

DIVERGENT FORAGING STRATEGIES OF TWO NEOTROPICAL MIGRANT WARBLERS: IMPLICATIONS FOR WINTER HABITAT USE

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ABSTRACT.—To address whether foraging strategies affect habitat-use patterns of non-breeding warblers, I quantified foraging behavior, bill dimensions, and diet (based on regurgitation samples) of Ovenbirds (*Seiurus aurocapillus*) and Swainson's Warblers (*Limnothlypis swainsonii*) wintering in three habitats in Jamaica. Ovenbirds primarily gleaned prey from the surface of the leaf litter (95% of foraging maneuvers), resulting in a diet comprised predominantly of ants (62% of all prey items), seeds (18%), and beetles (9%). Swainson's Warblers foraged by lifting leaves (80% of foraging maneuvers), resulting in a significantly different diet dominated by beetles (39%), spiders (22%), and ants (19%). More than 60% of the regurgitation samples from Swainson's Warblers contained orthopterans and/or gecko (*Sphaerodactylus goniirhynchus*) bones. Averaged across all habitat types, Ovenbirds consumed ants in direct proportion to their abundance based on visual counts of arthropods. Swainson's Warblers consumed beetles more than expected based on the abundance of beetles in visual counts and Berlese funnels. The use of a diversity of habitats by Ovenbirds may be related to their ability to feed opportunistically on ants, which are a widespread, abundant, and reliable resource. In contrast, based on their foraging behavior and diet, Swainson's Warblers may be restricted to habitats with a well-developed canopy and an abundant sub-surface leaf-litter fauna. Received 26 October 1998, accepted 1 October 1999.

AVIAN FORAGING STRATEGIES combine complex interactions among morphology, prey preference, foraging behavior, habitat selection, prey availability, and relationships with predators and competitors (Morrison et al. 1990). Quantifying these components of a species' foraging strategy can elucidate niche relationships (Robinson and Holmes 1982), patterns of habitat use (Karr and Brawn 1990), and community structure (MacArthur 1958) and also can help to focus conservation efforts (Petit et al. 1995). However, much of the data necessary to characterize a species' foraging strategy are lacking, including dietary information (Rosenberg and Cooper 1990). This is especially true for insectivorous Neotropical-Nearctic migrants on their wintering grounds (but see Morton 1980, Poulin and Lefebvre 1996).

Neotropical-Nearctic migrant passerines consistently have been shown to occupy a broad range of habitats on their wintering grounds (Hagan and Johnston 1992, Wunderle and Waide 1993, Petit et al. 1995). Rappole (1996) summarized two hypotheses to account

for this phenomenon. First, migrants may be generalists, using a diverse set of food resources across a variety of habitats. Second, high productivity on the breeding grounds can lead to an abundance of birds on the wintering grounds, forcing migrants to expand into a diversity of habitats. To test these hypotheses for Neotropical-Nearctic migrants, an understanding of their foraging behavior, diet, and patterns of prey availability is necessary across a broad array of habitats (Petit et al. 1995).

I studied two species of ground-foraging warblers that winter in Jamaica, the Ovenbird (*Seiurus aurocapillus*) and the Swainson's Warbler (*Limnothlypis swainsonii*). These species exhibit different patterns of habitat use: Ovenbirds are habitat generalists, whereas Swainson's Warblers are restricted to mature forested habitats (Wunderle and Waide 1993). The essentially two-dimensional foraging substrate used by these two species potentially simplifies some of the biases associated with estimating prey availability (Hutto 1990, Wolda 1990). Although both species are leaf-litter specialists, they differ in their foraging behavior, with Ovenbirds primarily gleaning prey from the leaf-litter surface (Zach and Falls 1979) and Swainson's Warblers manipulating the leaf litter to

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search for concealed prey (Lack and Lack 1972, Graves 1998). Little is known about the natural history of either species in winter (Van Horn and Donovan 1994, Graves 1996), and the Swainson's Warbler in particular is a species of conservation concern (Hunter et al. 1993, Thompson et al. 1993).

Here, I address three questions about the winter foraging strategies of Ovenbirds and Swainson's Warblers. First, do Ovenbirds and Swainson's Warblers consume different types of prey, and if so, are the differences related to foraging behavior and bill morphology? Second, do these species show different patterns of prey selection relative to prey abundance? Third, do differences in diet, foraging behavior, and prey selectivity provide an explanation for the contrasting patterns of winter habitat use by these species?

STUDY AREA AND METHODS

Study sites.—I collected data on two study plots of approximately 5 ha in each of three structurally and ecologically distinct habitat types in Jamaica: shade coffee, second-growth scrub, and undisturbed dry limestone forest. The shade coffee plots, James Hill (18°10'N, 77°20'W; 630 m elevation) and Baronhall Estates (18°12'N, 77°22'W; 555 m elevation), had well-developed overstories consisting primarily of *Pseudalbitzizia berteriana* (mean canopy height = 18.6 ± SD of 6.9 m; M. D. Johnson unpubl. data) and *Inga vera* (mean canopy height = 10.0 ± 2.1 m), respectively. Rainfall is seasonal and averages more than 160 cm per year (Lack 1976). Litter consisted almost entirely of the leaves of coffee and shade trees and generally was evenly distributed, but areas of herbaceous vegetation (11% of substrate) and bare soil (4% of substrate) were present. The mean dry mass of litter was 57.6 ± 30.2 g per 0.1 m².

