ARTHROPOD ABUNDANCE AND SEASONAL BIRD USE OF BOTTOMLAND FOREST HARVEST GAPS

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ABSTRACT.—We investigated the influence of arthropod abundance and vegetation structure on shifts in avian use of canopy gap, gap edge, and surrounding forest understory in a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. We compared captures of foliage-gleaning birds among locations during four periods (spring migration, breeding, post-breeding, and fall migration). Foliage arthropod densities were greatest in the forest understory in all four seasons, but understory vegetation density was greatest in gaps. Foliage-gleaning bird abundance was positively associated with foliage-dwelling arthropods during the breeding ($F = 18.5$, $P < 0.001$) and post-breeding periods ($F = 9.4$, $P = 0.004$), and negatively associated with foliage-dwelling arthropods during fall migration ($F = 5.4$, $P = 0.03$). Relationships between birds and arthropods were inconsistent, but the arthropod prey base seemed to be least important during migratory periods. Conversely, bird captures were positively correlated with understory vegetation density during all four periods ($P < 0.001$). Our study suggests high bird abundance associated with canopy gaps during the non-breeding period resulted less from high arthropod food resource availability than from complex understory and midstory vegetation structure. *Received 25 January 2011. Accepted 8 August 2011.*

Many bird species, including those of early-successional habitats and those of small tree-fall gaps within mature forest, select disturbed habitats during some portion of the year (Hunter et al. 2001). Several studies have documented greater bird abundance in forest canopy gaps created by natural treefalls (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986) or group-selection harvest (Kilgo et al. 1999, Moorman and Guynn 2001) than in the mature forest surrounding gaps. Some mature-forest breeders 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; Vitz and Rodewald 2006). Birds use a variety of forested habitats during migratory periods (Petit 2000, Rodewald and Brittingham 2002), but mature-forest edges and early-succession habitats may experience relatively greater use (Rodewald and Brittingham 2004). Reasons for greater use of disturbed habitats by birds during certain periods remain speculative, but abundant food and protection from predators have been proposed (Marshall et al. 2003).

Arthropod populations also are influenced by season and habitat type (Johnson and Sherry 2001, Greenberg and Forrest 2003) as well as canopy gap size (Shure and Phillips 1991). It should be advantageous for birds to choose sites with the greatest resource availability (Martin and Karr 1986), and greater invertebrate biomass has been positively correlated to bird abundance (Blake and Hoppes 1986, Holmes et al. 1986), daily nest survival rates, growth rates of nestlings (Duguay et al. 2000), and timing of warbler migration (Graber and Graber 1983). Studies of experimental prey removal have not linked decreased prey abundance with negative consequences for the local bird community (Nagy and Smith 1997, Marshall et al. 2002, Champlin et al. 2009).

Bowen et al. (2007) documented seasonal shifts in relative use by birds of canopy gap and forest habitat. They speculated these shifts may be driven by seasonal changes in arthropod abundance in gaps. Previous studies have not investigated seasonal shifts in avian habitat use as related to resource availability over multiple periods.

Our objectives were to: (1) investigate whether bird use of forest gaps was associated with arthropod abundance or vegetation structure, and (2) ascertain if shifts in relative use of gap and forest understory were related to spatial and temporal variation in arthropod abundance. We predicted positive relationships between avian habitat use and arthropod abundance (i.e., relative bird use of gap vs. forest understory will shift based on changes in local arthropod abundance) from spring migration through fall migration.

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METHODS

Study Area.—We sampled foliage-gleaning birds and foliage-dwelling arthropods within forest canopy gaps, gap edges, and mature bottomland forest understory during 2001 and 2002 at the Savannah River Site, a 78,000-ha National Environmental Research Park owned by the U.S. Department of Energy. The site was a mature stand of bottomland hardwoods, 120 ha in size, in Barnwell County in the Upper Coastal Plain Region of South Carolina. Birds, arthropods, and vegetation structure were surveyed in 12 group-selection gaps harvested in December 1994 and in the mature forest understory adjacent to gaps. Minimum spacing between gap centers was 100 m, and the mean distance between a gap's edge and the edge of its nearest neighbor was 102.7 m (range = 44–230 m). 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. Previous research within this size range in these gaps 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 patchily developed, consisting primarily of red mulberry (*Morus rubra*), ironwood (*Carpinus carolinianus*), and American holly (*Ilex opaca*). The understory contained patches of dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). Vegetation in the gaps varied from 1 to 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.

