

ABSTRACT

CHAMPLIN, TRACEY BERNICE. Do Food Availability and Microclimate Determine Bird use of Forest Canopy Gaps? (Under the direction of Christopher E. Moorman.)

We investigated the influence of arthropod availability and microclimate on avian use of forest canopy gaps in 2002 and 2003. We used mist netting and observation of foraging effort (attack rates) to determine the influence of arthropod abundance on avian habitat use of three sizes (0.13, 0.26, and 0.50 ha) of 2- to 3-year-old group-selection timber harvest openings during four periods (spring migration, breeding, post-breeding, and fall migration). We sprayed a broad-spectrum insecticide to reduce arthropod abundance in six of 12 gaps (2 of each size) from April through October in both years. We used a D-Vac backpack vacuum to monitor treatment efficacy across the four seasons. We used four-channel HOBO[®] H-8 data loggers to measure temperature, light intensity, and relative humidity at netting stations in canopy gaps without arthropod reduction.

Arthropods were effectively reduced in both years in treated gaps, but bird response to arthropod reduction varied among gap sizes and between years. In 2002, we generally captured more birds in treated than control gaps of the smallest size (0.13 ha) and fewer birds in treated than control gaps of the larger two sizes. In 2003, we recorded few differences between the number of captures in treated and control gaps. Relationships between bird captures and microclimate (temperature, light intensity, and relative humidity) were inconsistent. For example, fewer birds were captured where temperatures were higher during the breeding and post-breeding periods in 2002 and more birds were captured where temperatures were higher in spring 2003.

We suggest that birds in bottomland forests of the relatively mild southeastern U.S. select gap habitats based primarily on the dense vegetation structure that provides protection

from predators during times of vulnerability (e.g., post-breeding molts, migration). Other factors, including food availability and microclimate, likely play lesser roles in the habitat selection process, except during the breeding season when exposure to predators is less severe.

**DO FOOD AVAILABILITY AND MICROCLIMATE DETERMINE BIRD USE OF
FOREST CANOPY GAPS?**

By
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BIOGRAPHY

I am very pleased to have completed my Masters of Science at North Carolina State University. My interest in the natural world started in early childhood at Cape Cod National Seashore, where my family and I spent many weeks every summer camping on the beach. While there, I would spend much of my time searching out local wildlife, collecting seaweed and shells, and watching birds. Many years later I held my first job as a Biological Technician at Cape Cod National Seashore, where I learned about the local ecology and answered visitors' questions regarding the subject matter. Hooked on the prospects of a future in the sciences, I attended a local community college the rest of the year. During the summers, I would seek out any job that remotely resembled science and sign up. During my 14 years as a field biologist, I gained experience as a herpetologist, entomologist, ornithologist, mammologist, and wildlife biologist. Most of the 14 years have been spent in the U.S. However, I took a 6-week expedition to Belize and lived for one year in Peru and Bolivia. While in South America, my husband and I observed and inventoried all faunas with an emphasis on the Neotropical bird communities and created lists for ecotourism lodges along the Rio Tombopata, Rio Alto Madre de Dios, Rio Madre de Dios, and Rio Heath in the Amazon basin. I received my BS degree from the University of Massachusetts, Amherst in 1995 in Fisheries and Wildlife Science. My career goal includes applying my interest in the sciences while conducting field research, specifically with birds, conservation, writing, and photography. Personal interests include listening to international music, hiking, camping, and general exploration of the outdoors, and being a very involved parent of a wonderful little girl.

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TABLE OF CONTENTS

LIST OF TABLES.....	v
LIST OF FIGURES	vi
1. DOES FOOD AVAILABILITY DETERMINE BIRD USE OF FOREST CANOPY GAPS?	1
Abstract.....	2
Introduction.....	3
Study Site.....	5
Methods.....	6
Data Analysis.....	10
Results.....	12
Discussion.....	14
Acknowledgments.....	18
Literature Cited.....	19
Appendices.....	39
2. AVIAN RESPONSE TO MICROCLIMATE IN CANOPY GAPS IN A BOTTOMLAND HARDWOOD FOREST.....	43
Abstract.....	44
Introduction.....	45
Study Site.....	47
Methods.....	48
Data Analysis.....	50
Results.....	51
Discussion.....	53
Acknowledgments.....	56
Literature Cited.....	57

