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Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest

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ABSTRACT. Little is known about how insectivorous bird diets are influenced by arthropod availability and about how these relationships vary seasonally. We captured birds in forest-canopy gaps and adjacent mature forest during 2001 and 2002 at the Savannah River Site in Barnwell County, South Carolina, and flushed their crops to gather information about arthropods eaten during four periods: spring migration, breeding, postbreeding, and fall migration. Arthropod availability for foliage- and ground-gleaning birds was examined by leaf clipping and pitfall trapping. Coleopterans and Hemipterans were used by foliage- and ground-gleaners more than expected during all periods, whereas arthropods in the orders Araneae and Hymenoptera were used as, or less than, expected based on availability during all periods. Ground-gleaning birds used Homopterans and Lepidopterans in proportions higher than availability during all periods. Arthropod use by birds was consistent from spring through fall migration, with no apparent seasonal shift in diet. Based on concurrent studies, heavily used orders of arthropods were equally abundant or slightly less abundant in canopy gaps than in the surrounding mature forest, but bird species were most frequently detected in gaps. Such results suggest that preferential feeding on arthropods by foliage-gleaning birds in gap habitats reduced arthropod densities or, alternatively, that bird use of gap and forest habitat was not determined by food resources. The abundance of arthropods across the stand may have allowed birds to remain in the densely vegetated gaps where thick cover provides protection from predators.

SINOPSIS. **Dieta estacional de aves insectivoras usando huecos del docel en bosques de maderas duras**

Se conoce poco de como la dieta de insectívoros está influenciada por la disponibilidad de artrópodos y de como estas interacciones varían estacionalmente. Capturamos aves en huecos o aberturas del docel de un bosque, adyacente a un bosque maduro durante el 2001 y el 2002 en Savannah River Site, Condado Garnwell, Carolina del Sur. A las aves le lavamos el buche para obtener información sobre los artrópodos utilizados como alimento durante la migración primaveral, durante la época reproductiva, post-reproductiva y durante la migración otoñal. Para determinar la disponibilidad de artrópodos en el follaje y en el suelo, usamos la técnica de cortar hojas con artrópodos y la de trampas de envases en el suelo. Los coleópteros y los hemípteros fueron utilizados como fuente de alimento, más de lo esperado tanto por aves que se alimentaron en el follaje como en los suelos, durante todos los periodos. Por su parte, los arácnidos y los himenópteros, fueron utilizados menos de lo esperado, basándose en la disponibilidad de estos durante todos los periodos de estudio. Las aves que se alimentaron en los suelos utilizaron homópteros y lepidópteros en mayor proporción que lo esperado, dada su disponibilidad, durante todos los periodos. Los artrópodos utilizados por las aves fueron consistentes desde la primavera hasta la migración otoñal, sin que hubiera desplazamiento o cambios estacionales en la dieta. Basado en estudios concurrentes, los ordenes de artrópodos más utilizados como alimento, estuvieron en similar o un poco más bajo en abundancia en los huecos del docel que en los alrededores de bosque maduro, pero las especies de aves se detectaron con mayor frecuencia en los huecos. Estos resultados sugieren que la alimentación preferencial de artrópodos por aves que se alimentan buscando insectos entre el follaje en habitats con huecos, reducen la densidad de artrópodos, o que el uso de los huecos o de bosque maduro no esta determinado por los recursos alimentarios. La abundancia de artrópodos a lo largo del rodal puede haber permitido que la aves permanecieran en los huecos o aperturas con alta densidad de plantas, en donde el follaje provee de protección contra los depredadores.

Key words: arthropods, bird diets, Coleoptera, crop flushing, migration, postbreeding

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Passerine birds may feed almost continuously during daylight hours (Stevenson 1933), and food availability is thought to be a driving force behind habitat selection (Blake and Hoppes 1986, Holmes et al. 1986, Johnson and Sherry 2001). Avian prey selection is influenced by prey availability, including proximity, detectability, acceptance, and ability to successfully capture a potential prey item (Wolda 1990). However, little is known about the food preferences of many passerine species (Evans Ogden and Stutchbury 1994, McDonald 1998), or about how prey selection changes across seasons, particularly in bottomland forests in the southeastern United States.

