

EVALUATION OF AN ARTHROPOD SAMPLING TECHNIQUE FOR MEASURING FOOD AVAILABILITY FOR FOREST INSECTIVOROUS BIRDS

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Abstract.—I provide a detailed description of an arthropod sampling technique, “branch clipping,” and evaluate its efficacy in measuring food availability for three foliage-gleaning migratory warbler species wintering in Jamaica. I incorporated foraging observations into the sampling protocol to facilitate a match between the distribution of branch-clip samples and the distribution of warbler foraging attacks over available microhabitats. Where the match was imprecise, I weighted branch clip samples accordingly. Foraging observations indicated that most foraging maneuvers used by the warblers were directed at prey located on foliage, which are likely to be well sampled by branch clipping. Published diet analyses permitted the elimination of prey taxa and sizes that were not eaten by the warblers, and suggested that nearly all of the items eaten were captured by branch clipping. Habitat-specific warbler attack rates, which can be used as independent evaluations of food availability measurements, closely matched prey density as estimated by branch clips across three habitat types (citrus orchard, coffee plantation, and dry limestone forest). These data suggest that branch clipping effectively measured food availability for foliage-gleaning warblers in Jamaica. The method is probably also well suited for other foliage-gleaning species, particularly in habitats and seasons in which birds feed largely on prey residing on or flying near leaf surfaces. Branch clipping is probably ill suited for species that feed heavily on either large, fast flying insects (e.g., Odonata), or on large masses of flies (e.g., Chironomidae) that seldom land on forest foliage.

EVALUACIÓN DE UNA TÉCNICA PARA MUESTREAR ARTRÓPODOS PARA MEDIR LA DISPONIBILIDAD DE ALIMENTO PARA AVES DE BOSQUE INSECTÍVORAS

Sinopsis.—Proveo una descripción detallada de una técnica para muestrear artrópodos, “recortar ramas”, y evaluar la eficacia en medir la disponibilidad de comida para tres especies de aves migratorias que rebuscan en las hojas mientras invernan en Jamaica. Incorporé las observaciones de forrajeo al protocolo de muestreo para facilitar una asociación entre la distribución de las muestras de ramas recortadas y la distribución de los ataques de forrajeo de las especies sobre el microhabitat disponible. Cuando la asociación era imprecisa, pesé las muestras de las ramas de la misma forma. Las observaciones indican que la mayoría de las maniobras de forrajeo usadas se dirigieron a presas halladas en las hojas, que deben estar bien muestreadas en los cortes de ramas. Los análisis de las dietas publicados permiten la eliminación de taxones de presas y/o tamaños que no fueron tomados por las aves, y sugieren que básicamente todos los alimentos comidos fueron capturados por este método. Las tasas de ataque específicas al habitat, que son usables para evaluar independientemente cuan disponible está el alimento, se asociaron cercanamente a la densidad de presas según estimadas por este método a través de tres tipos de hábitat (siembra de *Citrus* sp., plantación de *Coffea* sp. y bosque cársico seco). Estos datos sugieren que el método de cortar ramas midió efectivamente la disponibilidad para las aves que rebuscan ramaje en Jamaica. Este método parece ser apropiado para otras especies que rebuscan ramaje, en particular en hábitats y temporadas en que las aves se alimentan grandemente en presas que residen o vuelan cerca de la superficie de las hojas. Recortar ramas es probablemente poco adecuado para estudiar especies que se alimentan mayormente de insectos grandes, de vuelo rápido

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(e.g., Odonata), o en grandes masas (e.g., Chiromidae) que rara vez se posa en ramaje del bosque.

Ornithologists have long recognized difficulty in effectively quantifying food availability for insectivorous birds (Morris 1960, Southwood 1980, Wiens 1984, Smith and Rotenberry 1990, Poulin and Lefebvre 1997). The principal problem is that due to prey choice and microhabitat selection, the abundance of arthropods in an environment does not necessarily correspond to the amount of food available for a foraging bird. For a given species, only some of the prey in an environment are encountered, and of those, only some are considered potential food items (Wolda 1990). Furthermore, a given insectivore does not search for prey in all microhabitats, and those in which it does search may not be visited with equal frequency (Hutto 1990). The result is that many arthropods present in an environment are not available as prey for an insectivore, and their inclusion in estimates of food availability may confound results (Wiens 1984, Cooper and Whitmore 1990).

Based on these considerations, Wolda (1990) operationally defined food availability as “the abundance of potential prey items in microhabitats used by an insectivore when searching for food.” Thus, in measuring food availability, it is crucial to take steps (via field and/or analytical methods) to exclude those prey that are not available to the species of interest—that is, those arthropods that are either sampled in inappropriate microhabitats, or not eaten (Cooper and Whitmore 1990).

“Branch clipping” is an arthropod sampling technique that has been used primarily to describe arthropod communities (Schowalter et al. 1981, Majer and Recher 1988, Majer et al. 1990, Schowalter 1994). Because it samples a wide range of arthropod groups from regions of vegetation frequently used by foraging birds, branch clipping could provide measurements of food availability useful for avian ecologists (Majer and Recher 1988, Cooper and Whitmore 1990), yet it has received relatively little attention (Gibb and Betts 1963). This may be in part because a discussion of its effectiveness in measuring food availability and a detailed description of a sampling protocol tailored for use in studies of avian ecology are lacking. In this paper, I evaluate the efficacy of branch clipping in measuring food availability for American Redstarts (*Setophaga ruticilla*), Northern Parulas (*Parula americana*), and Prairie Warblers (*Dendroica discolor*) wintering in three habitats in Jamaica, West Indies. In so doing, I provide a detailed description of a branch clipping sampling protocol and a discussion of its application for other species in other regions. First, using data on foraging behavior, I compare the distributions of warbler attacks to branch clip samples among microhabitats within the foliage profile. Second, I quantify the use of foraging maneuvers and discuss the capacity for branch clips to sample arthropods likely to be eaten by foraging warblers. Third, I review the literature to identify the potential prey taxa for the study species, and compare these to the arthropod taxa trapped in branch clip samples. Last, I test the reliability

of the protocol for measuring food availability for American Redstarts, Northern Parulas, and Prairie Warblers wintering in Jamaica by comparing habitat-specific foraging attack rates to food availability estimates derived from branch clip samples.

STUDY AREAS AND METHODS

Study Sites.—During the winter of 1996–1997, I sampled arthropods with branch clips in two sites of each of three habitats: shade coffee plantation, citrus orchard, and dry limestone forest. Below, I briefly describe the habitat types briefly below. Detailed site descriptions are available in Johnson (1999).

