

Food abundance does not determine bird use of early-successional habitat

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Abstract. Few attempts have been made to experimentally address the extent to which temporal or spatial variation in food availability influences avian habitat use. We used an experimental approach to investigate whether bird use differed between treated (arthropods reduced through insecticide application) and control (untreated) forest canopy gaps within a bottomland hardwood forest in the Upper Coastal Plain of South Carolina, USA. Gaps were two- to three-year-old group selection timber harvest openings of three sizes (0.13, 0.26, and 0.50 ha). Our study was conducted during four bird use periods (spring migration, breeding, post-breeding, and fall migration) in 2002 and 2003. Arthropods were reduced in treated gaps by 68% in 2002 and 73% in 2003. We used mist-netting captures and foraging attack rates to assess the influence of arthropod abundance on avian habitat use. Evidence that birds responded to arthropod abundance was limited and inconsistent. In 2002, we generally captured more birds in treated gaps of the smallest size (0.13 ha) and fewer birds in treated gaps of the larger sizes. In 2003, we recorded few differences in the number of captures in treated and control gaps. Foraging attack rates generally were lower in treated than in control gaps, indicating that birds were able to adapt to the reduced food availability and remain in treated gaps. We conclude that arthropod abundance was not a proximate factor controlling whether forest birds used our gaps. The abundance of food resources may not be as important in determining avian habitat selection as previous research has indicated, at least for passerines in temperate subtropical regions.

Key words: *arthropods; canopy gaps; early-successional habitat; food availability; food reduction; foraging; forest birds; habitat use; South Carolina, USA.*

INTRODUCTION

The importance of food availability in determining habitat use by birds has long been a focus of ecological research (Lack 1954, MacArthur 1958, MacArthur and Pianka 1966, reviewed in Cody 1985). One reason for this may be that the consequences of selecting a habitat with limited food resources can be significant in the life history of birds. Limited food abundance may result in delayed nest initiation (Marshall et al. 2002), fewer nesting attempts (Rodenhouse and Holmes 1992), reduced nest provisioning rates (Rodenhouse and Holmes 1992, Nagy and Smith 1997), and reduced overall reproductive success (Rodenhouse and Holmes 1992). It is therefore important to understand whether food availability is the mechanism driving habitat selection, or more specifically, whether the process of habitat selection is sufficiently flexible to allow birds to respond to variation in food abundance over both space and time.

Considerable correlative evidence suggests that food availability could be a primary factor determining avian habitat use. Positive relationships have been demonstrated both for avian frugivores and fruit (Blake and Hoppes 1986, Kwit et al. 2004) and for avian insectivores and arthropods (Hutto 1985, Blake and Hoppes 1986, Holmes et al. 1986, Johnson and Sherry 2001). Experimental work by Rey (1995), Moegenburg and Levey (2003), and Borgmann et al. (2004) confirmed that habitat use by frugivorous birds can indeed track fruit resources. However, few studies have experimentally addressed the impacts of arthropod food availability on habitat use by terrestrial birds, and the limited available information is inconsistent. Johnson and Sherry (2001) made use of an insect eruption as a natural experiment to confirm the prediction that winter birds in Jamaica would respond to elevated numbers of arthropods. Conversely, Cooper et al. (1990) failed to detect a numerical response by forest birds in West Virginia, USA, to experimental application of the insecticide diflubenzuron. Given the general lack of experimental work on the topic and the discrepancy among available information, more work is clearly needed.

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Forest canopy gaps, with their early-successional vegetation, provide a convenient setting in which to experimentally evaluate the influence of arthropod food resources on avian habitat use. Young gaps represent well-defined habitats that can be controlled for size and that can be replicated. Such discrete patches more readily facilitate manipulation of arthropod abundance. Gaps can be important habitat for many birds during a portion or all of their life cycle, including breeding, post-breeding, and migratory periods. Several studies have reported greater abundance and richness of breeding and migrating birds in canopy gaps than in the surrounding mature forest (Kilgo et al. 1999, Moorman and Guynn 2001, Bowen et al. 2007). Additionally, Pagen et al. (2000) and Vitz and Rodewald (2006) demonstrated that early-successional habitat can be important to forest-breeding songbirds during the post-breeding period, i.e., following breeding but prior to fall migration. Correlative studies suggest that high bird use of gaps results from the greater availability of food resources there (Schemske and Brokaw 1981, Blake and Hoppes 1986, Martin and Karr 1986, Levey 1988).

