.39 (0.08)	1.49 (0.43)	7:1
(May 1984)	0.37 (0.18)	0.30 (0.22)	33:1
(June 1984)	0.12 (0.06)	0.14 (0.08)	22:1
(July 1984)	0.36 (0.09)	2.46 (0.39)	4:1

the winter shows that the overall ratio of dead leaf:live leaf biomass was slightly lower at the Hummingbird Highway site (100 vs. 134:1) and considerably higher at the Salamanca site (493:1 vs. 90).

TAXONOMIC COMPOSITION OF DEAD LEAF AND LIVE LEAF ARTHROPOD FAUNAS

To assess the degree of similarity between various faunas, I calculated Schoener's overlap index (Schoener 1968, Table 7 based on data in Table 6). These values indicate that comparisons between tropical samples are quite similar (approximately 0.70) and that comparisons made between regions (West Indies vs. Belize) and seasons (Belize February vs. September) were as similar as those made within region and seasons.

In contrast, comparisons between the temperate-zone site and the nonbreeding site indicate much lower similarity and the difference between the within tropical versus the tropical-temperate comparisons is highly significant ($P < 0.001$). This suggests that the change from temperate to tropical latitudes entails a much greater shift in foliage arthropod faunas than does movement among the tropical sites.

For live leaves the major difference between the temperate and tropical sites is the higher relative abundance of lepidopteran larvae and beetles and the relative scarcity of spiders on the temperate foliage (Table 6). For dead leaves, Orthoptera were relatively less abundant and spiders, beetles, and caterpillars were relatively more common in the temperate-zone leaves. The small

TABLE 6. The gross taxonomic composition (%) of arthropod collections from dead and live leaves collected.

Site	n	Spiders	Orthop-tera	Lepidop-tera	Coleop-tera	Homop-tera	Hemip-tera	Others
Live leaves								
Monte Bonito, Dominican Republic	98	48	1	2	1	36	10	2
Windsor, Jamaica	32	72	3	0	0	15	6	4
Hardwar Gap, Jamaica	28	79	3	0	0	14	0	4
Hummingbird, Belize	41	68	5	0	12	12	2	0
Salamanca, Belize	23	35	22	8	4	24	4	3
Maryland	256	9	8	34	15	33	—	—
Dead leaves								
Monte Bonito, Dominican Republic	216	52	32	2	3	0	1	10
Windsor, Jamaica	111	26	54	4	9	0	1	6
Hardwar Gap, Jamaica	38	18	42	8	8	0	16	8
Hummingbird, Belize	92	27	52	5	10	0	3	3
Salamanca, Belize	123	10	70	2	17	0	2	9
Maryland	272	53	3	12	25	1	3	2

* All Belize samples are from February.

differences between the pooled Central American and Antillean samples include a consistently lower frequency of Orthoptera and beetles in the Antillean sample.

RELATIVE ABUNDANCE OF DEAD AND LIVE LEAVES

This ratio was only measured in the low understory of the Maryland and Belizean study sites. The transects produced very similar mean live : dead leaf ratios: 29:1 (6 SE, $n = 10$ transects) for Belize and 32:1 (9 SE, 10 transects) for Maryland. Although the data are limited, the results conform to my subjective impression that although the absolute abundance of dead leaves is often quite high in wet tropical forests, the *ratio* of live to dead leaves is no higher than in many temperate forests with shrub understories (e.g., typical breeding habitat for Worm-eating Warblers). It should be emphasized that some of the tropical habitats I visited, most notably the montane forest of Jamaica, are noticeably free of aerial leaf litter. However, the Belizean data were not gathered during the dry season when dead leaf abundance may be somewhat higher.

DISCUSSION

Worm-eating Warblers show marked seasonal change in their foraging behavior. During the breeding season I found them to be typical foliage-gleaning insectivores, occurring in all strata of the deciduous woodland study site, and only occasionally investigating dead leaves or bark. During the mid-winter, they become highly specialized on searching dead curled leaves suspended in the understory of tropical forests. The next most preferred substrate was bark, with live foliage gleaning rare and nearly restricted to damaged or heavily curled leaves. Nonbreeding Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*) have also been reported to be aerial leaf litter foragers (Morton 1980, Willis 1980). My winter observations of the former, however, suggest it is not as specialized on dead leaves (40% of 75 maneuvers, $n = 17$ individuals) as is the Worm-eating Warbler.

Along with a shift in substrate search, Worm-eating Warblers change the maneuvers used to locate and capture arthropods. As a typical foliage insectivore during the breeding season, Worm-eating Warblers glean prey from exposed surfaces. However, when foraging for prey hid-

TABLE 7. Similarity values for arthropod faunas on dead and live leaves censused at the various study sites (based on Table 6 and Schoener's index of overlap).

Sites	n of comparisons	Live leaves	Dead leaves
All Tropical*	10	0.70	0.71
West Indies-Belize*	6	0.69	0.73
Within Tropical Region*	4	0.71	0.68
Belize Fall–Winter	1	0.71	0.83
Maryland-Tropical	5	0.49	0.47

* Based on February data from Belize.

den in leaf curls and crevices, Worm-eating Warblers hang in a variety of postures, gape into holes, and occasionally grab and manipulate the leaves. Such a shift towards more specialized and presumably more energetically costly foraging maneuvers during the winter has been found for other migrant species as well (Bennett 1980, Mallory 1981).