Sampling Design.—We surveyed birds and arthropods during four avian activity periods in 2001 and 2002: spring migration (25 Mar through 15 May), breeding (16 May through 30 Jun), post-breeding (1 Jul through 31 Aug), and fall migration (1 Sep through 18 Oct). These beginning and ending dates are estimates of biologically meaningful periods, and each overlaps extensively with the other. Many individuals initiated breeding on our study area before 16 May, but transient species that bred to the north continued to migrate through South Carolina until mid-May. Similarly, some individuals migrated from or through our study area before 1 September, but most fall migration occurred after 1 September. We established a sampling transect radiating southward from the center of each gap to investigate bird-arthropod relationships within each period with three bird and arthropod sampling stations along each transect: one in the gap center, one at the southern edge of the gap, and one 50 m into the forest.

Vegetation Measurements.—We measured vegetation structure during June 2001 and 2002 along 10-m transects on each side of and parallel to all mist-net stations, 1.5 m from each net. We measured vertical distribution of vegetation modified from Karr (1971) at 1-m intervals along each 10-m transect (total 20 points). We recorded the number of times vegetation touched a 2-m pole or the height intervals directly above the pole at 12 height intervals (0–0.25, 0.26–0.50, 0.51–0.75, 0.76–1, 1.1–1.5, 1.6–2, 2.1–3, 3.1–5, 5.1–10, 11–20, 21–25, and 26–30 m). Touches >2 m high were estimated visually. The percent cover for each height interval was calculated from the percentage of the 20 sampling points with vegetation touches in that interval. We calculated the mean number of pole touches for height intervals ≤3 m as an index of foliage density for understory vegetation.

Arthropod Collection.—We sampled foliage-dwelling arthropods at each station during each avian activity period in 2001 and 2002. 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 [*Q. michauxii*], overcup oak [*Q. lyrata*], Durand oak [*Q. durandii*]), (2) lobed red oaks (cherrybark oak), (3) unlobed red oaks (water oak [*Q. nigra*], laurel oak, willow oak [*Q. phellos*]), (4) sweetgum, and (5) switchcane. This suite of species was selected to represent dominant members of the understory and overstory, as well as species important as avian foraging substrates (Buffington et al. 2000, Kilgo 2005). 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 2.54–15.24 cm in length and usually came from the end of a branch where most leaves

were clustered on the target plant species groups (Cooper and Whitmore 1990). We collected foliage from ground level to about 2.5 m. We placed clippings immediately in plastic bags to avoid evasive movements of arthropods, but highly mobile arthropods (a group of less interest for this study) were not as effectively sampled. We did not sample above 2.5 m because we considered it appropriate to sample arthropods only in the same stratum in which we sampled birds (i.e., 3-m mist nets). Samples were placed in a freezer for 24 hrs to kill all arthropods. We then shook the foliage to collect the arthropods, placed them in alcohol, and identified them to Order. Foliage was oven-dried for 48 hrs at 40°C and weighed.

Mist Netting.—We placed a single mist net (12 m long × 3 m tall with 30-mm mesh) at each of the three sampling stations at each of the 12 study gaps. Netting was conducted once each week at each station during the spring migration, post-breeding, and fall migration periods, rotating between stations on a regular weekly schedule. Nets were operated once every 2 weeks during the breeding period, because birds remain fairly stationary during this period. Nets were opened at first light and operated for 4–6 hrs, depending on daily weather conditions. Netting was not conducted when wind exceeded 16 km/hr or during steady rainfall. We banded captured birds with a U.S. Geological Survey aluminum leg band.

Statistical Analyses.—We assigned birds (Table 1) to the foliage-gleaning guild following Ehrlich et al. (1988) and Hamel (1992). Birds considered winter residents, present only from late fall through early spring, were not included in analyses.

We used a linear mixed model (PROC MIXED) (SAS Institute 2000) to conduct analysis of variance (ANOVA) with covariates and interactions to analyze the effects of net location (gap, edge, forest understory), period, and arthropod abundance on bird captures. We used mean captures of foliage-gleaning birds/100 net hrs as the dependent variable. We considered net location and period as fixed effects with net location as a split plot factor and period as the repeated measure. Arthropod abundance was a continuous covariate. We included all two-way interactions. We used a linear mixed model to examine the relationship between bird captures and understory (0–3 m) vegetation density with

TABLE 1. Foliage-gleaning bird species captured in mist nets at least once during 2001–2002 in South Carolina, USA.

