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Dissimilar Bill Shapes in New World Tropical Versus Temperate Forest Foliage-Gleaning Birds

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Summary. The bill shape of foliage-gleaning birds in temperate and tropical new world forests is dissimilar. Tropical species have longer and narrower bills than their temperate zone counterparts. In addition, their bills are longer for a given body size. These differences cannot be readily explained as phylogenetic artifacts. I suggest that the distinct bill morphology of the two assemblages is determined by the type of insects that comprise the largest size classes of potential prey. These large insects are particularly important since they generally comprise the bulk of the nestling diet for insectivorous birds. In tropical forests Orthoptera are probably the most abundant large soft-bodied arthropods; they form an important resource for foliage-gleaning birds during the breeding (rainy) seasons. Most temperate zone foliage-gleaning birds rely almost entirely upon caterpillars when breeding. Long, narrow bills are thought to close more rapidly than shorter, broader bills. These long, "fast" bills may be required to efficiently harvest active Orthoptera. Migrant warblers may face morphological constraints from breeding successfully in lowland tropical forests. While the short-billed temperate zone birds can survive the tropical dry season by foraging on small arthropods, they may be inefficient at handling large Orthoptera to feed to nestlings.

Introduction

Morphology is often used to test hypotheses concerning ecological relationships within avian guilds (e.g., Schoener 1965; Root 1967; Hespenheide 1976; Ricklefs 1977) and avian communities (e.g., Karr and James 1975; Ricklefs and Travis 1980). These analyses explore the distribution of species in morphological space, concentrating on limiting similarity within communities and convergence between communities. Studies have not explored morphological differences in equivalent guilds between communities. If identified, such multi-species morphological dissimilarities can provide a basis for examining underlying ecological differences between communities. In this paper I present and discuss the non-overlapping distributions of bill shape in foliage-gleaning birds of temperate and tropical broad-leafed forests.

Methods

I restricted my analysis to gleaning passerines that hop about actively searching for arthropods on leaf surfaces (Table 1). In many species, bird bills function in several ways for capturing, seizing, and handling prey, including ripping into hiding places. But by examining only insectivores that forage off broad leaves, I focused on birds that use their bills primarily to pluck and manipulate prey. The diverse morphologies can be interpreted in this light. Not included are species that are mostly nectarivorous (*Cyanerpes, Chlorophanes, Conirostrum*); species that often capture arthropods from twigs (*Parus, Trogolodytes, Polioptila, Ramphocaenus, Microbates, Vireo solitarius*); species that rip or probe into live or dead curled leaves (*Philydor, Automolus, Myrmotherula fulviventris, Cacicus uropygialis, Dacnis*); terrestrial species that might forage from leaf litter (*Myrmeciza, Oporornis*); and species that hover-glean or sally to capture flushed or aerial insects (*Dysithamnus puncticeps, Terenotriccus, Empidonax*, other hover-gleaning tyrannids, *Setophaga, Wilsonia*).

Tropical species include foliage-gleaners found in lowland or foothills forest (0–1,500 m) of Panama (from Ridgely, 1976). I have watched all of the species forage except *Terenura* (see Greenberg and Gradwohl, 1980), but my experience with *Hemithraupis, Chrysothlypis, Thamnistes*, and *Smaragdolanius* is quite limited. Temperate species include those breeding in eastern hardwood forests; foraging data for many species at Hubbard-Brook, New Hampshire is presented in Holmes et al. (1979). In addition, I will present an analysis comparing resident versus migrant foliage-gleaners (regardless of breeding habitat) on Barro Colorado Island, Panama.

Bills of 2–12 specimens of both sexes for species represented in the collections of the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley or the Museum of Zoology, Louisiana State University (LSU) were measured. I measured the culmen from the front edge of the nares to the tip of the upper mandible and bill width at the nares with dial calipers. Specimens of temperate zone species were randomly selected from the geographic range represented in the MVZ. Specimens of tropical species were primarily from Panama and Costa Rica, and were supplemented by material from nearby areas of Central and South America. Since I am not concerned here with interspecific interactions within communities, the broad range from which specimens were collected should not pose a serious problem. Weights of temperate zone species came from Holmes and Sturges (1975) and museum skin labels. Weights for tropical species came from our own banding data from Barro Colorado Island (Gradwohl and Greenberg, unpubl.), Karr (1971), and museum skin labels. Weights were converted to cube roots to compare with linear bill measurements. Unless otherwise stated, significance was determined with a Mann-Whitney U test (two-tailed).