LIST OF TABLES

	Page
Chapter 1	
Table 1. Mean arthropod abundance by treatment and period.....	25
Table 2. Mean bird captures in treated and control gaps.....	26
Table 3. Foraging attack rates in treated and control gaps.....	32
Table 4. Percent vegetation cover and stem density.....	34
Chapter 2	
Table 1. Percent vegetation cover in gaps.....	62
Table 2. Microclimate by gap size and net location.....	64
Table 3. Relationship between microclimate and bird activity....	67

LIST OF FIGURES

	Page
Chapter 1	
Figure 1. Mean number of arthropods per five samples.....	36
Figure 2. Foliage height profiles.....	37

CHAPTER 1

Food availability-bird use

Does Food Availability Determine Bird Use of Forest Canopy Gaps?

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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 untreated forest canopy gaps within a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. Gaps were 2- to 3-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 effectively reduced in both years in treated gaps. We used mist netting and foraging attack rates to determine the influence of arthropod abundance on avian habitat use. Bird response to arthropod reduction varied among gap sizes and between years. 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. Captures of foliage gleaners in 0.50-ha gaps during fall migration were inconsistent, with more captures in control gaps in 2002 and more captures in the treated gaps in 2003. We suggest that arthropod abundance was not a limiting factor for forest birds on our study site. Instead, birds likely used gaps for their dense vegetation that provided protection from predators during times of vulnerability (e.g., migratory periods and molt) while concurrently offering adequate food resources.

Key words: arthropods; canopy gaps; Coleoptera; food availability; food reduction; foraging; forest birds; habitat use; South Carolina.

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). Some evidence suggests that food availability could be the most important factor determining avian habitat use (Hutto 1985, Johnson and Sherry 2001, Kwit et al. 2004). 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). However, studies directly addressing impacts of food availability on habitat use are not consistent. Some studies have documented positive relationships (Goss-Custard 1970, Davies and Houston 1981, Marcotullio and Gill 1985) and others negative relationships (Alatalo 1980, Rotenberry 1980, Rosenberg et al. 1982) between food abundance and avian habitat use.

Patterns of avian habitat use change across seasons (Hutto 1985, Bowen et al. 2007), and, depending upon particular seasonal needs, habitat selection may be influenced by arthropod abundance. Several works have suggested that higher bird abundance may be associated with greater arthropod abundance (White 1969, Blake and Hoppes 1986, Holmes et al. 1986, Johnson and Sherry 2001). Depending on season and habitat type, individual bird species may respond differently to arthropod availability (Holmes et al. 1986, Blake and Loiselle 1991, Johnson and Sherry 2001).

Early-successional vegetation, such as canopy gaps, can be important habitat for some 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 early-successional 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 forest-breeding songbirds were more abundant in early-successional habitat than in mature forest during the post-breeding period. After fledging, forest birds tend to disperse from their natal habitats into large openings or patches of early-successional habitat with little to no canopy and a dense understory (Anders et al. 1998, Vega Rivera et al. 1998).

Although avian use of early-successional habitat is well documented, the reasons for the apparently preferential use are less clear. Some birds, especially shrub nesting species, select gaps as breeding habitat because the canopy openings often have a denser understory than adjacent mature forest (Robinson and Robinson 1999, Moorman and Guynn 2001). The gap understory may offer greater nest concealment (Rudnický and Hunter 1993) or favorable thermal environments (Walsberg 1985, Wachob 1996). Others have proposed that naïve fledglings, migrating individuals, and molting adults may use gaps as a refuge from predators (Winker et al. 1992, Moore et al. 1993, Anders et al. 1998, Vega Rivera 1998, Marshall et al. 2003) because of increased foliage density (Martin & Karr 1986, Levey 1988, Anders et al. 1998). Lastly, many researchers have suggested that high bird use of early-successional habitat results from the greater availability of food resources there (Blake and Hoppes 1986, Vega Rivera et al. 1998, Martin and Karr 1986, Levey 1988). Using a correlative approach, Bowen (2004) concluded that vegetation structure was likely more important than arthropod abundance in determining avian use of canopy gaps. Few researchers, however, have attempted to experimentally address the extent to which temporal or spatial variation in food availability influences avian habitat use patterns.