Bottomland hardwood forests provide important habitat for a variety of birds across all seasons (Dickson 1978, Pashley and Barrow 1993). Canopy gaps in mature bottomland forests can be an important habitat for many forest birds (Guilfoyle et al. 2005). Natural gaps (Willson et al. 1982, Martin and Karr 1986) and group-selection harvest gaps (Kilgo et al. 1999, Moorman and Guynn 2001) contain greater numbers of birds than surrounding forest. Arthropod populations are also affected by forest-canopy gaps and earlier stages of gap succession may support greater arthropod abundance than older forest-canopy gaps (Ulyshen et al. 2004, 2005, Ulyshen 2005). Flying arthropods may be more abundant in gap habitats than surrounding forest, whereas other groups, such as ground-dwelling arthropods, are less abundant in gap habitat (Greenberg and Forrest 2003, Ulyshen 2005).

Accurately determining prey availability, as perceived by birds, is a research challenge with many potential biases (Johnson 1980, Cooper and Whitmore 1990, Rosenberg and Cooper 1990, Wolda 1990). A bird's ability to capture prey is determined, in part, by vegetation structure in the foraging habitat (Robinson and Holmes 1982), arthropod prey characteristics, such as life stage, activity level, and palatability (Cooper and Whitmore 1990), and the bird's behavior and search tactics (Hutto 1990). Several direct observations of bird diets have shown certain arthropod groups to be preferred over others (Raley and Anderson 1990, Sillett 1994, Deloria-Sheffield et al. 2001, McMartin et al. 2002, Yard et al. 2004), but none of these studies addressed bird diets from spring through fall when Neotropical migratory birds are in the temperate zone.

Forest-breeding birds may be more abundant in early-successional than mature forest habitat, especially during the postbreeding (Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003) and migratory (Rodewald and Brittingham 2002) periods. The reasons for these patterns are unclear, but food abundance and protection from predators have been proposed (Marshall et al. 2003). However, information about the food preferences of forest-breeding birds in different seasons is lacking. Such information, coupled with data on the distribution of preferred foods among early- and late-successional habitats, could aid researchers examining habitat use by birds in forest habitats during different times of the year.

Our objective was to examine seasonal patterns in arthropod availability and prey selection by insectivorous birds in and around small forest-canopy gaps in a bottomland hardwood forest in the southeastern United States. To determine whether birds selected arthropod prey items in relative proportion to their availability, we compared percentages of arthropod groups both available to and consumed by foliage-gleaning and ground-gleaning passerine birds in four avian activity periods. We hypothesized that the proportion of prey in bird diets would be equal to the proportion available in the habitat.

METHODS

Study area. We conducted our research during 2001 and 2002 at the Savannah River Site, a 78,000-ha National Environmental Research Park owned and operated by the United States Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size in Barnwell County in the Upper Coastal Plain of South Carolina. We surveyed birds and arthropods in 12 group-selection gaps harvested in December 1994 and in the mature forest adjacent to gaps. Gaps were of three sizes (0.13, 0.26, and 0.50 ha), with four replicates of each size. Gaps were cleared to bare ground and circular in shape. Some downed tree tops and small-diameter stems were left as slash, but most wood was removed during logging. At the time of this study (7–8 years postharvest), most logging debris had decayed completely. After harvest, the gaps were allowed to regenerate naturally from stump sprouts and seed. The mature forest canopy was dominated by laurel oak (*Quercus laurifolia*), cherrybark oak (*Q. falcata* var. *pagodaefolia*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). The midstory was poorly developed, consisting primarily of red mulberry (*Morus rubra*), ironwood (*Carpinus carolinianus*), and American holly (*Ilex opaca*). The understory was dominated by dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). Vegetation in the gaps varied from approximately 1–8 m in height and was dominated by regenerating trees, primarily sweetgum, loblolly pine, sycamore (*Platanus occidentalis*), green ash (*Fraxinus pennsylvanica*), oaks, and black willow (*Salix nigra*), and dense stands of blackberry (*Rubus* spp.), dwarf palmetto, and switchcane.

Design. We surveyed birds and arthropods during four periods in 2001 and 2002: spring migration (25 March–15 May), breeding (16 May–30 June), postbreeding (1 July–31 August), and fall migration (1 September–18 October). As part of a larger study (Bowen 2004), we established sampling transects radiating southward from the center of each of 12 gaps with three bird and arthropod sampling stations along each transect: one in the gap center, one at the southern gap edge, and one in the forest 50 m from the edge.