Results

Lowland tropical forest foliage-gleaners have bill shapes that are quite distinct from their temperate zone counterparts (Fig. 1). Tropical species have longer bills averaging 1.01 cm versus 0.88 cm ($U_{16,12} = 144$, $p < 0.001$). In addition to length, tropical species tend to have relatively narrower bills. Bill width to length ratios (Table 1) average 0.40 for tropical and 0.47 for temperate zone species ($U_{16,12} = 157$, $p < 0.05$). The regression lines of length to width for the two groups (Fig. 1) are parallel and significantly different (ANCOVA $F_{1,25} = 38$, $p < 0.001$) indicating that for a given bill length, tropical birds have narrower bills. The migrant foliage gleaners that pass through or spend the

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Table 1. Morphological data for foliage-gleaning birds from the temperate (eastern U.S.) and tropical zones (Panama) of the new world

Species	Code	Family	*N*	Wt (g)	Culmen Length (cm)	Bill Width (cm)	Relative Bill Width (cm)
Temperate Species:							
Yellow-throated Vireo (*Vireo flavifrons*)	1	Vireonidae	6	15	0.83 (0.02)[a]	0.44 (0.02)	0.53 (0.02)
Red-eyed Vireo (*Vireo olivaceus*)	2	Vireonidae	6	17	0.92 (0.02)	0.38 (0.006)	0.42 (0.01)
Philadelphia Vireo (*Vireo philadelphicus*)	3	Vireonidae	6	12	0.68 (0.01)	0.31 (0.005)	0.45 (0.02)
Warbling Vireo (*Vireo gilvus*)	4	Vireonidae	6	15	0.78 (0.02)	0.34 (0.01)	0.43 (0.02)
Northern Parula Warbler (*Parula americana*)	5	Parulidae	6	8	0.72 (0.02)	0.30 (0.007)	0.43 (0.01)
Black-throated Blue Warbler (*Dendroica caerulescens*)	6	Parulidae	6	9	0.70 (0.01)	0.30 (0.003)	0.41 (0.01)
Black-throated Green Warbler (*Dendroica virens*)	7	Parulidae	6	9	0.73 (0.02)	0.29 (0.003)	0.40 (0.005)
Cerulean Warbler (*Dendroica cerulea*)	8	Parulidae	6	9	0.75 (0.01)	0.32 (0.005)	0.42 (0.01)
Blackburnian Warbler (*Dendroica fusca*)	9	Parulidae	6	10	0.77 (0.01)	0.33 (0.01)	0.43 (0.01)
Chestnut-sided Warbler[b] (*Dendroica pensylvanica*)	10	Parulidae	6	9	0.75 (0.02)	0.32 (0.01)	0.43 (0.01)
Bay-breasted Warbler[b] (*Dendroica castanea*)	11	Parulidae	6	11	0.78 (0.01)	0.43 (0.01)	0.43 (0.01)
Summer Tanager (*Piranga rubra*)	12	Thraupidae	6	27	1.36 (0.04)	0.75 (0.04)	0.55 (0.01)
Scarlet Tanager (*Piranga olivacea*)	13	Thraupidae	6	27	1.11 (0.02)	0.65 (0.01)	0.60 (0.02)
Rose-breasted Grosbeak	14	Fringillidae	6	41	1.19 (0.03)	0.74 (0.01)	0.62 (0.01)
Temperate Species means					0.88 (0.07)	0.43 (0.05)	0.47 (0.02)
Tropical Species:							
Slaty Antshrike (*Thamnophilus punctatus*)	A	Formicariidae	10	23	1.27 (0.02)	0.46 (0.01)	0.36 (0.01)
Russet Antshrike (*Thamnistes anabatinus*)	B	Formicariidae	8	21	1.28 (0.08)	0.63 (0.005)	0.51 (0.01)
Plain Antvireo (*Dysithamnus mentalis*)	C	Formicariidae	10	13	0.91 (0.02)	0.35 (0.007)	0.39 (0.005)
Pygmy Antwren (*Myrmotherula brachyura*)	D	Formicariidae	7	7	0.88 (0.01)	0.31 (0.01)	0.36 (0.01)
White-flanked Antwren (*Myrmotherula axillaris*)	E	Formicariidae	14	8	0.88 (0.01)	0.29 (0.01)	0.33 (0.01)
Slaty Antwren (*Myrmotherula schisticolor*)	F	Formicariidae	10	9	0.85 (0.01)	0.33 (0.006)	0.39 (0.004)
Dot-winged Antwren (*Microrhopias quixensis*)	G	Formicariidae	13	8	0.91 (0.01)	0.33 (0.006)	0.39 (0.01)
Rufous-rumped Antwren (*Terenura callinota*)	H	Formicariidae	4	8	0.87 (0.01)	0.33 (0.01)	0.38 (0.02)
Green Shrike-Vireo (*Smaragdolanius pulchellus*)	I	Vireolaniidae	4	27	1.07 (0.04)	0.46 (0.005)	0.43 (0.01)
Lesser Greenlet (*Hylophilus decurtatus*)	J	Vireonidae	12	9	0.86 (0.02)	0.27 (0.01)	0.32 (0.01)
Tawny-crowned Greenlet (*Hylophilus ochraceiceps*)	K	Vireonidae	10	11	0.85 (0.02)	0.34 (0.01)	0.40 (0.01)
Carmiol's Tanager[c] (*Chlorothraupis carmioli*)	L	Thraupidae	6	40	1.27 (0.02)	0.62 (0.01)	0.48 (0.01)
White-shouldered Tanager (*Tachyphonus luctuosus*)	M	Thraupidae	4	13	1.02 (0.04)	0.48 (0.02)	0.48 (0.02)
Scarlet-browed Tanager[d] (*Heterospingus xanthopygius*)	N	Thraupidae	2	36	1.35 (0.07)	0.56 (0.03)	0.42 (0.03)
Yellow-backed Tanager (*Hemithraupis flavicollis*)	O	Thraupidae	7	11	0.89 (0.02)	0.34 (0.007)	0.39 (0.01)
Black-and-yellow Tanager (*Chrysothlypis chrysomelas*)	P	Thraupidae	2	11	1.02 (0.02)	0.33 (0.02)	0.33 (0.02)
Tropical species means					1.01 (0.05)	0.40 (0.03)	0.40 (0.01)