Citrus orchards contained *Citrus sinensis*, *C. s.* × *reticulata*, and *C. paradisi*, and ranged from a large, homogeneous, intensively managed farm to small, diverse, little-managed plots. Trees were arranged in widely spaced rows (approx. 6 m between rows, approx. 4 m between trees in a row) and were thickly foliated, ranging from 3–7 m in height. Orchards were harvested January–March, but because fruit ripens asynchronously, unripe, overripe, and fruit rotting on the ground were usually present over most of the winter. Sites were located at middle elevations (200–310 m) near Rat Trap (Westmoreland Parish) and Comfort Hall (Manchester Parish), and they received moderate rainfall (250–375 cm annually, Lack 1976).

Coffee plantations (shade coffee) contained two distinct vegetation layers: the canopy (4–10 m) was comprised mainly of *Inga vera* and banana trees (*Musa* sp.), while the short (usually <3 m) understory was made up entirely of coffee (*Coffea arabica* var. *typica*), and ranged from thin to dense in cover (25–100%) depending on pruning history. Canopy cover varied from 30–85% depending on the age of the plantation and its pruning history. Sites were located at higher elevations (550–700 m) near Cave Valley (Clarendon Parish) and Coleyville (Manchester Parish), and they received annual rainfall similar to that of the citrus sites.

Dry limestone forest sites supported thin to sparse canopies (0–50% cover), containing many drought-deciduous trees such as *Bursera simaruba*, *Metopium brownii*, and *Peltophorum linnaei*, which are facultatively deciduous in the late dry season (late February–March). Both of these relatively undisturbed forest sites received little rainfall (<125 cm annually) but local topographic conditions resulted in different local moisture conditions. One site was located in a shallow valley, was more mesic, and supported canopy heights ranging from 5–15 m. The other site was located along a ridgeline, was drier, and had canopy heights from 3–12 m. Subcanopies and understories were moderately thick, containing *Ateramnus lucidus*, *Oxandra lanceolata*, *Pithecelobium* sp., and *Erithalis fructosa*. Cacti and *Agave* sp. were common in the driest microhabitats, such as on ridge tops. Both sites were located on Portland Ridge (Clarendon Parish), a peninsular forest property leased from the Jamaican government by the P. W. D. Gun Club (80–120 m elevation).

Foraging Observations and Diet Information.—Any study of food avail-

ability must be based on an analysis of the foraging ecology of the study species (Hutto 1990, Smith and Rotenberry 1990). Before arthropod samples are taken, a researcher should determine the following for a given insectivore: (1) the distribution of searching behaviors over available microhabitats (Greenberg and Gradwohl 1980, Morrison 1980, Airola and Barrett 1985, Holmes and Recher 1986, Wolda 1990), (2) the spectrum of hunting techniques used (Robinson and Holmes 1982, Rosenberg et al. 1982), and (3) the identity of potential prey species (Holmes and Schultz 1988, Chapman and Rosenberg 1991, Poulin and Lefebvre 1997).

I conducted observations by walking slowly through a habitat until I detected a foraging warbler. Once a warbler was detected, I continuously recorded foraging behaviors into a portable cassette recorder for up to 300 s. The first attack was excluded from analyses to avoid a bias toward more conspicuous behaviors (Wunderle and Latta 1998), and only those foraging bouts of at least 20 s were included for analyses (Robinson and Holmes 1982). Only a single foraging bout was recorded from an individual during a morning to avoid autocorrelation (Wagner 1981, Wunderle and Latta 1998). All observations were conducted 0600–1000 h or 1530–1730 h CST, times of day when these birds were most active (Sliwa and Sherry 1992, Lovette and Holmes 1995). Foraging maneuvers were classified into 6 types following the protocol of Remsen and Robinson (1990): leaf glean (surface maneuvers directed at prey on leaves), bark glean (surface maneuvers directed at prey on twigs and/or bark), probe, sally-strike, sally-hover, and flush-pursue (included flutter-chase). To describe the microhabitats used by the warblers, the horizontal (inner, middle, or outer [away from center] third of tree/shrub foliage) and vertical (lowest, second, third, or highest quartile of tree/shrub foliage) position of each attack maneuver was also recorded. Observations were unlikely to be heavily biased by conspicuous outer branch maneuvers in this study because the agricultural canopies and winter-defoliated forests in which I worked afforded favorable viewing opportunities. Differences in the relative use of attack maneuvers and microhabitats between the three study species and habitats were examined with profile analyses (an application of MANOVA, Tabachnick and Fidell 1996), in which the proportion of attacks in each attack type and microhabitat (per foraging bout) served as dependent variables, and species and habitat were grouping factors. Analyses were conducted with SYSTAT 5.2.1 for the Macintosh (Wilkinson 1989). The results of these observations were incorporated into the insect sampling protocol (see *Calculations*, below) to ensure that branch clip samples were taken from microhabitats used by the study species.

Winter analyses of prey taxa were available for all three species, and of prey sizes for American Redstarts. These studies provided prey identity predominately to order or, in some cases, family, which may be insufficient taxonomic precision for studies of food availability (Wolda 1990). Rather than undertake a precise diet analysis, I chose to minimize this problem by quantifying food availability for the three warbler species together. When these species were pooled into a guild (migrant canopy

TABLE 1. Frequency use (%) of foraging attack maneuvers of three canopy insectivorous warblers wintering in Jamaica. Values indicate the mean percentage of foraging attacks of each type per foraging bout, n = number of foraging bouts (20–300 s).

Species	Foraging attack maneuver						Attacks at foliage prey ^a	n
	Glean	Probe	Peck	Sally-strike	Sally-hover	Flush-pursue		
Prairie Warbler	57.5	0	19.0	2.0	18.4	3.1	98.0	68
N. Parula	74.7	1.1	8.6	0.2	12.7	2.7	99.8	64
Am. Redstart	24.5	0	2.5	15.8	28.2	29.0	84.2	100
Guild	52.2	0.4	10.0	6.0	19.8	11.6	94.0	232

^a Sum of glean, peck, sally-hover, and flush-pursue attacks.

insectivores), the combined diet was more broad than for any one species alone (Table 1), thereby comprising a resource base that was more likely to be sampled by a broad insect sampling technique like branch clipping.

Materials and Apparatus Construction.—The branch clip apparatus was easily and inexpensively assembled from three primary components (Fig. 1): a ring pole mechanism (A–I), a collapsible bag equipped with a drawstring (J–O), and a pruner pole (Q). To assemble the ring pole mechanism, first a steel spring net ring (A) was attached to a short aluminum pole (G; these two pieces are available through Bioquip Products Inc. and screw together; parts 7353 and 7324A). The pole and net ring were fastened to the top of a set of aluminum/fiberglass telescoping poles (I; Mr. Long Arm Inc. model #6618) with two medium, screw-adjustable hose clamps (H). To ensure that the bag was held open and outstretched when the apparatus was held vertically, 1-m lengths of heavy-duty plastic covered wire (three of them, B) were wrapped around the net ring and brought together behind it, creating a triangular frame. Where they came together, a large safety pin (C) or binder clip was attached. In addition, four binder clips (D) were clamped onto the net ring. Lastly, a short length of plastic tubing (E) was firmly duct-taped (F) to the short aluminum pole just beneath the net ring.