Species	Scientific name
Yellow-billed Cuckoo	*Coccyzus americanus*
Ruby-throated Hummingbird	*Archilochus colubris*
White-eyed Vireo	*Vireo griseus*
Blue-headed Vireo	*V. solitarius*
Red-eyed Vireo	*V. olivaceus*
Carolina Chickadee	*Poecile carolinensis*
Tufted Titmouse	*Baeolophus bicolor*
Blue-gray Gnatcatcher	*Polioptila caerulea*
Gray Catbird	*Dumetella carolinensis*
Worm-eating Warbler	*Helmitheros vermivorum*
Golden-winged Warbler	*Vermivora chrysoptera*
Blue-winged Warbler	*V. cyanoptera*
Kentucky Warbler	*Geothlypis formosa*
Common Yellowthroat	*G. trichas*
Hooded Warbler	*Setophaga citrina*
American Redstart	*S. ruticilla*
Northern Parula	*S. americana*
Magnolia Warbler	*S. magnolia*
Chestnut-sided Warbler	*S. pensylvanica*
Black-throated Blue Warbler	*S. caerulescens*
Pine Warbler	*S. pinus*
Prairie Warbler	*S. discolor*
Yellow-breasted Chat	*Icteria virens*
Summer Tanager	*Piranga rubra*
Northern Cardinal	*Cardinalis cardinalis*

vegetation as the covariate. Vegetation was only recorded once each year, so this model did not include a repeated measure. Year and gap size were not significant ($P > 0.05$) in any models, and these variables were not included in final models. Arthropod captures were standardized by number of arthropods/100 g of dry foliage. We modeled bird abundance with abundance of Lepidoptera because previous studies have shown Lepidoptera to be a primary avian food source (Holmes et al. 1986, McMartin et al. 2002).

RESULTS

The greatest understory vegetation density occurred in gaps (Fig. 1). Gaps had dense understory vegetation with no canopy, whereas forest had relatively open understory and midstory and well-developed canopy.

We captured arthropods representing 21 Orders during 2001 and 2002. Total arthropod density (number of arthropods/100 g of foliage) was lower during spring migration than in the other three periods and greater in the forest understory than in gaps and at gap edges (Table 2). Total arthropod
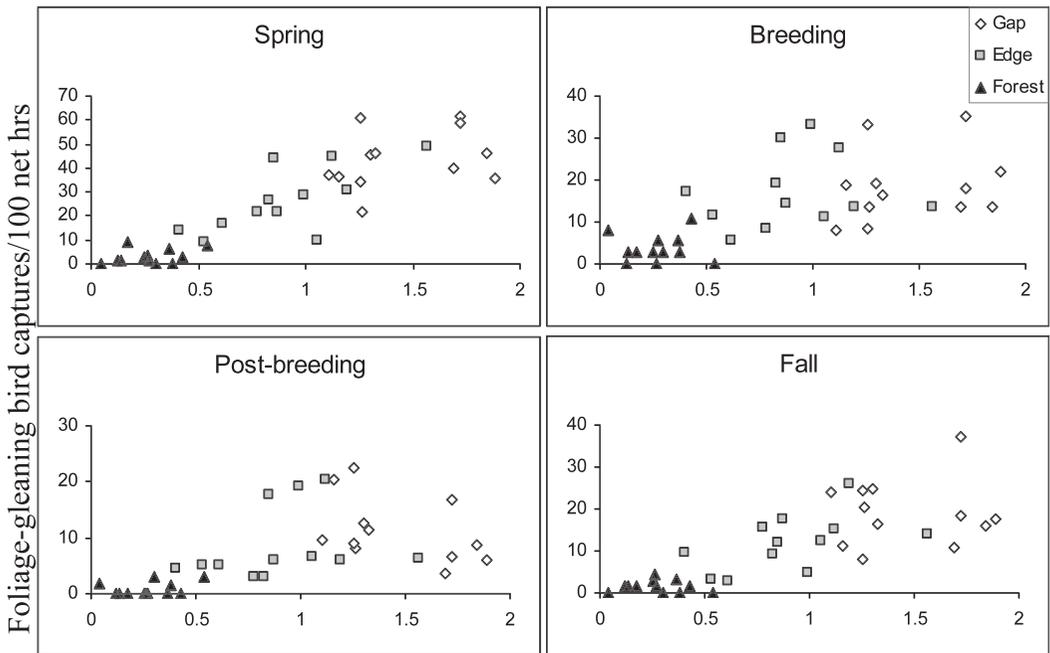
FIG. 1.   Seasonal foliage-gleaning bird captures plotted against mean understory foliage density (mean vegetation pole touches per understory height interval) for each net location in a bottomland forest during 2001–2002 in South Carolina, USA.