Herein we present a field-scale experiment investigating the influence of arthropod food availability on avian habitat use. Our objective was to assess, via experimental food reduction, whether causal relations exist between arthropod abundance and avian habitat selection in early-successional habitats. If avian use of food-reduced areas declined, we could conclude that food is a proximate cue in the habitat selection process. Alternatively, if birds did not alter their use of such areas, we must conclude that although food abundance still could be the ultimate evolutionary reason birds use gaps (i.e., over time, birds may have learned that certain habitat structures tend to provide certain levels of food resources), they either do not respond to varying food resource levels as a proximate cue when selecting habitat or food is not a limiting factor in early successional habitat. We hypothesized that: (1) fewer arthropods in experimental canopy gaps would lead to reduced use of these areas by birds, especially insectivorous species, from spring migration through fall migration; and (2) reduced use of such gaps by insectivorous birds could be explained by reduced foraging efficiency in food-reduced gaps.

METHODS

We conducted our study during four bird use periods (spring migration, breeding, post-breeding, and fall migration) in 2002 and 2003 at the U.S. Department of Energy's Savannah River Site, a 78 000-ha National Environmental Research Park in the Upper Coastal Plain of South Carolina. Our 120-ha study site was located within a 70- to 100-year-old, seasonally flooded bottomland hardwood forest. The forest canopy of the study site included typical bottomland hardwood species: cherrybark (*Quercus falcata* var. *pagodaefolia*), laurel (*Q. laurifolia*), willow (*Q. phellos*), overcup (*Q.*

lyrata), and swamp chestnut (*Q. michauxii*) oaks, sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). The understory was dominated by dwarf palmetto (*Sabal minor*) and giant switchcane (*Arundinaria gigantea*), and a poorly developed midstory consisted primarily of American holly (*Ilex opaca*), red mulberry (*Morus rubra*), and ironwood (*Carpinus carolinianus*).

We created 12 experimental canopy openings (hereafter gaps) via group selection timber harvest in August 2000. Four replicates each of three sizes (0.13, 0.26, and 0.50 ha) were harvested, with the boundary of each gap at least 150 m from the nearest adjacent gap. We selected these sizes because they are within the size range of group selection timber harvest openings, thus enhancing application of the research to forest management. Additionally, previous research at our study site has documented high avian use of gaps of these sizes during both nesting and migratory periods (Kilgo et al. 1999, Moorman and Guynn 2001, Bowen et al. 2007). We defined a gap to include all of the cleared area within the circumference delineated by the boles of trees left standing at the gap perimeter. To ensure that all gaps were as homogeneous as possible, they were cleared to ground level and nearly all debris was removed, although small amounts of slash and small-diameter woody debris were left behind. During our study, the gaps were dominated by early pioneering species such as grasses (Poaceae), sedges (Cyperaceae), dogfennel (*Eupatorium capillifolium*), dwarf palmetto (*Sabal minor*), switchcane (*Arundinaria gigantea*), and some woody stump sprout regenerative growth. Conducting the experiment during the second (2002) and third (2003) years postharvest allowed us to sample gaps after substantial vegetation structure had recovered but before plants were mature enough to fruit, thus ensuring that arthropods were the primary food source available to birds in the gaps.

Arthropod removal

We randomly selected six of the 12 gaps (two of each size) for experimental arthropod reduction and left six as untreated controls. In the southeastern United States, Neotropical migrants begin to arrive from wintering grounds during late March and early April; thus, we initiated arthropod removal treatments on 1 April. The same gaps were assigned to treatment and control during both years. We applied Ambush (25.6% permethrin; Zeneca Ag Products, Wilmington, Delaware, USA), a commercially available broad-spectrum pyrethroid insecticide, at labeled rates using SOLO-450 backpack mist blowers (Solo, Newport News, Virginia, USA) that projected a droplet cloud 7.6–10.6 m, depending on wind conditions. Pyrethrins have very low vertebrate toxicity and a labeled residual period of two to four weeks. We sprayed only when winds were <16 km/h, temperatures were <35°C, relative humidity was >30%, and no rain was expected for ≥24 h.

Spraying was conducted in a systematic manner so that each gap received uniform coverage throughout.