To assemble the collapsible bag component, fabric was sewn into a rectangular bag (60 × 100 cm, J) furnished with a small (approx. 5 cm wide) sleeve (K) at the open end, creating a bag which resembled a long pillow case. I found that most arthropods were easiest to locate on light colored fabric, and polyester was preferable to 100% cotton because it was lighter and dried more quickly. Next, a rope was passed through an opening in the sleeve (M), around the bag's circumference, and out again through another opening next to the first (L). The rope was then tied with a slip knot (N) large enough so that it could not pass through the plastic tube (E) on the net pole.

The loose end of the bag's rope (O) was passed through the plastic tube (E) on the net pole apparatus, and the bag was loosely clipped to

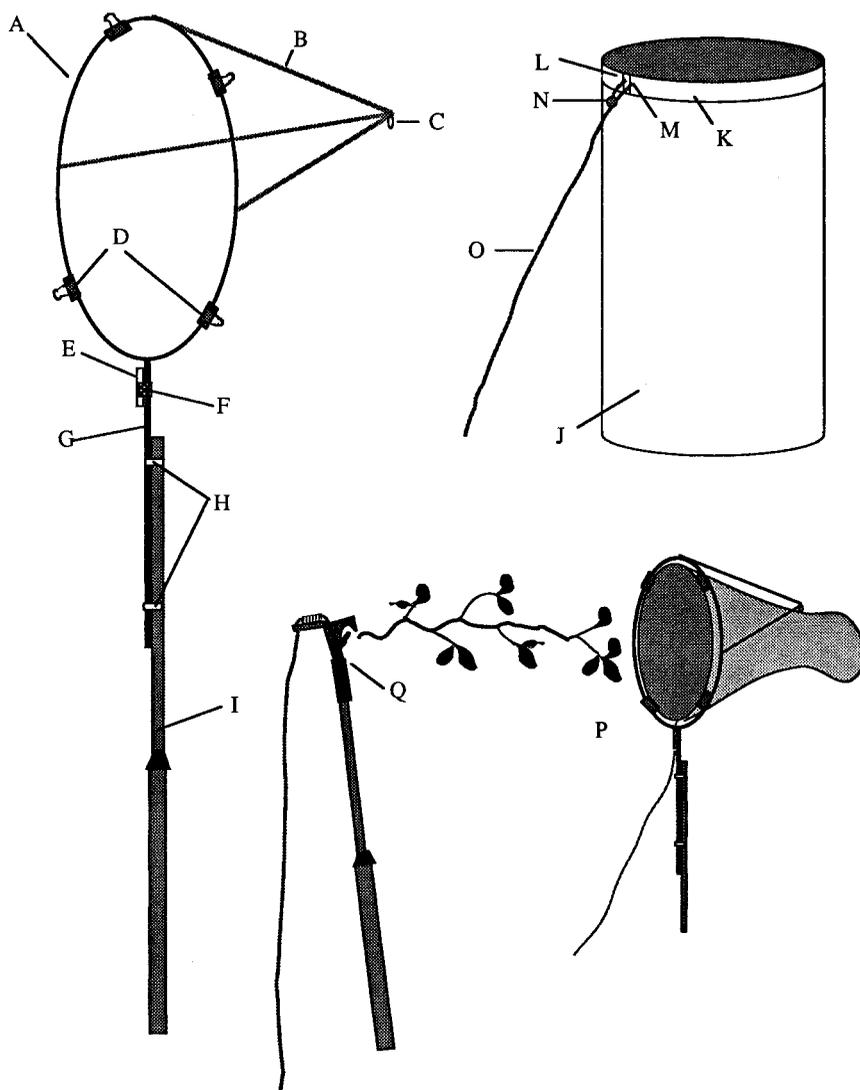


FIGURE 1. Branch clip apparatus comprised of three components: a ring pole (A-I), a collapsible bag (J-O), and a pruning pole (Q). See text for details.

the binder clips (D) and safety pinned (C) so that it was held open and extended (P).

Last, the pruner pole was assembled by attaching a tree pruner (Q; a hook-and-knife style pruner with a drawstring and retracting spring, often sold in garden stores already attached to a short, unusable pole) to a second set of telescoping poles. Attachment technique will vary depend-

ing on the type of pruner; in this case machine screws and nuts were adequate.

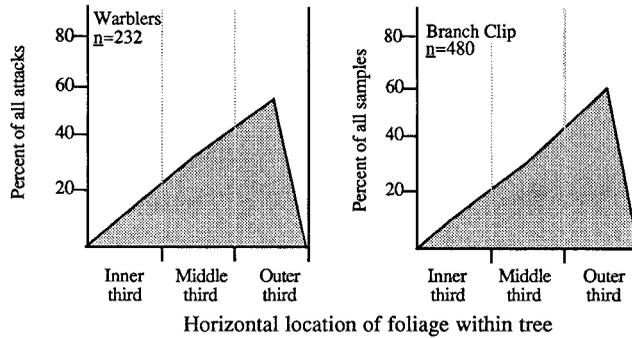
Arthropod Sampling.—In each study site, I sampled arthropods at points located at 50-m gridded intersections of 5-ha study plots. These plots are part of an ongoing study of wintering warbler ecology; further details concerning their locations and layouts are available upon request. Preliminary power analyses (Tabachnick and Fidell 1996) suggested that among habitats in Jamaica, approximately 16–20 branch clips were needed per site to demonstrate significant differences between habitats (unpubl. data). Therefore, I collected 20 branch-clip samples from each study site two times during the 1997 winter: once in mid-winter (January–February), and again in late winter (late February–March). The same trees, but different locations within trees, were sampled in each of the two sampling periods.

At each point, I selected a branch for sampling non-randomly, choosing areas of the foliage profile in an attempt to generally match the frequency of microhabitat use by the study guild (Fig. 2, see below). After a branch was selected, I extended the pole to the height of the branch, and, as quickly as possible, enclosed the branch and pulled the drawstring, cinching the bag tightly around the branch. The pruning pole was extended to the bagged branch, which was then clipped free from surrounding vegetation. Both poles were then lowered. With the telescoping poles I used, the maximum obtainable height was 8.5 m (including the length of the short aluminum pole [G] and my own height). This was adequate for most locations in the habitats studied here, although the top of the canopy was inaccessible in some areas of dry limestone forest.