Mist netting. Mist nets were located at each of the three sampling stations at each of the 12 study gaps. During the spring migration, postbreeding, and fall migration periods, netting was conducted once each week at each station, rotating between stations on a weekly schedule. During the breeding period, nets were operated once every 2 weeks because birds tend to be fairly stationary during this period. Nets were opened at first light and operated for 4–6 h, depending on weather conditions. We did not conduct netting when wind velocity exceeded 16 km per hour or during steady rainfall. Nets were 12-m long × 3-m tall with 30-mm mesh.

Crop flushing. We flushed bird crops to identify the proportions of various arthropod orders consumed (Rosenberg and Cooper 1990). We selected several target species for crop flushing, including Carolina Wren (*Thryothorus ludovicianus*), Hooded Warbler (*Wilsonia citrina*), Kentucky Warbler (*Oporornis formosus*), and White-eyed Vireo (*Vireo griseus*). The crops of other medium-sized, insectivorous species were also flushed as time permitted (Table 1). We did not flush crops of the same individuals twice in one period or if an individual bird appeared stressed. We flushed crops by inserting a thin (2-mm inside diameter), flexible, 10-cm long plastic tube down the throat and into the crop. A small syringe attached to the tube was used to slowly squirt warm water into the crop as the tube was withdrawn. The resulting regurgitate was collected in a shallow plastic dish and preserved in 70% alcohol. Regurgitated samples were sorted and counted, and arthropod fragments were identified to order using a dissecting microscope and entomology reference book (Gillott 1995). We identified the most frequently encountered orders using the following fragments (Fig. 1): Araneae (mouthparts and leg fragments), Coleoptera (mandibles, elytra, and leg fragments), Diptera (antennae, eyes, wings, and foot pads/empodium), Hemiptera (mouthparts, wing fragments, leg fragments, and scutella), Homoptera (mouthparts, leg fragments, and ovipositor), Hymenoptera (mouthparts, leg fragments, various body fragments, and wing fragments), Lepidoptera (adult wing scales, larval mandibles, setae, crochets, integument, and spiracle sieve plates), and Orthoptera (leg fragments, nymphal wingpads, and stridulatory organs). Exact numbers of individuals were difficult to estimate because of the high degree of fragmentation and, as a result, we estimated numbers conservatively. Multiple individuals were tallied only if we observed clearly identifiable fragments of the same type in excess of what might be expected on a single individual.

Arthropod sampling. During each period in 2001 and 2002, we sampled foliage-dwelling and ground-dwelling arthropods at each station. We used foliage clipping (Cooper and Whitmore 1990) to sample arthropods on each of five target plant species groups: (1) white oaks (white oak [*Quercus alba*], swamp chestnut oak [*Q. michauxii*], overcup oak [*Q. lyrata*], and Durand oak [*Q. durandii*]), (2) lobed red oaks (cherrybark oak), (3) unlobed red oaks [water oak (*Q. nigra*), laurel oak, and willow oak (*Q. phellos*)], (4) sweetgum, and (5) switchcane. These groups were selected to represent dominant members of the understory and overstory, and species important as avian foraging substrates (JCK and CEM, pers. obs.). Each sample consisted of

Table 1. Availability and seasonal use (percent of individuals in arthropod samples and crops, respectively) of arthropods by birds in a bottomland forest in South Carolina, 2001–2002.