[a] Numbers in parentheses are standard errors

[b] These species winter in broad-leafed forests (BCI), but breed in other habitats

[c] The closely related Yellow-olive Tanager (*Chlorothraupis olivacea*) of eastern Panama has not been included since it is so morphologically similar

[d] The closely related Sulphur-rumped Tanager (*Heterospingus rubrifrons*) has not been included

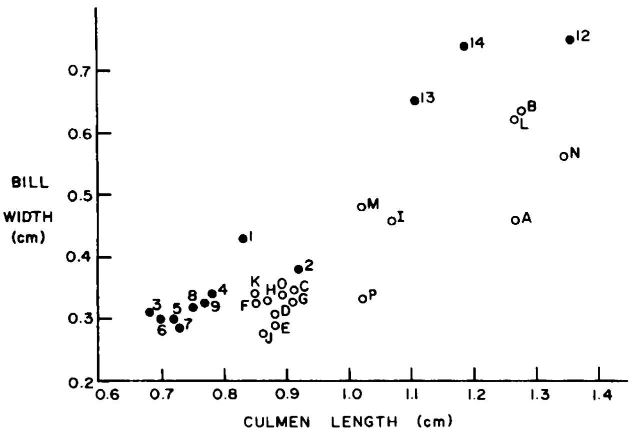

Fig. 1. Species' means of culmen length (cm) by bill width at nares. Tropical species (o) regression equation: $y=0.58x-0.19$ ($r=0.89$). Temperate species (●) regression equation: $y=0.67x-0.25$ ($r=0.97$). See Table 1 for species corresponding to symbols