density was greater at gap edges than in gaps except during the breeding season when densities were greater in gaps (Table 2). The five most frequently encountered arthropod Orders, representing at least 150 individuals, were Araneae, Coleoptera, Homoptera, Hymenoptera, and Lepidoptera. Aranids, hymenopterans, and lepidopterans followed the same general pattern as all arthropods combined, but coleopteran density decreased from spring to fall migration. Lepidoptera density was highest in the forest during spring migration, breeding, and post-breeding periods, but densities were similar among sampling locations during fall migration.

Bird and arthropod relationships were inconsistent across the four seasons (Table 3). Foliage-gleaning bird abundance was positively associated with foliage-dwelling arthropods during the breeding ($F = 18.5$, $P < 0.001$) and post-breeding periods ($F = 9.4$, $P = 0.004$), and negatively associated with foliage-dwelling arthropods during fall migration ($F = 5.4$, $P = 0.03$) (Table 3). There was no relationship between foliage-gleaning bird captures and foliage-dwelling lepidopterans ($F =$

1.2, $P = 0.28$) (Table 3). Foliage-gleaning birds were positively associated with understory vegetation density during all periods (Table 4; Fig. 1).

DISCUSSION

Seasonal shifts in relative bird use of gaps and forest understory in bottomland hardwood forests were not driven by changes in arthropod availability. Bowen et al. (2007) documented a seasonal shift in habitat use for several bird groups at our site with relative bird use of mature forest habitat greatest during the breeding period; they speculated these shifts may correspond to seasonal changes in arthropod abundance among habitats. However, arthropod abundance remained greater in forest understory than in gaps in all seasons, and we did not document an increase in total arthropods or any arthropod Order in the forest during the breeding season when relative bird use of forest understory was greatest. The highest arthropod densities in gaps occurred during the breeding season, the period when birds least used gaps. Foliage-gleaning birds on our study site, based on crop flushes, consumed

TABLE 2. Mean ± SE number of arthropods/100 g of dry foliage for most abundant arthropod Orders by period and net location in a bottomland forest during 2001–2002, South Carolina, USA.

	Spring			Breeding			Post-breeding			Fall		
	Gap	Edge	For	Gap	Edge	For	Gap	Edge	For	Gap	Edge	For
All arthropods	6.7 ± 1.3	9.3 ± 1.3	12.9 ± 1.3	18.1 ± 2.1	14.0 ± 2.1	22.3 ± 2.1	9.6 ± 2.9	13.1 ± 2.9	20.0 ± 2.9	12.1 ± 2.3	17.6 ± 2.3	23.5 ± 2.3
Araneae	1.7 ± 0.6	2.4 ± 0.6	2.8 ± 0.6	5.2 ± 0.6	3.5 ± 0.6	6.8 ± 0.6	5.5 ± 0.8	5.5 ± 0.8	8.2 ± 0.8	7.1 ± 0.8	6.7 ± 0.8	9.1 ± 0.8
Coleoptera	2.0 ± 0.8	2.7 ± 0.8	4.4 ± 0.8	1.7 ± 0.5	1.9 ± 0.5	3.9 ± 0.5	0.9 ± 0.2	1.3 ± 0.2	1.3 ± 0.2	0.7 ± 0.3	1.0 ± 0.3	2.1 ± 0.3
Homoptera	0.3 ± 0.2	0.3 ± 0.2	0.5 ± 0.2	2.5 ± 0.4	0.8 ± 0.4	2.4 ± 0.4	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.6 ± 0.2	0.4 ± 0.2	0.5 ± 0.2
Hymenoptera	0.8 ± 0.6	2.3 ± 0.6	3.0 ± 0.6	3.1 ± 1.4	3.7 ± 1.4	3.4 ± 1.4	0.0 ± 0.9	2.0 ± 0.9	2.1 ± 0.9	1.2 ± 1.3	4.9 ± 1.3	3.2 ± 1.3
Lepidoptera	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.9 ± 0.4	1.5 ± 0.4	2.3 ± 0.4	2.3 ± 1.2	3.2 ± 1.2	5.3 ± 1.2	2.3 ± 0.9	2.5 ± 0.9	2.3 ± 0.9
Orthoptera	0.0 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	2.0 ± 0.4	1.8 ± 0.4	2.0 ± 0.4	1.0 ± 0.3	1.1 ± 0.3	1.2 ± 0.3	0.0 ± 0.1	0.2 ± 0.1	0.3 ± 0.1