Once the bag was lowered, I pulled it free from the net ring. Next, the top of the clipped, bagged branch was held and the bag vigorously shaken to dislodge arthropods. The bag was opened just enough to remove the branch which was examined for arthropods and weighed to the nearest g with a Pesola scale. Finally, I placed my head inside the bag and held the opening loosely around my neck to prevent any arthropods from escaping. All arthropods were identified to appropriate taxa (see below), and grouped by 1-mm size intervals. I found it useful to have a hand lens and an aspirator tied around my neck to aid in collecting and identifying arthropods. Also, I taped a small (3 cm) plastic ruler to the aspirator vial to assist with length estimation. All data were recorded in the field. In sites or habitats with abundant arthropods, it was helpful to have a recorder, so that I could call out tallied arthropods from the bag and not repeatedly pull away from the bag to record data. With practice, I could consistently complete a branch clip sample in approximately 15–20 min.

The identification of trapped arthropods should match the level of identification of available diet analyses. In this study, I classified arthropods into the following 18 taxonomic groups corresponding closely to order: Aranae, Orthoptera, Dictyoptera, Isoptera, Psocoptera, Hemiptera, scale insects (Coccoidea: Homoptera), other Homoptera, Neuroptera, Coleoptera, Lepidoptera adults, Lepidoptera larvae, Nematocera, other

A. Overall Horizontal Microhabitat Use vs. Branch Clip Distribution



B. Overall Vertical Microhabitat Use vs. Branch Clip Distribution

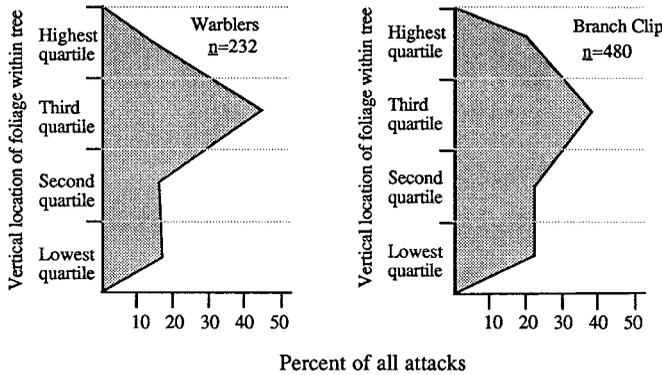


FIGURE 2. The distribution of warbler foraging attacks and branch clip samples among horizontal (A) and vertical foliage microhabitats (B) pooled across three habitats in Jamaica. Overall distributions of branch clip samples and microhabitat use did not differ statistically. n refers to the number of foraging bouts (20–300 s) or number of branch clip samples.

Diptera, Formicidae (Hymenoptera), other Hymenoptera, unidentified adult arthropods, and unidentified larvae. Wolda (1990) illustrated the potential for error when an inadequate level of identification is used, and recommended that avian ecologists identify prey to the (morpho)species level. In practice however, this is difficult because diet analyses often permit the identification of prey fragments only to the order or family level (Cooper et al. 1990, Rosenberg and Cooper 1990, Chapman and Rosenberg 1991, Lefebvre et al. 1992), and therefore any finer discrimination in identifying arthropod samples yields data that are not immediately applicable to studies of food availability. Consequently, most studies of insect

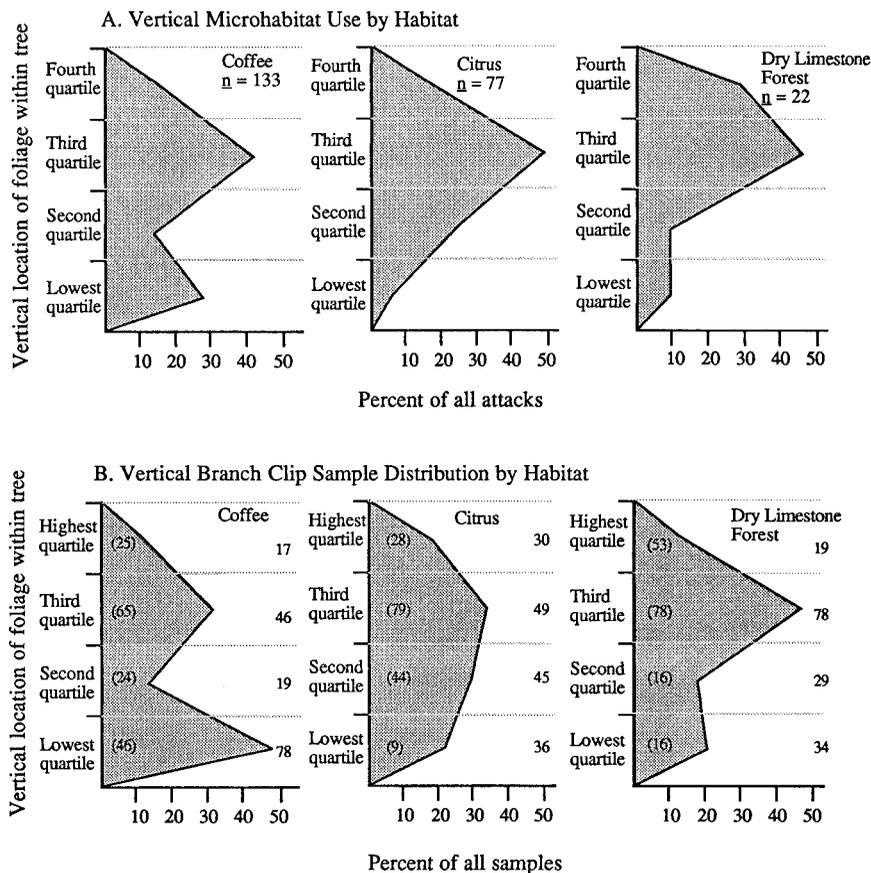


FIGURE 3. Use of vertical foliage microhabitats (A) and distribution of branch clip samples (B) in three Jamaican habitats: coffee plantation, citrus orchard, and dry limestone forest. Numbers in (B) indicate the number of samples in each foliage quartile ($n_{\text{actual}(i)}$) and (in parentheses) number of samples which would result in a precise match between warbler microhabitat use and branch clip sample distribution ($n_{\text{ideal}(i)}$). Branch clip samples were statistically weighted using the formula $W_i = n_{\text{ideal}(i)} / n_{\text{actual}(i)}$. See text for details.

food availability have identified potential prey to order (Hutto 1980, Terrill and Ohmart 1984, Holmes and Schultz 1988, Sherry 1990).