		Foliage gleeners[b]		Ground gleaners[c]	
Period	Order[a]	Availability	Use	Availability	Use
Spring migration			$N = 35$		$N = 11$
	Araneae	37	18	23	18
	Coleoptera	19	35	11	40
	Diptera	1	5	31	2
	Hemiptera	1	9	2	4
	Homoptera	5	6	0	13
	Hymenoptera	17	3	22	0
	Lepidoptera	6	15	0	18
	Orthoptera	0	3	3	5
Breeding			$N = 48$		$N = 9$
	Araneae	29	16	29	25
	Coleoptera	15	37	14	36
	Diptera	2	4	28	0
	Hemiptera	4	7	1	4
	Homoptera	8	6	0	6
	Hymenoptera	11	3	16	0
	Lepidoptera	18	18	0	21
	Orthoptera	7	6	8	8
Postbreeding			$N = 46$		$N = 17$
	Araneae	44	16	16	15
	Coleoptera	7	34	15	23
	Diptera	1	5	12	8
	Hemiptera	3	7	0	10
	Homoptera	5	5	0	4
	Hymenoptera	12	9	34	4
	Lepidoptera	11	18	1	25
	Orthoptera	13	4	8	9
Fall migration			$N = 62$		$N = 28$
	Araneae	43	15	19	14
	Coleoptera	5	38	15	46
	Diptera	2	4	23	5
	Hemiptera	2	7	1	6
	Homoptera	6	6	0	2
	Hymenoptera	20	3	11	2
	Lepidoptera	17	19	1	16
	Orthoptera	2	3	6	5

[a] Orders included comprised 96% of the prey items identified in crop samples.

[b] Includes Kentucky Warbler, Hooded Warbler, White-eyed Vireo, Tufted Titmouse (*Baeolophus bicolor*), Red-eyed Vireo (*Vireo olivaceous*), Black-throated Blue Warbler (*Dendroica caerulescens*), Worm-eating Warbler (*Helmitheros vermivorus*), Common Yellowthroat (*Geothlypis trichas*), and Yellow-breasted Chat (*Icteria virens*).

[c] Includes Carolina Wren, Veery (*Catharus fuscescens*), Gray-cheeked Thrush (*Catharus minimus*), Swainson's Thrush (*Catharus ustulatus*), Swainson's Warbler (*Limnothlypis swainsonii*), and Ovenbird (*Seiurus aurocapilla*).

25 branch tips from each target species group (total sample = 125 branch tips) collected near each sampling station (i.e., within the target habitat type while moving in or around the gap). Each branch-tip clipping was between 2.54- and 15.24-cm stem length and usually came from the end of a branch that included several attached leaves. We collected foliage from ground level to about 2.5 m and immediately placed clippings in plastic bags. Sampling from higher in the canopy would have been problematic because arthropods may have been dislodged while remotely harvesting samples. Additionally, we considered it appropriate to sample arthropods in the same

Fig. 1. Photograph illustrating high degree of fragmentation of arthropod prey items from crop-flushing samples taken from insectivorous birds in a bottomland forest in South Carolina (2001–2002). Top row, L–R: Coleopteran elytra, Coleopteran elytra, and Coleopteran leg. Bottom row, L–R: Coleopteran mandible, Coleopteran prothorax, Lepidopteran (larval) mandible, and Coleopteran mandible.

stratum where we sampled birds (i.e., 3-m mist nets). Two of the species we sampled (Carolina Wren and Kentucky Warbler) forage on or near the ground (Haggerty and Morton 1995, McDonald 1998), whereas Hooded Warblers and White-eyed Vireos forage mainly in understory and lower mid-story vegetation (mean height 6.4 m; Buffington et al. 2000). We acknowledge that crop-flush samples from birds that had foraged at heights greater than 3 m could have biased our data if arthropods were distributed variably between vegetation heights <3 m and >3 m. Once collected, samples were frozen for 24 h, and then shaken to collect arthropods that were preserved in 70% alcohol and identified to order.

We sampled ground-dwelling arthropods using two pitfall traps (Cooper and Whitmore 1990) at each sampling station. We used 7-day trapping periods in 2001, but shifted to 2-day trapping periods in 2002 because large numbers of arthropods were captured each day. We operated the traps once during each period. Pitfall traps consisted of a 480-ml plastic cup buried to ground level, with a funnel (8.4 cm diameter) to direct arthropods into a smaller 120-ml specimen cup. The trap was positioned at the intersection of two 1-m long drift fences. Two pitfall traps were placed 5 m apart at each station. The collecting cups were filled with an NaCl-formaldehyde solution with a drop of detergent added to reduce surface tension (New and Hanula 1998). Samples were dried, weighed, stored in 70% alcohol, and identified to order.