The second-growth scrub plots were 10 km west of Black River (18°02'N, 77°57'W; 5 m elevation). The plots, approximately 1 km apart, receive less than 125 cm of rainfall per year (Lack 1976). Both were dominated by logwood (*Haematoxylum campechianum*), an introduced tree that formed a roughly monospecific overstory across the majority of both plots (mean canopy height = 6.0 ± 0.9 m). The plots were characterized by frequent human disturbance (cutting for fence posts and charcoal, and clearing for small agricultural plots). One of the second-growth scrub sites was younger and had more well-developed shrub and herbaceous layers. On both plots, the leaf litter was interspersed with patches of herbaceous vegetation (15% of substrate) and bare soil (2% of substrate). The mean dry mass of litter was 98.0 ± 28.7 g per 0.1 m².

The dry limestone forest plots were on Portland Ridge, 12 km southeast of Lionel Town (17°44'N, 77°09'W; 100 to 120 m elevation). The plots were less than 2 km apart and received less than 125 cm of rainfall per year (Lack 1976). Mean canopy heights were 9.3 ± 1.9 m (Portland Ridge lower) and 10.2 ± 2.9 m (Portland Ridge upper), and canopies were dominated by *Metopium brownii*, *Bursera simaruba*, and *Thrinax parviflora*. The subcanopy was dominated by *Ateramnus lucidus* and *Oxandra lanceolata*. Although 95% of the forest floor was covered by leaf litter, limestone outcrops were common on both plots. The mean dry mass of litter was 65.6 ± 33.9 g per 0.1 m².

Foraging behavior.—I quantified the foraging behavior of Ovenbirds and Swainson's Warblers during the winters of 1993–1994 to 1996–1997; observations of foraging behavior were opportunistic, but I attempted to observe both species throughout each winter (1 November to 25 March), at various times of day, and in all habitat types. I categorized foraging behaviors using the terminology of Remsen and Robinson (1990) and Graves (1998) as glean (ground), leaf-lifting (ground), and "other" (<10% of all foraging behaviors), the latter consisting of lunge (ground), leap (from ground toward the undersurface of low leaves), and glean while in a tree or shrub (which was not differentiated from gleaning from the ground by Remsen and Robinson [1990]). Graves (1998) used Meanley's (1970) characterization of leaf-lifting as a tactic in which "the bird pokes its bill under a leaf, pushing it upwards, searching the ground beneath it or examining its underside." I also considered leaf-lifting to include cases where a bird pushed a leaf upward and then flicked the leaf aside with its bill closed. I included data only from foraging sequences that lasted at least 10 s but no more than 5 min, and only when I felt I had not disturbed the bird's foraging routine (e.g. when birds were not flushed from the ground and when they appeared to behave naturally). Although many birds were not marked, observations were temporally and spatially separated such that observations were probably taken from different individuals.

Diet composition and bill dimensions.—During the winters of 1993–1994 to 1996–1997, I assessed the diet of Ovenbirds and Swainson's Warblers captured in mist nets by forcing the birds to regurgitate after giving them an emetic (antimony potassium tartrate; Poulin et al. 1994). At each site, I attempted to collect an equal number of regurgitation samples in early (November to December) and late (February to March) winter. Birds were marked with a unique combination of two colored leg bands and an aluminum U.S. Fish and Wildlife Service leg band to ensure that only one regurgitation sample was collected per individual. On all birds captured, I measured the length, width, and depth of the bill at or to the distal edge of the nares.

I stored regurgitated samples in 70% ethanol and then examined them in the laboratory using a 7.5 to 64 \times dissecting microscope. I identified prey items to order in most cases, with the following exceptions (for both prey use and prey abundance): larvae refer to holometabolous larvae, which were dominated by Coleoptera, Lepidoptera, and Diptera; non-insect arthropods were divided into spiders, harvestmen, pseudoscorpions, mites, and "arthropods" (centipedes, millipedes, isopods, and amphipods); Dicotyledon (roaches) were combined with Orthoptera; and Hymenoptera were divided into ants (Formicidae) versus other Hymenoptera. All vertebrate prey were geckos (*Sphaerodactylus goniorhynchus*).

Dietary studies based on data from emetic samples have been criticized because of the potential for differential digestibility of soft- versus hard-bodied prey (Rosenberg and Cooper 1990). However, familiarity with potential prey items greatly enhances recognition of even soft-bodied prey from diagnostic undigestible body parts such as wings, elytra, mandibles, or chelicerae (Calver and Wooler 1982, Ralph et al. 1985, Chapman and Rosenberg 1991). In addition, a laboratory study using captive Ovenbirds showed that the proportion of prey regurgitated did not vary across prey types (Zach and Falls 1976a). I identified prey by diagnostic body parts and by comparison with voucher specimens or published descriptions (Calver and Wooler 1982, Ralph et al. 1985, Chapman and Rosenberg 1991). To control for changes in my ability to recognize fragmented remains, I examined each regurgitation sample a second time after all samples had been examined once. Minimum estimates of prey numbers were based on anatomical characteristics (e.g. number of spiders of a given size class = number of spider fangs of that size class divided by 2). Diets were characterized by numerical abundance, because estimates of mass or volume from fragmented food items were difficult to determine consistently among taxa.