Our objective was to assess whether observed patterns of bird use of early-successional habitat in various periods could be explained by the relative availability of arthropod food resources there. We used experimental arthropod reductions to examine whether causal relations exist between arthropod abundance and avian habitat selection in early-successional habitats. Specifically, we hypothesized that: (1) fewer arthropods in experimental canopy gaps would lead to reduced use by birds from spring migration through fall migration; (2) insectivorous birds would be a stronger treatment indicator than all birds because the former rely on arthropods as a food resource; (3) reduced use of gaps by insectivorous birds could be explained by reduced foraging efficiency in treated gaps.

STUDY SITE

We conducted our study during four bird-use periods (spring migration, breeding, post-breeding and fall migration) in 2002 and 2003 at the Department of Energy's Savannah River Site, a 78,000-ha National Environmental Research Park in the Upper Coastal Plain of South Carolina. The 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*).

METHODS

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 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 post harvest 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 April 1. The same gaps were assigned to treatment and control during both years. We applied Ambush[®] (25.6% permethrin), a commercially available broad-spectrum pyrethroid insecticide (Zeneca Ag Products Inc.) at labeled rates using SOLO[®]-450 backpack mist blowers 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 2 - 4 weeks. We sprayed only when winds were less than 16 km per hour, temperatures were $<35^{\circ}\text{C}$, relative humidity was $>30\%$, and no rain was expected for ≥ 24 hours. 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 3 weeks, (mean number of arthropods 149.2 ± 28.0 per sample in control gaps and 60.00 ± 28.0 per sample in treated gaps; $F_{1,6} = 10.17$, $P = 0.019$), so we re-treated gaps at 3-week intervals from April through October in both years. Once the 3-week spray schedule was established, we used a D-Vac backpack vacuum to assess efficacy of arthropod removal in each period (4 times per year) midway through a spray rotation (i.e., 1.5 weeks post applications) at each of the 60 bird sampling sites described below. 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 hours to kill arthropods. We then placed the contents of each bag on a sheet of white paper for sorting with a hand lens, and then counted and identified each arthropod to order.

Avian Response

Mist-net captures--We estimated bird use of gaps with mist netting. One gap of each size was netted daily during spring migration (Apr 1 - May 12), breeding (May 13 - Jul 7), post-breeding (Jul 8 - Aug 31), and fall migration (Sep 1 - Oct 18). We deployed five nets (4-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 approximately 3 - 5 hours 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 collected behavioral observations in combination with mist netting to examine whether arthropod removal affected foraging efficiency of birds present in treated and untreated gaps. Foraging observations were conducted an equal number of times in each gap during each period. To account for possible variability in foraging activity throughout the day, start times were staggered 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. The observer recorded the bird's incidence of prey attack, and activity time. We spent ≥ 30 minutes observing birds in each gap but no more than 60 minutes 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 less than 20 seconds also were

excluded (Robinson and Holmes 1982, Cimprich et al. 2005). Attack rates were standardized to 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 meters. Vegetation touches were recorded along a 2-cm x 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 average 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 (James and Shugart 1970). 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 analysis of variance (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 was used to obtain homogeneity of variance for arthropod abundance [Log(x+1)].

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, foliage and ground gleaning foraging guilds (Hamel 1992), and individual species. Birds considered winter residents (Hamel 1992), 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 (scientific names in Appendix 1), we included only those with ≥ 30 captures per year. We conducted separate analyses for initial captures and for recaptures. Within-year recaptures represented a sub-set 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.

Because Coleoptera was the only order that was more abundant in treated gaps (see results below) and because they are an important food source 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 x Coleoptera was included in all models. The model for the response is:

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

where β_0 intercept, β_1 = slope, X_{ijk} = log coleoptera count, γ_i = modifies intercept for gap size i, g_i modifies slope for gap size i, δ_{ij} = random error among gaps in same treatment and gap size, S_k modifies slope for season k, and ε_{ijk} = random error within a gap.

Foraging observations-- We had a sufficient number of observations to analyze all species 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. To minimize autocorrelation, foraging observations were at least four days apart.

