ABSTRACT

BOWEN, LIESSA THOMAS. Seasonal Relationships Between Birds and Arthropods in Bottomland Forest Canopy Gaps. (Under the direction of Christopher E. Moorman and Daniel J. Robison.)

I investigated the influence of arthropod availability and vegetation structure on avian habitat use at the center, edge, and adjacent to forest canopy gaps in 2001 and 2002. I used mist-netting and plot counts to estimate abundance of birds using three sizes (0.13, 0.26, and 0.5 ha) of 7-8 year old group-selection timber harvest openings during four seasons (spring migration, breeding, post-breeding, and fall migration) in a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. I used foliage clipping, Malaise trapping, and pitfall trapping to determine arthropod abundance within each habitat, and I used a warm water crop-flush on captured birds to gather information about arthropods eaten.

I observed more birds, including forest interior species, forest-edge species, field-edge species, and several individual species, in early-successional canopy gap and gap-edge habitats than in surrounding mature forest during all seasons. I found a significant interaction between season and habitat type for several groups and individual species, suggesting a seasonal shift in habitat use. Captures of all birds, insectivorous birds, foliage-gleaners, ground-gleaners, aerial salliers, Hooded Warbler (*Wilsonia citrina*), Northern Cardinal (*Cardinalis cardinalis*), White-eyed Vireo (*Vireo griseus*), and Black-throated Blue Warbler (*Dendroica caerulescens*) were positively correlated with understory vegetation density during two or more seasons. I found relationships between insectivorous birds and leaf-dwelling Lepidoptera, insectivorous birds and ground-dwelling arthropods, foliage-gleaning birds and foliage-dwelling arthropods, and aerial salliers and flying arthropods, as well as between individual bird species and arthropods. Relationships were inconsistent, however, with many species being negatively correlated with arthropod abundance. Coleopteran, Lepidopteran, and Aranid prey items represented the greatest proportions of crop-flush samples during all seasons. Proportional consumption of Coleopteran and Hemipteran prey items was higher than their proportional availability, and consumption of Aranid and Hymenopteran prey items was lower than their proportional availability during all seasons. Individual bird species and guilds consistently consumed similar proportions of certain groups of arthropods from spring through fall migration, with no apparent seasonal shift in diet composition.

My research suggests that many species of birds selectively choose mid-successional gap and gap-edge habitat over surrounding mature forest during the non-breeding season, and the creation of small canopy gaps within a mature forest may increase local bird species richness. It is less obvious how arthropod availability affects bird habitat use across seasons. A structurally diverse mosaic of habitat types, including regenerating canopy gaps within a mature forest, may provide valuable habitat for birds and a variety of arthropod prey items across multiple seasons.

SEASONAL RELATIONSHIPS BETWEEN BIRDS AND ARTHROPODS IN BOTTOMLAND FOREST CANOPY GAPS

by
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BIOGRAPHY

I am very happy to have completed my PhD from North Carolina State University. My interest in nature began in early childhood during family weekend retreats in rural Washington County, Missouri, collecting frogs, fish, crawdads, and aquatic insects from a small stream. My first biological internship was at the University of Chicago, assisting with a study of inbreeding depression in two species of morning glory. My first position as a field technician for a bird project was located on the rainforest-covered slopes of Mauna Kea volcano on the Big Island of Hawaii. After that incredible experience, I was definitely hooked on both birds and field research. Other biology-related jobs have included studying aquatic insect larvae in Illinois, bird nesting success in Iowa and Wisconsin, plant conservation in Missouri, and public outreach in Virginia. I received my MS degree from Iowa State University in 1999 for my work studying bird response to a large-scale tallgrass prairie restoration. My career goal includes a combination of field research, birds, conservation, public outreach, writing, and photography. Personal interests include folk music and dance, hiking, camping, and exploring the outdoors, and being a very involved parent of a wonderful little boy.

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TABLE OF CONTENTS

LIST OF TABLES

Page

Chapter 1

Chapter 2

Chapter 3

LIST OF FIGURES

Page

Chapter 1

Chapter 2

Chapter 3

CHAPTER 1

Seasonal bird use of canopy gaps

SEASONAL BIRD USE OF FOREST CANOPY GAPS IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT

Bird use of small canopy gaps within mature forests has not been well studied, particularly across multiple seasons. We investigated seasonal differences in bird use of forest and gap habitat within a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. Gaps were 0.13-0.5-ha, 7 to 8-year-old group-selection timber harvest openings. Our study occurred during four bird-use seasons (spring migration, breeding, post-breeding, and fall migration) in 2001 and 2002. We used plot counts and mist netting to estimate bird abundance in canopy gaps and surrounding forest habitats. Using both survey methods, we observed more birds, including forest-interior species, forest-edge species, field-edge species, and several individual species, in mid-successional canopy gap and gap-edge habitats than in surrounding mature forest during all seasons. We found a significant interaction between season and habitat type for all birds, forest interior birds, forest-edge birds, and field-edge birds, as well as several individual species. These interactions suggest a seasonal shift in habitat use, often as bird activity shifted between canopy gaps and the immediate gap edge, or as the proportion of birds using forested habitat increased during the breeding season. Our research suggests that many species of birds selectively choose early successional gap and gap-edge habitat over surrounding mature forest during the non-breeding season, and the creation of small canopy gaps within a mature forest may increase local bird species richness. The reasons for increased bird activity in gaps, however, remain unclear.

Human attempts to eliminate or control natural periodic disturbance is a leading cause of landbird declines (Askins 2000), and as a result, many disturbance-dependent birds have been identified as species of conservation concern (Hunter et al. 2001). Many species of birds, including several species of conservation concern that breed in mature forests, require some amount of forest disturbance (e.g., fire, ice, or wind) resulting in treefall gaps to create ideal habitat (Hunter et al. 2001). One type of disturbance common in mature forests is the creation of small light gaps in the forest canopy, often caused by natural treefall occurrences. Canopy gaps created by small-scale timber harvest operations may mimic these natural disturbances, providing different microclimates and habitat patches, leading to a unique assortment of gap-associated flora and fauna (Watt 1947; Canham et al. 1990).

Birds select habitat based largely upon vegetation structure (Holmes et al. 1979), and some may prefer early successional gap habitat based on the unique qualities of the vegetation there (e.g., dense foliage, well-developed herb and shrub layer). Several bird species seem to prefer small-scale canopy gap openings to mature forested habitat during migration or the breeding season (Martin and Karr 1986; Germaine et al. 1997; Kilgo et al. 1999; Moorman and Guynn 2001). Forest canopy gaps may be used differently throughout the year, depending on the availability of protective cover, desirable nesting habitat, or suitable prey items (Robinson and Holmes 1982; Willson et al. 1982; Blake and Hoppes 1986).

During migration, birds pass through a series of unfamiliar habitats and tend not to spend much time in any one location (Moore et al. 1993). Habitat selection during this time may be influenced by accessible food resources, competition with other species, and risk of predation (Petit 2000). During the breeding season, birds require habitat with suitable nesting sites. Early-successional-nesting birds, such as Common Yellowthroat and Indigo Bunting, use regenerating canopy gaps for nesting (Moorman and Guynn 2001). During the post-breeding period, adult birds may select densely vegetated habitats as refugia during their molt (Vega Rivera et al. 1999), and young birds may seek the protective cover from predators offered by gaps (Anders et al. 1998; Vega Rivera et al. 1998), as each group is particularly vulnerable during these times.

The use of artificial, small-scale disturbances by birds within mature forests has not been well studied, particularly across multiple seasons. Approximately 70 species of birds use bottomland hardwood forests for breeding (Pashley and Barrow 1993), and bottomland forests typically contain higher densities of birds than adjacent upland forests in all seasons (Dickson 1978). Our goal was to determine relative use of gap and forest habitat by birds during four seasons (spring, breeding, post-breeding, and fall) within a bottomland hardwood forest. This study should aid land managers in assessing habitat needs for certain bird species that use bottomland forests for migration or breeding.

STUDY AREA

We studied birds during 2001 and 2002 at the Savannah River Site (SRS), a 78000-ha National Environmental Research Park owned and operated by the U. S. Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size, and located in Barnwell County in the Upper Coastal Plain of South Carolina. Birds were surveyed in 12 group-selection gaps harvested in December 1994 and in the mature forest adjacent to gaps. The gaps were of three sizes (0.13, 0.26, and 0.50 ha) with four replicates of each size. It is within this size range that previous research has identified a threshold in response by breeding (Moorman and Guynn 2001) and fall migrant birds (Kilgo et al. 1999). 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 was 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.

METHODS

We surveyed birds during four avian activity periods in 2001 and 2002: spring migration (25 March through 15 May), breeding (16 May through 30 June), post-breeding (1 July through 31 August), and fall migration (1 September through 18 October).

Plot counts.-

Plot counts were conducted within each of the 12 experimental gaps and within 12 forested control plots of equivalent size. The 12 forested control plots were randomly placed a minimum of 100 m from the nearest gap center within the mature forest surrounding the study gaps. The forest plot perimeters were flagged so that observers could easily determine plot boundaries. Each of the 24 plot count plots was visited three times during each season and counts were averaged over the three visits. For approximately one half of the plot counts and equally distributed across treatment types, two observers walked slowly around the perimeter of each plot. When the observers met on the opposite side of the plot, they compared observations and agreed upon a total number of each bird species observed within the gap/edge habitat. When only one observer was available, the single observer walked slowly around the entire plot, recording all birds seen and heard. At both forest and gap plots, birds observed within the actual plot and at the immediate edge (0-10 m from the bole line or flagged boundary into the forest) were included in the count. Larger plots and plots with more bird activity took longer to survey.

Mist netting.-

Constant effort mist nets were located at each of three sampling stations (gap, edge, and forest) at each of the 12 study gaps. During the spring migration, post-breeding, and fall migration seasons, netting was conducted once each week at each station, rotating between stations on a regular weekly schedule. During the breeding season, nets were operated once every two weeks because birds tend to remain fairly stationary during this period. Nets were opened at first light and operated for 4-6 h, depending on daily weather conditions. Netting was not conducted when wind exceeded 16 km per hour or during steady rainfall. Nets were 12-m long x 3-m tall, with 30-mm mesh. Captured birds were aged and sexed (Pyle et al. 1987), weighed, and banded with a USGS Biological Resources Division aluminum leg band.

Statistical analysis.-

We used a linear mixed model (PROC MIXED, SAS Institute 1990) to perform repeated measures analysis of variance (ANOVA). We analyzed the effects of habitat type, season, and the interaction between habitat and season on bird abundance. For mist-netting data analysis, habitats included gap, edge, and forest; for plot count data analysis, habitats included gap/edge and forest. We used mean captures per 100 net hours as the dependent variable for mist-netting analyses and mean birds per ha as the dependent variable for plot count analyses. We considered habitat type and season as fixed effects, with habitat type as a split plot factor and season as the repeated measure. Year was not significant ($p>0.05$), so years were pooled in the final analyses, and these pooled data are represented in tables and figures.

Birds were assigned to habitat-use groups (Appendix 1): (1) all birds, (2) forest interior species, (3) forest-edge species, and (4) field-edge species (Ehrlich et al. 1988; Hamel 1992). We analyzed mist-netting captures and plot count detections for each group. Individual species (see scientific names in Appendix 1) were chosen for analysis if they accounted for at least 80 detections over both years for plot counts (Blue-gray Gnatcatcher, Carolina Wren, Eastern Tufted Titmouse, Northern Cardinal, Northern Parula, and White-eyed Vireo) or at least 80 captures over both years for mist netting (Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, Northern Cardinal, and White-eyed Vireo). Birds considered winter residents, present only in early spring or late fall, were not included in analyses.

RESULTS

Plot counts.-

From April through October, 2001 and 2002, we counted 1711 individuals representing 70 species in gap/edge habitat and 38 species in forest habitat. We detected more individuals in the gaps than in the surrounding forest during all seasons for all bird groups and individual species analyzed (Table 1; Fig. 1). The abundance of forest-interior birds, field-edge birds, Blue-gray Gnatcatcher, Carolina Wren, Eastern Tufted Titmouse, Northern Cardinal, and Northern Parula differed among seasons, but no consistent patterns were evident, as seasonal use varied considerably by species or group (Table 1). We documented a significant interaction between season and habitat type for field-edge birds, Blue-gray Gnatcatcher, and Northern Parula (Table 1). Field-edge birds were detected most often during spring and fall migration and primarily in gap/edge habitat. The greatest proportion of forest detections of field-edge birds occurred during the post-breeding season. Blue-gray gnatcatcher was most abundant in gap/edge habitat during all seasons, but forest detections dropped to almost zero during fall migration. Northern Parula used both gap/edge and forest habitat during spring migration and breeding season, and then dropped to near zero occurrence in the forest during the post-breeding season and fall migration.

Mist netting.-.

From April through October, 2001 and 2002, during 7669 net hours, we recorded 1476 captures representing 56 species. We captured 55 species in gap/edge habitat and 26 species in forest habitat across all seasons. We captured more individuals in the gaps and at their edges than in the surrounding forest during all seasons for all bird groups and individual species except for Carolina Wren, which was captured more frequently at edge or forest habitats than gaps during all seasons (Table 2; Fig. 2). Number of captures differed among seasons for all groups and species analyzed except Kentucky Warbler and Northern Cardinal, with most groups being most frequently captured during spring (Table 2). There was an interaction between season and habitat type, suggesting a seasonal shift in habitat use, for all birds, forest interior birds, forest-edge birds, field-edge birds, Black-throated Blue Warbler, and Kentucky Warbler (Table 2). Some species (e.g., forest interior specialists and Kentucky Warbler) shifted from gap during spring migration to edge during the breeding season, and back to gap habitat after the breeding season. Forest-edge birds were most abundant in the gap habitat during spring and fall migration, but both gap and edge were used equally during the breeding and post-breeding seasons. Total mist-net captures tended to shift slightly between gap and edge habitat (gap during spring and fall migratory periods, edge during breeding and post-breeding), with forest captures representing just a small proportion of captures during each season. The highest proportion of forest captures, however, occurred during the breeding season (Fig. 3). Forest interior birds, forest-edge birds, Carolina Wren, and Hooded Warbler used forested habitat most during the breeding season as well.

DISCUSSION

We observed and captured more birds in gap and gap-edge habitat than in the surrounding mature forest during all bird-use seasons. Generally, bird detections in edge habitat were more similar to detections in gap habitat than forested habitat. Carolina Wren was the only species to show a distinct forest/edge preference, but based only upon mist-netting captures. Many birds that are forest interior specialists or forest breeders, for example, may seek out early successional habitats for foraging or shelter outside of the breeding season. Other studies also have reported more bird activity in gaps than mature forest, including migrating foliage gleaning insectivores (Willson et al. 1982; Blake and Hoppes 1986; Martin and Karr 1986), fall migrants (Kilgo et al. 1999), breeding birds (Smith and Dallman 1996; Germaine et al. 1997; King et al. 2001; Moorman and Guynn 2001) and post-breeding birds (Anders et al. 1998; Vega Rivera et al. 1998, 1999, 2003; Pagen et al. 2000). Migrating birds also may prefer forest edge habitat to forest interior habitat during fall migration (Rodewald and Brittingham 2002). Other researchers have found that individual species, including Hooded Warbler (Annand and Thompson 1997; Robinson and Robinson 1999), Carolina Wren (Robinson and Robinson 1999; Moorman and Guynn 2001), and White-eyed Vireo (Robinson and Robinson 1999; Moorman and Guynn 2001) use regenerating group selection openings more than mature forest during the breeding season. Hooded Warblers breed in the forest understory on our site (Moorman et al. 2002), but were often seen foraging in the gap habitat during all seasons, and with young in gap habitat during the post-breeding season (L. T. Bowen, pers. obs.).