I calculated the mean proportion of the diet for each taxon by averaging across regurgitation samples the proportion of prey in each category. I analyzed diets both with and without seeds (assuming one seed per fruit); however, I omitted seeds in analyses of prey use versus abundance because they could not be quantified in Berlese funnels (see below). In addition, because fleshy fruits in regurgitation samples were represented by seeds, and many plants on the study site contained multiseeded fruits, counts of seeds alone may lead to overestimation of fruit in the diet.

For most analyses of prey use and abundance, I used five categories: ants, beetles, spiders, holometabolous larvae, and "other" (all remaining prey types). For all analyses, larger or smaller subdivision of prey categories did not change the relationship of the test statistic to the critical value ($\alpha = 0.05$). To evaluate the adequacy of sample sizes for dietary

data, I selected regurgitation samples at random (with replacement) from the pooled data set (within species, across habitats) and determined asymptotic values for cumulative percent prey in the random sample (Chapman and Rosenberg 1991). This procedure was repeated 10 times and the mean value reported. An asymptotic value indicates the number of regurgitation samples at which little additional dietary information is added.

Prey abundance.—Because no known sampling method assesses prey availability in the same way that a bird does (Cooper and Whitmore 1990), I estimated prey abundance in the leaf litter in two ways: Berlese funnels and visual counts. Berlese funnels use heat and light to extract arthropods from a cross-sectional sample of leaf litter and thus sample potential prey from throughout the leaf-litter strata. In contrast, visual counts of arthropods sample only prey that occur at or near the leaf-litter surface (Holmes 1966). Berlese funnels were better for sampling beetles (the most frequently consumed prey items of Swainson's Warblers), whereas visual counts were better for sampling ants (the most frequently consumed prey items of Ovenbirds). Thus, the two methods provided complementary assessments of prey abundance.

Samples of leaf litter that were placed in Berlese funnels were collected from February 1995 to March 1997. To obtain these samples, I pushed a 0.1-m² cylindrical core into the subsoil and then collected all leaves and leaf fragments within the core. Samples were stored in plastic bags and then placed in Berlese funnels, usually on the evening of the day of collection. I followed the protocol of Levings and Windsor (1982), with the exception of extraction time, which I decreased from 24 to 14 h (because at most sites I did not have continuous access to electricity for 24 h). On a subset of samples, I conducted an additional 10-h extraction immediately after the first 14-h extraction and found that $97.1 \pm 3.5\%$ ($n = 10$) of the arthropods were extracted within 14 h. For Berlese funnels, I chose sample locations on each plot by generating 30 to 55 pairs of random distances (0 to 25 m) and compass bearings (0° to 359°) paced from 50-m grid-plot intersections. About half of the samples were collected in early winter and half in late winter.

I conducted visual counts of arthropods from November 1995 to March 1996. For these counts, observers identified to the lowest possible taxon all arthropods seen during 5-min scans of 0.25-m² quadrats of the forest floor. Each quadrat consisted of four stakes connected by string. Stakes were pushed into the forest floor such that the string rested 8 cm above the leaf litter, minimizing disturbance to the fauna. Observers knelt approximately 0.2 m in front of the quadrat and leaned over the count area with their eyes approximately 1.5 m above the leaf-litter surface. Visual counts were conducted from 1100 to 1600 EST. Hourly sampling at fixed locations showed

no diurnal variation in prey numbers (repeated-measures ANOVA, $F = 1.85$, $df = 7$ and 35 , $P = 0.19$). I found no difference among observers in the total number of arthropods counted in the early ($t = 0.31$, $df = 838$, $P > 0.50$) and late winter ($t = 0.12$, $df = 808$, $P > 0.70$), or in the distribution of numbers of arthropods within prey categories ($G = 0.5$, $df = 8$, $P > 0.90$). Visual counts were taken at 20 random distances (0 to 25m) and bearings (10 in early winter and 10 in late winter) from each Ovenbird and Swainson's Warbler capture location on the study plots, resulting in 200 to 360 visual counts per plot.

For both methods of estimating prey abundance, I calculated the mean proportion of prey in each category by averaging across samples the proportion of prey within each prey category. More than 60% of the prey items in Berlese funnel samples (hereafter "Berlese samples") consisted of mites, Psocoptera, Colembola, and Thysanoptera, which combined accounted for less than 0.5% of the diets of Ovenbirds and Swainson's Warblers. Thus, to provide a more meaningful description of the composition of potential prey, I eliminated these four prey categories from estimates of prey abundance for both sampling methods. Berlese samples ($n = 8$) and visual counts ($n = 86$) that contained no prey items were omitted from the analyses.