Vegetation

We used a two-factor analysis of variance (PROC ANOVA, SAS Institute 1990) to perform an ANOVA to assess the effects of gap size and treatment on vegetation. We used the same model as above without transformation of the dependent variable, and 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 approximately 68 percent in 2002 and 73 percent in 2003 (Figure 1). We collected 29,034 arthropods that were identified to 15 orders and an unknown category. In 2002, we collected 8,535 arthropods in controls and 2,767 in treated gaps ($F_{1,6} = 53.72$; $P < 0.001$; Appendix 2). In 2003, we collected 13,951 arthropods in controls and 3,781 in treated gaps ($F_{1,6} = 92.80$; $P < 0.001$; Appendix 2). Fewer arthropods were collected in treated gaps than control gaps in all seasons (Table 1).

Arthropod abundance generally increased 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 (see Appendix 2), which was more abundant in 0.13-ha treated gaps than controls in 2002.

Mist Net Captures

Mist nets were open for 15,860 net hours. We captured 1,153 individual birds (not counting recaptures) representing 52 species. In 2002, we operated mist nets for 7,698 hrs

and captured 562 individuals representing 47 species (Appendix 1). Of these, 94 individuals (11 species) were subsequently recaptured 224 times. In 2003, mist nets were operated for 8,162 hrs, and 591 individuals were captured representing 42 species (Appendix 1). Of these, 89 individuals (6 species) were subsequently recaptured 212 times.

Initial captures--In 2002, total captures and insectivore captures were higher in 0.13-ha treatment gaps than in similar-sized control gaps (Table 2). In 2003, captures of these groups did not differ between treatment and control gaps. Total bird captures were positively correlated with Coleoptera abundance in 2002 ($F_{1,30} = 4.09$, $SE = 0.140$, $P = 0.05$) but not in 2003 ($F_{1,30} = 1.90$, $SE = 0.270$, $P = 0.18$) after adjusting for treatment effect.

During fall migration in 2002, we captured more foliage gleaners in 0.50-ha control gaps than in like-sized treatment gaps and fewer foliage gleaners in 0.13-ha control gaps than like-sized treatment gaps (Table 2). In fall 2003, we captured fewer foliage gleaning birds in 0.50-ha control gaps than equally sized treatment gaps (Table 2).

Of the species captured, Carolina wren, common yellowthroat, hooded warbler, and northern parula had sufficient captures for analyses in both years (Table 2). 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 2).

Recaptures--The number of recaptures did not differ between treatments and control gaps in either year (Table 2).

Foraging observations

In 2002 and 2003, we collected 372 foraging observations of ≥ 20 seconds. We collected more observations in controls than treatments in 2002 (92 and 77, respectively) and 2003 (121 and 82, respectively; Table 3). Attack rates generally were higher in control gaps than in treatment gaps, but this pattern was strongest in the spring of 2003 (Table 3). Common yellowthroat attack rates were higher in control than treated gaps in 2003 (Table 3).

Vegetation

All percent vegetative cover and total stem density measures were similar among gaps in each year. (Table 4; Figure 2).

DISCUSSION

Response by birds to arthropod reduction was inconsistent. In some cases, bird use of treated gaps, where arthropod abundance had been reduced, was greater than use of control gaps. Similarly, captures of insectivores, foliage gleaning birds, and individual bird species also were inconsistent. These results suggest that birds did not alter their use of the canopy gaps according to arthropod abundance.

Selecting a habitat in which to forage optimally is critical to basic survival (MacArthur and Pianka 1966). Therefore, a relationship between food resource levels and both bird densities and foraging attack rates 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 hypotheses that reduced foraging efficiency would occur where food resources were reduced. Kilgo (2005), working in the forest surrounding our gaps, documented a positive relationship between arthropod abundance and foraging attack rate of Hooded Warblers. Similarly, Cooper et al. (1990) demonstrated a negative relationship

between arthropod abundance and foraging area of the Red-eyed Vireo, which was two to three times smaller in control than in arthropod reduced plots.

Birds that used the treated gaps generally did so with a cost of reduced foraging efficiency. Even so, birds used the treated and control gaps equally, indicating that factors other than arthropod abundance attracted birds to gaps. Birds may have been unable to recognize reduced food resources, or our treatments may not have reduced arthropods below a critical threshold. Even with an overall arthropod reduction of two-thirds and reduced foraging efficiency, birds appeared able to find sufficient food. Kilgo (2005) suggested that arthropods might not be a limiting factor in determining avian habitat selection in some regions or habitat types. Rather, birds might select the dense gap vegetation because of the cover provided during migration (Cimprich et al. 2005), breeding (Robinson and Robinson 1999, Moorman and Guynn 2001), and post-breeding (Pagen et al. 2000, Vitz and Rodewald 2006) periods.