It is possible that we captured more birds in gap habitat than forest habitat because of differences in habitat structure (Remsen and Good 1996). Birds using the low early successional vegetation within the gaps were more available for sampling with a 3-m high net than birds in the forest. However, comparisons among seasons at a given location are not subject to this potential bias. Additionally, our plot counts corroborated our mist-net data; they sampled both the understory and canopy and also detected more birds using gap habitat than forest habitat. Plot counts also included birds using the immediate edge of gaps, a mix of habitat types and vegetation structures, which may have attracted forest-interior birds more than the actual gap center. Detectability of birds in gaps during plot counts likely was lower than in the forest because of the dense vegetation in the gaps, so our estimates of bird use of gaps may actually be conservative. Seasonal differences in both bird captures and plot counts may be attributed, in part, to more birds being available during spring and fall migratory periods, yet within each season during this study, we consistently detected more birds using the canopy gaps than forest.

While most birds used gap and edge habitat more than forested habitat during all seasons, we also detected a seasonal shift in habitat use for several groups, as proportions of gap, edge, and forest captures varied between seasons. Generally, bird use of gap and edge habitats was highest during spring and fall migration, while use of forested habitat tended to be greatest during the breeding season and lowest during the post-breeding period. Other researchers have documented seasonal shifts in habitat use between the breeding and post-breeding periods, particularly as fledgling birds moved from forested habitat into early and mid-successional habitats (Anders et al. 1998; Vega Rivera et al. 1998, 2003; Pagen et al. 2000), possibly in search of greater cover or more abundant food resources. Regenerating forest canopy gaps may provide a necessary habitat type for birds during these seasons of increased mobility, such as migration and post-breeding dispersal.

Gap interiors were not only densely vegetated, but also contained mid-successional fruiting species (e.g., sumac and blackberry), while other fruiting species such as poison ivy (*Toxicodendron radicans*) and hawthorn (*Crataegus sp.*) were common at the immediate gap edge (L. T. Bowen, pers. obs.). We observed omnivorous birds eating fruits in gaps, including American beautyberry (*Callicarpa americana*), flowering dogwood (*Cornus florida*), grape (*Vitis sp.*), hawthorn, poison ivy, and winged sumac (*Rhus copallinum*) (L. T. Bowen pers. obs.). Fruiting vegetation typically is most abundant in late summer to early fall (McCarty et al. 2002). Willson et al. (1982) found that avian frugivores preferentially visited natural forest openings during migratory periods, even when these gaps provided no more fruit than surrounding forest habitat. We did not, however, find a corresponding shift in habitat use for omnivorous species such as Northern Cardinal, suggesting that birds were meeting their nutritional needs without closely following seasonal fruit availability.

The creation of 0.13- to 0.5-ha canopy gaps can be used to increase habitat diversity within mature bottomland hardwood forest, thereby attracting a greater number of foraging, breeding, and migrating birds. Kilgo et al. (1999) and Moorman and Guynn (2001) worked in the same gaps at 2-5 years post-harvest and determined that larger gaps (e.g., 0.5 ha) supported greater bird abundance and species richness than uncut forest and smaller openings, particularly those less than 0.26 ha. In our study, however, bird use did not vary by gap size in any season. During our study, the 7-8 year-old canopy gaps were beginning to more closely resemble the surrounding forest. As these gaps regenerate and pass through successional stages, the bird community should also change accordingly. Robinson and Robinson (1999) noted that long-term effects of small-scale canopy gaps upon the forest bird community are unlikely because the regenerating forest matures and returns to pre-harvest conditions in a relatively short time.

We found birds using regenerating canopy gaps more than mature forested habitat during all seasons. Bird habitat use shifted slightly from gaps during spring migration to forest during breeding season, then back to gaps during post-breeding season and fall migration. Reasons for these habitat selections and seasonal shifts, however, remain speculative. It is possible that omnivorous birds use canopy gaps more during seasons of high fruit availability, but fruiting production within our canopy gaps was relatively low highly seasonal. Rather, we suspect birds may select regenerating canopy gaps for the protection offered by these densely vegetated areas, particularly during seasons of vulnerability, such as during migratory periods as birds move through unfamiliar areas and during the post-fledging periods when young are more vulnerable to predators.

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Table 1. Mean plot count detections per ha, for each season and count location (n=12) in a bottomland hardwood forest in South Carolina, USA (2001-2002) with associated p-values for season, habitat type, and season*habitat type interaction. Standard errors are in parentheses.

		Spring		Breeding		Post-breeding		Fall	
Species or group	P-value	gap/edg	for	gap/edg	for	gap/edg	for	gap/edg	for
All birds	0.3961[a]	38.58	6.92	38.19	10.35	35.15	7.70	39.34	7.66
	<0.0001[b]	(3.37)	(3.37)	(3.28)	(3.28)	(3.40)	(3.40)	(3.52)	(3.52)
	0.5797[c]								
Forest interior spp.	0.0026[a]	6.87	2.10	8.41	3.29	5.36	1.30	4.37	1.26
	<0.0001[b]	(0.83)	(0.83)	(1.26)	(1.26)	(0.87)	(0.87)	(0.61)	(0.61)
	0.4777[c]								
Forest-edge spp.	0.1022[a]	25.01	4.76	29.25	7.04	29.04	6.20	29.83	5.95
	<0.0001[b]	(2.24)	(2.24)	(2.29)	(2.29)	(2.38)	(2.38)	(2.72)	(2.72)
	0.6841[c]								
Field-edge spp.	<0.0001[a]	4.71	0.028	0.32	0.00	0.43	0.056	4.04	0.00
	<0.0001[b]	(0.41)	(0.41)	(0.11)	(0.11)	(0.13)	(0.13)	(0.45)	(0.45)
	<0.0001[c]								

Blue-gray Gnatcatcher	<0.0001[a]	3.06	0.59	3.05	0.35	3.29	0.51	0.89	0.00
	<0.0001[b]	(0.46)	(0.46)	(0.37)	(0.37)	(0.40)	(0.40)	(0.22)	(0.22)
	0.0009[c]								
Carolina Wren	<0.0001[a]	3.03	0.46	3.19	0.78	6.38	1.87	4.07	0.94
	<0.0001[b]	(0.37)	(0.37)	(0.40)	(0.40)	(0.57)	(0.57)	(0.50)	(0.50)
	0.1561[c]								
Eastern Tufted Titmouse	<0.0001[a]	1.62	0.46	1.85	1.38	2.80	0.22	3.91	1.74
	0.0003[b]	(0.31)	(0.31)	(0.40)	(0.40)	(0.46)	(0.46)	(0.47)	(0.47)
	0.0881[c]								
Northern Cardinal	0.0041[a]	3.10	0.14	4.12	0.68	4.21	1.23	3.86	0.46
	<0.0001[b]	(0.47)	(0.47)	(0.56)	(0.56)	(0.62)	(0.62)	(0.47)	(0.47)
	0.6130[c]								
Northern Parula	<0.0001[a]	3.87	0.73	3.42	0.78	1.51	0.053	1.38	0.028
	0.0002[b]	(0.59)	(0.59)	(0.54)	(0.54)	(0.35)	(0.35)	(0.29)	(0.29)
	0.0517[c]								
White-eyed Vireo	0.1458[a]	2.97	0	3.73	0.080	2.35	0	2.81	0.11
	<0.0001[b]	(0.39)	(0.39)	(0.59)	(0.59)	(0.42)	(0.42)	(0.41)	(0.41)
	0.2191[c]								

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[a] season

[b] habitat type

[c] season * habitat type

Table 2. Mean captures per 100 net hours per season and net location (n=12) in a bottomland forest in South Carolina, USA (2001-2002) with associated p-values for season, net location, and season*net location interaction. Standard errors are in parentheses.

		Spring			Breeding			Post-breeding			Fall		
Species or group	P-values[*]	gap	edg	for	gap	edg	for	gap	edg	for	gap	edg	for
All birds	<0.0001[a]	53.80	34.71	5.73	22.13	26.92	10.27	14.59	15.50	3.26	28.29	20.15	5.43
	<0.0001[b]	(3.48)	(3.48)	(3.48)	(2.42)	(2.42)	(2.42)	(1.98)	(1.98)	(1.98)	(2.01)	(2.01)	(2.01)
	<0.0001[c]												
Forest interior spp.	<0.0001[a]	21.87	15.27	2.08	7.07	11.86	3.19	5.99	6.38	1.17	15.11	11.24	2.07
	<0.0001[b]	(2.64)	(2.64)	(2.64)	(1.50)	(1.50)	(1.50)	(1.00)	(1.00)	(1.00)	(1.61)	(1.61)	(1.61)
	<0.0001[c]												
Forest-edge spp.	<0.0001[a]	21.87	12.84	3.47	13.92	14.37	6.84	7.81	8.99	2.08	9.82	6.59	2.71
	<0.0001[b]	(1.92)	(1.92)	(1.92)	(2.25)	(2.25)	(2.25)	(1.19)	(1.19)	(1.19)	(1.34)	(1.34)	(1.34)
	<0.0037[c]												
Field-edge spp.	<0.0001[a]	10.07	6.59	0.17	1.14	0.68	0.23	0.78	0.12	0.00	3.23	2.33	0.65
	<0.0001[b]	(1.24)	(1.24)	(1.24)	(0.34)	(0.34)	(0.34)	(0.22)	(0.22)	(0.22)	(0.66)	(0.66)	(0.66)
	<0.0001[c]												

Black-throated Blue Warbler	0.0045[a]	5.21	3.47	0.00							2.20	1.81	0.26
	<0.0001[b]	(0.61)	(0.61)	(0.61)							(0.61)	(0.61)	(0.61)
	0.0331[c]												
Carolina Wren	0.0111[a]	1.91	4.34	1.74	1.37	7.07	5.48	1.43	5.08	1.69	1.68	2.07	2.45
	0.0001[b]	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)	(0.99)
	0.0758[c]												
Hooded Warbler	0.0003[a]	6.94	7.12	0.87	2.28	4.11	2.05	2.87	3.26	0.13	2.20	2.84	0.52
	<0.0001[b]	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)	(0.94)
	0.0754[c]												
Kentucky Warbler	0.1087[a]	2.26	1.39	0.87	1.14	4.56	0.23	1.43	1.04	0.52	NA	NA	NA
	0.0008[b]	(0.56)	(0.56)	(0.56)	(0.56)	(0.56)	(0.56)	(0.56)	(0.56)	(0.56)			
	0.0005[c]												
Northern Cardinal	0.0854[a]	2.43	2.43	0.87	2.51	0.46	0.46	2.73	1.95	0.13	1.42	1.16	0.00
	<0.0001[b]	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)	(0.54)
	0.4216[c]												
White-eyed Vireo	0.0024[a]	6.07	2.26	0.17	5.70	3.42	0.23	1.30	1.04	0.00	3.23	1.81	0.00
	<0.0001[b]	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)	(0.83)
	0.0982[c]												

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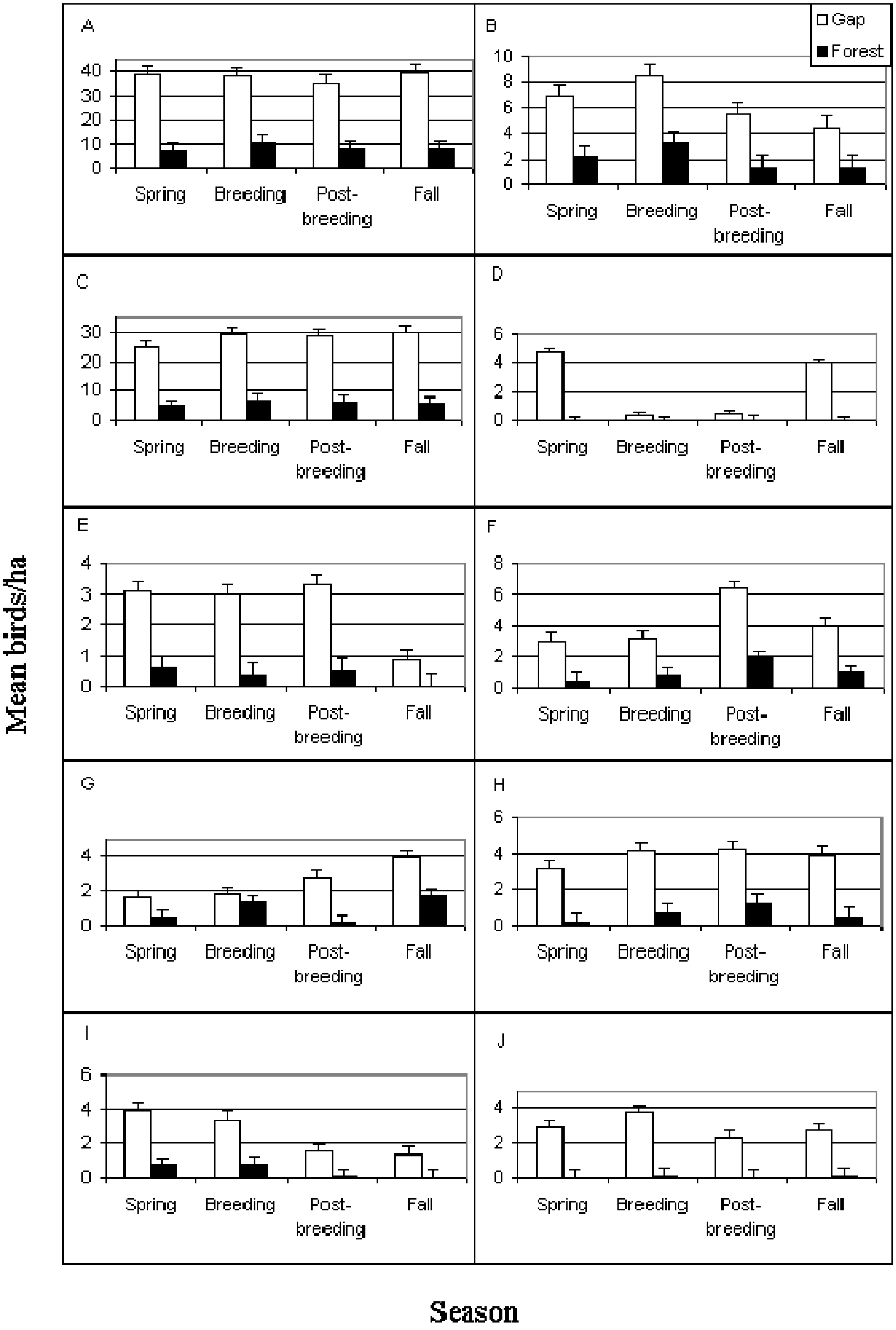
* [a] season