Statistical analyses.—I used repeated-measures ANOVA to compare variation in (1) percent of foraging maneuvers within behavioral categories (within and between species), (2) percent of diet in each prey category (among habitats and within and between species), and (3) percent of prey in each category in abundance samples (between sampling methods and within and among habitats). In each analysis, the repeated measures were percentages within each category of foraging maneuvers or prey categories, and the sampling units were individuals, regurgitation samples, visual counts, or Berlese samples (Greer and Dunlap 1997). I did not include the "other" category in the repeated-measures ANOVAs to avoid nonindependence of proportions (Aebischer et al. 1993). To maintain alpha at 0.05, I used the Huynh-Feldt epsilon correction for departures from sphericity in covariance matrices (Huynh and Feldt 1976). I calculated population dietary heterogeneity (PDH; Sherry 1984) as an index of the variability of prey types consumed for each species-habitat group, where PDH is the G -statistic divided by df . Larger PDH values indicate greater variation in prey use among individuals. Overall differences between prey use versus abundance were tested with MANOVA using the proportion of ants, beetles, holometabolous larvae, and spiders as dependent variables (Silleet et al. 1997). Indices of prey selection were obtained by averaging the difference between percent abundance and percent use for each prey category (Rosenberg 1990); positive and negative values indicate a prey type was taken more or less frequently

than predicted based on its abundance, respectively. Significance levels for use of individual prey categories relative to their abundance were obtained using t -tests. I used BMDP version 7.0 (Dixon 1992) for all statistical tests.

RESULTS

Bill morphology.—Compared with Ovenbirds ($n = 316$), Swainson's Warblers ($n = 31$) have a longer (11.62 ± 0.51 mm vs. 8.87 ± 0.51 mm), deeper (4.30 ± 0.16 mm vs. 4.10 ± 0.19 mm), and narrower bill (3.35 ± 0.35 mm vs. 3.75 ± 0.33 mm; t -tests, all $t > 5.96$, $df = 345$, all $P < 0.0001$). In addition, Swainson's Warblers have feathers covering their nares, but Ovenbirds do not.

Foraging behavior.—The types of foraging maneuvers used by Ovenbirds were consistent across habitats (repeated-measures ANOVA, behavior \times habitat interaction, $F = 0.43$, $df = 2$ and 32 , $P = 0.65$). More than 95% of their foraging maneuvers (10 birds in shade coffee, 19 in second-growth scrub, and 6 in dry limestone forest; $n = 413$ foraging maneuvers) consisted of gleans directed at the leaf-litter substrate (best characterized as pecks). In contrast, 80% of the foraging maneuvers of Swainson's Warbler (three birds in second-growth scrub and two in dry limestone forest; $n = 67$ foraging maneuvers) consisted of leaf-lifting, and the foraging maneuvers of the two species differed significantly (species \times behavior interaction, $F = 273.4$, $df = 1$ and 38 , $P < 0.0001$).

Diet composition.—I collected regurgitation samples from 53 Ovenbirds and 13 Swainson's Warblers. Although Swainson's Warblers occurred on both of the second-growth scrub sites, I collected too few regurgitation samples ($n = 2$) for statistical comparison; Swainson's Warblers occurred at low densities (0 to 1 per 5 ha) on the shade coffee plots. Saturation curves suggested that diets of Ovenbirds and Swainson's Warblers were adequately quantified by 12 to 15 and 7 to 9 samples, respectively (Fig. 1). I resighted or recaptured 28% and 18% of Ovenbirds and Swainson's Warblers, respectively, more than one day after administering emetics. Two of 17 (12%) Swainson's Warblers died immediately after I administered the emetic, but no Ovenbirds died at the time of forced regurgitation.

Ovenbird regurgitation samples contained 2,137 prey items in 19 prey categories ($\bar{x} = 40.3$,

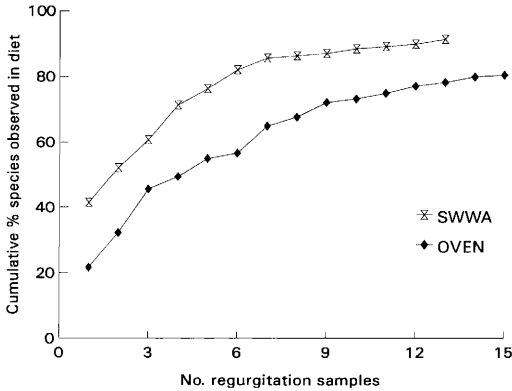


FIG. 1. Saturation curves for Ovenbirds (OVEN) and Swainson's Warblers (SWWA) representing the cumulative number of prey types in randomly selected (with replacement) regurgitation samples from the total population of regurgitation samples (all habitats combined). Each point represents a mean based on 10 sampling procedures.

range 2 to 177 prey items per sample; Table 1). Ants (62% of all prey items) were the most common prey type consumed in each habitat, followed by seeds (18%) and beetles (9%), and Ovenbirds did not use the four most commonly consumed prey types equally (repeated-measures ANOVA, $F = 56.39$, $df = 3$ and 150 , $P < 0.0001$; Fig. 2A). In combination, holometabolous larvae, snails, and spiders contributed less than 10% of the total diet, but each was present in more than 33% of the regurgitation samples. Ovenbird diets varied across habitats when seeds were included in the analysis (prey \times habitat interaction, $F = 3.86$, $df = 6$ and 150 , $P = 0.005$); seeds were more prevalent and ants less prevalent in the diets of Ovenbirds in shade coffee. When seeds were excluded from the analysis, Ovenbird diets were similar across habitats ($F = 0.88$, $df = 6$ and 150 , $P > 0.5$; Fig. 2B).