Post-spraying arthropod recovery assessments were conducted using sweep nets weekly for the first month to determine efficacy of the treatment. We determined that treatments were effective for three weeks (149.2 ± 28.0 arthropods per sample in control gaps and 60.00 ± 28.0 arthropods per sample in treated gaps [mean \pm SE]; $F_{1,6} = 10.17$, $P = 0.019$), so we retreated gaps at three-week intervals from April through October in both years. Once the three-week spray schedule was established, we used a D-Vac backpack vacuum (Rincon-Vitova Insectaries, Ventura, California, USA) to assess efficacy of arthropod removal in each period (four times per year) midway through a spray rotation (i.e., 1.5 weeks post applications) at each of the 60 bird sampling sites. Collections were made in 1.13-m diameter circular plots, located 1–2 m from cleared mist net lanes. Upon sampling the plot, the D-Vac collection bag was immediately inverted into a cotton bag and sealed. Samples were placed in a freezer for ≥ 24 h to kill arthropods. We then placed the contents of each bag on a sheet of white paper for sorting with a hand lens and counted and identified each arthropod to order.

Avian response

Mist net captures.—We estimated bird use of gaps with mist netting during spring migration (1 April–12 May), breeding (13 May–7 July), post-breeding (8 July–31 August), and fall migration (1 September–18 October). We netted three gaps per day, one of each size, rotating through all 12 gaps in succession at least once per week. Each gap was netted 30 times in 2002 and 31 times in 2003. We deployed five nets (four-panel, 30-mm mesh) in each gap, one each on the north and south edges perpendicular to the gap edge, one at the center, and one each to the east and west of center, halfway to the gap edge. We operated nets from first light until ~ 3 –5 h after sunrise, depending on weather conditions. Netting was not conducted during strong winds or rain. Captured birds were banded with a metal USGS Biological Resources Division band, identified to species, aged, sexed, and released (Pyle 1997). Numbers of captures were standardized as captures per 100 net-hours for all analyses. We felt mist netting was more appropriate for sampling birds than visual or auditory surveys because our study spanned seasons in which birds are less vocal. Additionally, dense vegetation in the gaps made visual detection difficult. Vegetation structure was generally similar among gaps, and < 3 m tall, which minimized bias associated with mist net sampling (Remsen and Good 1996).

Foraging observations.—We conducted behavioral observations in combination with mist netting to examine whether arthropod removal affected foraging efficiency of birds present in treated and control gaps. We conducted foraging observations an equal number of times in each gap during each period. To account for

possible variability in foraging activity throughout the day, we staggered start times among gap sizes within and among days, ensuring that each gap size was observed at all times of day throughout a period. A single observer moved slowly through a gap until a bird was sighted. Although birds were not uniquely marked, observers attempted to minimize the likelihood of obtaining multiple observations of the same individual by considering species, sex, whether banded or not, and location. Additionally, foraging observations in each gap were at least four days apart to further minimize any impacts of autocorrelation. However, we acknowledge that observations were not completely independent if we observed the same bird more than once. The observer recorded the starting and ending time of visual contact and the bird's incidence of prey attacks. We spent ≥ 30 min observing birds in each gap but no more than 60 min to assure that one gap of each size was observed for foraging activity during each day. Individual birds were observed for as long as they remained visible. Observations in which a bird was obviously engaged in activities other than foraging were not included. Observations lasting < 20 s also were excluded (Robinson and Holmes 1982, Cimprich et al. 2005). Attack rates were standardized to number of attacks per minute for analysis.

Vegetation sampling

Vertical vegetation structure was recorded at each mist net during July and early August in 2002 and 2003 using a modification of the techniques of Karr (1971) and Schemske and Brokaw (1981). Two 12-m transects were established parallel to and 2 m distant from each side of each net. At 10 sampling points (1.2-m intervals) along each transect, the presence or absence of vegetation in each of 12 height intervals was recorded for a total of 20 points per height interval per net. Height intervals were 0–0.25, > 0.25 –0.50, > 0.50 –0.75, > 0.75 –1.00, > 1.0 –1.5, > 1.5 –2, > 2 –3, > 3 –5, > 5 –10, > 10 –20, > 20 –25, and > 25 –30 m. Vegetation touches were recorded along a 2 cm \times 2 m vertical pole at each sampling point and were tallied as grass/sedge, herb/forb, woody, or vine. For height intervals > 2 m, we sighted along the pole and recorded the presence or absence of vegetation. We grouped all height intervals ≤ 3 m to calculate percent cover for each of the four types, because most vegetation occurred within 3 m of the ground and nets sampled only the lowest 3 m of vegetation. A gap's percent cover was calculated by averaging the coverage values for the four vegetation types at the five nets.

Density of stems < 3 cm was recorded in five 1-m² plots randomly placed within a 0.04-ha circle centered on each net lane in 2002 and a 0.011-ha circle in 2003. Tallied stems were recorded as grass/sedge, herb/forb, woody, or vine. Average stem density for each gap was calculated by averaging over all plots. Plot size was adjusted from 0.04 ha to 0.011 ha in 2003 to eliminate

the potential for overlap between plots sampled from adjacent nets in the smaller gap sizes.