[b] net location

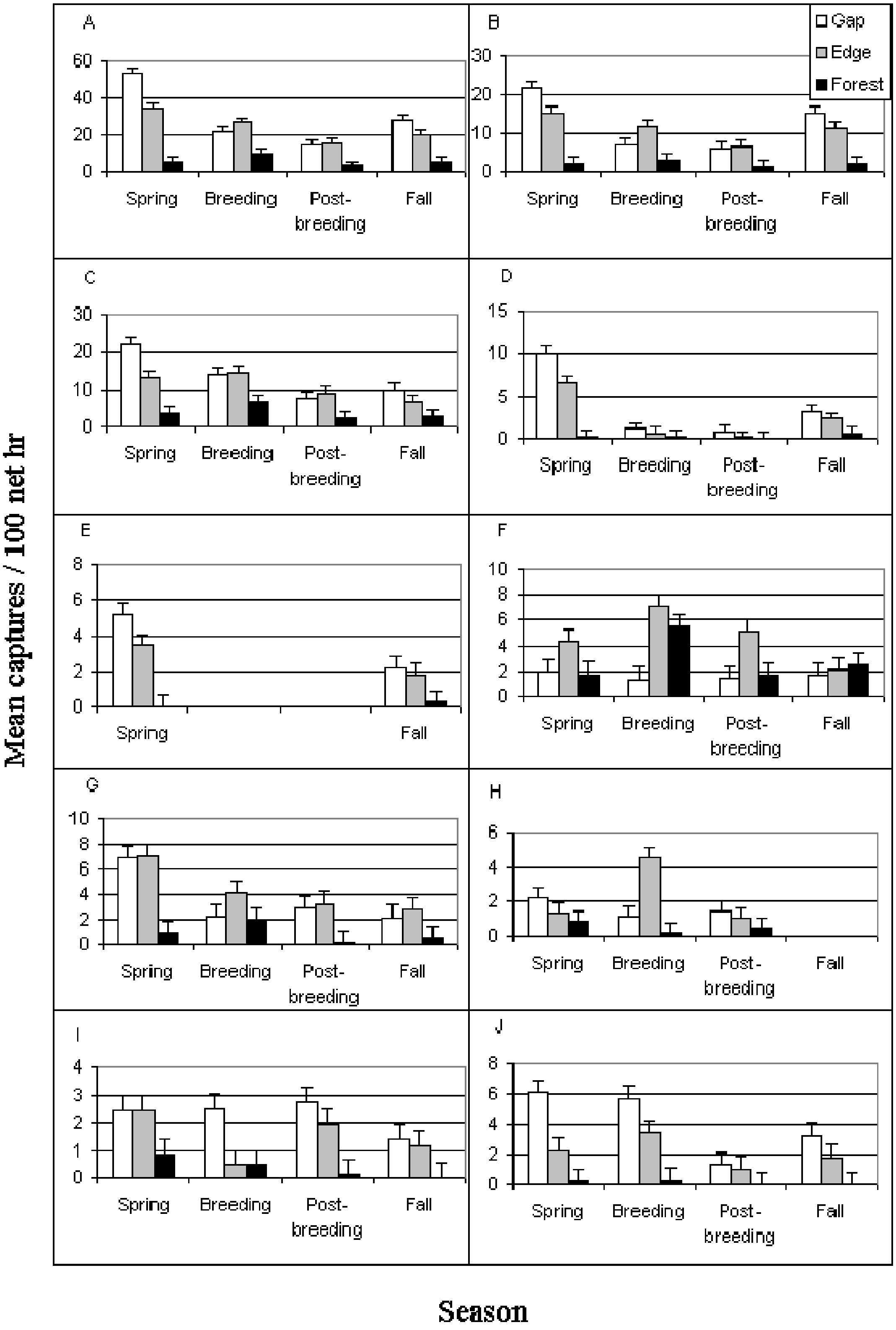
[c] season * net location

Fig. 1. Seasonal bird counts (birds per ha) for gap/edge and forest habitats, with standard error bars (2001 and 2002 in South Carolina, USA). (A) all birds, (B) forest interior species, (C) forest-edge species, (D) field-edge species, (E) Blue-gray Gnatcatcher, (F) Carolina Wren, (G) Eastern Tufted Titmouse, (H) Northern Cardinal, (I) Northern Parula, and (J) White-eyed Vireo



Mean birds/ha
Season
☐ Gap
■ Forest
A
0
10
20
30
40
B
0
2
4
6
8
10
C
0
10
20
30
D
0
2
4
6
E
0
1
2
3
4
F
0
2
4
6
8
G
0
2
4
H
0
2
4
6
I
0
2
4
6
J
0
2
4
Spring
Breeding
Post-breeding
Fall

Fig. 2. Mean bird captures per 100 net hours for each habitat and season with standard error bars (2001 and 2002 in South Carolina, USA). (A) all birds, (B) forest interior species, (C) forest-edge species, (D) field-edge species, (E) Black-throated Blue Warbler, (F) Carolina Wren, (G) Hooded Warbler, (H) Kentucky Warbler, (I) Northern Cardinal, and (J) White-eyed Vireo


Mean captures / 100 net hr
Season
Gap
Edge
Forest
A
0
20
40
60
B
0
10
20
30
C
0
10
20
30
D
0
5
10
15
E
0
2
4
6
8
F
0
2
4
6
8
10
G
0
2
4
6
8
10
H
0
2
4
6
I
0
1
2
3
4
J
0
2
4
6
8
Spring
Breeding
Post-breeding
Fall

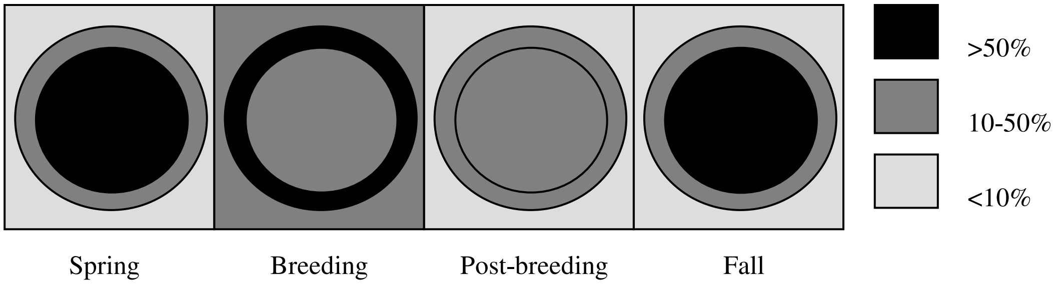


Fig. 3. Percent of captures per season and habitat type (gap, edge, forest) in a bottomland forest (2001 and 2002 in South Carolina, USA). Darker shades represent proportionally more captures.

Appendix 1. List of all birds observed with habitat group associations. Species included in this list were detected by plot counts or mist-netting at least once.

Species[a]	Scientific Name	Habitat Group
Acadian Flycatcher	*Empidonax virescens*	forest interior
American Crow	*Corvus brachyrhynchos*	forest edge
American Goldfinch	*Carduelis tristis*	field
American Redstart	*Setophaga ruticilla*	forest interior
Barred Owl	*Strix varia*	forest interior
Bicknell's Thrush	*Catharus bicknelli*	forest interior
Black and White Warbler	*Mniotilta varia*	forest interior
Black-throated Blue Warbler	*Dendroica caerulescens*	forest interior
Black-throated Green Warbler	*Dendroica virens*	forest interior
Blue Jay	*Cyanocitta cristata*	forest edge
Blue-gray Gnatcatcher	*Polioptila caerulea*	forest edge
Blue-headed Vireo	*Vireo solitarius*	forest interior
Blue-winged Warbler	*Vermivora pinus*	field edge
Brown Thrasher	*Toxostoma rufum*	field edge
Brown-headed Cowbird	*Molothrus ater*	forest edge
Brown-headed Nuthatch	*Sitta pusilla*	forest edge
Canada Warbler	*Wilsonia canadensis*	forest interior
Carolina Chickadee	*Poecile carolinensis*	forest edge
Carolina Wren	*Thryothorus ludovicianus*	forest edge
Chestnut-sided Warbler	*Dendroica pensylvanica*	field edge
Chimney Swift	*Chaetura pelagica*	field
Common Grackle	*Quiscalus quiscula*	field edge
Common Yellowthroat	*Geothlypis trichas*	field edge

Downy Woodpecker	*Picoides pubescens*	forest edge
Eastern Phoebe	*Sayornis phoebe*	forest edge
Eastern Towhee	*Pipilo erythrophthalmus*	field edge
Eastern Tufted Titmouse	*Baeolophus bicolor*	forest edge
Eastern Wood-Pewee	*Contopus virens*	forest edge
Fish Crow	*Corvus ossifragus*	forest edge
Golden-Winged Warbler	*Vermivora chrysoptera*	forest edge
Gray Catbird	*Dumetella carolinensis*	field edge
Gray-cheeked Thrush	*Catharus minimus*	forest interior
Great Crested Flycatcher	*Myiarchus crinitus*	forest edge
Hairy Woodpecker	*Picoides villosus*	forest interior
Hermit Thrush	*Catharus guttatus*	forest interior
Hooded Warbler	*Wilsonia citrina*	forest interior
Indigo Bunting	*Passerina cyanea*	field edge
Kentucky Warbler	*Oporornis formosus*	forest interior
Louisiana Waterthrush	*Seiurus motacilla*	forest interior
Magnolia Warbler	*Dendroica magnolia*	forest interior
Mourning Dove	*Zenaida macroura*	field edge
Northern Cardinal	*Cardinalis cardinalis*	forest edge
Northern Flicker	*Colaptes auratus*	forest edge
Northern Parula	*Parula americana*	forest edge
Northern Waterthrush	*Seiurus noveboracensis*	forest interior
Orange-crowned Warbler	*Vermivora celata*	forest edge
Ovenbird	*Seiurus aurocapillus*	forest interior
Pileated Woodpecker	*Dryocopus pileatus*	forest interior
Pine Warbler	*Dendroica pinus*	forest edge
Prairie Warbler	*Dendroica discolor*	field edge

Red-bellied Woodpecker	*Melanerpes carolinus*	forest edge
Red-eyed Vireo	*Vireo olivaceus*	forest interior
Red-headed Woodpecker	*Melanerpes erythrocephalus*	forest edge
Red-shouldered Hawk	*Buteo lineatus*	forest edge
Red-winged Blackbird	*Agelaius phoeniceus*	field
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	forest interior
Ruby-crowned Kinglet	*Regulus calendula*	forest edge
Ruby-throated Hummingbird	*Archilochus colubris*	forest edge
Scarlet Tanager	*Piranga olivacea*	forest interior
Summer Tanager	*Piranga rubra*	forest edge
Swainson's Thrush	*Catharus ustulatus*	forest interior
Swainson's Warbler	*Limnothlypis swainsonii*	forest interior
Swamp Sparrow	*Melospiza georgiana*	field
Turkey Vulture	*Cathartes aura*	field edge
Veery	*Catharus fuscescens*	forest interior
White-breasted Nuthatch	*Sitta carolinensis*	forest edge
White-eyed Vireo	*Vireo griseus*	forest edge
White-throated Sparrow	*Zonotrichia albicollis*	field
Winter Wren	*Troglodytes troglodytes*	forest edge
Wood Thrush	*Hylocichla mustelina*	forest interior
Worm Eating Warbler	*Helmitheros vermivorus*	forest edge
Yellow-bellied Sapsucker	*Sphyrapicus varius*	forest edge
Yellow-billed Cuckoo	*Coccyzus americanus*	forest edge
Yellow-breasted Chat	*Icteria virens*	field edge
Yellow-rumped Warbler	*Dendroica coronata*	forest edge
Yellow-throated Vireo	*Vireo flavifrons*	forest edge

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[a] American Ornithologists' Union (1998) common and scientific names.

CHAPTER 2

Seasonal bird-arthropod-vegetation relationships

SEASONAL RELATIONSHIPS BETWEEN ARTHROPOD ABUNDANCE, VEGETATION STRUCTURE, AND BIRD USE OF FOREST CANOPY GAPS IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT

We investigated the influence of arthropod abundance and vegetation structure on avian habitat use in three sizes (0.13, 0.26, and 0.5 ha) of 7-8 year old group-selection timber harvest openings during four seasons (spring migration, breeding, post-breeding, and fall migration) in a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. We used mist netting to estimate abundance of birds using canopy gap, gap edge, and surrounding forest habitats. We used foliage clipping, Malaise trapping, and pitfall trapping to determine arthropod abundance at the same locations. We captured more birds, including insectivores, foliage gleaners, and ground gleaners, in mid-successional canopy gap and edge habitats than in surrounding mature forest habitat during all seasons. Foliage-dwelling arthropod density generally was highest in forest habitats, while flying arthropod biomass was greatest in the gap habitats during all seasons. Ground-dwelling arthropods did not differ among habitats, but were dramatically less abundant during fall migration than the previous three seasons. We found significant relationships between insectivorous birds and leaf-dwelling Lepidoptera, insectivores and ground-dwelling arthropods, foliage-gleaning birds and foliage-dwelling arthropods, and aerial salliers and flying arthropods, as well as several relationships between individual bird species and arthropods. Relationships were inconsistent, however, with many groups or species being negatively correlated with arthropod abundance. Captures of all birds, insectivorous birds, foliage gleaners, ground gleaners, aerial salliers, Hooded Warbler (*Wilsonia citrina*), Northern Cardinal (*Cardinalis cardinalis*), White-eyed Vireo (*Vireo griseus*), and Black-throated Blue Warbler (*Dendrouca caerulescens*) each were positively correlated with understory vegetation density during two or more seasons. We conclude that the high bird abundance associated

with canopy gaps may have resulted less from high food resource availability than from complex understory and midstory vegetation structure.

Canopy gaps created by small-scale harvest operations can be used to mimic natural treefall disturbances. Canopy gaps within a mature forest habitat contain different microclimates, leading to a unique assortment of gap-associated flora and fauna (Watt 1947; Canham et al. 1990). Across multiple seasons, birds tend to be more abundant in forest canopy gaps created either by natural treefalls (Willson et al. 1982; Martin and Karr 1986) or group-selection harvest (Kilgo et al. 1999; Moorman and Guynn 2001; Bowen 2004).

Bird habitat use patterns change across seasons (Bowen 2004), depending upon particular seasonal needs, including protective cover, abundant food resources, appropriate breeding habitat, and places to raise young during breeding and post-breeding seasons (Robinson and Holmes 1982; Willson et al. 1982; Blake and Hoppes 1986; Moore et al. 1995; Petit 2000; Vega Rivera et al. 2003). Passerines often shift into more densely vegetated habitats between breeding and post-breeding periods (Anders et al. 1998; Vega Rivera et al. 1998, 2003; Pagen et al. 2000) and use a wider variety of forested habitats during migratory periods (Petit 2000; Rodewald and Brittingham 2002). Not only do habitat needs change across seasons, each species responds differently to its habitat on a local scale, including vegetation structure and food resource availability (Holmes et al. 1986). Like birds, arthropod populations may use habitats differently, depending upon seasonality and habitat type (Johnson and Sherry 2001; Greenberg and Forrest 2003) as well as canopy gap size (Shure and Phillips 1991).

Avian needs vary by season, but birds may benefit by selecting habitat based upon arthropod abundance, as they require food resources during all seasons. It would be advantageous for birds to choose sites with the greatest resource availability (Martin and Karr 1986), and indeed, it has been suggested that greater invertebrate biomass is linked to higher bird abundance (Blake and Hoppes 1986; Holmes et al. 1986), higher daily nest survival rates and faster growth rates of nestlings (Duguay et al. 2000), and timing of warbler migration (Graber and Graber 1983). Studies of experimental prey removal, however, have not linked decreased prey abundance with negative consequences for the local bird community (Nagy and Smith 1997; Marshall et al. 2002; T. Champlin, unpublished data).

Previous studies have not investigated seasonal shifts in avian habitat use as related to resource availability over multiple seasons. Using sampling stations established within forest canopy gaps, gap edges, and mature bottomland forest, we sampled birds, foliage-dwelling arthropods, ground-dwelling arthropods, flying arthropods, and understory vegetation density. Our goal was to examine the influences of both arthropod abundance and vegetation structure on seasonal avian habitat use, from spring migration through fall migration.

STUDY AREA

We conducted the study during 2001 and 2002 at the Savannah River Site (SRS), a 78000-ha National Environmental Research Park owned and operated by the U. S. Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size, located in Barnwell County in the Upper Coastal Plain region of South Carolina (Fig. 1). Birds, arthropods, and vegetation structure were surveyed in 12 group-selection gaps harvested in December 1994 and in the mature forest adjacent to gaps. The gaps were in their seventh and eighth growing seasons post-harvest during the study. They were of three sizes (0.13, 0.26, and 0.50 ha) with four replicates of each size. It is within this size range that previous research has identified a threshold in response by breeding (Moorman and Guynn 2001) and fall migrant birds (Kilgo et al. 1999). 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 patches of blackberry (*Rubus* spp.), dwarf palmetto, and switchcane.

METHODS

We surveyed birds and arthropods during four avian activity periods (hereafter, seasons) in 2001 and 2002: spring migration (25 March through 15 May), breeding (16 May through 30 June), post-breeding (1 July through 31 August), and fall migration (1 September through 18 October). We established a sampling transect radiating southward from the center of each gap with three bird and arthropod sampling stations along each transect, one in the gap center, one at the southern edge, and one 50 m into the forest.

Vegetation.-

During June 2001 and 2002, we measured vegetation structure along 10-m transects on each side of and parallel to all mist-net stations at least 1.5 m from each net. Following techniques modified from Karr (1971), we measured vertical distribution of vegetation at 1-m intervals along each 10-m transect (total 20 points). At 12 height intervals (0-0.25, 0.25-0.5, 0.5-0.75, 0.75-1, 1-1.5, 1.5-2, 2-3, 3-5, 5-10, 10-20, 20-25, and 25-30 m), we recorded whether vegetation touched a 2-m pole or the height intervals directly above the pole. Touches >2 m high were estimated visually. The percent cover for each height interval was determined by calculating the percentage of the 20 sampling points with vegetation touches in that interval. We grouped height intervals to calculate an index of foliage cover for vegetation layers by taking the mean percent cover of the height intervals in 0-3 m (understory), 3-20 m (midstory), and 20-30 m (canopy).