Data analyses. For each of the four periods, we examined relationships between foraging guild (foliage gleaners and ground gleaners) and potential arthropod prey items. Bark-gleaning birds were not included in our analyses because few were captured. Birds were assigned to foraging guilds following Ehrlich et al. (1988) and Hamel (1992). We summarized both bird crop-flush samples and arthropod samples from foliage clipping and pitfall trapping as frequencies (i.e., the percentage of the number of a particular arthropod order in the total sample). Bird abundance did not differ among gaps sizes or years (Bowen et al. 2007). Although bird and arthropod abundance varied among sampling stations (Ulyshen et al. 2004, Ulyshen et al. 2005, Bowen et al. 2007), stations were sufficiently close that birds may have consumed a prey item at one location (gap, edge, or forest) and then been captured at another location before the item passed from the crop. Therefore, data were averaged between years, among gap sizes, and among sampling locations (gap, edge, and forest).

Table 2. Index[a] of seasonal arthropod use by birds relative to availability in a bottomland forest in South Carolina, 2001–2002.

Bird grouping	Period [b]	*N*	Araneae	Coleoptera	Diptera	Hemiptera	Homoptera	Hymenoptera	Lepidoptera	Orthoptera
Foliage gleaners	1	35	− −	+	++	+++	0	− −	++	++
	2	48	− −	++	++	+	−	− −	0	0
	3	46	− −	++	++	+	0	0	+	− −
	4	62	− −	++	+	++	+	− −	0	0
	all	191	− −	++	++	++	0	− −	+	−
Ground gleaners	1	11	−	++	− − −	++	+++	− − −	+++	+
	2	9	0	++	− − −	++	+++	− − −	+++	0
	3	17	0	+	−	+++	+++	− − −	+++	0
	4	28	−	+	− −	+++	+++	− −	+++	0
	all	65	−	++	− −	++	+++	− − −	+++	0

[a] For each order, D_{hb} values (Morrison 1982) are represented as follows: − − − = −1 to −0.81; − − = −0.80 to −0.41; − = −0.40 to −0.16; 0 = −0.15 to 0.15; + = 0.16 to 0.40; ++ = 0.41 to 0.80; and +++ = 0.81 to 1.

[b] 1 = spring migration, 2 = breeding period, 3 = postbreeding period, 4 = fall migration, and all = all periods combined.

The degree to which prey items are located, captured, and eaten is affected by arthropod size, life stage, palatability, color, and activity pattern (Cooper and Whitmore 1990). Therefore, arthropod abundance may not reflect actual prey availability because birds may not eat or be able to capture all potentially available arthropods. In addition, differences between availability and use of arthropod prey items may be influenced by bird foraging strategies and arthropod distribution (Raley and Anderson 1990). Bird diets also may differ with season, time of day, habitat type, and sex of the bird (Wheelwright 1986). Because birds do not forage equally on all available potential prey items and because of the great number of factors affecting prey selection, it is difficult to interpret bird diet analyses. We attempted to minimize this bias by matching as closely as possible each species' preferred foraging strategy with the most readily available arthropods. Hence, we compared foliage-gleaning birds with foliage-dwelling arthropods and ground-gleaning birds with ground-dwelling arthropods.

Our goal was to determine whether birds consumed arthropods in proportion to their availability. We used an index developed by Jacobs (1974) to evaluate seasonal use of each arthropod order relative to availability:

$$D_{hb} = \frac{r - p}{r + p - 2rp},$$

where D_{hb} is the index of arthropod use, r represents the percentage of an arthropod order in the crop-flush sample, and p represents the percentage of a particular arthropod order in the total arthropod sample. Values of D_{hb} range from −1 to 1. We then followed Morrison's (1982) categorization of D_{hb} for preference and avoidance. Because the terms preference and avoidance imply aspects of food selection difficult to assess in the field (Litvaitis et al. 1994), we generally avoided their use. Instead, we modified the terminology associated with relative values of the index as follows: −1 to −0.81 = used much less than availability, -0.80 to -0.41 = used moderately less than availability, −0.40 to −0.16 = used slightly less than availability, −0.15 to 0.15 = use equals availability, 0.16 to 0.40 = use slightly exceeds availability, 0.41 to 0.80 = use moderately exceeds availability, and 0.81 to 1 = use greatly exceeds availability (Table 2). We chose the Jacobs (1974) index because it allows comparison of food types with different relative abundances (Jacobs 1974). In addition, the index is sensitive to slight preference, although it fails to account for the possibility that birds affect prey density (Cock 1978).