Swainson's Warbler regurgitation samples contained 267 prey items in 14 categories ($\bar{x} = 20.5$, range 8 to 79 prey items per sample; Table 1). Beetles (39%), spiders (22%), and ants (19%) were the most commonly consumed prey items, and Swainson's Warblers also did not use the four most commonly consumed prey types equally ($F = 15.0$, $df = 3$ and 36 , $P = 0.0001$). Orthopterans and bones of geckos occurred in more than 60% of the regurgitation samples.

Ovenbird and Swainson's Warbler diets in

TABLE 1. Number of prey items (percent of total in parentheses) and frequency of occurrence (percent of individuals that contained prey type) of prey types in regurgitation samples taken from Ovenbirds ($n = 53$) and Swainson's Warblers ($n = 13$) in Jamaica during the winters of 1993-1994 to 1996-1997.

Prey type	Ovenbird		Swainson's Warbler	
	Number ^a	Frequency	Number ^a	Frequency ^a
Formicidae	1,323 (62)	100	51 (19)	77
Seeds	395 (18)	49	7 (3)	31
Coleoptera	198 (9)	96	103 (39)	100
Larvae ^b	54 (3)	51	10 (4)	54
Snails	33 (2)	42	1 (tr)	8
Spiders	32 (1)	38	58 (22)	100
Hymenoptera ^c	20 (1)	30	1 (tr)	8
Orthoptera ^d	15 (1)	25	13 (5)	62
Dermaptera	9 (tr)	8	5 (2)	31
Homoptera	8 (tr)	8	0 (0)	0
Mites	7 (tr)	6	2 (1)	15
Hemiptera	6 (tr)	8	3 (1)	15
Diptera	6 (tr)	4	0 (0)	0
Arthropods ^e	4 (tr)	8	0 (0)	0
Odonata	2 (tr)	4	0 (0)	0
Isoptera	2 (tr)	4	0 (0)	0
Egg	1 (tr)	2	0 (0)	0
Psocoptera	1 (tr)	2	0 (0)	0
Pseudoscorpion	0 (0)	0	3 (1)	23
Vertebrate ^f	0 (0)	0	9 (3)	69
Unknown	21 (1)	13	1 (tr)	8
Total	2,137		267	

^a tr = <1%.

^b Includes all holometabolous larvae.

^c Excluding Formicidae.

^d Also includes Dictyoptera (roaches).

^e Only Diplopoda found in emetics (see text for definition used in prey abundance samples).

^f The gecko *Sphaerodactylus goniorhynchus*.

dry limestone forest habitat were significantly different from each other regardless of whether seeds were included in the analysis (species \times prey interaction, both $F > 7.0$, $df = 3$ and 78 , both $P < 0.02$; Fig. 2). PDH values were consistent among habitats for Ovenbirds (2.1 to 2.2), in contrast to the lower value (1.2) for Swainson's Warblers in dry limestone forest.

Prey abundance.—I found significant effects of sampling method (prey category \times sampling method interaction, $F = 510.6$, $df = 3$ and $5,535$, $P < 0.0001$) and habitat (prey category \times habitat type, $F = 64.3$, $df = 6$ and $5,535$, $P < 0.0001$) on prey abundance, as well as a significant prey category \times habitat type \times sampling method interaction ($F = 47.8$, $df = 6$ and $5,535$, $P <$

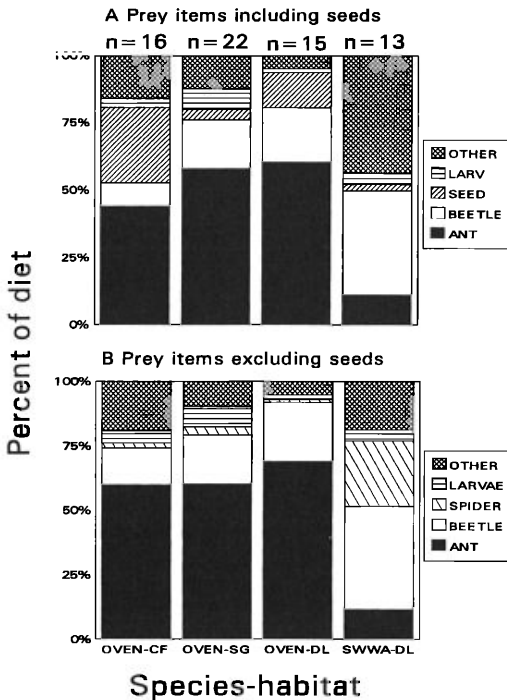


FIG. 2. Percent of diet in the five most frequently consumed prey categories for Ovenbirds (OVEN) and Swainson's Warblers (SWWA) in shade coffee (CF), second-growth scrub (SG), and dry limestone (DL) habitats. (A) includes seeds, (B) excludes seeds.