Arthropod collection.-

During each season in 2001 and 2002, we sampled foliage-dwelling, ground-dwelling, and flying arthropods at each station. We used foliage clipping (Cooper and Whitmore 1990) to sample foliage-dwelling arthropods on each of five target plant species groups. (1) white oaks [white oak (*Quercus alba*), swamp chestnut oak (*Quercus michauxii*), overcup oak (*Quercus lyrata*), Durand oak (*Quercus durandii*)], (2) lobed red oaks (cherrybark oak), (3) unlobed red oaks [water oak (*Quercus nigra*), laurel oak, willow oak (*Quercus phellos*)], (4) sweetgum, and (5) switchcane. This suite of species was selected to represent dominant members of both the understory and overstory, as well as species important as avian foraging substrates (J. C. Kilgo and C. E. Moorman, pers. obs.). Each sample consisted of 25 branch tips from each target species group (total sample=125 branch tips) collected in the vicinity of each sampling station (i.e., staying within the target habitat type). Each branch-tip clipping was between 2.54 and 15.24 cm and usually came from the end of a branch that included several leaves. We collected foliage from ground level to about 2.5 m, and clippings were immediately placed in plastic bags. Samples of target species occasionally were difficult to find, so not all samples included 125 clippings. Once the samples were collected, they were placed in a freezer for 24 hrs to kill all arthropods. We then shook the foliage to collect the arthropods, put them in alcohol, and identified them to order. Foliage was oven-dried for 48 h at 40^{o} C.

We used Malaise traps (Cooper and Whitmore 1990) to sample flying arthropods during each season, using 7-day trapping periods in 2001 and 2-day trapping periods in 2002. The Malaise traps (Sante Traps, Lexington, KY) were modified from the traditional Malaise trap design (Townes 1972) and allowed arthropod collection from any direction. Collecting jars were located both at the top and bottom of each trap to collect arthropods that, when trapped, either dropped or flew upward. The traps were suspended from EMT electrical conduit approximately 3 m off the ground, thereby leaving the traps hanging slightly above the ground. The 3-m section of conduit was connected by an elbow to a 1-m section of conduit that had a hook at the end, which allowed traps to be suspended. One lower corner of the trap was connected to the conduit pole to hold the trap in place during windy conditions. At the end of each trapping period, arthropods were collected from the jars, sorted by order, and recorded as dry weight (g) per day (to account for different collecting periods in different years).

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 and 2-day trapping periods in 2002, and operated the traps once during each season. The pitfall traps consisted of a 480-ml plastic cup buried to ground level, with a small funnel (8.4 cm diameter) to direct arthropods into a smaller 120-ml specimen cup. The cup 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 jars were filled with a detergent and NaCl-formaldehyde solution (New and Hanula 1998). Samples were dried, weighed, stored in 70% alcohol, and identified to order.

Mist netting.-

Continuous operation mist nets were located at each of the three sampling stations at each of the 12 study gaps. During the spring migration, post-breeding, and fall migration seasons, netting was conducted once each week at each station, rotating between stations on a regular weekly schedule. During the breeding season, nets were operated once every two weeks because birds tend to remain fairly stationary during this period. Nets were opened at first light and operated for 4-6 h, depending on daily weather conditions. Netting was not conducted when wind exceeded 16 km per hour or during steady rainfall. Nets were 12-m long x 3-m tall with 30-mm mesh. Captured birds were aged and sexed (Pyle et al. 1987), weighed, and banded with a USGS Biological Resources Division aluminum leg band.

DATA ANALYSIS

We assigned birds to several foraging guilds (Appendix 1): (1) all birds, (2) insectivores, (3) foliage gleaners, (4) ground gleaners, and (5) salliers (Ehrlich et al. 1988; Hamel 1992). Birds considered winter residents, present only in early spring or late fall, were not included in analyses. We analyzed mist-netting captures for each of the above guild groups. Individual species were chosen for analysis if they accounted for at least 80 captures over both years. These included Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, Northern Cardinal, and White-eyed Vireo (see scientific names in Appendix 1). Black-throated Blue Warbler is a transient species so data analysis only included spring and fall migratory periods, and Kentucky Warbler is an early migrant, so analysis of this species did not include fall migration.

We used a linear mixed model (PROC MIXED, SAS Institute 1990) to conduct analysis of variance (ANOVA) with covariates and interactions to analyze the effects of net location (gap, edge, forest), season, and arthropod abundance on bird captures. We used mean captures per 100 net hours for each guild or species as the dependent variable. We considered net location and season as fixed effects, with net location as a split plot factor and season as the repeated measure. Arthropod abundance was a continuous variable. We included all two-way interactions. We used a PROC MIXED model to examine the relationship between bird captures and understory (0-3 m) vegetation density with vegetation as the covariate. Because vegetation was only recorded once each year, this model did not include season. Year and gap size were not significant ($p \leq 0.05$) in any models, so these variables were not included in final models. Arthropod captures were standardized by g/day for Malaise traps and pitfall traps and by number of arthropods per g of foliage for foliage clippings. We compared captures of the foliage-gleaning guild to foliage-dwelling arthropod abundance, captures of the aerial sallier guild to flying arthropod abundance, and captures of the ground-gleaning guild to ground-dwelling arthropod abundance. We modeled bird abundance with Lepidopteran abundance based upon previous studies that have shown Lepidopterans to be a primary avian food source (Holmes et al. 1986; McMartin et al. 2002). We modeled each individual bird species abundance with Aranids and Coleopterans only when deemed important based on diets of individual species analyzed (Haggerty and Martin 1995; Halkin and Linville 1999; Whitehead and Taylor 2002; Bowen 2004).

RESULTS

Vegetation structure and diversity.-

The highest understory vegetation density occurred in the early successional gap habitat. Gaps tended to have very dense understory vegetation with little or no canopy cover, whereas forested habitat tended to have a relatively open understory, moderately developed midstory, and closed canopy (Fig. 2).

Arthropods.-

We captured arthropods representing 21 orders using foliage clipping during 2001 and 2002. Total arthropod density (number of arthropods per g of foliage) generally was slightly lower during spring migration than the other three seasons, and tended to be slightly greater at edge and forest habitats than in the gaps (Table 1). The five most frequently encountered arthropod orders, representing at least 150 individuals, were Araneae, Coleoptera, Homoptera, Hymenoptera, and Lepidoptera. Aranids, Hymenopterans, and Lepidopterans tended to follow the same general pattern as all arthropods. Coleopteran density tended to be greatest in the forest and edge habitats and lowest during post-breeding season and fall migration. Homopteran density was highly variable by habitat with the greatest density at the edge during fall migration.

We captured arthropods representing 17 orders using Malaise traps during 2001 and 2002. There were more arthropods (g/day) collected from gap habitats than either edge or forest during every season (Table 1). Total arthropod biomass was highest during the breeding season and lowest during post-breeding season and fall migration. The five most abundant arthropod orders were Diptera, Lepidoptera, Coleoptera, Hymenoptera, and Orthoptera; these represented biomass of at least 1 g/day. Coleopterans and Dipterans were most abundant at the edge but other orders tended to be more abundant in gaps. Coleopterans and Hymenopterans were most abundant during spring migration, Dipterans were most abundant during breeding season, and Lepidopterans were most abundant during fall migration.

We captured arthropods representing 23 orders using pitfall traps during 2001 and 2002. Total arthropod biomass (g/day) was greater during spring migration through post-breeding seasons than during fall migration, but it did not differ among habitat types (Table 1). The five most abundant arthropod orders were Diptera, Hymenoptera, Araneae, Coleoptera, and Orthoptera, which represent biomass of at least 100 g/day. These five orders all followed the same general pattern as total arthropod biomass.

Arthropod effects on birds.-

Bird captures were not consistently related to arthropod abundance (Table 2). We found an interaction between foliage-dwelling arthropods and season. Therefore, when the relationships between foliage-gleaning birds and foliage-dwelling arthropods was broken down by season, we found foliage-gleaning bird abundance to be positively associated with foliage-dwelling arthropods during the breeding and post-breeding seasons, and negatively associated during fall migration (Table 2; Fig. 3). There was a positive relationship between foliage-dwelling Lepidoterans and both White-eyed Vireo (during spring migration and breeding season) and Kentucky Warblers (Table 2), but a negative overall relationship between insectivorous birds and foliage-dwelling Lepidopterans (Table 2; Fig. 4). Northern Cardinals were negatively associated with foliage-dwelling arthropods, Aranids, and breeding-season Lepidopterans (Table 2). Insectivorous birds tended to be negatively associated with ground-dwelling arthropods during spring migration and the post-breeding season, but ground-gleaning birds were not associated with ground-dwelling arthropods during any season (Table 2; Fig. 5). Both aerial sallier and Acadian Flycatcher abundance tended to be negatively associated with all flying arthropods (Table 2; Fig. 6).

Vegetation structure effects on birds.-

All birds and foliage-gleaning birds were positively associated with understory vegetation density during all seasons (Table 3). Insectivorous birds were positively associated with understory vegetation density during spring and fall migration and during the breeding season (Table 3; Fig. 7). Ground gleaners were positively associated with understory foliage density only during spring and fall migratory periods, and aerial salliers only during the post-breeding season and fall migration (Table 3). All groups of birds, except Carolina Wren and Kentucky Warbler, were positively associated with understory vegetation density during at least one season (Table 3).

DISCUSSION

Our study suggests that birds do not closely follow local variations in arthropod availability. From spring migration through fall migration, we found no consistent relationships between arthropod availability and bird abundance for any group of birds or arthropods. When we did find bird-arthropod relationships, some were positive and some were negative depending upon the season and groups analyzed. A manipulative study conducted concurrent to ours at the SRS showed no effect of arthropod removal on breeding, post-breeding, and migrating bird communities using forest canopy gaps (T. Champlin, unpublished data). In other studies, the removal of Lepidopteran larvae had little or no effect on avian site fidelity or reproductive success (Nagy and Smith 1997; Marshall et al. 2002). Some studies, however, have suggested that birds may be able to follow changes in invertebrate abundance (Graber and Graber 1983; Blake and Hoppes 1986; Holmes et al. 1986; Gray 1993; Duguay et al 2000; Johnson and Sherry 2001). For example, Duguay et al. (2000) found a positive correlation between invertebrate biomass and daily nest survival rates of breeding birds and faster growth rates of nestlings in forest stands with greater invertebrate biomass. Graber and Graber (1983) determined that warbler migration coincides with the peak spring outbreak of Lepidopteran larvae, and Holmes et al. (1986) reported that bird abundance often is related to outbreaks of Lepidopteran larvae, a primary component of the warbler diet.

While birds were consistently more abundant in gap habitat than forested habitat, we found different patterns of abundance between foliage-dwelling, ground-dwelling, and flying arthropods. Foliage-dwelling arthropods were most abundant in forested habitat and most abundant during the breeding season, ground-dwelling arthropods varied by season for each habitat but abundance dropped dramatically during fall migration, and flying arthropods were most abundant in gap habitat but declined in abundance in the fall. In other studies of seasonal arthropod abundance, arthropod biomass increased through multiple seasons (Duguay et al. 2000; Greenberg and Forrest 2003), and bird habitat use was generally positively associated with prey availability. Greenberg and Forrest (2003) reported invertebrate biomass to be highest in the summer and greater in forested plots than in canopy gaps, while Blake and Hoppes (1986) found certain types of insects to be more abundant in canopy gaps during migratory periods. Duguay et al. (2000) reported mean invertebrate biomass was similar for selection cut and unharvested forests early in the breeding season, but was higher in unharvested stands than group-selection stands during the post-breeding season.

The inconsistent relationships between arthropods and birds, especially the negative relationships we found, indicate that arthropod abundance is not the prime factor influencing bird use of forest canopy gaps. Instead, the relationships documented in our study may be artifacts of the different habitat relations of the bird and arthropod groups we compared. The relationships were sometimes consistent with each other (resulting in positive correlations) and sometimes inconsistent (resulting in negative correlations). It is possible that potential relationships between birds and arthropods occurred at a different scale than we were able to detect, or that birds perceive prey on a different scale than we were able to represent with our collection techniques. For example, because birds were sampled continually throughout each season and arthropods were collected just once (1-day sampling periods for foliage-dwelling arthropods and 2- or 7-day sampling periods for ground-dwelling and flying arthropods), the arthropod data may not accurately represent actual prey availability during all periods in a season. Because we found no consistent bird-arthropod relationships, our data indicate that arthropods may not be a limiting resource for birds in southeastern bottomlands (i.e., they are capable of finding sufficient food resources across the area, even in areas of relatively low arthropod abundance), and that bird use of gaps is more closely related to the vegetation structure important for other aspects of their life history (e. g., cover for fledglings, foraging, and molting). It is not clear whether this relationship between bird use and vegetation structure adequately explains bird use of gaps in other regions and habitats.

Conservation Implications.-

Birds tended to respond positively to understory vegetation structure. We consistently detected more birds in the gap and edge habitats during all seasons, and the understory vegetation density also is highest in these habitats. Dense understory vegetation could be associated with increased foraging substrate density, thereby increasing foraging efficiency, even if the number of arthropods per g of foliage was equal to or lower than areas with less complex vegetation structure. Nets placed in dense understory vegetation also were more likely to capture birds, as any bird moving through this habitat would encounter the net, unlike a bird using the forest canopy out of range of our nets (Remsen and Good 1986). Birds foraging in forested habitat would only be available to netting if they were using the relatively sparse forest understory rather than the canopy vegetation. We were, therefore, only able to compare bird captures in the understory vegetation representing each habitat type.

Bowen (2004) documented a seasonal shift in habitat use for several bird groups, where birds used each habitat type differently during different seasons. Generally, the greatest bird use of gap habitat occurred during spring and fall migration, with the highest proportion of both edge and forest captures occurring during the breeding season. This seasonal shift in habitat use, however, was not explained by arthropod abundance. Rather, the avian shifts in habitat use that we observed may be the result of several factors, including a slight shift to forested habitat during breeding season for forest breeders, and an overall increase in the numbers of birds using the bottomland forest during spring and fall migration.

Other studies also have shown that forest stands with greater foliage density and understory habitat structure, such as in small-scale canopy gaps, tend to have more birds than mature forest (Blake and Hoppes 1986; Martin and Karr 1986; Kilgo et al. 1999; Moorman and Guynn 2001; Wilson and Twedt 2003). Birds may select mid- successional habitat with greater foliage density during migratory periods as well as during breeding and post-breeding seasons because of increased foraging substrate and protective cover. These factors may be particularly important during migration when birds move through unfamiliar territories and for fledgling birds during the post-breeding season. Dense understory vegetation also offers birds a number of perching sites, protection from the elements, greater cover during molt (Anders et al. 1998; Vega Rivera et al. 1998; 2003), protective habitat for young during the post-breeding period (Pagen et al. 2000), or protection from predators (Moore et al. 1995).

Future work on bird use of gaps in other regions should consider the influence of arthropod abundance to determine its universal importance relative to vegetation structure. For the greatest benefit to Neotropical migrant birds locally, Pashley and Barrow (1993) recommended a management regime that mimics natural disturbances to maintain habitat heterogeneity. In order to provide suitable habitat for a variety of birds during breeding, post-breeding, and migratory periods, all season-specific requirements (e.g. foraging substrates, nesting sites, protection from predators) must be available within close proximity. Future research should examine the relationship among birds, vegetation density, and arthropod abundance continually throughout several seasons to isolate the factors most important in determining seasonal shifts in bird habitat use.

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Table 1. Mean arthropod abundance with standard error in parentheses for each arthropod trapping method and most abundant arthropod orders by season and net location in a bottomland forest (2001-2002, South Carolina, USA).