RESULTS

Crop flushing. We flushed 255 crops of 15 bird species (Table 1) and identified 703 individual prey items representing 15 arthropod orders. Carolina Wrens comprised 74% of the ground-gleaning birds sampled. Kentucky Warblers, Hooded Warblers, and White-eyed Vireos comprised 17%, 43%, and 24%, respectively, of the foliage-gleaning birds sampled. The most commonly identified prey were in the orders Coleoptera (29% of arthropods collected during crop flushing), Lepidoptera (19%), Araneae (17%), Hemiptera (9%), Homoptera (7%), Diptera (5%), Hymenoptera (5%), and Orthoptera (5%). Together these orders comprised 96% of the arthropods identified in crops. Other orders detected included Acarina, Mallophaga, Neuroptera, Pseudoscorpiones, Psocoptera, and Thysanoptera.

Other items identified from crop contents included a few small feathers, insect eggs, a small flower, and small seeds. We determined percentages of arthropods in bird diets based only on the total arthropods identified; other items were disregarded. Plant material (usually seeds) was found in only 10 (4%) of 255 crops.

Arthropod sampling. Arthropods in eight orders comprised 95% of all arthropods captured by foliage clipping, including Araneae (39% of total arthropods captured), Hymenoptera (15%), Lepidoptera (13%), Coleoptera (12%), Homoptera (6%), Orthoptera (6%), Hemiptera (3%), and Diptera (1%). These same eight orders comprised 93% of all arthropods captured in pitfall traps, including Diptera (24%), Hymenoptera (23%), Araneae (22%), Coleoptera (15%), Orthoptera (6%), Hemiptera (1%), Homoptera (1%), and Lepidoptera (1%).

Arthropod use and availability. Proportional use of arthropod orders was similar between foliage-gleaning and ground-gleaning birds (Table 1). Differences in use relative to availability indices between the two groups (Table 2) stemmed from the differences in proportional availability of foliage-dwelling and ground-dwelling arthropods (Table 1). Coleopterans and Hemipterans made up a greater proportion of prey items in crop samples than expected based on the proportion of individuals of these orders in foliage and pitfall samples (i.e., were used more than expected) in all periods, and arthropods in the orders Araneae and Hymenoptera were used in proportion to or less than availability by birds in all periods (Table 2). Dipterans were well represented in pitfall traps, but poorly represented in foliage clippings (Table 1). Ground-gleaning birds used Dipterans little relative to availability, whereas foliage-gleaning birds used them heavily compared to their low frequency in foliage samples (Table 2). Similarly, Lepidopterans were well represented in foliage samples and poorly represented in pitfall traps, thereby indicating apparently heavy use by ground gleaners and use either equal to or exceeding availability by foliage gleaners (Tables 1 and 2). Although we did not distinguish between larval and adult Lepidopterans, most flushed from crops were larvae.

Ground-gleaning and foliage-gleaning birds exhibited few seasonal changes in relative use of arthropod orders (Table 2). Of the arthropod orders most frequently identified from crops, foliage-gleaning birds used Coleopterans more than all others during all periods (Table 1). Of the orders most frequently identified from crops, ground-gleaning birds used Coleopterans more than others during all periods except the postbreeding period, when consumption of Coleopterans was similar to that of Lepidopterans (Table 1). Relative use of Orthopterans by foliage gleaners and ground gleaners was highest during spring migration (Table 2), but availability was lowest during the spring (Table 1). Similarly, foliage-gleaning birds showed highest relative use of Lepidopterans during spring migration (Table 2), but availability was lowest during this period (Table 1). Relative use of Hemipterans by foliage gleaners was highest during migration periods (Table 2), but proportional use was nearly identical for all periods (Table 1). Ground-gleaning birds used Araneae during the breeding period more than in other periods, and foliage-gleaning birds used Hymenopterans during the postbreeding period more than in other periods (Tables 1 and 2).