Data analysis

Arthropods.—Because of extreme differences in environmental conditions between sampling years, with drought in 2002 and flooding in 2003, we analyzed years separately. We used a linear mixed model (PROC MIXED, SAS Institute 1990) to perform split-plot-in-time ANOVA. We studied the effects of treatment, gap size, period, and their interactions on arthropod abundance. We considered gaps as the replicate whole-plot units, gap size and treatment as whole-plot factors, and period as the split-plot factor. Data transformation [$\log(x + 1)$] was used to obtain homogeneity of variance for arthropod abundance.

Mist-net captures.—We used a linear mixed model (PROC MIXED, SAS Institute 1990) to perform a split-plot-in-time ANOVA to test the effects of arthropod removal on all birds, insectivores as a group, the foliage-gleaning foraging guild (Hamel 1992), and individual species. Birds considered winter residents (Hamel 1992), those present only in early spring or late fall, and hummingbirds were not included in analyses. We assessed the effects of treatment, gap size, period, and the interactions among treatment, gap size, and period on bird abundance. For analysis of individual species and guilds (see Appendix D for scientific names and guild designations), we included only those with ≥ 30 captures per year.

We conducted separate analyses for initial captures and for recaptures. Within-year recaptures represented a subset of birds (many of which had established territories) that theoretically had had time to assess habitat quality and food availability between their first and subsequent captures. Hence, within-year recaptures may have provided an even more appropriate, if less powerful (because of limited sample sizes), test of our hypotheses.

We tested the effects of one arthropod order, Coleoptera, on bird captures because it was the only order that was more abundant in treated gaps (see *Results*) and because it was one of the two most important food sources for birds in our gaps (Moorman et al. 2007). We used a linear mixed model (PROC MIXED, SAS Institute 1990) to analyze the effects of gap size, period, and Coleopteran abundance on bird captures. We used mean captures per 100 net-hours for each guild or species as the dependent variable. Gap size and period were considered fixed effects, with period considered as a split-plot factor. Coleopteran abundance was considered a continuous variable. The interaction of gap size \times Coleoptera was included in all models. The model for the response was:

$$Y_{ijk} = \beta_0 + \beta_1 X_{ijk} + \gamma_i + g_i X_{ijk} + \delta_{ij} + S_k + \epsilon_{ijk} \quad (1)$$

where β_0 is the intercept, β_1 is the slope, X_{ijk} is the log(Coleoptera count), γ_i is the modified intercept for

gap size i , gamma g_i is the modified slope for gap size i , δ_{ij} is a random error among gaps in the same treatment and gap size, S_k is the modified slope for season k , and ϵ_{ijk} is the random error within a gap.

Foraging observations.—We had a sufficient number of observations to analyze all species of birds combined in both years and of the individual species, only enough to analyze Common Yellowthroat in 2003. We used a linear mixed model (PROC MIXED, SAS Institute 1990) to perform a split-plot-in-time ANOVA to assess the effects of gap size, period, and treatment on avian foraging success. We used mean attack rate for all species or for Common Yellowthroat as the dependent variable.

Vegetation.—We used a two-factor ANOVA (PROC ANOVA, SAS Institute 1990) to assess the effects of gap size and treatment on vegetation. We used the same model as above without transformation of the dependent variable, but the model did not include period because vegetation was collected only once per year.

RESULTS

Arthropods

Insecticide treatments reduced arthropod abundance in treated gaps by 68% in 2002 and 73% in 2003 (Appendix A). We collected 29 034 arthropods that were identified to 15 orders and an unknown category (Appendix B). In 2002, we collected 8535 arthropods in controls and 2767 in treated gaps ($F_{1,6} = 53.72$, $P < 0.001$). In 2003, we collected 13 951 arthropods in controls and 3781 in treated gaps ($F_{1,6} = 92.80$, $P < 0.001$). Fewer arthropods were collected in treated gaps than control gaps in all seasons (Appendix C).

Arthropod abundance generally increased in both treated and control gaps from 2002 to 2003. Six orders (Araneae, Coleoptera, Diptera, Homoptera, Hymenoptera, and Orthoptera), representing 800 or more individuals, dominated abundance in 2002, and four orders (Araneae, Diptera, Homoptera, and Hymenoptera) dominated abundance in 2003. All orders of arthropods were less abundant in treated than in control gaps except for Coleoptera (Appendix B), which was more abundant in 0.13-ha treated gaps than controls in 2002.