Our results indicate that bird habitat use is not governed solely by variations in local food resource availability. Other studies, however, have shown a positive correlation between the distribution of birds and arthropod abundance and several have concluded that food availability is the driving force behind habitat selection in birds (Blake and Hoppes 1986, Holmes et al. 1986, Johnson and Sherry 2001). Martin (1980) suggested that spring migrants dispersed among habitat "islands" on the Great Plains in relation to available food supply. Hutto (1985), investigating the distribution and density of insectivorous migrant birds in Arizona, determined that seasonal change in bird densities across different habitat types closely matched seasonal changes in food availability. Thus, these studies indicate that

birds may be able to "track" variations in local food resources (Rotenberry 1980, Hutto 1985, Martin and Karr 1986, Johnson and Sherry 2001).

Despite the effectiveness of our treatments in reducing arthropod abundance (mean overall reduction of approximately 70%), a sufficient arthropod prey base appears to have persisted in our study plots. A correlative study conducted concurrent to ours in the same bottomland hardwood forest stand suggested that there was limited relationship between arthropod availability and bird abundance (Bowen 2004). 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. Rotenberry (1980) and Rosenberg et al. (1982) suggested that a bird's energy demands are small compared to the available food in a habitat.

Birds' inherent flexibility allows them to adapt to changes by altering their foraging behavior or primary food item (Alatalo 1980, Rotenberry 1980, Hutto 1981). Because birds are flexible in both their foraging behavior and the foods they select, they may locate sufficient food without having to leave areas of low insect abundance (i.e., without having to leave a reduced-insect plot). This plasticity in behavior allows migrants to adaptively exploit unfamiliar or unpredictable habitats as they are encountered (Petit 2000).

Although we believe that our treatment design and scale were suitable to test our hypotheses, artifacts of our sampling methods may have obscured our ability to detect treatment response. As birds move from place to place, they presumably are assessing food resources and adjusting their movements accordingly (Davies and Houston 1981). However, birds continued to forage in our treated gaps, albeit less successfully. These individuals may have been sampled before they had time to assess and respond to food availability.

Landscape level food abundance may have been adequate enough that a localized (i.e., gaps) reduction in food resources did not preclude the use of that location. Several birds nesting in treated gaps foraged outside of them and returned to feed nestlings (T. B. Champlin, pers. obs.). Additionally, birds passing through a gap on their way to another location were captured and presumably would have been sampled without assessment of food resources. Finally, birds may not have selected gap habitat based on proximate factors like food but rather based on an innate response to ultimate factors such as habitat structure for nesting (Rudnicky and Hunter 1993), brood rearing, and molt (Winker et al. 1992, Vega Rivera et al. 1998). Petit (2002) describes that the general habitat selection pattern of Neotropical migrants is more closely related to the within habitat structural characteristics rather than to measures of food abundance. Thus, continued bird use of treated gaps may indicate that birds keyed on the structure and composition of the gap habitat because in their experience such habitat typically provides the necessary resources.

The pattern of increased avian use of 0.13-ha treated gaps in 2002 may be explained by the higher abundance of Coleoptera there. Total bird abundance was positively associated with Coleoptera abundance in that year. Further, Coleoptera was the most frequent order found in gut flush samples on the study site (Moorman et al. 2007). Other works also have demonstrated the importance of Coleoptera in the diets of forest passerines (Holmes and Robinson 1988, Raley and Anderson 1990, McMartin et al. 2002). Ulyshen et al. (2004) determined that our recently created canopy gaps had approximately twice the species richness and about 6 times the abundance of Coleopterans than did the surrounding forest. Collectively, this evidence suggests that birds are capable of selecting habitat based primarily

on physical characteristics but that selection may become more precise when a preferred food is available.

Birds using the early-successional canopy gaps did not alter habitat use in response to arthropod reduction. It is possible that birds responded to arthropod abundance, as is evident in reduced foraging efficiency in treated gaps, yet the scale at which the capture data was collected may have been inadequate to detect a similar response in habitat use of the bird assemblages measured. We suspect, however, that the cover and protection offered by these regenerating canopy gaps attracted birds during times of vulnerability (e.g., migratory periods, and molt) and likely also offered sufficient food resources.