Calculations.—In this study, foraging observations and branch clipping were conducted concurrently. As a result, I selected branches for sampling based on gestalt approximations of warbler microhabitat use. Consequently, although the distribution of branch clips among horizontal foliage strata matched the frequency of microhabitat use by the study guild, the distribution of branch clips and microhabitat use among vertical foliage strata did not match well (Fig. 3). To amend this, I weighted branch clip samples obtained from different vertical regions of the foliage profile so

as to match microhabitat use by the study guild. This was accomplished using the following formulae for each microhabitat (i):

$$W_i = n_{\text{ideal}(i)} / n_{\text{actual}(i)} \quad (1)$$

$$n_{\text{ideal}(i)} = U_i \cdot n_{\text{total}} \quad (2)$$

where

W_i = the weighting factor by which all branch clip samples in microhabitat (i) were multiplied,

$n_{\text{ideal}(i)}$ = the number of branch clip samples from i if the match between warbler microhabitat use and branch clip sample distribution was precise,

$n_{\text{actual}(i)}$ = the actual number of branch clip samples taken from i ,

U_i = the percent use of microhabitat i by the study guild,

n_{total} = the total number of branch clip samples among all microhabitats.

The weighted sample totals were subsequently used in further calculations of food availability.

The food value of a prey item is closely related to its mass (Krebs and McCleery 1984, Karasov 1990), and since prey size and mass often vary significantly between sites (Janzen 1973), calculating food availability simply from the abundance of prey in each prey taxon could be misleading. Therefore, it is advisable to use arthropod biomass in calculations of food availability. I accomplished this by using length-mass regression equations derived from locally collected arthropods for each relevant prey taxon (Johnson and Strong manuscript). Other published length-mass regressions are available for some habitats in various regions, such as Costa Rica and Massachusetts (Schoener 1980), Washington (Rogers et al. 1977), and West Virginia (Sample et al. 1993). If length-mass regressions are unavailable for a particular study region or habitat, they should be computed from collected voucher specimens (Hodar 1996). Collecting vouchers from branch clip samples is relatively easy with an aspirator, forceps, and vials. Sample sizes required for generating reasonably accurate regressions are generally small (20–50 individual arthropods per prey taxon spanning as wide a range of lengths as possible), and the technique is straightforward (Hodar 1996).

For statistical calculations, each branch clip sample served as the unit of replication (i.e., rows in a database), and the biomass of trapped arthropods in each relevant prey taxon (one column per taxon) comprised the cell values. The principal index of food availability derived from branch clipping was the density of prey in the environment. The prey density of a branch clip sample was calculated as the biomass of all trapped arthropods per gram of clipped and inspected vegetation in that

sample. To examine differences in food availability between habitats, I ran an ANOVA in which habitat type served as the grouping factor, and prey density (in mg arthropods per gram clipped and inspected vegetation [$\times 1000$]) served as the dependent variable. There were no significant effects of winter period on prey density (ANOVA; $F_{1,478} = 0.59$, $P = 0.44$), therefore, samples from the early and late winter periods were pooled for further analyses.

Comparing Food Estimates With Attack Rates.—Many researchers have recognized that an effective way to evaluate the reliability of food availability measurements is to compare them to quantitative measures of foraging behaviors (Smith and Rotenberry 1990, Wolda 1990), but few arthropod sampling techniques have been evaluated in this way (Hutto 1990). By testing the prediction that food availability and foraging attack rate are positively correlated among habitats (Hutto 1990), foraging observations can provide an independent evaluation of food availability estimates. Here, I calculated foraging attack rates for each warbler species as the number of attacks per second observed in a foraging bout, and compared them to the estimates of food availability derived from branch clips.

RESULTS

Branch Clips vs. Foraging Locations.—The use of microhabitats by American Redstarts, Northern Parulas, and Prairie Warblers was quantified for purposes of measuring food availability for the three species together as a guild. Because profile analyses demonstrated that there were no significant differences ($P > 0.05$) between the species in microhabitat use, all observations of the guild were pooled for further comparisons. Among horizontal foliage strata, the guild tended to concentrate its foraging toward the outer edges of foliage and tree branches; 55.6% of all attacks by the guild occurred in the outer (away from trunk) third of tree foliage (Fig. 2a). Among vertical foliage strata, the guild attacked prey most frequently in the third quartile (50–75% of canopy height), and distributed its attacks relatively evenly across the other strata (Fig. 2b). However, profile analyses indicated that microhabitat use differed between habitats ($F_{4,223} = 2.53$, $P < 0.05$; Fig. 3a). In coffee, the guild tended to attack most often in the first and third foliage quartiles (28.7 and 40.7% of all attacks, respectively), whereas in citrus and dry limestone forest, the first quartile was used infrequently (5.4 and 9.7%, respectively).

Over all habitats, the distribution of branch clip samples closely matched the microhabitat use of the study guild. Chi-square analyses demonstrated that the overall distribution of foraging attacks and branch clip samples did not statistically differ among horizontal ($X^2 = 5.3$, $P = 0.07$, $df = 2$; Fig. 2a) or vertical strata ($X^2 = 7.6$, $P = 0.06$, $df = 3$; Fig. 2b). The use of vertical microhabitats varied between habitats, however (Fig. 3a), and when habitats were analyzed separately, the match between microhabitat use and branch clip sample distribution was not as close (Fig. 3b). To amend this, I statistically weighted branch clip samples by multi-

plying samples in each vertical microhabitat by a weighting factor derived from the use of that microhabitat by the study guild, as described in Calculations (Methods). Because horizontal microhabitat use did not differ among habitats and closely matched branch clip sample distribution (Fig. 2a), weighting samples also by horizontal microhabitat use was not necessary.

Foraging Attack Maneuvers.—Most attack maneuvers used by the study guild were probably directed at prey on foliage. More than any other maneuver, Prairie Warblers and Northern Parulas gleaned from surfaces of leaves (Table 1). Prairie Warblers also often pecked at the ends of small branches, again probably attacking small, sessile prey (Remsen and Robinson 1990). American Redstarts showed more variation in their attack types, including the use of sally-hover and flush-pursue maneuvers (Table 1). Nonetheless, even these more active maneuvers were usually directed at prey on (or flushed from) foliage (Remsen and Robinson 1990). Only the sally-strike attacks, which comprised 15.8% of American Redstart attacks, were likely to have been directed at free-flying insects (Remsen and Robinson 1990). Overall, 94% of the attack maneuvers used by the study guild (mean of the three species) were directed at prey located on foliage (Table 1).

Arthropod Taxa and Sizes.—Numerous taxonomic groups were trapped in branch clip samples (Table 2). Four orders—spiders (Aranae), leaf hoppers, psyllids, etc. (Homoptera), beetles (Coleoptera), and ants and wasps (Hymenoptera)—together comprised approximately 75% of the total trapped biomass. Flies (Diptera), and moths and caterpillars (Lepidoptera) comprised 7% and 6%, respectively, while the remaining groups combined accounted for 12.3% of total biomass.