	Spring			Breeding			Post-breeding			Fall		
	Gap	Edge	For	Gap	Edge	For	Gap	Edge	For	Gap	Edge	For
Foliage Clippings[a, b]												
All arthropods	6.7	9.3	13	18	14	22	9.5	13	20	12	18	23
	(1.3)	(1.3)	(1.3)	(2.1)	(2.1)	(2.1)	(2.9)	(2.9)	(2.9)	(2.3)	(2.3)	(2.3)
Araneae	1.4	2.4	2.8	5.2	3.5	6.8	5.5	5.5	8.1	7.1	6.7	9.1
	(0.56)	(0.56)	(0.56)	(0.57)	(0.57)	(0.57)	(0.77)	(0.77)	(0.77)	(0.80)	(0.80)	(0.80)
Coleoptera	2.0	2.7	4.3	1.7	1.9	3.9	0.89	1.3	1.3	0.70	0.97	2.1
	(0.78)	(0.78)	(0.78)	(0.51)	(0.51)	(0.51)	(0.24)	(0.24)	(0.24)	(0.27)	(0.27)	(0.27)
Homoptera	0.25	0.28	0.48	2.5	0.83	2.4	0.38	0.30	0.24	0.56	0.40	0.46
	(0.15)	(0.15)	(0.15)	(0.41)	(0.41)	(0.41)	(0.11)	(0.11)	(0.11)	(0.20)	(0.20)	(0.20)
Hymenoptera	0.77	2.3	3.0	3.1	3.7	3.4	0.021	2.0	2.1	1.2	4.9	3.2
	(0.64)	(0.64)	(0.64)	(1.4)	(1.4)	(1.4)	(0.93)	(0.93)	(0.93)	(1.3)	(1.3)	(1.3)

Lepidoptera	0.058	0.24	0.38	0.94	1.5	2.3	2.3	3.2	5.3	2.3	2.5	2.3
	(0.12)	(0.12)	(0.12)	(0.40)	(0.40)	(0.40)	(1.2)	(1.2)	(1.2)	(0.87)	(0.87)	(0.87)
Orthoptera	0.027	0.22	0.16	2.0	1.8	2.0	1.0	1.1	1.2	0.031	0.20	0.26
	(0.057)	(0.057)	(0.057)	(0.38)	(0.38)	(0.38)	(0.28)	(0.28)	(0.28)	(0.069)	(0.069)	(0.069
Malaise Trapping[c]												
All arthropods	0.048	0.022	0.016	0.050	0.013	0.010	0.015	0.011	0.010	0.025	0.010	0.004
	(0.007)	(0.007)	(0.007)	(0.012)	(0.012)	(0.012)	(0.002)	(0.002)	(0.002)	(0.004)	(0.004)	(0.004)
Coleoptera	0.039	0.600	0.053	0.024	0.027	0.030	0.010	0.019	0.015	0.003	0.006	0.004
	(0.006)	(0.006)	(0.006)	(0.005)	(0.005)	(0.005)	(0.003)	(0.003)	(0.003)	(0.001)	(0.001)	(0.001)
Diptera	0.198	0.051	0.032	0.322	0.027	0.009	0.054	0.009	0.006	0.024	0.008	0.001
	(0.036)	(0.036)	(0.036)	(0.10)	(0.10)	(0.10)	(0.010)	(0.010)	(0.010)	(0.004)	(0.004)	(0.004)
Hymenoptera	0.090	0.041	0.021	0.018	0.014	0.006	0.008	0.012	0.012	0.011	0.008	0.004
	(0.014)	(0.014)	(0.014)	(0.004)	(0.004)	(0.004)	(0.005)	(0.005)	(0.005)	(0.003)	(0.003)	(0.003)
Lepidoptera	0.074	0.021	0.013	0.023	0.018	0.015	0.021	0.024	0.032	0.100	0.030	0.009
	(0.020)	(0.020)	(0.020)	(0.004)	(0.004)	(0.004)	(0.005)	(0.005)	(0.005)	(0.020)	(0.020)	(0.020)
Pitfall Traps[c]												

All arthropods	1.2	0.75	0.91	1.3	1.0	0.67	0.71	0.99	1.1	0.35	0.28	0.28
	(0.17)	(0.17)	(0.17)	(0.19)	(0.19)	(0.19)	(0.14)	(0.14)	(0.14)	(0.053)	(0.053)	(0.053)
Araneae	2.3	1.2	1.3	2.8	2.1	1.1	0.85	1.8	0.68	0.46	0.42	0.27
	(0.45)	(0.45)	(0.45)	(1.0)	(1.0)	(1.0)	(0.43)	(0.43)	(0.43)	(0.11)	(0.11)	(0.11)
Coleoptera	0.59	0.74	1.0	0.77	1.6	0.59	0.54	0.91	1.7	0.62	0.71	0.56
	(0.23)	(0.23)	(0.23)	(0.41)	(0.41)	(0.41)	(0.18)	(0.18)	(0.18)	(0.13)	(0.13)	(0.13)
Diptera	4.4	2.2	1.7	3.3	1.7	0.98	0.84	0.81	1.2	0.85	0.49	0.35
	(0.83)	(0.83)	(0.83)	(0.50)	(0.50)	(0.50)	(0.16)	(0.16)	(0.16)	(0.16)	(0.18)	(0.16)
Hymenoptera	1.3	1.3	1.9	1.4	0.96	0.89	2.2	2.2	2.8	0.24	0.17	0.28
	(0.47)	(0.47)	(0.47)	(0.24)	(0.24)	(0.24)	(0.69)	(0.69)	(0.69)	(0.077)	(0.077)	(0.077)
Orthoptera	0.35	0.43	0.27	0.59	0.88	0.52	0.49	0.66	0.61	0.15	0.15	0.10
	(0.11)	(0.10)	(0.10)	(0.14)	(0.15)	(0.14)	(0.10)	(0.10)	(0.10)	(0.03)	(0.029)	(0.03)

[a] number of arthropods/g dry foliage

[b] numbers in table for foliage clipping arthropods are estimate*100

[c] g/day

Table 2. Relationship between bird abundance (mist net captures per 100 net hrs) and arthropod availability in a bottomland hardwood forest on the Savannah River Site, South Carolina, 2001-2002. Positive or negative relationships are indicated in parentheses.

Dependent variable	Independent variables[a]	F	DF	P
Bird and foliage-dwelling arthropods				
All birds	All Arthropods (-)	1.47	1/33	0.234
	All arthropods*season	1.16	3/33	0.340
	Lepidoptera (-)	3.19	1/33	0.0831
	Lepidoptera*season	1.62	3/33	0.202
Insectivores	All arthropods (-)	0.05	1/33	0.825
	All arthropods*season	0.83	3/33	0.489
	Lepidoptera (-)	5.08	1/33	0.0312
	Lepidoptera*season	2.25	3/33	0.101
Foliage gleaners	All arthropods (-)	0.48	1/33	0.493
	All arthropods*season	5.44	3/33	0.0044
	Spring (-)	1.17	33	0.287
	Breeding (+)	18.49	33	0.0001
	Post-breeding (+)	9.36	33	0.0044
	Fall (-)	5.43	33	0.0261
	Lepidoptera (-)	1.22	1/33	0.277
	Arthropod*season	1.60	3/33	0.207
Hooded Warbler	All arthropods (-)	0.11	1/33	0.748
	All arthropods*season	0.53	3/33	0.668
	Araneae (-)	2.02	1/33	0.164
	Araneae*season	1.24	3/33	0.311

	Coleoptera (+)	4.61	1/33	0.0391
	Coleoptera*season	5.79	3/33	0.0027
	Spring (-)	6.60	33	0.0150
	Breeding (+)	1.69	33	0.201
	Post-breeding (-)	4.67	33	0.0384
	Fall (+)	5.62	33	0.0235
	Lepidoptera (-)	1.30	1/33	0.0621
	Lepidoptera*season	0.70	3/33	0.560
Northern Cardinal	All Arthropods (-)	6.06	1/33	0.0192
	All arthropods*season	2.03	3/33	0.129
	Araneae (-)	4.22	1/33	0.0479
	Araneae*season	2.15	3/33	0.113
	Coleoptera (-)	3.66	1/33	0.0645
	Coleoptera*season	0.49	3/33	0.693
	Lepidoptera (-)	1.08	1/33	0.307
	Lepidoptera*season	3.14	3/33	0.0381
	Spring (-)	1.23	33	0.274
	Breeding (-)	7.24	33	0.0111
	Post-breeding (+)	1.77	33	0.193
	Fall (+)	3.57	33	0.0675
White-eyed Vireo	All arthropods (+)	2.93	1/33	0.0965
	All arthropods*season	1.48	3/33	0.237
	Araneae (+)	1.18	1/33	0.285
	Araneae*season	2.16	3/33	0.112
	Coleoptera (+)	2.60	1/33	0.117
	Coleoptera*season	1.07	3/33	0.376
	Lepidoptera (+)	31.51	1/33	0.0001

	Lepidoptera*season	20.62	3/33	0.0001
	Spring (+)	5.43	33	0.0261
	Breeding (+)	46.51	33	0.0001
	Post-breeding (-)	0.0025	33	0.964
	Fall (-)	0.073	33	0.789
Black-throated Blue Warbler	All arthropods (-)	0.85	1/33	0.363
	All arthropods*season	3.13	3/33	0.0862
	Araneae (-)	0.21	1/33	0.651
	Araneae*season	2.87	1/33	0.0994
	Coleoptera (-)	0.00	1/33	0.957
	Coleoptera*season	0.10	1/33	0.758
	Lepidoptera (-)	0.00	1/33	0.964
	Lepidoptera*season	0.26	1/33	0.613
Kentucky Warbler	All arthropods (+)	1.05	1/33	0.312
	All arthropods*season	1.54	2/33	0.229
	Araneae (-)	0.04	1/33	0.846
	Araneae*season	0.08	2/33	0.921
	Coleoptera (-)	0.35	1/33	0.559
	Coleoptera*season	0.09	2/33	0.911
	Lepidoptera (+)	5.52	1/33	0.0249
	Lepidoptera*season	1.91	2/33	0.164
Birds and ground-dwelling arthropods				
All birds	All arthropods (+)	0.72	1/33	0.401
	All arthropods*season	5.79	3/33	0.0027
	Spring (-)	2.69	33	0.111
	Breeding (+)	0.058	33	0.811

	Post-breeding (-)	3.53	33	0.0695
	Fall (+)	0.59	33	0.448
Insectivores	All arthropods (+)	0.00	1/33	0.959
	All arthropods*season	5.37	3/33	0.0040
	Spring (-)	3.92	33	0.0561
	Breeding (+)	0.56	33	0.460
	Post-breeding (-)	5.24	33	0.0283
	Fall (+)	1.90	33	0.178
Ground gleaners	All arthropods (-)	2.06	1/33	0.161
	All arthropods*season	0.62	3/33	0.606
Carolina Wren	All arthropods (-)	1.98	1/33	0.169
	All arthropods*season	0.35	3/33	0.789
	Araneae (-)	0.00	1/33	0.968
	Aranae*season	0.37	3/33	0.778
	Coleoptera (+)	0.01	1/33	0.943
	Coleoptera*season	0.28	3/33	0.837
Birds and flying arthropods				
All birds	All arthropods (+)	0.16	1/33	0.690
	All arthropods*season	0.27	3/33	0.843
Insectivores	All arthropods (+)	0.07	1/33	0.787
	All arthropods*season	0.79	3/33	0.511
Aerial salliers	All arthropods (-)	4.02	1/33	0.0531
	All arthropods*season	1.29	3/33	0.293
Acadian Flycatcher	All arthropods (-)	6.15	1/33	0.0184
	All arthropods*season	2.23	3/33	0.104
	Coleoptera (+)	2.38	1/33	0.133

Coleoptera*season	0.71	3/33	0.555

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[a] Each arthropod variable was tested against bird abundance in a separate model, which also included season and net location as fixed effects to control for their influence. Given here are the results only for arthropod variables and their interactions with season.

Table 3. Relationship between bird abundance (mist net captures per 100 net hrs) and understory (0-3 m) vegetation density in a bottomland hardwood forest on the Savannah River Site, South Carolina, 2001-2002. Numerator DF is 1 and denominator DF is 26 for each category.

Bird Group	Season	F	P
All birds	Spring (+)	114.65	0.0001
	Breeding (+)	7.38	0.0116
	Post-breeding (+)	9.56	0.0047
	Fall (+)	62.37	0.0001
Insectivores	Spring (+)	111.97	0.0001
	Breeding (+)	5.56	0.0261
	Post-breeding (+)	3.14	0.0884
	Fall (+)	49.19	0.0001
Foliage gleaners	Spring (+)	131.37	0.0001
	Breeding (+)	22.64	0.0001
	Post-breeding (+)	17.08	0.0003
	Fall (+)	47.07	0.0001
Ground gleaners	Spring (+)	9.99	0.0040
	Breeding (-)	1.00	0.327
	Post-breeding (-)	3.89	0.0592
	Fall (+)	16.60	0.0004
Aerial salliers	Spring (-)	2.45	0.130
	Breeding (+)	0.02	0.890

	Post-breeding (+)	6.19	0.0196
	Fall (+)	4.60	0.0415
Carolina Wren	Spring (+)	0.08	0.777
	Breeding (-)	2.05	0.164
	Post-breeding (-)	3.69	0.0659
	Fall (-)	0.38	0.543
Hooded Warbler	Spring (+)	17.00	0.0003
	Breeding (+)	0.81	0.376
	Post-breeding (+)	8.61	0.0069
	Fall (+)	3.68	0.0662
Northern Cardinal	Spring (+)	1.23	0.278
	Breeding (+)	2.24	0.147
	Post-breeding (+)	8.53	0.0071
	Fall (+)	10.34	0.0035
White-eyed Vireo	Spring (+)	40.88	0.0001
	Breeding (+)	13.83	0.0010
	Post-breeding (+)	2.82	0.105
	Fall (+)	6.47	0.0172
Black-throated Blue Warbler	Spring (+)	27.16	0.0001
	Fall (+)	5.71	0.0244
Kentucky Warbler	Spring (+)	0.90	0.351
	Breeding (+)	0.14	0.711
	Post-breeding (+)	1.07	0.311

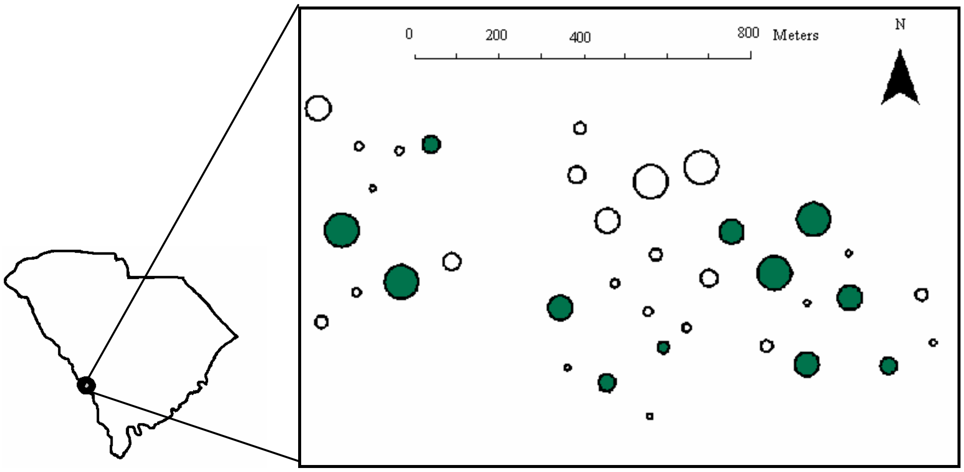

Fig. 1. Forest canopy gaps at Savannah River Site, Barnwell County, in the coastal plain of South Carolina, USA. Gaps used for this study were 0.13, 0.26, and 0.5 ha and are shown as solid circles. Other gaps not used for this study were <0.13, 0.13, 0.26, and 0.5 ha and are shown as outlines.