Worm-eating Warblers encounter a marked shift in the relative biomass of arthropods in dead or on live foliage between the breeding and winter range. This shift is far greater than the variation found among tropical sites, even when comparing Antillean and Central American sites. Although the numbers of total arthropods in both dead and live leaves are similar between the breeding and nonbreeding sites, in the tropical samples the number of large arthropods in dead leaves is greater and large prey on live foliage are almost nonexistent. Such a shift in the relative available arthropod biomass (which must be largely determined by the larger arthropods) is probably sufficient to change the relative profitability of dead leaf specialization and compensate for the energetic cost of the more acrobatic foraging maneuvers and increased travel associated with foraging in aerial leaf litter. Consistent with these availability data is the observation that although overall foraging success rates at dead leaves differed little between the temperate and tropical sites, the proportion of large prey captured was greater on the tropical site.

In addition to the latitudinal change in insect numbers and biomass is the systematic shift in the type of arthropods available. Temperate zone leaves support high abundances of easily captured, soft-bodied caterpillars (Holmes et al. 1979, this study). In contrast, live leaf faunas in the tropics during the dry season are dominated by fast and active arthroods (such as spiders and

homopterans, Janzen 1973, this study). The leaves of West Indian forests in particular are strongly dominated by small spiders (this study). A foliage-gleaning bird that rarely employs hovering to capture prey may find the small amount of gleanable insect biomass on live leaves in these forests uneconomical to pursue. It is interesting to note that the most common foliage-gleaning birds in the West Indian forests are small, active migrant warblers (American Redstart *Setophaga ruticilla,* Black-throated Blue Warbler *Dendroica caerulescens,* Northern Parula Warbler *Parula americana*) and todies (*Todus*). On the other hand, potential prey in dead leaves (even members of highly active groups such as spiders and Orthoptera) almost invariably remain immobile within leaves to avoid detection, even when prodded (J. Gradwohl, pers. comm.). Therefore, the most important adaptation for dead leaf foragers is the ability to reach open and peer into the leaves. Appropriate behaviors are well developed in Worm-eating Warblers. It is likely that certain unusual morphological characteristics of Worm-eating Warblers, such as their disproportionately large bills (Remsen and Parker 1984) and short tarsi, are adaptations for dead leaf foraging as well.

The change in relative profitability of dead versus live leaves to Worm-eating Warblers is probably based on the activity pattern of the dominant herbivorous arthropods. The largest soft-bodied arthropods in the temperate zone are lepidoptera larvae, which generally forage on leaves during the day to take advantage of warm temperatures for rapid growth (Heinrich 1979). The largest tropical arthropods are usually active on foliage at night (pers. observ.) and seek refuge during the day.

It appears that the shift in relative abundance and type of dead leaf and live leaf arthropods, rather than the relative abundance of dead versus live leaves (cf. Remsen and Parker 1984), is the driving ecological force in the behavioral shift of the Worm-eating Warbler. I did not observe any consistent difference in the relative abundance of dead and live leaves between the temperate and tropical sites. In areas where dead leaves are scarce (e.g., montane and dry limestone forests), the few birds I observed were searching twigs, vines and branches. Within study sites dead leaves were patchily distributed, yet I observed no tendency for Worm-eating Warblers to forage on live leaf arthropods when in open understory with few dead leaves. Nor did they become specialized on searching dead leaves when in the dense laurel understory of the Maryland site which was so rich in dead leaves. Much more censusing of the relative abundance of dead leaves and arthropods is necessary to determine which is more important for supporting the great increase in resident dead-leaf-foragers between subtropical and tropical areas (Remsen and Parker 1984).

Worm-eating Warblers arriving in the tropics appear to face a high degree of consistency between various tropical sites. The largest potential source of variation probably would be the location of a wintering site with respect to island versus mainland conditions. Comparing the West Indian sites to the Belizean sites, I found that there was no great shift in the relative representation of various major arthropod groups, in the relative abundance of dead leaf and live leaf arthropods, or in the size distribution of dead leaves. Lack (1976) hypothesized and Janzen (1973) and Andrews (1979) demonstrated through widescale sweep sampling that the Antilles have lower arthropod abundances than equivalent mainland tropical sites. In general I found lower arthropod abundances in the island samples, but no difference in the relative distribution of abundance in dead and live leaves.

Based on experiments with naive hand-raised Worm-eating Warblers (Greenberg, in press), I hypothesized that the preference for dead versus live leaves is largely determined by trial and error learning. Consistent with this hypothesis, Worm-eating Warblers that had recently arrived in Belize (September to October) were less specialized on dead leaves than in February at the same site. Although I detected a slight increase in the abundance of live leaf prey during this period over the mid-winter sample, the overall estimated biomass ratios suggest that dead leaf arthropods were relatively more plentiful during fall.

Other observations suggest some degree of behavioral plasticity as well. I observed a shift to dead leaf foraging after an initial use of live leaves on my Maryland study site in early May, presumably in response to inclement weather conditions. The most salient behavior of hand-raised Worm-eating Warblers is their tendency to manipulate and explore objects, particularly foliage (dead or alive), in the absence of specific reinforcement (Greenberg, in press). Such well developed exploratory behavior coupled with the dramatic shift in relative prey abundance is prob-

ably sufficient to account for, in a proximate sense, the seasonal change in specialization observed in the Worm-eating Warbler.

ACKNOWLEDGMENTS

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