Dietary information suggested that the study guild ingested a wide range of prey taxa (Table 2), necessitating the exclusion of relatively few arthropods from the branch clip samples. All groups eaten by the warblers were captured in branch clip samples except Odonata. Of the groups trapped by branch clips, only Isopterans were not reported to be eaten by any of the three warblers in the study guild. Therefore, I excluded Isoptera from calculations of food availability. Published analyses of prey sizes are lacking for wintering warblers, but observations suggest that large insects are rarely eaten (Greenberg 1995). Furthermore, a preliminary diet analysis indicated that among 100 stomach/emetic (regurgitation) samples from wintering American Redstarts, no arthropods were >10 mm in length, except for one 20 mm damselfly ($n = 322$ items, A. Medori and T. W. Sherry, unpubl. data). I rarely observed a warbler handling prey for more than a second, which further suggests that they were eating predominately small prey (pers. obs.). Warblers did occasionally glean large (>10 mm) caterpillars from new foliage or curled leaves (by probing, mostly done by Parulas), however, indicating that large caterpillars are potential prey for wintering warblers. Because caterpillars are digested quickly, they are poorly represented in diet analyses based on stomach contents (Rosenberg and Cooper 1990). Therefore, I excluded all ar-

TABLE 2. Taxonomic distribution (by mass) of branch clip samples, and summary of available diet information for three canopy insectivorous warblers in winter. X indicates that a taxon has been reported in the diet of a wintering warbler; no report indicates taxon has not to date been reported eaten; not spec. indicates for a sub-order taxon that the order was reported to be eaten, but finer classification was not specified.

Taxonomic unit	% by mass in branch clip samples	Prairie Warbler	Norther Parula	American Redstart
Aranae	18.1	X ^a	X ^{b,c,d}	X ^{e,f,g}
Odonata	not captured	no report	X ^c	X ^{e,f}
Orthoptera	2.3	X ^a	X ^d	X ^{e,f}
Dictyoptera	2.6	no report	no report	X ^f
Isoptera	0.2	no report	no report	no report
Psocoptera	1.7	no report	no report	6
Hemiptera	2.8	X ^a	X ^{b,d}	X ^{e,f,g}
Homoptera (all)	35.7	X ^a	X ^b	X ^{e,f,g}
Scale insects	4.8	not spec.	X ^d	no report
Other Homoptera	30.9	not spec.	X ^b	X ^{e,f}
Neuroptera	0.6	no report	no report	X ^e
Coleoptera	9.6	X ^a	X ^{b,c,d}	X ^{e,f,g}
Lepidoptera (all)	6.1	X ^a	X ^d	X ^{e,f}
Adults	0.8	not spec.	not spec.	X ^f
Larvae	5.3	not spec.	X ^h	X ^h
Diptera (all)	7.1	X ^a	X ^d	X ^{e,f}
Nematocera	1.2	not spec.	not spec.	X ^f
Non-Nematocera	5.9	not spec.	not spec.	X ^f
Hymenoptera (all)	11.1	X ^a	X ^{b,d}	X ^{e,f,g}
Formicidae	9.3	not spec.	X ^d	X ^f
Non-Formicidae	1.8	not spec.	X ^{b,d}	X ^f
Unknown (all)	2.1	—	—	—
Unknown adults	1.4	—	—	—
Unknown larvae	0.7	—	—	—
Length range	1–73 mm	no data	no data	<10.0 mm ^f

^a Bent (1953)

^b Wetmore (1916).

^c Danforth (1925).

^d Moldenhauer and Regelski (1996).

^e Lefebvre et al. (1992).

^f A. Medori and T. W. Sherry (unpubl. data).

^g Sherry and Holmes (1997).

^h Personal observation.

thropods >10 mm in length except caterpillars from analyses of food availability. Had they been captured, large Odonata (dragonflies) would have also been retained.

The size distribution of arthropods in branch clip samples differed significantly between the three habitats (Table 3). Citrus orchards supported high relative proportions of very small (<2 mm) and medium (4–5 mm) sized prey, but otherwise showed a similar prey size distribution to coffee plantations. Dry limestone forest contained proportionately more arthropods in the 2–3 mm and 6–10 mm ranges than the other habitats.

TABLE 3. Size distribution of arthropods trapped in branch clip samples in three habitats in Jamaica, showing total number of arthropods (percents) in each size class and chi-square test statistics.

Size class	Citrus	Coffee	Dry limestone forest
1-1.9 mm	100 (6.4)	55 (3.4)	21 (5.6)
2-2.9 mm	265 (16.9)	441 (27.3)	161 (42.8)
3-3.9 mm	982 (62.7)	1002 (62.1)	145 (38.6)
4-4.9 mm	150 (9.6)	76 (4.7)	24 (6.4)
5-5.9 mm	40 (2.6)	19 (1.2)	16 (4.3)
6-9.9 mm	28 (1.8)	20 (1.2)	9 (2.4)
Total no. arthropods	1566	1613	376

$\chi^2 = 187.0$, $df = 10$, $P < 0.001$

Habitat-Specific Food Availability vs. Foraging Attack Rate.—Food availability as indexed by branch clip samples differed significantly among habitats (ANOVA; $F_{2,477} = 21.87$, $P < 0.0001$; Fig. 4). Coffee plantations supported the greatest prey densities (2.43 mg arthropods/10 g vegetation), and dry limestone the least (0.66 mg arthropods/10 g vegetation, Tukey mean comparisons). Unweighted prey density was also highest in coffee and lowest in dry limestone forest ($F_{2,477} = 14.0$, $P < 0.0001$).

Foraging attack rates varied significantly among warblers in the study guild. American Redstarts and Northern Parulas attacked more often than did Prairie Warblers ($P < 0.05$, $F_{2,229} = 15.38$; ANOVA, with Tukey mean comparison). Within a species, small sample sizes (particularly in dry limestone forest) prohibited testing for differences in winter period

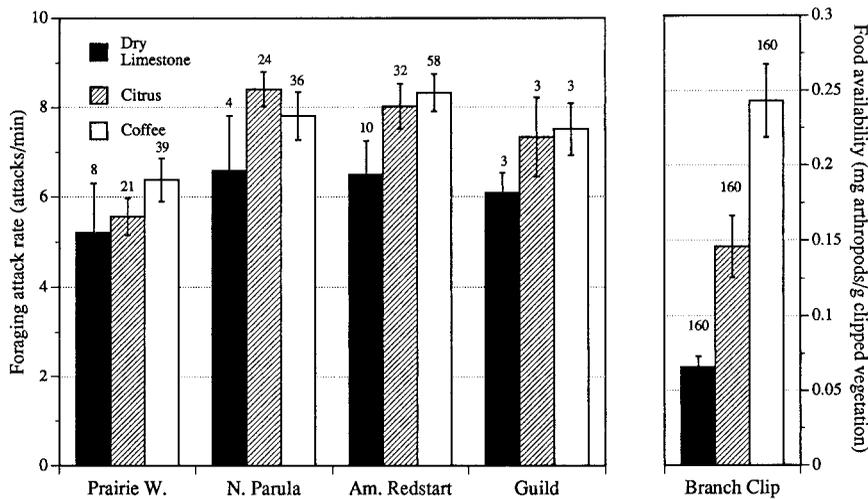


FIGURE 4. Foraging attack rates (± 1 SE) for three common migrant canopy insectivores in winter (and their average) versus food availability as measured by branch clips in three habitats in Jamaica (food data were natural log transformed for analyses).

or detecting significant differences between habitats. Nonetheless, all three species attacked at their lowest rates in dry limestone forest, and both Prairie Warblers and American Redstarts attacked most rapidly in coffee (Fig. 4).