Mist net captures

We operated mist nets for 15 860 net-hours. We captured 1153 individual birds (not counting recaptures), representing 52 species. In 2002, we operated mist nets for 7698 h and captured 562 individuals representing 47 species (Appendix D). Of these, 94 individuals (11 species) were subsequently recaptured 224 times. In 2003, mist nets were operated for 8162 h, and 591 individuals were captured representing 42 species (Appendix D). Of these, 89 individuals (six species) were subsequently recaptured 212 times.

Initial captures.—We detected few differences in initial captures between treated and control gaps. In 2002, total

captures and insectivore captures were higher in 0.13-ha treatment gaps than in like-sized control gaps (Table 1), but in 2003, captures of these groups did not differ between treated and control gaps of any size. Total bird captures were positively correlated with Coleoptera abundance after adjusting for treatment effect in 2002 ($F_{1,30} = 4.09$, $SE = 0.140$, $P = 0.05$) but not in 2003 ($F_{1,30} = 1.90$, $SE = 0.270$, $P = 0.18$).

We captured more foliage gleaners during fall migration 2002 in 0.50-ha control gaps than in like-sized treatment gaps but fewer foliage gleaners during that period in 0.13-ha control gaps than like-sized treatment gaps (Table 1). During fall 2003, we captured fewer foliage-gleaning birds in 0.50-ha control gaps than like-sized treatment gaps (Table 1).

Of the species captured, Carolina Wren, Common Yellowthroat, Hooded Warbler, and Northern Parula had sufficient captures for analyses in both years (Table 1). We captured fewer Common Yellowthroats in 0.50-ha control gaps than in treatment gaps during the 2002 post-breeding period, and fewer Northern Parulas in control gaps than treatment gaps during the 2003 fall migration (Table 1).

Recaptures.—The number of recaptures did not differ between treated and control gaps in either year (Table 1).

Foraging observations

In 2002 and 2003, we collected 372 foraging observations of ≥ 20 s. We collected more observations in controls than treated gaps in 2002 (92 and 77, respectively) and 2003 (121 and 82, respectively; Table 2). Attack rates generally were higher in control gaps than in treatment gaps, but this pattern was strongest in the spring of 2003 (Table 2). Common Yellowthroat attack rates were higher in control than treated gaps in 2003 (Table 2).

Vegetation

No percentage of vegetative cover or total stem density measure differed between treated and control gaps in either year (Appendix E).

DISCUSSION

Birds generally did not alter their use of canopy gaps according to food abundance. We documented few differences in mist net captures in response to arthropod reduction in our gaps, and those that existed were inconsistent. We did detect lower use of treated gaps by foliage-gleaning birds, but only during one season of one year (fall migration, 2002) and only in 0.5-ha gaps. More often where the few differences occurred, bird use of treated gaps actually was greater than that of control gaps, contrary to our expectations. Therefore, we cannot conclude that food is the proximate cue in avian selection of early successional habitat. Instead, birds either do not cue on food resources when selecting early

successional habitat or food is not limiting for them there, at least in our study site.

Selecting a habitat in which to forage optimally has been suggested as critical to basic survival (MacArthur and Pianka 1966). If it is, a relationship between food resource levels and both bird density and foraging attack rate might be expected to be most evident when food is limited (Wiens 1977). Attack rates generally were lower in treated than control gaps, supporting our hypothesis that reduced foraging efficiency would occur where food resources were reduced. Similarly, Kilgo (2005) documented a positive relationship between arthropod abundance and foraging attack rate of Hooded Warblers in the forest surrounding our gaps. Nevertheless, bird abundance was not affected by arthropod reduction. A correlative study conducted concurrent to ours in the same forest stand also concluded that there was limited relationship between arthropod availability and bird abundance (Bowen 2004).

Although artifacts of our sampling methods may have obscured our ability to detect treatment response, we believe that our treatment design and scale were suitable to test our hypotheses. Mist nets necessarily sample birds that are mobile. Captured individuals may have been sampled before they had sufficient opportunity to assess and respond to food availability. Additionally, our gaps were small relative to the movements of migrating birds, if not territorial birds, and individuals simply passing through a gap en route to another location presumably would have been sampled without assessment of food resources. However, our comparisons of recaptures between treatments should have eliminated these biases. Results obtained from both recaptures and initial captures were similar, further corroborating our conclusion that food did not drive bird use of our gaps. In addition to recapture evidence, during the breeding season we located nests and observed territorial behavior within the gaps, indicating that birds used gaps on an ongoing basis for extended periods. Finally, our ability to obtain foraging observations in all periods confirms that most birds did spend time foraging in the gaps and were not simply passing through.