DISCUSSION

Foliage-gleaning and ground-gleaning birds consumed similar proportions of Coleopterans and Hemipterans in our study, consistently consuming them in proportions greater than expected based on their availability during all periods. Although other investigators also have determined that birds prefer Coleopterans (Robinson and Holmes 1982, Wheelwright 1986, Raley and Anderson 1990, Sillett 1994, Poulin and Lefebvre 1996, McMartin et al. 2002, Yard et al. 2004), Hemipterans have not previously been identified as a primary food resource. We also determined that foliage- and ground-gleaning birds consumed Araneae and Hymenopterans in proportions equal to or lower than their availability during all periods, but both orders are reportedly common food items elsewhere (Robinson and Homes 1982, Poulin and Lefebvre 1996, Yard et al. 2004). Arthropod orders consumed in proportions lower than their relative availability likely still were an important component of bird diets (Raley and Anderson 1990).

Other researchers have reported that Lepidopterans are an important food resource for insectivorous birds (Robinson and Holmes 1982, Wheelwright 1986, McMartin et al. 2002, Yard et al. 2004). Similarly, we detected relative use of Lepidopterans by foliage-gleaning birds in proportion to or slightly greater than availability. We also recorded high relative use of insects in the orders Lepidoptera, Hemiptera, and Homoptera by ground-gleaning birds in every period. High relative use of these three arthropod orders by ground foragers, however, may have resulted from the low numbers of arthropods captured in pitfall traps.

Patterns of arthropod use by foliage-gleaning and ground-gleaning birds generally were consistent among periods. Many investigators have described changes in food habits within (e.g., Hejl and Verner 1990) or between (e.g., Martin and Karr 1990) seasons, probably due to changes in food availability. Arthropod availability, however, was relatively consistent among periods in our study. Seasonal consistency in the diets of our four focal bird species apparently reflects the seasonally stable arthropod prey base available to them. Further, we found little fruit in bird crops. Thus, not only was the arthropod composition of the diets of our focal species similar over time, these species did not switch to a fruit diet during fall as many migrants do. White-eyed Vireos reportedly consume some fruit throughout the year, but especially during the nonbreeding period (Hopp et al. 1995), whereas Hooded Warblers remain insectivorous year round (Evans Ogden and Stutchbury 1994). Whether the consistency we observed resulted from a more abundant and temporally stable arthropod prey base in the warm and humid southeastern United States or from a scarcity of fruit on our study sites, or whether it reflects more universal dietary patterns in these species is unclear.

Direct observations of avian diets are complicated by variable digestion rates of different arthropods (Mook and Marshall 1965, Swanson and Bartonek 1970, Rosenberg and Cooper 1990). Digestibility is affected by prey size, body type (soft or hard), and bird condition (Custer and Pitelka 1975). Caterpillars and other soft-bodied insect larvae are more easily digested than arthropods with hard body parts and, therefore, may be underrepresented in bird diet samples (Wheelwright 1986). Thus, proportions of soft-bodied arthropods, such as those in the orders Araneae and Lepidoptera, were probably underrepresented in our analyses and may be more important in bird diets than indicated by our results. Because we regularly identified both hard-bodied and soft-bodied prey items, however, we believe that our data represent the wide variety of prey items consumed by birds during different seasons.

The high use of Coleopterans by all birds in all periods may shed light on selection of early-versus late-successional habitats by forest birds. We generally detected more birds in regenerating canopy gaps than in the surrounding forest (Bowen et al. 2007), but foliage-dwelling arthropods, including the heavily used Coleoptera, were equally or less abundant in gaps than in adjacent mature forest (Bowen 2004). This may indicate that foliage-gleaning birds preferentially cropped arthropods or specific arthropod orders in gap habitats, thereby resulting in reduced arthropod densities in gaps (i.e., measurable arthropod abundance represents what birds leave rather than to what they respond). Alternatively, this conflicting pattern of bird and arthropod abundance in gap and forest habitat may indicate that bird use of gap and forest habitat was not determined by food resources. Working in riparian habitat in Arizona, Rosenberg et al.

(1982) concluded that arthropod abundance far surpassed the energy requirements necessary to sustain bird populations. We suspect that arthropods may have been sufficiently abundant across the stand that food did not limit or determine habitat use (Kilgo 2005), thus allowing birds to remain in the densely vegetated gaps where thick cover could provide protection from predators, especially during the postbreeding (Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003) and migratory periods (Rodewald and Brittingham 2002, Cimprich et al. 2005) when birds may be particularly vulnerable.

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