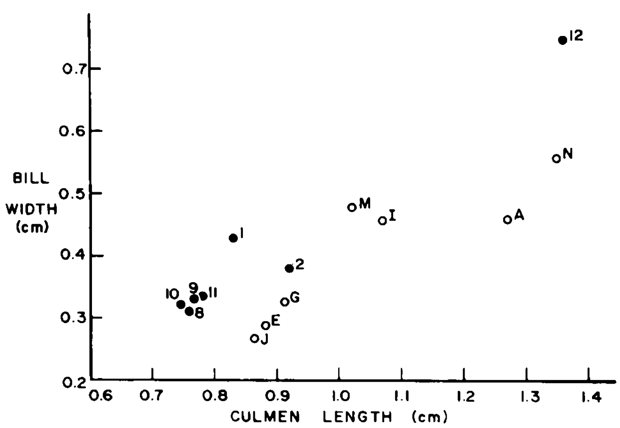

Fig. 2. Species' means of culmen length by bill width for foliage-gleaning birds on Barro Colorado Island, Panama. Migrants included irrespective of breeding habitat. Tropical residents are clear circles (o) and temperate zone species are darkened circles (●)

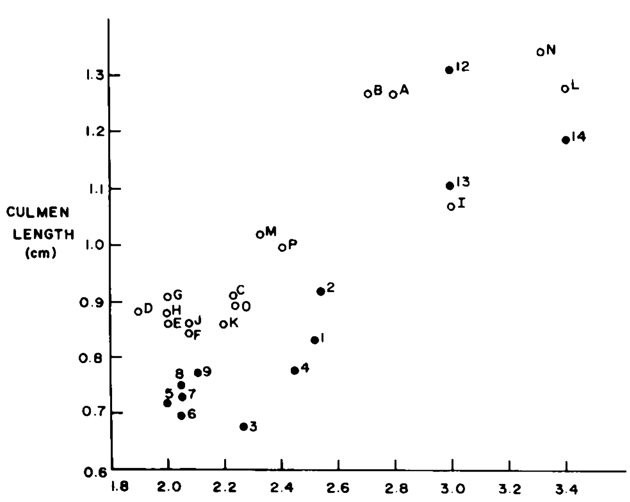

Fig. 3. Species' means of cube root of body weight by culmen length. Regression equations for tropical species (o): $y=0.35x+0.16$ ($r=0.92$). Regression equation for temperate zone species (●): $y=0.47x+0.35$ ($r=0.84$). See Table 1 for symbols

winter on Barro Colorado Island are also distinguished from the local residents by having shorter and relatively broader bills (Fig. 2).

The consistently greater bill length in tropical foliage-gleaners does not result from larger overall body size (Fig. 3). In fact, relative bill length (culmen length/cube root of body weight) is far greater in tropical species ($U_{16,12}=189$, $p<0.001$). The regression lines of mean bill length to cube root of body weight for tropical species and temperate species are significantly different (ANCOVA $F_{1,25}=26.4$, $p<0.001$). These results are relatively insensitive to inaccuracies in body weight data; an 8 g tropical species has a greater bill length than a 15 g temperate zone species.

Discussion

I will examine four factors that might account for the generally longer and narrower bills of tropical forest foliage-gleaners: physiological efficiency; phylogenetic artifact; prey size; and prey mobility.

Physiological Efficiency

Karr and James (1975) suggested that tropical birds are generally smaller than temperate zone species since temperatures are less often stressfully cold. This explanation, based on Bergmann's Rule, assumes that in the absence of physiologically based counter-selection, body size should tend to decrease. Newton (1967) suggested that birds should evolve the smallest body size possible for a given bill size since a smaller body requires less food. This would account for the increased relative bill length for tropical birds, but fails to explain the consistently greater absolute bill size.

Phylogenetic Artifact

Few major taxa are represented in the foliage-gleaning guild of nearctic or neotropical forests. The difference between temperate and tropical bills may be a result of the phylogenetic history of these few groups. It is conceivable that long, narrow bills are characteristic of Formicariidae and shorter bills are characteristic of Parulidae; antwrens and *Dendroica* have not diverged from this general pattern. Several observations suggest that this is not the case. The tropical foliage-gleaners represent four separate families; the temperate species show a similar familial diversity. Even within Formicariids there is a tremendous diversity of bill size and shapes, including some terrestrial species with relatively short, broad bills. *Dendroica* may have long, narrow bills in species that often probe into needle clusters of pine trees (Ficken et al. 1967). *Dendroica dominica*, for example, has a bill length of 1.0 cm (0.02 cm SE) and a relative bill width of only 0.29 (0.01 SE). Finally, temperate zone vireos (*Vireo*) have shorter, broader bills than lowland tropical vireos (*Hylophilus*).