0.0001; Fig. 3). The interaction terms were influenced strongly by the higher proportion of ants in the visual counts, the higher proportion of larvae and beetles in the Berlese funnels, and the variation in the proportion of these three prey categories across habitat types. Because of these significant interaction terms, I examined prey selection relative to both estimates of arthropod abundance.

Prey selection.—Ovenbirds exhibited significant differences between percent of prey items in their diet and percent abundance estimated from Berlese funnels (Wilks' lambda = 0.59, $F = 58.1$, $df = 4$ and 331, $P < 0.001$) and visual counts (Wilks' lambda = 0.77, $F = 119.7$, $df = 4$ and 1,608, $P < 0.001$; Fig. 4D). In addition, the patterns of prey use and abundance varied across habitats for abundance estimates based on Berlese funnels (Wilks' lambda = 0.92, $F = 3.5$, $df = 8$ and 662, $P = 0.001$) and visual counts (Wilks' lambda = 0.97, $F = 6.2$, $df = 8$ and 3,216, $P < 0.001$; Figs. 4A–C). Pooled across habitats, the proportion of prey con-

sumed was significantly different than the proportion in abundance samples with the exception of the comparison of ant use to abundance as measured by visual counts (Fig. 4D). Comparing use with abundance for Berlese funnels, Ovenbirds consumed ants and beetles more than expected and holometabolous larvae, spiders, and other prey types less than expected. Comparing use with abundance for visual counts, Ovenbirds consumed beetles and holometabolous larvae more than expected, spiders and other prey types less than expected, and ants in proportion to their abundance.

Swainson's Warblers also showed significant differences between percent of prey in their diets and percent abundance estimated from Berlese funnels (Wilks' lambda = 0.40, $F = 40.4$, $df = 4$ and 108, $P < 0.001$) and visual counts (Wilks' lambda = 0.42, $F = 124.6$, $df = 4$ and 336, $P < 0.001$; Fig. 4E). Regardless of sampling methodology, Swainson's Warblers consumed beetles and spiders more than expected based on their abundance. The differences between use and abundance for ants, larvae, and "other" prey types varied with methodology.

DISCUSSION

Sampling considerations.—Regurgitation samples yielded relatively large sample sizes (2 to 177 prey items per sample), and I documented no negative effects of the emetic on Ovenbirds. Swainson's Warblers may be more sensitive to the technique, based on the two individuals that died (both were immature females that died on the same day) and the lower resighting/recapture rate compared to Ovenbirds. The administration of emetics to captive Ovenbirds induced mortality in 10 of 20 individuals (Zach and Falls 1976a), whereas the mortality rate was only 2% in a sample of 3,419 wild individuals of 82 species that were given emetics in Venezuela (Poulin et al. 1994). The actual mortality rate is probably intermediate between these values, because captive birds may be exposed to the added stress of unfamiliar conditions. Moreover, Poulin et al. (1994) documented mortality only among individuals that did not survive the initial administration of the emetic. A more rigorous study of the effect of emetic administration would provide a better assessment of mortality rates, which may be species-specific.

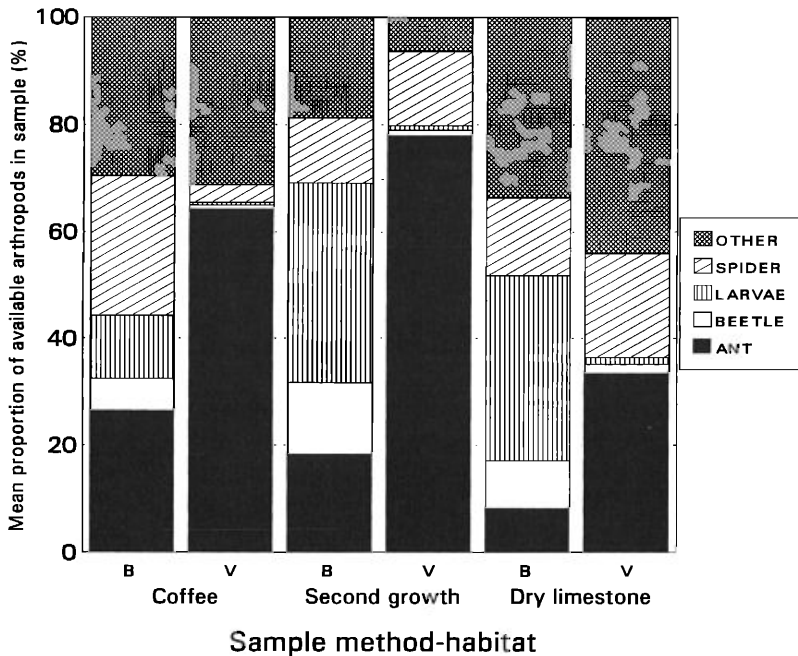


FIG. 3. Estimated abundance of prey types in five categories (ant, beetle, holometabolous larvae, spider, and other) from Berlese samples (B) and visual samples (V) in shade coffee, second-growth scrub, and dry limestone habitats.