The trends in foraging attack rates corresponded well to the pattern of food availability as measured by branch clipping (Fig. 4). The ranked order of habitats for American Redstarts' and Prairie Warblers' attack rates was identical to that of food availability, although the variation between habitats was more pronounced for the arthropod than foraging data. The average attack rate for the guild (arithmetic mean of 3 species) also had the same ranked order of habitats as food availability (Fig. 4). For Northern Parulas, attack rate was highest in citrus, but food availability as measured with branch clips was highest in coffee.

DISCUSSION

The results of this study suggest that branch clipping was effective in measuring food availability for the guild of common migrant canopy insectivores wintering in Jamaica (American Redstarts, Northern Parulas, and Prairie Warblers). By quantifying the foraging behaviors of the study species, I was able to sample arthropods from vegetation in a way that matched how the warblers used microhabitats within the foliage profile (Fig. 2). Where the match was poor, I statistically weighted branch clip samples accordingly (Fig. 3). Observations of foraging attack maneuvers indicated that 94% of the guild's attacks were directed at prey located on foliage (Table 1), which are likely to be well sampled by branch clipping (Schowalter et al. 1981, Majer and Recher 1988, Cooper and Whitmore 1990, Majer et al. 1990, Schowalter 1994). Published diet analyses identified potential prey, suggesting that termites (Isoptera) and large insects (except caterpillars) should be removed from food availability analyses (Table 2). Dietary information also indicated that nearly all of the items eaten by the guild were captured by branch clipping. Measurements of food availability corresponded to warbler foraging attack rates among three habitats in Jamaica; citrus orchards and especially dry limestone forests had lower prey densities and foraging rates than did shade coffee plantations (Fig. 4). Foraging attack rates, which can be used as an independent assessment of the reliability of food availability estimates (Hutto 1990), provided the strongest evidence suggesting that, once field and analytical steps were taken to exclude uneaten prey and unused microhabitats, branch clips effectively sampled food availability for American Redstarts, Northern Parulas, and Prairie Warblers wintering in Jamaica.

It should be noted that the utility of foraging attack rates as an assessment of food availability estimates rests on the assumption that other variables in food intake remain constant between habitats, such as time spent foraging (daily time budget), average prey size/nutritional value, and rate of energy expenditure (Hutto 1990). If these variables are markedly unequal between habitats, foraging attack rates can become decoupled from food availability. For example, in citrus orchards 6.4% of all

arthropods captured in branch clips were less than 2 mm in length, versus only 3.4% in coffee plantations (Table 3). Many of these small insects in citrus (81%) were bark lice (Psocoptera) typically found on small twigs (pers. obs.). Northern Parulas used bark gleans 12.4% of the time in citrus orchards, compared to only 7.0% in coffee. These data suggest that parulas in citrus orchards may have fed on many small prey (including many Psocopterans) rapidly gleaned from bark and leaf surfaces, while those in coffee may have fed at nearly the same rate but on larger prey. Thus, food may have been somewhat less available for Northern Parulas in citrus orchards than suggested by foraging attack rates, which may explain the single discrepancy between attacks rates and measures of food availability. Unlike foraging observations, branch clip data provide measurements of food availability in terms of arthropod biomass per foliage unit mass, and therefore may be more reliable than simple foraging attack rates, but again, other assumptions are operating (e.g., equal energy content per unit mass for all arthropod taxa).

Previous researchers have noted that branch clipping may be biased against "active arthropods" (Cooper and Whitmore 1990). In this study, no dragonflies were collected by branch clipping, even though they were present in the habitats studied (pers. obs.) and may have been used occasionally by foraging warblers as prey (Lefebvre et al. 1992; Medori and Sherry, unpubl. data). Although branch clipping failed to capture this "active" prey type, I argue that at least some other active insects are reasonably well sampled. Dragonflies are anomalous because they have exceptionally keen eyesight compared to other insects, particularly at long distances (Goldsmith and Bernard 1974, Hodgson 1974, Miller 1987). Long, keen eyesight is relatively rare among insects, being most evident in Odonata and very large Diptera and Hymenoptera (Goldsmith and Bernard 1974), which are important in the diets of only some forest insectivorous birds, such as large Neotropical flycatchers, swifts, and swallows (Hespenheide 1975, Sherry 1984). Thus, branch clipping probably traps most insects before they have time to detect, react to, and evade the bag (Majer et al. 1990, pers. obs.). Indeed, in this study, small flies (Diptera) contributed 7.1% to the total biomass of arthropods trapped by branch clipping. Both robust, fast flying non-Nematocerans (5.9%) and slower, seldom-landing, mosquito-like Nematocerans (1.2%) were captured, indicating that some "active" insects are frequently sampled.

Nonetheless, other arthropods may be poorly sampled by branch clips because they do not typically reside or fly near foliage where they may be captured. For example, midges (Diptera: Chironomidae) often occur in huge swarms which usually form in the evening in open spaces over wet meadows or clearings in forests (Borror et al. 1989), and are sampled poorly by branch clipping. In addition, arthropods that typically reside on very large branches, trunks, or in dense thickets cannot be easily accessed, and are therefore poorly sampled by branch clipping.

Usefulness of branch clipping for other species and habitats.—Although this study focused on migrant canopy insectivores in Jamaica, branch clipping

may also be a useful technique for measuring food availability for other species and in other habitats. Majer and Recher (1988) demonstrated that branch clipping samples most insect orders in forest habitats reasonably well, a finding that is corroborated here. Therefore, provided diet analyses are available to identify which prey are not eaten, branch clipping probably captures the potential prey of many species of forest insectivores. By using telescoping poles and/or canopy platforms (Schowalter 1994) to gain access to most regions of forest understories and canopies, branch clipping also enables a researcher to sample directly from the microhabitats used by foraging birds.