Prey Size

Schoener (1971) and Faaborg (1977) suggested that the relatively greater abundance of large arthropods in tropical regions might have a great effect on the bill size distribution of tropical birds. These workers and others (Karr and James 1976), have found, however, that avian guilds respond to an increased size range of prey with an increased range in bill size by the addition of a few, uncommon, large-billed species. This would not account for the consistently longer bills of tropical foliage-gleaning birds. Nor does it explain the narrower bills of tropical species.

Observations of temperate zone species that were feeding nestlings also suggests that differences in the size distribution alone may not account for their shorter, broader bills. Parent birds usually feed their young prey items larger than those they eat themselves (Betts 1955; Royama 1966; Root 1967; Nolan 1979), and these nestling prey items can be quite large. For example, the most common size class of caterpillars brought to nestling Prairie Warblers (*Dendroica discolor*) was 20–25 mm (Nolan 1979). The mean length of prey brought by the similar-sized Dot-winged Antwren (*Microrhopias quixensis*) to 10 nests (598 items) was 10–15 mm (Gradwohl and Greenberg in press). Even for the much more massive Slaty Antshrike (*Thamnophilus punctatus*) the most common length for items brought to the nest was only 20–25 mm (Oniki 1975). All foliage gleaners, tropical or temperate, can consistently handle large prey items when raising families.

Prey Mobility

The largest prey items handled by foliage-gleaning birds are probably the greatest ecological challenge to a particular bill design. These large prey items are usually both the fastest and the strongest within a particular taxon. If this assumption is accepted, then it follows that the period of a bird's life history during which the largest prey are handled is probably the period that exerts the strongest selective force in molding bill shapes. The largest prey handled by foliage-gleaners are usually those fed to nestling or to mates during courtship feeding (Royama 1966; Root 1967; Nolan 1979; Gradwohl and Greenberg in press).

Breeding in insectivorous forest birds generally occurs in response to blooms of arthropods during the temperate zone summer or tropical rainy seasons. These resource blooms are qualitatively different between temperate and lowland tropical forests. In temperate forests, Lepidoptera larvae become the abundant arthropods of leaf surfaces (Holmes et al., 1979). In tropical forests various groups of Orthoptera (crickets, katydids, and roaches) appear to be the most abundant large prey on foliage (Greenberg and Gradwohl in press; Greenberg in prep.). The few in-depth studies of nesting birds indicate that these differences are reflected in nestling diet. Caterpillars appear to be nearly universal food of young temperate zone foliage-gleaners. For example, during June and July 1980 I observed that of 249 large prey carried by 13 species of nesting warblers in Maine, 91% were caterpillars between 1–2 cm in length. Observations and experiments by Holmes et al. (1979) and Heinrich (1979) indicate that large green caterpillars suffer severe predation by nesting birds. On the other hand, Orthoptera may be far more important to tropical forest insectivores. I observed that Orthoptera dominated the nestling diet of *Microrhopias*, and Oniki (1975) made similar observations for *Thamnophilus* (Table 2). Most large prey items handled by other foliage-gleaning birds on Barro Colorado Island were Orthoptera (Table 2). Yet even in Panama, the most common large prey items of wintering *Dendroica* were grubs.

Orthoptera and caterpillars of equivalent size are markedly different prey for birds. Orthoptera are highly mobile, but essentially powerless to escape once the body is seized and the legs are held free. Caterpillars are easily seized but can struggle considerably with body contractions once captured. While beating caterpillars to immobilize them requires strength, the removal of the potentially dangerous hind legs of Orthoptera demands quick, deft bill movements.

The difference in bill morphology of tropical and temperate foliage-gleaners is consistent with the qualitative difference in prey behavior. Beecher (1962) argued, based on functional analysis and correlation, that longer bills can handle more mobile prey. Ashmole (1968) suggested that terns with longer and narrower bills capture faster fish. Lederer (1975, 1980) suggested that for tyrant flycatchers, longer billed species can capture more mobile prey of similar size than short-billed species. The longer, narrower bills of tropical foliage-gleaners may function to capture the highly active Orthoptera and hold their struggling legs free from their face. The broader bills of temperate zone species may increase their strength to resist the movements of struggling larvae. In addition, temperate zone foliage-gleaners often carry simultaneously several large prey items, presumably because grubs are easily captured, even with a full mouth. I have never observed such multiple loadings in tropical foliage-gleaning species. Multiple loadings should also favor strength over speed.