Foraging strategies.—Despite foraging nearly exclusively on the leaf-litter substrate, Ovenbirds and Swainson’s Warblers used different foraging behaviors that resulted in access to different types of prey. Ovenbirds consistently gleaned prey from the leaf-litter surface, whereas Swainson’s Warblers lifted leaves to search actively for concealed prey. These divergent foraging behaviors led to significantly different diets. Ovenbirds consumed primarily ants, which were the most abundant prey type on the leaf-litter surface. By foraging on prey concealed beneath the leaf litter, the diet of Swainson’s Warblers was dominated by beetles, spiders, and frequently orthopterans and small vertebrates (geckos).

Morphological differences between the species also probably affected dietary differences. Based on comparative data in Ridgway (1902), Swainson’s Warblers have the longest bill of any parulid that nests in North America. Thus, they appear to be specialized morphologically, and their long, deep bill may facilitate the capture of large, fleeing prey (e.g. spiders, orthopterans, and geckos) that are uncovered under the leaf litter. In other avian guilds, longer bills

have been shown to be advantageous in capturing large, fast insects (Lederer 1975, Greenberg 1981). Additionally, the heavier bill of the Swainson’s Warbler may be advantageous in flipping leaves and probing beneath the leaf-litter surface. The low PDH for Swainson’s Warblers suggests that the prey types they encountered beneath the leaf-litter surface are remarkably consistent, which is similar to findings for canopy dead-leaf specialists in the Amazon (Rosenberg 1993) and for several resident flycatchers in Costa Rica (Sherry 1984). Furthermore, the feathers covering the nares of Swainson’s Warblers may function to reduce the inhalation of dust or debris while the birds search under leaves. Although the sample size for quantifying Swainson’s Warbler foraging behaviors was small, the foraging behaviors observed were similar to those used by Swainson’s Warblers during the breeding season (Meanley 1970), supporting the conclusion that the foraging behavior of this species is highly stereotyped (Graves 1998).

Prey selection.—Ovenbirds were highly selective for ants when comparing prey use with abundance as measured by Berlese funnels.

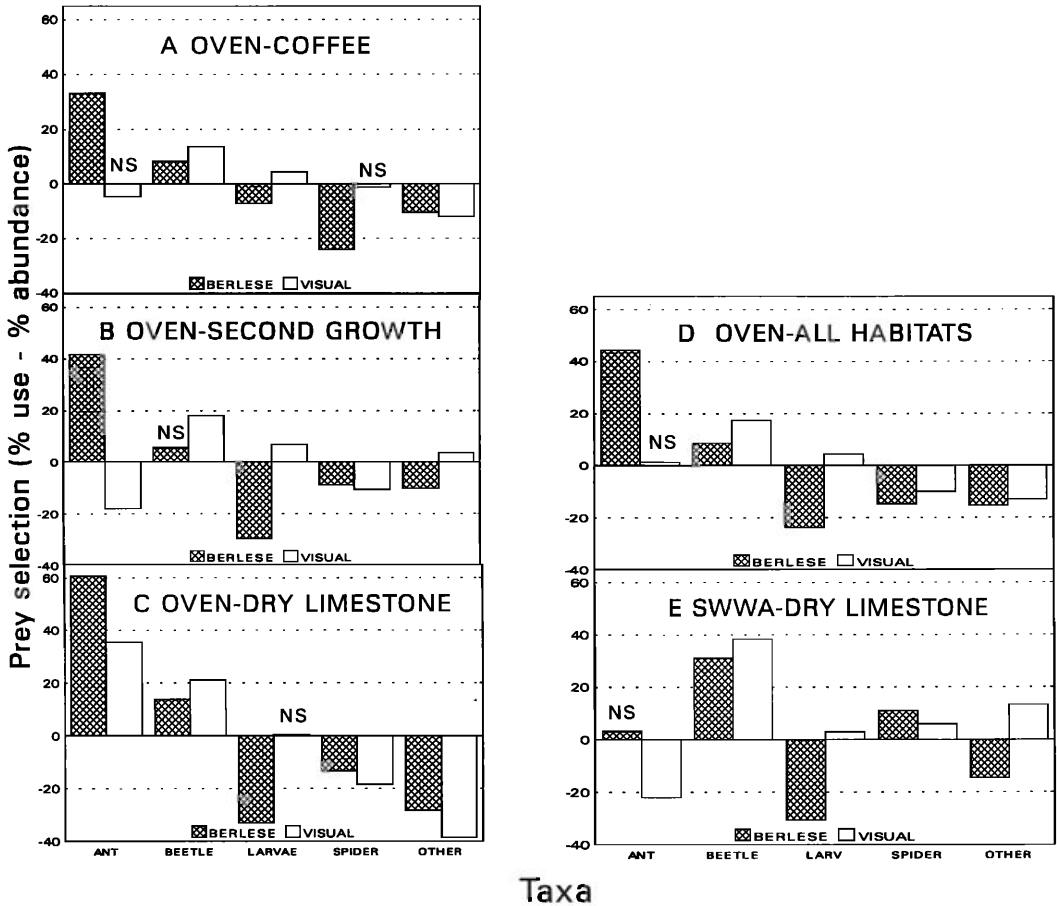


FIG. 4. Percent use minus percent abundance of ants, beetles, spiders, holometabolous larvae, and other prey types for Ovenbirds (A–D) and Swainson's Warblers (E). Positive and negative values indicate percent use was greater than or less than percent abundance, respectively. All differences were significant ($P < 0.05$) unless indicated by NS.