However, an understanding of the foraging ecology of the focal species and the ecological characteristics of the habitats studied may also identify species and/or habitats for which branch clipping is ill-suited. For example, the diets of some forest insectivores, such as wood-pewees (Sherry 1984), are comprised mainly of insects that fly quickly and possess keen eyesight (e.g., large Diptera or Odonata); other birds, such as swallows (Hespenheide 1975), frequently feed on large aggregations of flying insects that seldom land (e.g., Nematocerans). These insects are poorly sampled by branch clipping. Thus, to generalize, branch clipping is probably ineffective in measuring food availability for bird species that rely predominantly on sally-strike attacks directed toward aerial prey or that feed in flight on flying masses of small insects.

In addition, species that typically prey upon foliage-dwelling insects may shift their behavior toward more aerial prey in certain habitats or seasons, which may make branch clipping useful only in some habitats and times of year. For example, Black-throated Green Warblers (*Dendroica virens*) generally feed on small sessile insect prey located near the ends of branches (Morse 1993), which suggests that they would be a species for which branch clipping may be well-suited for measuring food availability. Yet Smith et al. (1998) demonstrated that during spring migration near the shores of the Great Lakes, Black-throated Green Warblers feed heavily on midges (Diptera: Chironomidae). Consequently, branch clipping would ineffectively sample food availability for Black-throated Green Warblers in near-shore habitats at that time of year. Similarly, in a Jamaican mangrove swamp, American Redstarts used attack maneuvers directed at flying prey proportionately more often than in the drier habitats studied here (see Lovette and Holmes 1995), and diet analyses suggest they ingest more Nematoceran flies in the mangrove than in dry limestone forest (A. Medori and T. W. Sherry, unpubl. data). Thus, in mangroves, branch clipping alone may not adequately sample food availability. Other species probably show similar shifts toward flying insects with aquatic larvae in habitats (or seasons) that contain standing water. In these instances, combining branch clipping results with those from sweep nets (Terrill and Ohmart 1984), Malaise traps (Parrish and Sherry 1994), or water pan traps (Cooper and Whitmore 1990) may provide more accurate measures of food availability.

Nonetheless, using branch clips to measure food availability for “fo-

liage-gleaning" insectivores in densely forested habitats is overly restrictive because many semi-aerial insectivores (redstarts, gnatcatchers, some flycatchers) actually ingest prey which typically reside on foliage (Remsen and Robinson 1990), even if such prey are often captured in flight after being flushed from their perches. In addition, the sally-strike attacks of some birds, such as Least and Hammond's Flycatchers (*Empidonax minimus* and *E. hammondi*), are often aimed at insects flying close to canopy foliage (Via 1979, Sakai and Noon 1990, Briskie 1994, Sedgewick 1994), where they could be sampled by branch clipping. Thus, branch clipping could be a useful sampling technique even for some flycatchers, although complimentary methods may also be needed.

Methodological variations.—The sampling protocol described in this study was designed specifically for the species and habitats studied here. However, variations in this protocol may prove useful for researchers working with other species in other habitats.

In this study, I collected branch clip samples with a reusable cloth bag and inspected samples in the field because it was time efficient and amenable to use in remote sites where laboratory conditions were unavailable. As an alternative however, disposable plastic trash bags could be used in place of the re-usable cloth bag. These bags could be transported to a lab or field station where they may be frozen or fumigated with pesticides to immobilize or kill arthropods to facilitate counting and measuring (Schowalter et al. 1981, Majer and Recher 1988). This variation has the added benefit of preserving the sampled arthropods and vegetation so that arthropod captures could be expressed in relation to dry mass and/or leaf area, depending on the needs of the researcher.

The branch clip apparatus and branch selection technique I describe effectively accessed the microhabitats used by foraging warblers in the habitats studied here, but other forests and/or study designs may require different methods. Longer telescoping poles could be used in forests where birds frequently forage at heights greater than 9 m, although they become prohibitively unwieldy above 15 m. The use of platforms (Schowalter et al. 1981) or a mobile cherry picker (Majer et al. 1990) may be required in the tallest forests. I selected branches for sampling so as to match the use of microhabitats by foraging warblers, but random or stratified branch selection could be useful for other studies (Schowalter 1994), such as those comparing used to unused microhabitats (Cooper and Whitmore 1990). In these cases, a researcher could randomly select "sampling frames" at each sampling location by positioning oneself a random distance and direction from a central point (e.g., tree trunk) and sighting through a restrictive frame (e.g., a toilet paper tube). Then a branch(es) could be enumerated and randomly selected within the sampling frame.

The methods described here were designed to compare the availability of food between habitats, but some researchers will wish to quantify food availability on smaller spatial scales (e.g., per nesting site or territory), which requires a different sampling protocol. Branch clipping has been found to be effective in capturing sessile prey such as lepidopteran larvae

useful for many birds as nestling food (Gibb and Betts 1963, Majer et al. 1990), but whether multiple samples within such a limited area as a bird's nesting site could detect variation between sites and remain statistically independent is uncertain. For cases in which the change in food availability over time is important, Poulin and Lefebvre (1997) describe a useful technique to quantify the relative change in abundance of arthropod taxa. Because this approach is based on the summation of percent abundances, it has the added benefit of permitting the combination of results from different arthropod trapping techniques, or even different food types (e.g., arthropods, seeds, fruit).

As an alternative to prey density, one could quantify foliage volume in each study site (MacArthur and Horn 1969) and multiply it by prey density to obtain total prey abundance as an index of food availability (adjusted insect density; Hutto 1985). This may be useful if sites differ greatly in foliage volume. However, the energetics of foraging act upon prey ingestion rates (Krebs and McCleery 1984, Karasov 1990), which are probably closely related to rates of potential prey encounter, and hence, foraging movement speeds (Robinson and Holmes 1982, Hutto 1990). Therefore, food availability is higher in sites with high foliage volume only if birds also consume (move) at faster rates in them. Due to vegetation obstruction, the reverse may be more likely. Prey density (prey per unit of vegetation weight or area) is probably more closely correlated with ingestion rates and may therefore be a more meaningful index of food availability than total prey abundance.

Lastly, to compare arthropod communities between groups, rather than total arthropod availability, one should use a profile analysis (an application of MANOVA) (Johnson, in press). With this analysis, each taxon serves as a dependent variable; between subjects tests reveal differences in absolute arthropod abundance (the "size" of the arthropod community), whereas within subjects tests reveal differences in relative arthropod abundances (community "shape") (Boecklen and Price 1989, Tabachnick and Fidell 1996). For descriptive statistics, the ratio of means (mean arthropod biomass of all samples in a site/mean vegetation mass of all samples in that site) may provide the best estimate of the true mean when the sample unit size is variable (Cochran 1977, Schowalter et al. 1981).

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