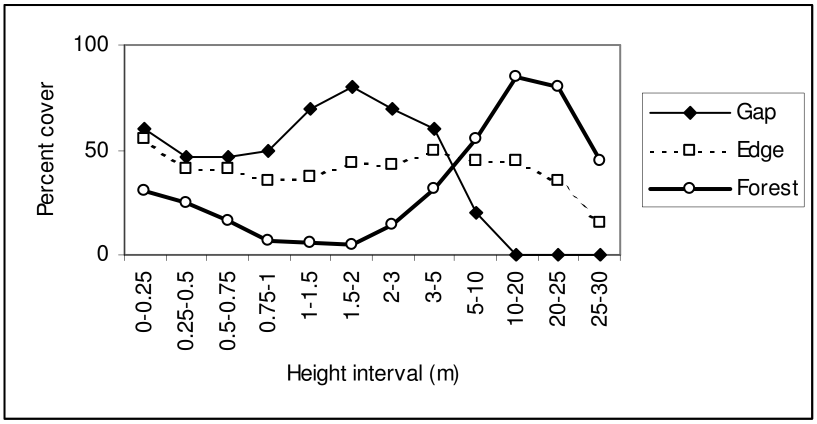

Fig. 2. Foliage height profiles for gap, edge, and forest net locations in a bottomland forest in South Carolina, USA (2001-2002). Vegetation measures were collected in June of each year.

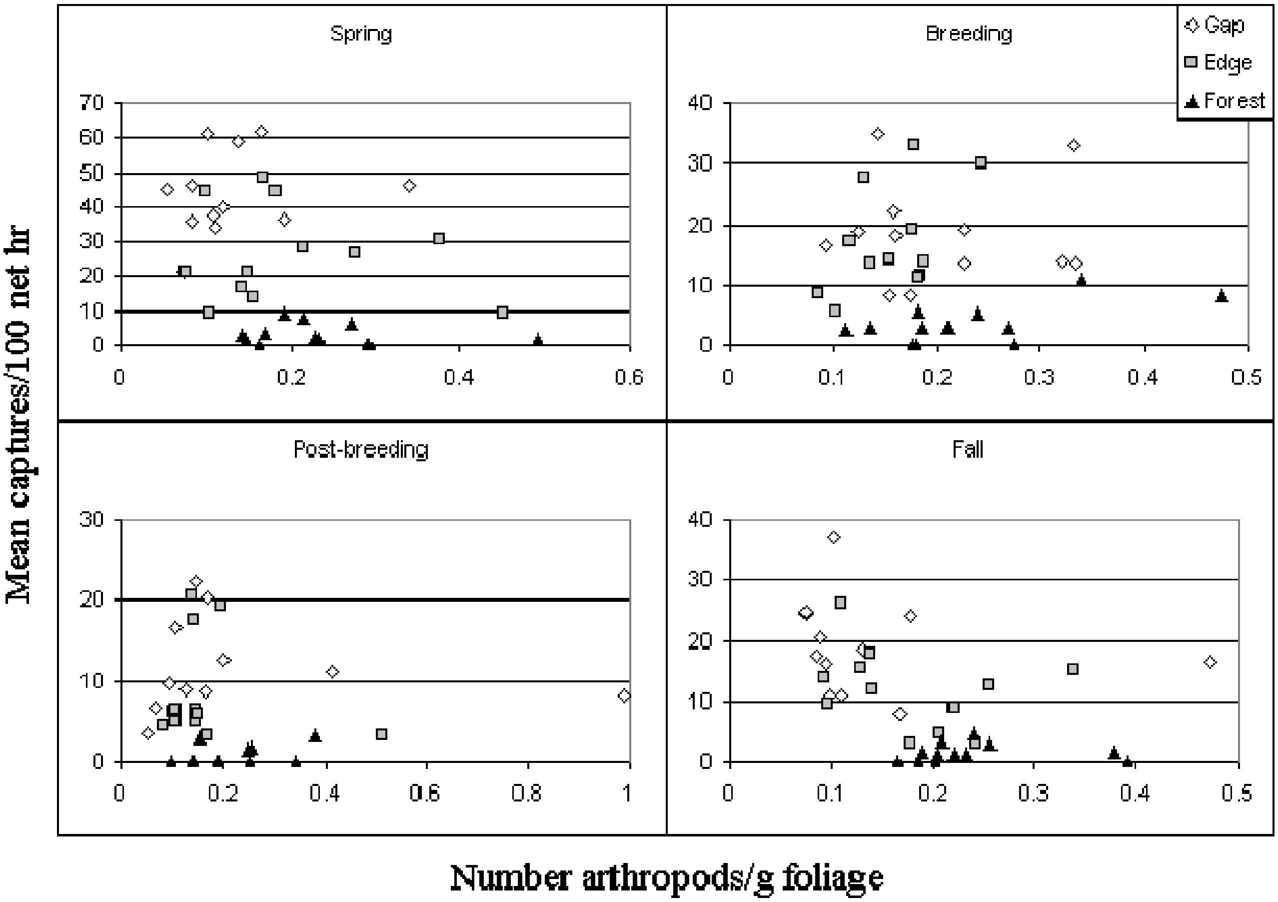

Fig. 3. Seasonal foliage-gleaning bird captures plotted against arthropod density (number of arthropods per g of foliage) from foliage clippings for each net location in a bottomland forest in South Carolina, USA (2001-2002).

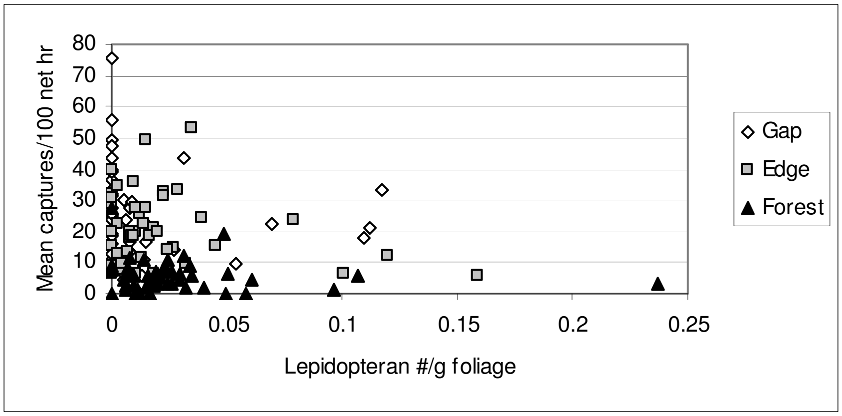

Fig. 4. Insectivore captures plotted against Lepidopteran density (number of Lepidopterans per g of foliage) from foliage clippings for each net location in a bottomland forest in South Carolina, USA (2001-2002).

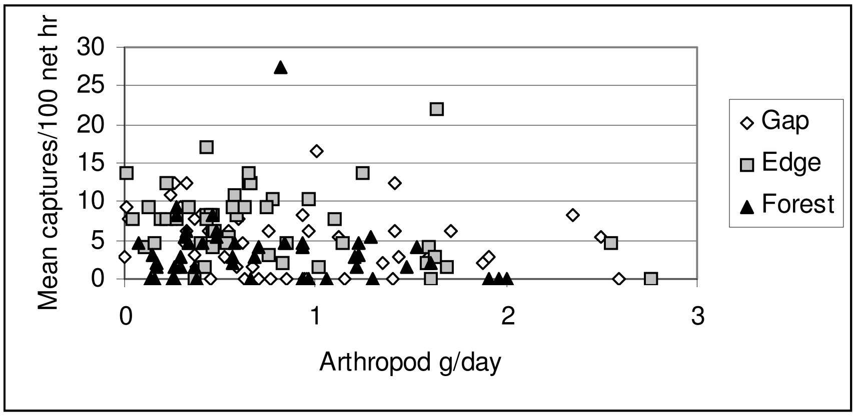

Fig. 5. Ground gleaner bird captures plotted against arthropod biomass (g/day) from pitfall trapping for each net location in a bottomland forest in South Carolina, USA (2001-2002).

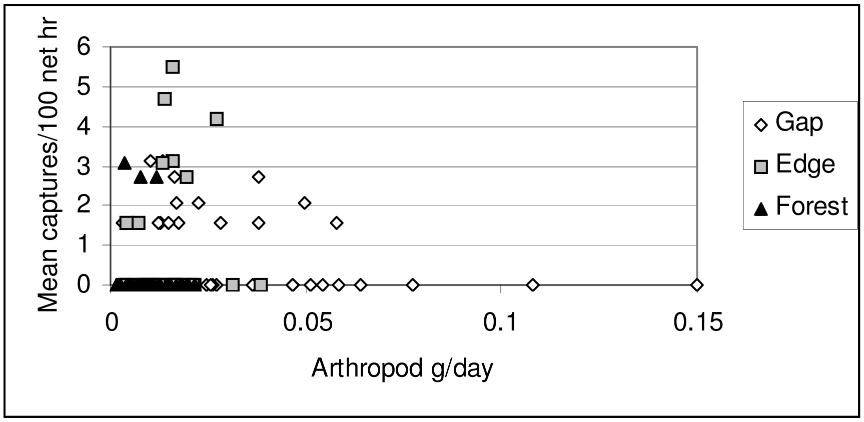

Fig. 6. Aerial sallier bird captures plotted against arthropod biomass (g/day) from Malaise trapping for each net location in a bottomland forest in South Carolina, USA (2001-2002).

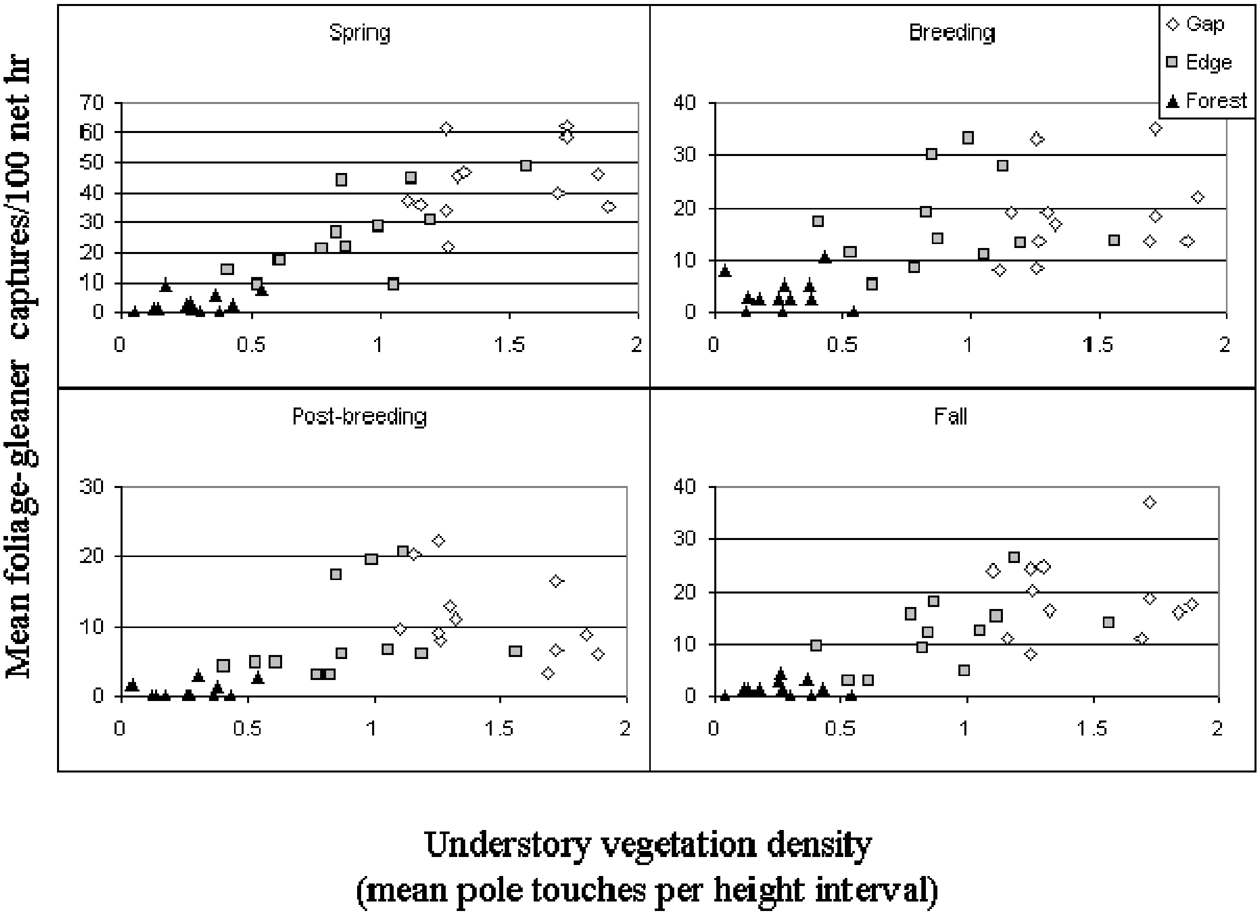

Fig. 7. Seasonal foliage gleaner captures plotted against mean understory foliage density (mean vegetation pole touches per understory height interval) for each net location in a bottomland forest in South Carolina, USA (2001-2002).

Appendix 1. List of all birds observed with habitat, foraging, migration, and food preference guild associations. Species included in this list were detected by mist netting or area counts at least once.

Species[a]	Scientific Name	Foraging Group	Food Type
Acadian Flycatcher	*Empidonax virescens*	sallier	insectivore
American Redstart	*Setophaga ruticilla*	foliage gleaner	insectivore
Bicknell's Thrush	*Catharus bicknelli*	ground gleaner	omnivore
Black and White Warbler	*Mniotilta varia*	bark gleaner	insectivore
Black-throated Blue Warbler	*Dendroica caerulescens*	foliage gleaner	insectivore
Blue-gray Gnatcatcher	*Polioptila caerulea*	foliage gleaner	insectivore
Blue-headed Vireo	*Vireo solitarius*	foliage gleaner	insectivore
Blue-winged Warbler	*Vermivora pinus*	foliage gleaner	insectivore
Brown Thrasher	*Toxostoma rufum*	ground gleaner	omnivore
Carolina Chickadee	*Poecile carolinensis*	foliage gleaner	insectivore
Carolina Wren	*Thryothorus ludovicianus*	ground gleaner	insectivore
Chestnut-sided Warbler	*Dendroica pensylvanica*	foliage gleaner	insectivore
Common Yellowthroat	*Geothlypis trichas*	foliage gleaner	insectivore
Downy Woodpecker	*Picoides pubescens*	bark gleaner	insectivore
Eastern Towhee	*Pipilo erythrophthalmus*	ground gleaner	omnivore
Eastern Tufted Titmouse	*Baeolophus bicolor*	foliage gleaner	omnivore
Golden-winged Warbler	*Vermivora chrysoptera*	foliage gleaner	insectivore
Gray Catbird	*Dumetella carolinensis*	foliage gleaner	omnivore
Gray-cheeked Thrush	*Catharus minimus*	ground gleaner	omnivore
Great Crested Flycatcher	*Myiarchus crinitus*	sallier	insectivore
Hooded Warbler	*Wilsonia citrina*	foliage gleaner	insectivore
Indigo Bunting	*Passerina cyanea*	ground gleaner	omnivore

Kentucky Warbler	*Oporornis formosus*	foliage gleaner	insectivore
Louisiana Waterthrush	*Seiurus motacilla*	ground gleaner	insectivore
Magnolia Warbler	*Dendroica magnolia*	foliage gleaner	insectivore
Northern Cardinal	*Cardinalis cardinalis*	foliage gleaner	omnivore
Northern Parula	*Parula americana*	foliage gleaner	insectivore
Northern Waterthrush	*Seiurus noveboracensis*	ground gleaner	insectivore
Orange-crowned Warbler	*Vermivora celata*	foliage gleaner	insectivore
Ovenbird	*Seiurus aurocapillus*	ground gleaner	insectivore
Pileated Woodpecker	*Dryocopus pileatus*	bark gleaner	insectivore
Pine Warbler	*Dendroica pinus*	foliage gleaner	insectivore
Prairie Warbler	*Dendroica discolor*	foliage gleaner	insectivore
Red-bellied Woodpecker	*Melanerpes carolinus*	bark gleaner	insectivore
Red-eyed Vireo	*Vireo olivaceus*	foliage gleaner	insectivore
Red-headed Woodpecker	*Melanerpes erythrocephalus*	bark gleaner	insectivore
Ruby-crowned Kinglet	*Regulus calendula*	foliage gleaner	insectivore
Ruby-throated Hummingbird	*Archilochus colubris*	foliage gleaner	omniivore
Summer Tanager	*Piranga rubra*	foliage gleaner	insectivore
Swainson's Thrush	*Catharus ustulatus*	ground gleaner	insectivore
Swainson's Warbler	*Limnothlypis swainsonii*	ground gleaner	insectivore
Swamp Sparrow	*Melospiza georgiana*	ground gleaner	omnivore
Traill's Flycatcher	*Empidonax spp.*	hover gleaner	insectivore
Veery	*Catharus fuscescens*	ground gleaner	omnivore
White-eyed Vireo	*Vireo griseus*	foliage gleaner	insectivore
White-throated Sparrow	*Zonotrichia albicollis*	ground gleaner	omnivore
Winter Wren	*Troglodytes troglodytes*	ground gleaner	insectivore
Wood Thrush	*Hylocichla mustelina*	ground gleaner	omnivore
Worm Eating Warbler	*Helmitheros vermivorus*	foliage gleaner	insectivore