Although our results indicate that bird habitat use is not governed solely by variations in local food resource availability, correlative studies have shown a positive relationship between the distribution of birds and arthropod abundance, indicating that birds are able to "track" variations in local food resources in many situations (Hutto 1985, Blake and Hoppes 1986, Johnson and Sherry 2001). Hutto (1985), investigating the distribution and density of insectivorous migrant birds in Arizona, USA, determined that seasonal change in bird densities across different habitat types closely matched seasonal changes in food availability. Blake and Hoppes (1986) correlated bird and arthropod abundance across both treefall gaps and mature forest. Thus, both of these studies, in contrast to ours, assessed

TABLE 1. Mean bird captures/100 net-hours in six treated (arthropods removed) and six control canopy gaps (0.13, 0.26, and 0.50 ha) at the Savannah River Site, South Carolina, USA (2002–2003).

Guild or species, gap size, and period†	2002					2003				
	Control	Treated	SE	<i>F</i>	<i>P</i>	Control	Treated	SE	<i>F</i>	<i>P</i>
All birds‡						7.48	7.36	1.48	0.01	0.942
0.13 ha	4.31	8.74	1.50	8.76	0.025					
0.26 ha	7.54	5.22	1.50	2.41	0.172					
0.50 ha	10.44	6.96	1.50	5.40	0.059					
Insectivores‡						5.50	5.91	1.15	0.13	0.736
0.13 ha	2.93	5.77	1.11	6.58	0.043					
0.26 ha	4.98	3.11	1.11	2.86	0.142					
0.50 ha	7.35	5.20	1.11	3.78	0.100					
Foliage gleaners§										
Spring										
0.13 ha	3.47	6.18	1.42	1.85	0.190	4.18	4.01	1.98	0.00	0.950
0.26 ha	0.36	1.74	1.42	0.47	0.500	4.83	3.96	1.98	0.10	0.758
0.50 ha	5.26	2.49	1.42	1.90	0.185	6.34	7.19	1.98	0.09	0.766
Breeding										
0.13 ha	3.12	2.87	1.42	0.02	0.901	2.55	2.62	1.98	0.00	0.983
0.26 ha	5.87	5.31	1.42	0.08	0.782	3.13	3.87	1.98	0.07	0.796
0.50 ha	5.12	3.08	1.42	1.02	0.325	6.26	2.98	1.98	1.38	0.256
Post-breeding										
0.13 ha	0.75	3.11	1.42	1.38	0.256	3.04	2.59	1.98	0.03	0.874
0.26 ha	2.69	0.76	1.42	0.93	0.348	3.31	4.38	1.98	0.15	0.706
0.50 ha	0.38	3.77	1.42	2.86	0.108	5.17	9.81	1.98	2.74	0.115
Fall migration										
0.13 ha	1.17	5.60	1.42	4.87	0.041	6.23	2.03	1.98	2.25	0.151
0.26 ha	6.11	2.31	1.42	3.56	0.075	3.39	6.16	1.98	0.97	0.337
0.50 ha	10.63	4.06	1.42	10.72	0.004	1.95	9.92	1.98	8.09	0.011
Carolina Wren	1.62	1.26	0.35	1.09	0.336	0.75	0.70	0.14	0.12	0.750
Hooded Warbler¶						0.21	0.19	0.14	0.01	0.907
Spring	0.10	0.36	0.32	0.66	0.427					
Breeding	0.83	0.26	0.32	3.17	0.092					
Post-breeding	0.51	0.76	0.32	0.60	0.448					
Fall	0.18	0.10	0.32	0.07	0.788					
Common Yellowthroat§						2.00	2.33	0.59	0.31	0.600
Spring										
0.13 ha	0.37	0.38	0.61	0.00	0.982					
0.26 ha	0.00	0.00	0.61	0.00	1.000					
0.50 ha	1.50	1.55	0.61	0.01	0.938					
Breeding										
0.13 ha	1.42	0.77	0.61	1.12	0.304					
0.26 ha	2.23	1.13	0.61	3.20	0.090					
0.50 ha	1.04	1.14	0.61	0.03	0.871					
Post-breeding										
0.13 ha	0.38	0.00	0.61	0.38	0.546					
0.26 ha	1.15	0.00	0.61	3.54	0.076					
0.50 ha	0.00	1.89	0.61	9.52	0.006					
Fall migration										
0.13 ha	0.86	1.07	0.61	0.11	0.745					
0.26 ha	1.67	1.75	0.61	0.02	0.894					
0.50 ha	3.27	2.32	0.61	2.42	0.137					
Northern Parula¶	0.22	0.58	0.24	2.20	0.188					
Spring						0.67	0.13	0.72	0.55	0.466
Breeding						0.69	0.43	0.72	0.13	0.725
Post-breeding						1.22	1.45	0.72	0.10	0.751
Fall						0.11	1.86	0.72	5.98	0.025
Recaptures	3.17	2.55	0.62	0.95	0.368	2.35	2.75	0.78	0.26	0.628