However, much of this selectivity disappeared when estimates of prey abundance were limited to the litter surface (i.e. visual counts), implying that Ovenbirds do not feed on ants selectively, but take them opportunistically in proportion to their abundance. Ants have been shown to be an unprofitable prey item (energy/handling time) owing to their low mass and high concentration of chitin (Zach and Falls 1978). During the breeding season, captive Ovenbirds consistently avoided ants in an extensive series of paired prey-selection tests (Zach and Falls 1978), and although ants made up 4 to 21% of the diet of breeding adults, ants were not found in nestling diets (Stenger 1958). Combined, these results suggest that ants are profitable only when present in high densities.

More surprising was that Ovenbirds showed the strongest selection for ants in dry limestone forests, where ants made up the lowest proportion of prey on the leaf-litter surface. Sites in dry limestone forest supported significantly lower total arthropod biomass than did sites in shade coffee or second-growth scrub (Strong 1999), suggesting that Ovenbirds foraged on ants because ant colonies represented predictable locations with high densities of prey (Zach and Falls 1976b, 1979).

Regardless of sampling methodology, my analyses showed that both species consistently selected beetles. Thus, they may use a nonrandom search pattern to increase the probability of encountering beetles. A similar explanation may apply to the consumption by Swainson's

Warblers of relatively large active prey that may occur more frequently in certain microhabitats within the leaf litter (i.e. spiders, geckos, and orthopterans). This could be tested with more detailed foraging observations and stratified sampling of leaf-litter fauna. An additional (but not mutually exclusive) hypothesis is that Swainson's Warblers ignore less-profitable (i.e. smaller) prey types. This hypothesis is supported by their lack of selection for larvae, many of which were small in the Berlese samples. However, both measures of prey abundance may quantify prey in ways that do not mirror the search images of the two warbler species, creating discrepancies between estimated prey abundance and actual availability (Cooper and Whitmore 1990).

Habitat-use patterns.—Are the divergent foraging strategies of Ovenbirds and Swainson's Warblers responsible for differences in their patterns of habitat use? Ovenbirds, typical of many Neotropical-Nearctic migrant parulids that winter in the Caribbean, use a diversity of habitat types during the nonbreeding season (e.g. Wunderle and Waide 1993). Rappole (1996) summarized two hypotheses for this general habitat-use pattern: (1) species may use a diversity of prey types across habitats, and (2) high breeding-season productivity may force individuals into suboptimal habitats. In contrast to hypothesis one, Ovenbirds exhibit a relatively consistent diet across habitats. My results suggest a third hypothesis for the general pattern of habitat use by Ovenbirds, simply that the ubiquity of ants makes a wide array of habitats suitable for wintering Ovenbirds. Although the abundance of ants declines in the dry season (Levings 1983, Strong 1999), ants have access to underground refugia and therefore may provide a more stable prey base (i.e. a renewable resource) in habitats with a pronounced dry season. Even in dry limestone forests, where surface prey biomass is significantly lower than in other habitats (Strong 1999) and ants make up a decreased proportion of available prey, Ovenbird diets still are dominated by ants. However, it is plausible that by being forced to expand into a diversity of habitats through high productivity in the breeding season, Ovenbirds may specialize on a widely distributed prey type. Investigation of Ovenbird diets in other portions of their nonbreeding range, especially in areas where ants are

less abundant, might provide a better test of hypotheses two and three.

In contrast to the generalized pattern of habitat occupancy by Ovenbirds, Swainson's Warblers are restricted to forested habitats with a continuous overstory (Arendt 1992, Wunderle and Waide 1993). Because of their stereotyped foraging behavior and morphological specialization, Swainson's Warblers may be limited to habitats with a well-developed canopy and litter layer that support a more abundant subsurface leaf-litter fauna. As estimated by Berlese funnels, dry limestone forests supported the highest subsurface prey biomass of the three habitats (Strong 1999), providing an explanation for the high density of Swainson's Warblers in this habitat and supporting the hypothesis that food availability is the most important factor determining intrinsic habitat quality for nonbreeding migrant landbirds (Hutto 1980).

Understanding the foraging strategies of multiple species can provide insight into why some species are more vulnerable than others to conversion of natural landscapes (Petit et al. 1995). This is especially pertinent for Swainson's Warblers. The abundance and diversity of leaf-litter fauna are reduced through increased desiccation resulting from forest fragmentation (Kapos 1989) or from increased radiation reaching the leaf litter in early successional and most agricultural habitats (see Lee 1989). Although the foraging strategy of Swainson's Warblers may facilitate prey capture in heavily forested areas, their foraging behavior requires an abundance of subsurface leaf-litter fauna, and their lack of dietary opportunism may make them vulnerable to human perturbation of forested habitats.

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