Table 2. The large prey of foliage-gleaning birds on Barro Colorado Island, Panama

Species	N	Percent Orthoptera	Percent Larvae
Dot-winged Antwren (nest)[a]	539	57 (3)	9 (1.6)
(away from nest)	60	55	13
White-flanked Antwren	37	58	11
Slaty Antshrike (nest)[b]	174	44	17
(away from nest)	52	42	37
Bay-breasted Warbler	25	14	65
Chestnut-sided Warbler	35	14	78
Dendroica (total)	60	14	73
Lesser Greenlet	23	61	26
White-shouldered Tanager	52	62	15

[a] Mean and standard error (parentheses) based on samples observed at 10 different nests (Gradwohl and Greenberg, in press)
[b] From Oniki (1975)

Caterpillar Foragers in Lowland Tropical Forests

In this discussion I do not wish to imply that no bird species forages primarily upon caterpillars when foraging for large prey in lowland tropical forests. In fact, my limited observation of the Blue Dacnis (*Dacnis cayana*) suggest they feed heavily upon larvae that live in leaf curls or mines; twenty-four of twenty-five large prey items were grubs. *Dacnis* use their narrow icterid-like bills to probe into crannies and gaps to extract hidden grubs. My few observations of the Scarlet-rumped Cacique (*Cacicus uropygialis*) indicate that it also probes into leaf curls for larvae. By excluding probing species I probably excluded the major caterpillar foraging species. This may say something about the distribution of caterpillars in lowland tropical forests. Unlike many cryptic caterpillars in the temperate zone (Heinrich 1979), many tropical cryptic species hide by sewing into leaf material. These may require special bill shapes and searching behavior to locate and extract.

Other Tropical Habitats

The analysis presented here was restricted to lowland tropical forests because it is quite likely that major changes in available prey occur as one moves up a tropical mountain. Orthoptera, for example, apparently drop out at high elevations (above 1,500 m) in the mountains of Costa Rica (Janzen 1973). This suggests that the caterpillar-Orthoptera ratio could approach temperate zone conditions. The change in bill morphology of birds along an altitudinal gradient would provide an interesting test of the ideas presented here. I have also excluded lowland second-growth and dry forest species because it is also likely that the availability of major insect groups is quite different from moist forest. Orthoptera, for example, were found to be less numerous in drier forests of Costa Rica (Janzen and Schoener 1968). These comparisions, as well as similar analyses on other continents could provide natural tests for the hypothesis presented in this paper.

Bill Shape of Temperate Zone Migrants Wintering in Lowland Tropical Forests

The migrant foliage gleaners in a lowland Panamanian forest (Fig. 2) are distinct from the local residents in having shorter, broader bills. The bill morphology of these species supports the hypothesis that it is breeding resources that most strongly influence the shape of foliage-gleaning bills. In this way foliage gleaners may differ from finches (Fretwell 1972) and shorebirds, which appear to have winter-selected bill morphology. In fact, bill shape is the only feature that distinguishes temperate zone foliage-gleaners, as a group, from tropical resident foliage-gleaners. For ecological variables, each migrant species more closely resembles some tropical resident species than it resembles other migrants (Greenberg 1979; Morton 1980; Greenberg in prep). This suggests a line of speculation for why these successfully wintering migrant species have not established breeding populations in lowland tropical forests. It is possible that these temperate zone breeding migrants are unable to efficiently gather large Orthoptera. The few large prey items observed taken by *Dendroica* on Barro Colorado Island support this idea; seventy-six percent ($n=60$) were large grubs (Table 2). In addition, Morton (1980) found larvae, but no Orthoptera in the stomachs of *Dendroica* from the Canal Zone. Restriction to less mobile prey in smaller size classes could require a tremendous number of trips to the nest. This would be both energetically demanding and attractive to predators (Skutch 1949). During the winter months, large Orthoptera are scarce (Gradwohl and Greenberg, in press) and residents and migrants must both rely upon small arthropods for self-maintenance.

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