Yellow-bellied Sapsucker	*Sphyrapicus varius*	bark gleaner	insectivore
Yellow-billed Cuckoo	*Coccyzus americanus*	foliage gleaner	insectivore
Yellow-breasted Chat	*Icteria virens*	foliage gleaner	insectivore

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[a] American Ornithologists' Union (1998)

CHAPTER 3

Seasonal bird diets

SEASONAL BIRD DIETS IN A BOTTOMLAND FOREST

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Abstract. Canopy gaps in bottomland hardwood forests provide important habitat for a wide variety of both migratory and resident bird species. Little is known about how birds forage in relation to arthropod availability, and less is known about how these patterns vary seasonally. We captured birds using mist netting and then used a warm water crop-flush to gather information about arthropods eaten over multiple bird-use seasons. We used leaf clipping and pitfall trapping to determine which arthropod groups were available to foliage-gleaning birds and ground-gleaning birds. Individual bird species and foraging guilds analyzed included Carolina Wren (*Thryothorus ludovicianus*), Hooded Warbler (*Wilsonia citrina*), Kentucky Warbler (*Oporornis formosus*), White-eyed Vireo (*Vireo griseus*), foliage-gleaning birds and ground-gleaning birds. The arthropod orders Coleoptera, Lepidoptera, and Araneae represented the highest percentages of total bird diet for each bird species and group analyzed. We compared bird use vs. availability of potential prey items and ranked the most frequent prey items by degree of selection or avoidance. In general, birds selected Coleopterans and Hemipterans during all seasons and avoided Aranids and Hymenopterans during all seasons. Bird diet analysis did not demonstrate a consistent selection pattern for other arthropod orders (Dipterans, Homopterans, Lepidopterans, and Orthopterans). Ground-gleaning birds demonstrated a stronger selection for Homopterans and Lepidopterans than foliage-gleaners. Individual bird species and guilds tended to consistently select or avoid certain groups of arthropods from spring through fall migration, with no apparent seasonal shift in diet preference among arthropod orders.

Key words: Birds, bottomland forest, crop flushing, diet analysis, prey selection

INTRODUCTION

Passerine birds feed almost continuously during daylight hours (Stevenson 1933), and food resource availability is thought to be a driving force behind habitat selection (Blake and Hoppes 1986, Holmes et al. 1986, Johnson and Sherry 2001). Bird prey selection is influenced by prey availability, including proximity, detection, acceptance, pursuit, and successful capture of a potential prey item (Wolda 1990). However, little is known about food preferences of certain passerine species (Evans and Stutchburg 1994, McDonald 1998), or about how birds' prey-selection patterns change across seasons.

Canopy gaps within mature forest provide additional habitat for birds. Both natural gaps (Willson et al. 1982, Martin and Karr 1986) and group-selection harvest gaps (Kilgo et al. 1999, Moorman and Guynn 2001) typically contain greater numbers of birds than the surrounding mature forest. Arthropod populations also are 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). Flying arthropods may be more abundant in gap habitats than surrounding forest, while other groups, such as ground-dwelling arthropods have been reported in lower numbers in gap habitat (Greenberg and Forrest 2003).

Accurately determining prey availability, as perceived by a bird, 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 has addressed bird-arthropod relationships in eastern deciduous forests.

Our goals were to examine both arthropod availability and prey selection by insectivorous birds, both in and around small-scale forest canopy gaps in a southeastern bottomland hardwood forest. We sought to determine whether birds exhibited a seasonal shift in prey use from spring migration through fall migration. We compared percentages of arthropod groups both available to and consumed by foliage-gleaning and ground-gleaning passerine birds to determine whether birds selected arthropod prey items in relative proportion to their availability.

METHODS

We surveyed birds and arthropods during four avian activity periods (hereafter, seasons) in 2001 and 2002: spring migration (25 March through 15 May), breeding (16 May through 30 June), post-breeding (1 July through 31 August), and fall migration (1 September through 18 October). We established a sampling transect 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 edge; and one 50 m into the forest.

STUDY AREA

We conducted this research during 2001 and 2002 at the Savannah River Site (SRS), a 78000-ha National Environmental Research Park owned and operated by the U. S. Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size, located 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. The gaps were of three sizes (0.13, 0.26, and 0.50 ha) with four replicates of each size. 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.

MIST NETTING

Continuous operation mist nets were located at each of the three sampling stations at each of the 12 study gaps. During the spring migration, post-breeding, and fall migration seasons, netting was conducted once each week at each station, rotating between stations on a regular weekly schedule. During the breeding season, nets were operated once every two weeks because birds tend to remain fairly stationary during this period. Nets were opened at first light and operated for 4-6 h, depending on daily weather conditions. We did not conduct netting when wind exceeded 16 km per hour or during steady rainfall. We used 12-m long x 3-m tall nets, with 30-mm mesh. Captured birds were aged and sexed (Pyle et al. 1987), weighed, and banded with a USGS Biological Resources Division aluminum leg band.

CROP-FLUSHING

We used a warm water crop-flush to identify the proportions of various arthropod orders consumed by birds (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*). Other medium-sized insectivorous species caught were also crop-flushed, but in lower numbers (TABLE 1). We did not crop-flush the same individual twice in one season and did not crop-flush individual birds that appeared stressed. We inserted a thin, flexible, 10-cm plastic tube down the throat and into the crop. Using a small syringe, we slowly squirted warm water into the crop as we withdrew the tube, and caught the regurgitate in a shallow plastic dish. We preserved samples in 70% alcohol. We then sorted, counted, and identified arthropod fragments to order using a dissecting microscope and entomology reference book (Gillott 1995). We identified the most frequently encountered orders by the following fragments (FIGURE 1): Araneae (mouthparts, leg fragments); Coleoptera (mandibles, elytra, leg fragments); Diptera (antennae, eyes, wings, foot pads/empodium); Hemiptera (mouthparts, wing fragments, leg fragments, scutella); Homoptera (mouthparts, leg fragments, ovipositor); Hymenoptera (mouthparts, leg fragments, various body fragments, wing fragments); Lepidoptera (adult wing scales, larval mandibles, setae, crochets, integument, and spherical plates); and Orthoptera (leg fragments, nymphal wingpads, and stridulatory organ). Exact numbers of individuals were difficult to estimate because of the high degree of fragmentation, and as a result, we estimated numbers conservatively.

ARTHROPOD SAMPLING

During each season 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 foliage-dwelling arthropods on each of five target plant species groups. (1) white oaks (white oak [*Quercus alba*], swamp chestnut oak [*Quercus michauxii*], overcup oak [*Quercus lyrata*], Durand oak [*Quercus durandii*]), (2) lobed red oaks (cherrybark oak), (3) unlobed red oaks [water oak (*Quercus nigra*), laurel oak, willow oak (*Quercus phellos*)], (4) sweetgum, and (5) switchcane. This group of species was selected to represent dominant members of both the understory and overstory, as well as species important as avian foraging substrates (J. C. Kilgo and C. E. Moorman, pers. obs.). Each sample consisted of 25 branch tips from each target species group (total sample=125 branch tips) collected in the vicinity of each sampling station (i.e. staying within the target habitat type). Each branch-tip clipping was between 2.54 and 15.24 cm and usually came from the end of a branch that included several leaves. We collected foliage from ground level to about 2.5 m, and immediately placed clippings in plastic bags. Samples of target species occasionally were difficult to find, so not all samples included 125 clippings. Once collected, we placed samples in a freezer for 24 hrs, shook the foliage to collect the arthropods, put them in alcohol, and identified them 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 and 2-day trapping periods in 2002, and operated the traps once during each season. The pitfall traps consisted of a 480-ml plastic cup buried to ground level, with a small 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 jars were filled with a detergent and NaCl-formaldehyde solution (New and Hanula 1998). Samples were dried, weighed, stored in 70% alcohol, and identified to order.

ANALYSIS

For each of the four bird-use seasons, we examined the relationships between bird species (Carolina Wren, Hooded Warbler, Kentucky Warbler, and White-eyed Vireo) or foraging guild (foliage-gleaners and ground-gleaners) and potential arthropod prey items. Both bird crop-flush samples and arthropod availability samples from foliage clipping and pitfall trapping were summarized by percentages, i.e., the percentage of the entire crop-flush or arthropod availability sample containing a particular arthropod order. Bird and arthropod data were averaged between years and among sampling locations (gap, edge, forest). Arthropod abundance may not reflect actual prey availability, as birds may not eat all potentially available arthropods, depending on prey size, life stage, palatability, color, and activity pattern (Cooper and Whitmore 1990). Differences in proportional availability vs. use of arthropod prey items may also be attributed to bird foraging strategy and arthropod distribution (Raley and Anderson 1990). Additionally, bird diets may differ depending upon 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 may be 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. 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 and whether proportional arthropod use changed seasonally. We used an index developed by Jacobs (1974) to evaluate seasonal bird use of each arthropod order in relation to its availability:

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

where D_{hb} is the index of arthropod use, r represents the mean percentage of the total crop-flush sample arthropods representing a particular arthropod order, and p represents the mean percentage of the total arthropod collection sample representing each arthropod order. We then followed Morrison's (1982) categorization of D_{hb} for selection and avoidance, ranging from -1 to 1, where -1 to -0.81 = strong avoidance, -0.80 to -0.41 = moderate avoidance, -0.40 to -0.16 = slight avoidance, -0.15 to 0.15 = no selection, 0.16 to 0.40 = slight selection, 0.41 to 0.80 = moderate selection, and 0.81 to 1 = strong selection.

RESULTS

CROP FLUSHING

We obtained 255 crop flushes from 15 bird species (TABLE 1) and identified 703 individual prey items representing 15 arthropod orders. The most frequently encountered arthropod orders, and those considered for analysis, included 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 arthropod orders comprised 96% of the arthropods encountered using crop-flushing. We counted only 11 entire arthropods representing several orders (Araneae, Diptera, Homoptera, Hymenoptera, Psocoptera, and Thysanoptera).

We also identified a category of "other" non-arthropod contents, including a few small feathers, insect eggs, a small flower, and small seeds. Percentages of arthropods found in bird diets represent only the total arthropod content of the crop-flushing, and any non-arthropod ("other") contents were disregarded. Plant material (usually seeds) occurred in only 10 of the 255 crop-flush samples from several species: Hooded Warbler, Kentucky Warbler, Ovenbird (*Seiurus aurocapillus*), Veery (*Catharus fuscescens*), and White-eyed Vireo.

ARTHROPOD SAMPLING

Eight arthropod orders comprised 95% of total arthropod captures from foliage clipping. These orders included 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 total pitfall captured arthropods: Diptera (24%), Hymenoptera (23%), Araneae (22%), Coleoptera (15%), Orthoptera (6%), Hemiptera (1%), Homoptera (1%), and Lepidoptera (1%).

ARTHROPOD USE VS. AVAILABILITY

Using Morrison's (1982) rankings of selection and avoidance, Coleopterans, Hemipterans, and Lepidopterans tended to be selected by all birds in all seasons, while Aranids and Hymenopterans tended to be avoided by all birds in all seasons (TABLE 2). Dipterans were well represented by pitfall traps but poorly represented by foliage clippings, and were avoided by ground-gleaning birds and highly selected by foliage-gleaning birds. Similarly, Lepidopterans were well represented by foliage clippings and poorly represented by pitfall trapping, leading to a seemingly strong selection by ground gleaners and either no selection or slight selection by foliage-gleaners. These data do not distinguish between larval and adult Lepidopterans, although most of the crop-flushed Lepidopterans represented larval individuals. Overall, the most abundant foliage-dwelling arthropods were Aranids, Lepidopterans, Coleopterans, and Hemipterans, and of these, foliage-gleaning birds selected Coleopterans above all others during all seasons (FIGURE 2). The most abundant ground-dwelling arthropods were Aranids, Coleopterans, Hemipterans, and Lepidopterans, and of these, ground-gleaning birds selected Coleopterans above all others during all seasons except the post-breeding season, when Coleopteran consumption was approximately equivalent to that of Lepidopteran consumption (FIGURE 3).

DISCUSSION

Each bird species and group studied consumed three arthropod orders in the highest overall proportions: Araneae, Coleoptera, and Lepidoptera. By comparing usage vs. availability of arthropod orders, however, both the foliage-gleaning and ground-gleaning birds we studied consistently consumed Coleopteran prey items in greater proportion than their relative availability during all seasons. Other direct observation studies of bird diets have also shown strong avian selection for 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). We also found proportionally greater consumption of Hemipteran prey items than relative availability during all seasons and for all bird groups analyzed. Hemipterans, however, represented a low proportion of total bird diet composition, and indeed, Hemipterans have not previously been identified as a selected food resource. Both foliage-gleaning and ground-gleaning birds in our study consistently consumed Aranid and Hymenopteran prey items in the lowest proportions relative to availability during all seasons, though both orders are reportedly common avian food items elsewhere (Robinson and Homes 1982, Poulin and Lefebvre 1996, Yard et al. 2004), and Aranids represented a high overall proportion of total bird diet composition in our study as well. Avian consumption or avoidance of other arthropod orders (Dipterans, Homopterans, Lepidopterans, and Orthopterans) during our study was less consistent, varying considerably between bird foraging guild and season. Other researchers have reported Lepidopterans as an important avian food resource for insectivorous birds (Robinson and Holmes 1982, Wheelwright 1986, McMartin et al. 2002, Yard et al. 2004), and our data suggests that Lepidopterans comprise a high percentage of total bird diet as well. We found the highest proportion of Lepidopterans, relative to availability, only in ground-gleaning birds. Homopterans were reported as a selected food item by Robinson and Holmes (1982) and Deloria-Sheffield et al. (2001) but Raley and Anderson (1990) found them to be avoided. In our study, the proportion of Homopterans in crop-flushes from ground-gleaning birds was higher than the percent available, but similar to the percent available for foliage-gleaning birds.

For individual species, our findings were generally consistent with previous reports, but some exceptions existed. For each individual species examined, Coleopterans, Aranids, and Lepidopterans comprised the highest percentages of the total diet. In our study, relative to availability, crop-flushes of both Hooded Warblers and Kentucky Warblers contained higher proportions of Coleopterans, Dipterans, and Hemipterans during all seasons, and lower proportions of Aranids, Hymenopterans, and Orthopterans. Evans and Stutchbury (1994) similarly reported that the main diet of Hooded Warblers included Coleopterans and Dipterans, but in contrast to our findings, they also reported that Aranids, Lepidopterans, and Orthopterans were important components of the diet. Likewise, our findings for

Kentucky Warblers contrast those of McDonald (1998), who reported that the primary diet this species consisted of Lepidopterans and Aranids. We found White-eyed Vireos consumed relatively higher proportions of Coleopterans, Dipterans, and Hemipterans during all seasons, but lower proportions of Aranids and Hymenopterans. Hopp et al. (1995) describe the White-eyed Vireo diet to consist primarily of Lepidopterans, Coleopterans, Dipterans, and Aranids. Finally, we found Carolina Wrens to consistently consume higher proportions of Coleopterans, Hemipterans, Homopterans, and Lepidopterans. Haggerty and Morton (1995) describe the diet of Carolina Wrens as consisting primarily of Lepidopterans, Hemipterans, and Coleopterans. Despite these inconsistencies in avian diet preferences, arthropod orders that are consumed in lower proportions than their relative availability may still be an important component of avian diets (Raley and Anderson 1990). Our sampling suggests that each species selects some arthropod groups before others, but also consumes a variety of other prey items as well, including several groups used less than their proportional availability.