Notes: Standard errors apply to all factor levels (i.e., all gap size × treatment combinations) of each bird group analysis. For gap size × treatment interactions, *df* = 1, 6, and for period × treatment and gap size × treatment × period interactions, *df* = 1, 18. *P* values are from PROC MIXED ANOVA.

† Levels of the factor interacting with treatment (i.e., gap size or period) are given.

‡ For 2002, gap size × treatment interaction; gap size analyzed separately.

§ Gap size × treatment × period interaction (gap size and treatment analyzed separately within period) for foliage gleaners in both 2002 and 2003 and for Common Yellowthroat in 2002.

¶ Treatment × period interaction (period analyzed separately) for Hooded Warbler in 2002 and Northern Parula in 2003.

TABLE 2. Foraging attack rates (attacks per minute) in treated (arthropods removed) and control canopy gaps in South Carolina, USA (2002–2003).

Variable	Control	Treated	SE	F	P
2002					
All species	3.78	2.75	0.68	2.33	0.178
2003					
All species					
Season†					
Spring	4.29	1.31	1.33	5.05	0.026
Breeding	2.07	2.79	1.04	0.47	0.496
Post-breeding	1.31	0.72	1.64	0.13	0.719
Fall	2.20	0.58	1.40	1.33	0.251
Common Yellowthroat	3.30	0.97	0.85	7.43	0.034

Notes: For treatment effect, $df = 1, 6$, and for the treatment \times period interaction, $df = 1, 184$. P values are from PROC MIXED ANOVA. "All species" includes the following (number of individuals given for 2002, 2003, respectively; see Appendix D for scientific names not given here): Yellow-billed Cuckoo (*Coccyzus americanus*) (4, 6); Ruby-throated Hummingbird (*Archilochus colubris*) (2, 4); Eastern Wood-Pewee (12, 5); Acadian Flycatcher (3, 5); Eastern Phoebe (0, 1); Great Crested Flycatcher (7, 4); White-eyed Vireo (1, 2); Yellow-throated Vireo (4, 0); Red-eyed Vireo (4, 1); Carolina Chickadee (1, 1); Tufted Titmouse (7, 0); White-breasted Nuthatch (2, 0); Carolina Wren (10, 6); House Wren (0, 1); Sedge Wren (*Cistothorus platensis*) (0, 1); Ruby-crowned Kinglet (*Regulus calendula*) (0, 1); Blue-gray Gnatcatcher (10, 9); Gray Catbird (1, 0); Northern Parula (7, 10); Magnolia Warbler (1, 0); Yellow-rumped Warbler (1, 2); Black-and-white Warbler (1, 0); American Redstart (3, 1); Northern Waterthrush (0, 1); Common Yellowthroat (38, 101); Yellow-breasted Chat (1, 0); Hooded Warbler (0, 2); Summer Tanager (11, 6); Scarlet Tanager (0, 1); Swamp Sparrow (*Melospiza georgiana*) (0, 1); Northern Cardinal (6, 4); Blue Grosbeak (7, 0); Indigo Bunting (24, 27); unknown (1, 0).

† Significant treatment \times period interaction; periods analyzed separately.

habitat selection at scales larger than the habitat patch. Johnson and Sherry (2001) documented a response by wintering warblers to a food pulse, as opposed to food reduction, in a single habitat patch, suggesting that food there may have been limited. Our findings were more consistent with those of Cooper et al. (1990), who found that none of the 21 breeding bird species they evaluated decreased in density in response to arthropod food reduction in an oak–hickory forest in West Virginia, USA.