TABLE 3. Relationship between foliage-gleaning bird captures (mist-net captures/100 net hrs) and foliage-dwelling arthropods in a bottomland hardwood forest on the Savannah River Site, South Carolina, 2001–2002. Positive or negative relationships are indicated in parentheses.

Independent variables[a]	F	df	P
All arthropods (−)	0.5	1/33	0.49
All arthropods*period (+)	5.4	3/33	0.004
Spring (−)	1.2	33	0.29
Breeding (+)	18.5	33	<0.001
Post-breeding (+)	9.4	33	0.004
Fall (−)	5.4	33	0.03
Lepidoptera (−)	1.2	1/33	0.28
Arthropod*period (−)	1.6	3/33	0.21

[a] The arthropod variables were tested against bird abundance in a model which also included period and net location as fixed effects to control for their influence. Only the results for arthropod variables and their interactions with period are provided.

Coleoptera in proportions greater than expected based on availability during all seasons (Moorman et al. 2007). Yet, foliage-dwelling Coleoptera were more abundant in the forest understory than in the gaps during all seasons, suggesting birds were not tracking important arthropod food resources.

We documented relationships between birds and arthropods during the breeding, post-breeding, and fall migration periods. However, the observed patterns may be artifacts of different and independent habitat associations of birds and arthropods. A positive correlation occurred when habitat associations of birds and arthropods were consistent with each other and, when inconsistent, there was a negative correlation. Conversely, the positive relationships between foliage-gleaning birds and foliage-dwelling arthropods during the breeding and post-breeding periods may indicate arthropod food resources are more important during these

TABLE 4. Relationship between foliage-gleaning bird captures (mist-net captures/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.

Period	F	P
Spring (+)	131.4	<0.001
Breeding (+)	22.6	<0.001
Post-breeding (+)	17.1	<0.001
Fall (+)	47.1	<0.001

periods than during migration, when cover may be more critical as birds move through unfamiliar habitats and are more vulnerable to predators (Petit 2000).

Arthropod biomass varies temporally and spatially, but arthropod numbers typically are greater in mature forest than in recently disturbed areas (Duguay et al. 2000, Greenberg and Forrest 2003, Ulyshen 2005). Blake and Hoppes (1986) found certain types of insects to be more abundant in canopy gaps during migratory periods, but Greenberg and Forrest (2003) reported invertebrate biomass to be greater in mature forest than in canopy gaps. Duguay et al. (2000) reported mean total invertebrate biomass was greater in unharvested stands than clearcut stands late in the breeding period when most birds had young in the nest. The interior of young (1 yr post-harvest) gaps may have greater arthropod abundance than adjacent mature forest, but the centers of old (7 yrs post-harvest) gaps, like those in our study, contained similar or fewer numbers of some arthropod Orders than adjacent mature forest (Ulyshen et al. 2004, 2005, 2006).

Previous studies suggested birds are 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). Duguay et al. (2000) documented 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) showed warbler migration coincided with the peak spring outbreak of lepidopteran larvae, and Holmes et al. (1986) reported bird abundance often is related to outbreaks of lepidopteran larvae, a primary component of the warbler diet. Supplementally-fed female Black-throated Blue Warblers (scientific names of birds are in Table 1) in New Hampshire produced more second broods and spent less time foraging away from the nest than did controls (Nagy and Holmes 2005).