Direct observations of avian diets, such as ours, are complicated by the highly variable digestion rates of different arthropod orders (Mook and Marshall 1965, Swanson and Bartonek 1970, Rosenberg and Cooper 1990). Prey item digestibility depends on prey size, prey body type (soft or hard), and the overall condition of the bird (Custer and Pitelka 1975). Caterpillars and other soft-bodied insect larvae are more easily digested than arthropods with hard body-parts and may, therefore, be underrepresented in bird diet samples (Wheelwright 1986). The time between prey ingestion and prey-item sampling must also be considered. Birds caught in nets continue to digest prey (Rosenberg and Cooper 1990), while in the nets and while being transported to the banding station (Mook and Marshall 1965, Rosenberg and Cooper 1990). In one study, invertebrate material in birds' stomachs became uncountable and unrecognizable after just 40 minutes, with soft-bodied (Aranid) arthropods disappearing faster than hard-bodied (Coleopteran) arthropods (Custer and Pitelka 1975). In another study, the average passage time from consumption to excretion was just 1.5 h (Stevenson 1933). Because of the lag between capture time and crop-flushing and the highly fragmented nature of the arthropods we found during crop-flushing, it seems likely that many of the prey items ingested were already moderately digested and may have moved further down the digestive tract before crop-flushing occurred. Thus, proportions of soft-bodied arthropods, such as Aranids and Lepidopterans, are probably underrepresented in our analyses, and may be more important in bird diets than indicated by our results. Additionally, when sampling occurs after prey items are partially digested, correct identification of highly fragmented arthropods can become very difficult (Rosenberg and Cooper 1990). These caveats notwithstanding, because we regularly identified both hard-bodied and soft-bodied prey items, we believe that our data represent the wide variety of prey items consumed by birds during different seasons.

Coleopterans comprised the highest overall proportions of all bird diet samples collected. Relative to proportional availability, the two most heavily selected arthropod orders overall, the Coleopterans and the Hemipterans, were generally more abundant in the forest than in gaps during all seasons (Bowen 2004). Forest habitat, therefore, appears to provide necessary arthropod prey items and valuable foraging opportunities. We detected many bird species and foraging groups, however, more commonly in regenerating canopy gaps (Bowen 2004). Increased foliage density in gaps was not accounted for when calculating overall arthropod availability and for foliage-dwelling arthropods in particular, prey items per g of foliage may be greater in gaps than our data suggests. Forest managers and those wishing to manage habitat for breeding and migratory birds should provide a forested landscape capable of supporting a variety of bird species but also a variety of arthropod prey items. A large mature bottomland forest perforated by small-scale canopy gaps may provide sufficient habitat and arthropod prey resources for foliage-gleaning and ground-gleaning birds across multiple seasons. Regenerating canopy gaps provide dense understory vegetation that may also offer valuable foraging and resting areas safe from predators.

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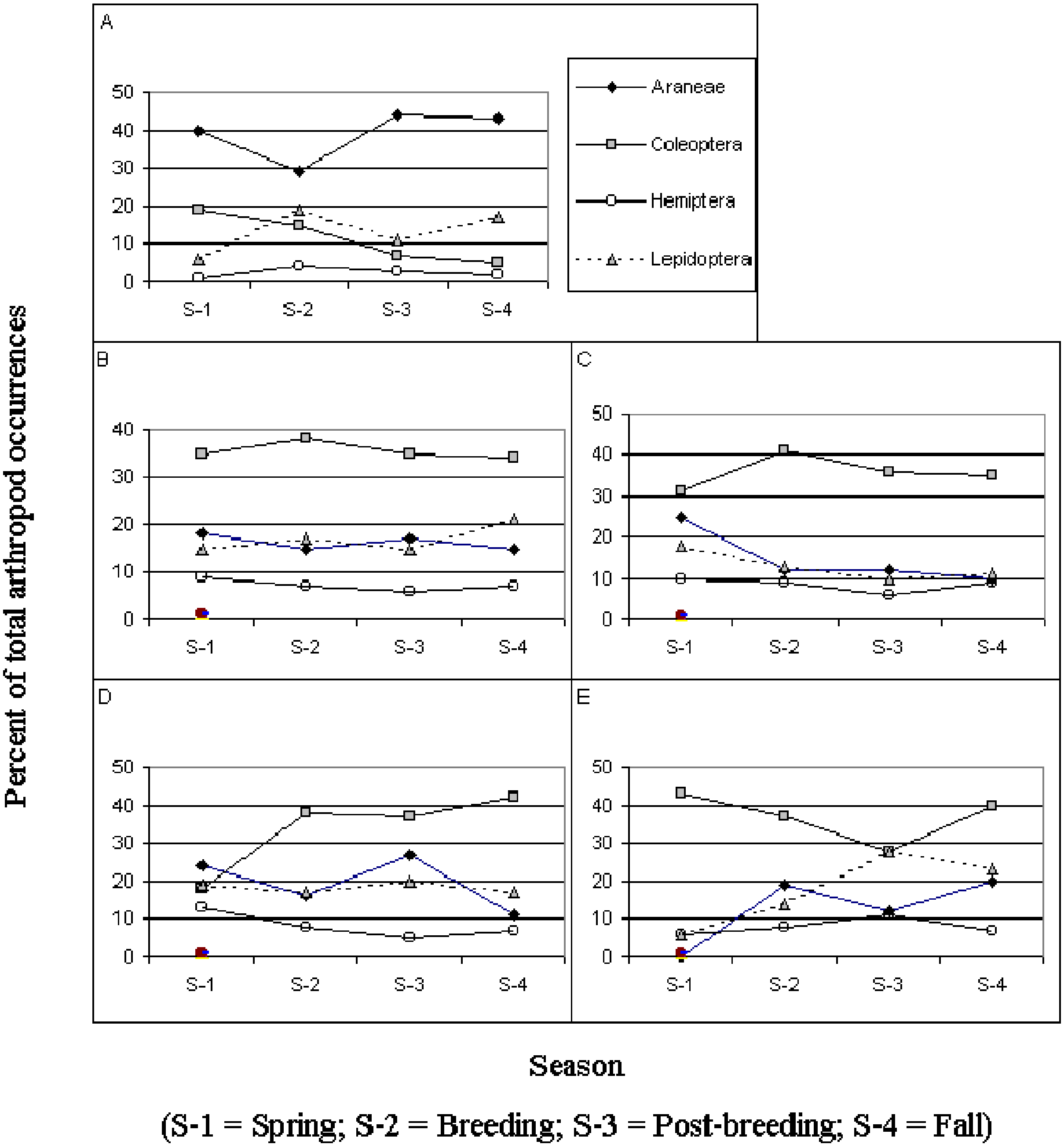
FIGURE 1. Photograph illustrating high degree of fragmentation of prey items from crop-flushing samples taken from insectivorous birds in a bottomland forest in South Carolina (2001-2002). Top row, L-R: Coleoptera elytra, Coleoptera elytra, Coleoptera leg. Bottom row, L-R: Coleoptera mandible, Coleoptera prothorax, Lepidoptera mandible, Coleoptera mandible.

FIGURE 2. Percent availability and consumption of four most frequently encountered (by crop-flushing) arthropod orders: comparison between foliage-gleaning birds and foliage-clipping arthropods in a bottomland forest in South Carolina (2001-2002). Percentages represent the percent of total arthropod sample containing each arthropod order. A = Foliage-clipping arthropods; B = Foliage-gleaning birds; C = Hooded Warbler; D = Kentucky Warbler; E = White-eyed Vireo


Percent of total arthropod occurrences
A
Araneae
Coleoptera
Hemiptera
Lepidoptera
B
C
D
E
0
10
20
30
40
50
S-1
S-2
S-3
S-4
Season
(S-1 = Spring; S-2 = Breeding; S-3 = Post-breeding; S-4 = Fall)

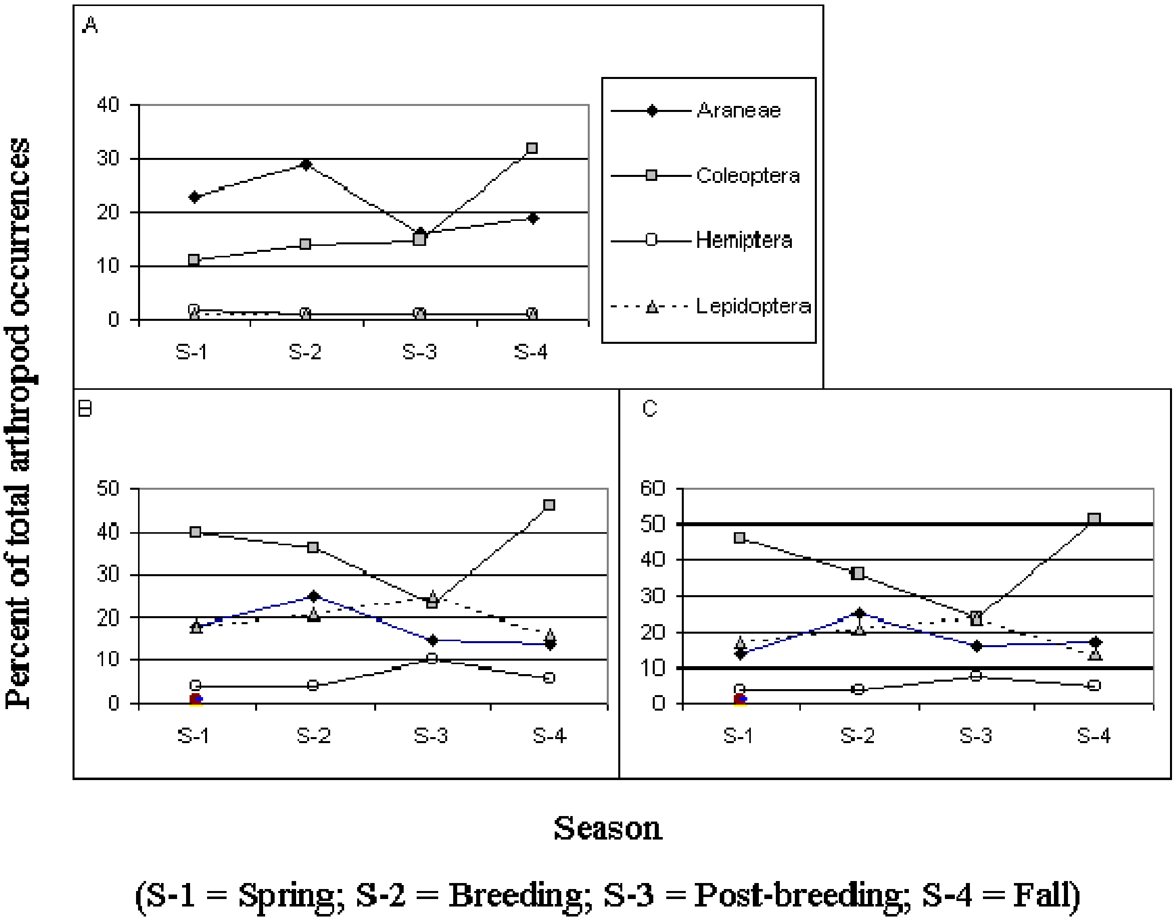


FIGURE 3. Percent availability and consumption of four most frequently encountered (by crop-flushing) arthropod orders: comparison between ground-gleaning birds and pitfall trapping for arthropods in a bottomland forest in South Carolina (2001-2002). Percentages represent the percent of total arthropod sample containing each arthropod order. A = Pitfall-trapped arthropods; B = Ground-gleaning birds; C = Carolina Wren

TABLE 1. Seasonal number of birds sampled using a warm water crop-flush in a bottomland forest in South Carolina, 2001-2002.

Common Name	Scientific Name	Guild[a]	S-1[b]	S-2	S-3	S-4
Black-throated Blue Warbler	*Dendroica caerulescens*	FG	0	0	0	11
Carolina Wren	*Thryothorus ludovicianus*	GG	9	9	15	15
Common Yellowthroat	*Geothlypis trichas*	FG	1	0	0	5
Eastern Tufted Titmouse	*Baeolophus bicolor*	FG	0	1	0	0
Grey-cheeked Thrush	*Catharus minimus*	GG	0	0	0	1
Hooded Warbler	*Wilsonia citrina*	FG	20	21	20	22
Kentucky Warbler	*Oporornis formosus*	FG	6	10	13	3
Ovenbird	*Seiurus aurocapillus*	GG	1	0	2	6
Red-eyed Vireo	*Vireo olivaceus*	FG	1	2	3	0
Swainson's Thrush	*Catharus ustulatus*	GG	0	0	0	3
Swainson's Warbler	*Limnothlypis swainsonii*	GG	1	0	0	0
Veery	*Catharus fuscescens*	GG	0	0	0	2
White-eyed Vireo	*Vireo griseus*	FG	6	14	9	17
Worm-eating Warbler	*Helmitheros vermivorus*	FG	1	0	0	4
Yellow-breasted Chat	*Icteria virens*	FG	0	0	1	0

[a] FG = Foliage-gleaner; GG = Ground-gleaner

[b] Sample size (*n*) per season: S-1 = Spring migration; S-2 = Breeding season; S-3 = Post-breeding season; S-4 = Fall migration

TABLE 2. Seasonal arthropod orders consumed by birds in a bottomland forest in South Carolina, 2001-2002.

Bird (arthropod sample)	Season	*n*	Araneae[a]	Coleoptera	Diptera	Hemiptera	Homoptera	Hymenoptera	Lepidoptera	Orthoptera
Carolina Wren	1	9	-	++	- - -	+	+++	- - -	+++	++
(pitfall traps)	2	9	0	++	- - -	++	+++	- - -	+++	0
	3	15	0	+	-	+++	+++	- - -	+++	0
	4	15	0	+	- - -	+++	+++	- -	+++	-
	all	48	0	++	- - -	++	+++	- - -	+++	0
Hooded Warbler	1	20	-	+	++	+++	0	- - -	++	++
(foliage clipping)	2	21	- -	++	++	+	0	-	-	-
	3	20	- -	++	++	+	0	+	0	- - -
	4	22	- -	++	++	++	++	- -	-	- -
	all	83	- -	++	++	++	0	-	0	-
Kentucky Warbler	1	6	-	0	++	+++	+	-	++	- - -
(foliage clipping)	2	10	-	++	++	+	-	- -	0	-
	3	13	-	++	- - -	+	+	- - -	+	- - -
	4	3	- -	+++	++	++	- - -	- -	0	- - -
	all	32	-	++	++	++	0	- -	+	- -

White-eyed Vireo	1	6	- - -	++	+++	++	0	- -	0	+++
(foliage clipping)	2	14	-	++	+	0	-	- - -	-	0
	3	9	- -	++	++	++	+	- - -	++	-
	4	17	- -	+++	- - -	++	0	- - -	+	-
	all	46	- -	++	++	++	0	- - -	+	0
Foliage gleaners	1	35	- -	+	++	+++	0	- -	++	++
(foliage clipping)	2	48	- -	++	++	+	-	- -	0	0
	3	46	- -	++	++	+	0	0	+	- -
	4	62	- -	++	+	++	+	- -	0	0
	all	191	- -	++	++	++	0	- -	+	-
Ground gleaners	1	11	-	++	- - -	++	+++	- - -	+++	+
(pitfall traps)	2	9	0	++	- - -	++	+++	- - -	+++	0
	3	17	0	+	-	+++	+++	- - -	+++	0
	4	28	-	+	- -	+++	+++	- -	+++	0
	all	65	-	++	- -	++	+++	- - -	+++	0

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[a] Arthropod order proportional use compared with proportional availability, referring to D_{hb}. + + + = use much greater than availability, + + = use moderately greater than availability, + = use slightly greater than availability, 0 = use same as

availability, - = use slightly lower than availability, - - = use moderately lower than availability, and - - - = use much lower than availability.