Ironically, partial support for the hypothesis that bird habitat use tracks food resources may be found in the unexpectedly greater use of our 0.13-ha treated gaps in 2002, which may be explained by the preference of birds for Coleoptera. For unknown reasons, Coleopterans were more abundant in 0.13-ha treated than control gaps in 2002. This order was the most frequent order found in avian gut flush samples on the study site (Moorman et al. 2007), and other research also has demonstrated the importance of Coleoptera in the diets of forest passerines (Holmes and Robinson 1988, Raley and Anderson 1990, McMartin et al. 2002). Further, total bird abundance was positively associated with Coleoptera abundance in that year. This finding suggests

that the abundance of particular preferred foods may occasionally be important in habitat choices. Still, most evidence from our study indicates that food abundance did not determine habitat selection.

That birds continued to use treated gaps at the cost of reduced foraging efficiency begs the question of how they were able to do so. Even with an overall arthropod reduction of $\sim 70\%$, birds apparently were able to find sufficient food. One explanation may be that food abundance at the landscape scale was adequate enough that a localized reduction in food resources did not preclude the use of that location. However, in addition to the fact that birds persisted in using treated gaps, two factors suggest that the gaps themselves remained important foraging areas for birds. First, research from other gaps at our study site has demonstrated that birds use gap habitat heavily relative to surrounding forest throughout the growing season (Kilgo et al. 1999, Moorman and Guynn 2001, Bowen et al. 2007); i.e., birds probably did not simply shift all of their foraging activity from gaps into the surrounding forest. Second, our gaps likely comprised substantial proportions of the areas used by birds. For example, territory size of our most abundant species, Common Yellowthroat, is usually < 1 ha (Guzy and Ritchison 1999) and our gaps averaged 0.3 ha. If gaps did remain important for foraging despite the food reduction, this suggests that our treatments may not have reduced arthropods below a critical threshold. Even one-third of the arthropod density occurring in these habitats conceivably is sufficient to meet the needs of foraging passerines. Some even have argued against the negative effects of food limitation. Kilgo (2005), working in our study site, suggested that arthropod abundance might not be a limiting factor in determining avian habitat selection in some regions or habitat types, and Rotenberry (1980) and Rosenberg et al. (1982) concluded that in some situations, the energy demands of birds are small compared to available food resources. In addition, the flexibility of avian foraging strategies (Alatalo 1980, Rotenberry 1980, Hutto 1981) may have allowed birds to adapt to reduced food availability. Because birds are capable of changing both their foraging behavior and the foods they select, they may locate sufficient food without having to leave areas of low insect abundance. This plasticity in behavior allows migrants to adaptively exploit unfamiliar or unpredictable habitats as they are encountered (Petit 2000).

Factors other than arthropod abundance must have attracted birds to gaps. Others have suggested that birds select dense early-successional vegetation because of the cover provided for migratory (Rodewald and Brittingham 2004, Cimprich et al. 2005), breeding (Robinson and Robinson 1999, Moorman and Guynn 2001), and post-breeding (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006) activities. Petit (2000) described the general habitat selection pattern of Neotropical migrants as being more closely related to

within-habitat structural characteristics than to measures of food abundance. It may be that neither food nor cover are proximate settling cues for birds, but rather ultimate benefits that are typically, in their experience, associated with the structure of early-successional habitats. Thus, persistent bird use of our treated gaps may indicate that birds keyed on the structure and composition of the gap habitat because such habitat typically provides the necessary resources.

In summary, bird use of our early-successional canopy gaps was not affected by arthropod reduction. Birds may have been negatively affected by the reduced arthropod abundance in treated gaps via reduced foraging efficiency, but even this did not induce them to abandon the area. Birds apparently were attracted to the regenerating canopy gaps by their overall vegetative structure rather than by the abundant food resource base there. We conclude that the abundance of food resources may not be as important in determining avian habitat selection as previous research has indicated, at least for forest-breeding passerines in temperate subtropical regions.

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APPENDIX A

Mean arthropod abundance in six treated and six control canopy gaps by year at the Savannah River Site, South Carolina (2002–2003) (*Ecological Archives* E090-109-A1).

APPENDIX B

Number of arthropods collected per gap in treatment and control canopy gaps of three sizes in a bottomland hardwood forest in South Carolina (2002–2003) (*Ecological Archives* E090-109-A2).

APPENDIX C

Mean arthropod abundance for all arthropods by treatment and period in six treated and six control canopy gaps at the Savannah River Site, South Carolina (2002–2003) (*Ecological Archives* E090-109-A3).

APPENDIX D

Number of individuals of each species (excluding recaptures) captured in experimental canopy gaps in South Carolina (2002–2003) (*Ecological Archives* E090-109-A4).

APPENDIX E

Percentage of vegetation cover and stem density in six treatment and six control canopy gaps at the Savannah River Site, South Carolina (2002–2003) (*Ecological Archives* E090-109-A5).