Several studies, however, have failed to detect positive relationships between birds and arthropods. Experimental reductions of arthropods in gaps similar to those in our study did not affect avian use of the gaps, even though foraging efficiency of birds using the gaps was reduced (Champlin et al. 2009). Falcone and DeWald (2010) detected no difference in bird densities between sites treated with Imidacloprid to kill hemlock wooly adelgid (*Adelges tsugae*) and untreated sites, even though larval Lepidoptera were reduced in treated sites. The removal of lepidopteran larvae in other studies had little effect on avian site fidelity or reproductive success (Nagy and Smith 1997, Marshall et al. 2002). Karr and Brawn (1990) reported bird captures in central Panama were not consistently correlated with arthropod abundance at capture locations; they concluded habitat associations of birds were not solely food-resource mediated. Vitz and Rodewald (2006) documented no relationships between the distribution of captures of forest-breeding songbirds in clearcuts and microhabitat characteristics, including arthropod abundance and vegetation structure. Kilgo (2005) examined the relationship between Hooded Warbler foraging success and arthropod abundance at our study site and concluded arthropods may not be a limiting resource for that species during the breeding period (i.e., they are capable of finding sufficient food resources across the area, even in areas of relatively low arthropod abundance). However, others have suggested birds can suppress arthropod prey so that measurable arthropod abundance represents what birds leave rather than to what they respond (Marquis and Whelan 1994, Strong et al. 2000). Increased bird activity in forest surrounding gaps during the breeding season in our study should have suppressed arthropod populations. Yet, numbers of all arthropods and Coleoptera remained high in forest habitats during the breeding period when bird numbers were greatest. The lack of consistent relationships in our data indicate Kilgo's (2005) conclusion may be more generally true for other bird species in southeastern bottomland hardwoods throughout the growing season.

We likely captured more birds in gap than forest understory because of differences in habitat structure (Remsen and Good 1996). Birds using low vegetation within the gaps were more available for sampling with a 3-m tall net than birds in the mature forest. However, count data from a concurrent study of the same gaps corroborated our mist-net data (Bowen et al. 2007). These counts sampled both the understory and forest canopy and also detected more birds using gap habitat than mature-forest habitat (Bowen et al. 2007). Our focus was more on shifts in bird use relative to gaps than on differences in bird abundance between gap and forest. Capture probabilities likely were higher in

gaps than in adjacent forest understory, but relative capture probabilities likely remained constant across seasons. Different capture probabilities among net locations should not have influenced our ability to detect seasonal shifts in relative bird use of the lowest stratum (<3 m) of vegetation in gaps and forest. Nets sampled only vegetation near the ground, and we could not address shifts in bird use of the forest canopy.

Birds may have used gaps in response to available fruits. Gap interiors contained early-successional fruiting species (e.g., winged sumac [*Rhus copallina*] and blackberry), while other fruiting species such as poison ivy (*Toxicodendron radicans*) and hawthorn (*Crataegus* spp.) were common at the immediate gap edge (LTB, pers. obs.). We observed omnivorous birds eating fruits in gaps, including American beautyberry (*Callicarpa americana*), flowering dogwood (*Cornus florida*), grape (*Vitis* spp.), hawthorn, poison ivy, and winged sumac (LTB, pers. obs.). Fruit typically is most abundant on the Savannah River Site from late summer through early fall (McCarty et al. 2002). Some bird species such as Summer Tanager and Gray Catbird are known to shift to diets higher in fruit during fall migration. 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 (Bowen et al. 2007). Vegetation matter, including fruit, comprised <5% of the crop contents of several of the birds most commonly captured during all four periods (Moorman et al. 2007). Fruit production within our canopy gaps was relatively low and highly seasonal with no fruit available during spring, one of the periods of highest bird use (Bowen et al. 2007).

Data from our study suggests bird use of gaps may be more closely related to vegetation structure, important for various aspects of their life history (e.g., cover for fledglings, foraging, and molting), than to arthropod abundance. We consistently detected more birds in the gap and edge habitats during all periods (Bowen et al. 2007), and the understory vegetation density also was highest in these locations. Dense understory vegetation could be associated with increased foraging substrate density, thereby increasing foraging efficiency, even if arthropod density on foliage was equal to or lower than areas with less complex vegetation structure. Other studies also have shown that small canopy gaps with greater foliage density and understory habitat structure tend to support more birds than mature forests (Blake and Hoppes 1986, Martin and Karr 1986, Kilgo et al. 1999, Moorman and Guynn 2001, Wilson and Twedt 2003). Forest-breeding birds may use early-successional habitat with greater foliage density because of increased protective cover, particularly during migration when birds move through unfamiliar areas. Dense understory vegetation provides birds more 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), and protection from predators (Moore et al. 1995).

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