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LITERATURE CITED

- Alatalo, R. V. 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in Northern Finland. *Oecologia* 45:190-196.
- Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349-358.
- Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103:328-340.
- Blake, J. G., and B. A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108:114-130.
- Bowen, L. T. 2004. Seasonal relationships between birds and arthropods in bottomland forest canopy gaps. Ph.D. dissertation, North Carolina State University, Raleigh, NC.
- Bowen, L. T., C. E. Moorman, and J. C. Kilgo. 2007. Seasonal bird use of canopy gaps in a bottomland forest. *The Wilson Journal of Ornithology* 119:77-88.
- Cimprich, D. A., M. S. Woodrey, and F. R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover. *Animal Behaviour* 69:1173-1179.
- Cody, M. L. ed. 1985. *Habitat Selection in Birds*. Academic Press, London and New York.
- Cooper R. J., K. M. Dodge, P. J. Martinat, S. B. Donahoe, and R. C. Whitmore. 1990. Effects of diflubenzuron applications on eastern deciduous forest birds. *Journal of Wildlife Management* 54:486-493.
- Davies, N. B., and A. I. Houston. 1981. Owners and satellites: the economics of territory defence in the Pied Wagtail, *Motacilla alba*. *Journal of Animal Ecology* 50:157-180.
- Goss-Custard, J. D. 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology* 39:91-113.

- Hamel, P. B. 1992. *Land Manager's Guide to the Birds of the South*. The Nature Conservancy, Chapel Hill, NC; USDA Forest Service, Southern Region, Atlanta, GA.
- Holmes, R. T., and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. *Wilson Bulletin* 100:377-394.
- Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. *Ecological Monographs* 56:201-220.
- Hutto, R. L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. *Auk* 98:765-777.
- _____, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: Competition mediated? *Auk* 102:120-132.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- Johnson, M. D., and T. W. Sherry. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70:546-560.
- Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs* 41:130-148.
- Kilgo, J. C., K. V. Miller, and W. P. Smith. 1999. Effects of group-selection timber harvest in bottomland hardwoods on fall migrant birds. *Journal of Field Ornithology* 70:404-413.
- Kilgo, J. C. 2005. Harvest-related edge effects on prey availability and foraging of Hooded

- Warblers in a bottomland hardwood forest. *Condor* 107:627-636.
- Kwit, C., D. J. Levey, C. H. Greenberg, S. F. Pearson, J. P. McCarty, S. Sargent, and R. L. Mumme. 2004. Fruit abundance and local distribution of wintering hermit thrushes (*Catharus guttatus*) and yellow-rumped warblers (*Dendroica coronata*) in South Carolina. *Auk* 121:46-57.
- Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69:1076-1089.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *In* Foundations of Ecology: Classic Papers with Commentaries (L. A. Real and J. H. Brown, Eds.). The University of Chicago Press, Chicago.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *In* Foundations of Ecology: Classic Papers with Commentaries (L. A. Real and J. H. Brown, Eds.). The University of Chicago Press, Chicago.
- Marcotullio, P. J., and F. B. Gill. 1985. Use of time and space by chestnut-backed antbirds. *Condor* 87:187-191.
- Marshall, R. M., R. J. Cooper, J. A. DeCecco, J. Strazanac, and L. Butler. 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the Red-Eyed Vireo. *Ecological Applications* 12:261-280.
- Marshall, R. M., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. *Forest Ecology and Management* 183:127-135.
- Martin, T. E. 1980. Diversity and abundance of spring migratory birds using habitat islands

- on the Great Plains. *Condor* 82:430-439.
- Martin, T. E. and J. R. Karr. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scandinavica* 17:165-174.
- McMartin, B., I. Bellocq, and S. M. Smith. 2002. Patterns of consumption and diet differentiation for three breeding warbler species during a spruce budworm outbreak. *Auk* 119:216-220.
- Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1993. Stopover habitat: Management implications and guidelines. Pages 58-69 *in* Status and Management of Neotropical migratory birds; 1992 (D. M. Finch and P. W. Stangel, Eds.). U.S. Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- Moorman, C. E., and D. C. Guynn, Jr. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11:1680-1691.
- Moorman, C. E., L. T. Bowen, J. C. Kilgo, C. E. Sorenson, J. L. Hanula, S. Horn, and M. D. Ulyshen. 2007. Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest. *Journal of Field Ornithology* 78:1-10.
- Nagy, L. R., and K. G. Smith. 1997. Effects of insecticide-induced reduction in lepidopteran larvae on reproductive success of Hooded Warblers. *Auk* 114:619-627.
- Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. *Condor* 102:738-747.
- Petit, D. R. 2000. Habitat use by landbirds along nearctic-neotropical migration routes:

- Implications for conservation and stopover habitats. Pages 15-33 *in* Stopover Ecology of Nearctic-Neotropical Migrants: Habitat Relations and Conservation Implications. (F. R. Moore ed.). Studies in Avian Biology No. 20.
- Pyle, P. 1997. Identification Guide to North American Birds. Slate Creek Press, Bolinas, CA.
- Raley, C. M., and S. H. Anderson. 1990. Availability and use of arthropod food resources by Wilson's Warblers and Lincoln's Sparrows in southeastern Wyoming. *Condor* 92:141-150.
- Remsen, J. V. Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113:381-398.
- Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.
- Robinson, W. D., and S. K. Robinson. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology* 13:58-66.
- Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357-372.
- Rosenberg, K. V., R. D. Ohmart, and B. W. Anderson. 1982. Community organization of riparian breeding birds: response to an annual resource peak. *Auk* 99:260-274.
- Rotenberry, J. T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment. *Ecological Monographs* 50:93-110.
- Rudnick, T. C., and M. L. Hunter, Jr. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358-364.
- SAS institute, 1990. SAS users guide version 6. SAS institute, Inc., Cary, NC.

- Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62:938-945.
- Ulyshen, M. D., J. L. Hanula, S. Horn, J. C. Kilgo, and C. E. Moorman. 2004. Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. *Forest Ecology and Management* 199:259-272.
- Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69-78.
- Vitz, A. C. and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127:477-486.
- Wachob, D. G. 1996. The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. *Condor* 98:114-122.
- Walsberg, G. E. 1985. Physiological consequences of microhabitat selection. *In* *Habitat Selection in Birds* (Cody, M. L. ed.), pp. 389-413. Academic Press, London and New York.
- White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of Psyllids in Australia. *Ecology* 50:905-909.
- Wiens, J. A. 1977. On competition and variable environments. *American Scientist* 65:590-597.
- Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384-402 *in* *Ecology and Conservation of Neotropical Migrant Landbirds*. (J. M. Hagan and D. W. Johnson, Eds.). Smithsonian Institution Press, Washington, DC.

Table 1. Mean arthropod abundance (log transformed [Log(x+1)] mean number of arthropods per period per five D-VAC samples in each gap) for all arthropods by treatment and period in six treated and six control canopy gaps at the Savannah River Site, South Carolina (2002 - 2003).

	Control	Treated	SE	$F_{3,30}$	P
2002					
Spring	31.39	15.49	5.50	8.36	0.007
Breeding	62.49	30.22	5.50	34.44	<0.001
Post-breeding	69.11	31.31	5.50	47.24	<0.001
Fall	68.66	27.73	5.50	55.38	<0.001
2003					
Spring	57.50	26.84	5.88	27.91	<0.001
Breeding	69.80	27.60	5.88	51.56	<0.001
Post-breeding	69.71	26.67	5.88	53.63	<0.001
Fall	79.27	32.29	5.88	63.87	<0.001

Table 2. Mean bird captures/100 net hrs in six treated (arthropods removed) and six control canopy gaps at the Savannah River Site, South Carolina (2002 - 2003). Degrees of freedom for gap size x treatment interactions is $F_{1,6}$ and for period x treatment and gap size x treatment x period interactions is $F_{1,18}$.

Year	Bird Group	Gap Size/Season ^c	Control	Treated	SE	<i>F</i>	<i>P</i> ^a
2002	All Birds ^b						
		Gap Size					
		0.13	4.31	8.74	1.50	8.76	0.025
		0.26	7.54	5.22	1.50	2.41	0.172
		0.50	10.44	6.96	1.50	5.40	0.059
	Insectivores ^b						
		0.13	2.93	5.77	1.11	6.58	0.043
		0.26	4.98	3.11	1.11	2.86	0.142
		0.50	7.35	5.20	1.11	3.78	0.100
	Foliage Gleaners ^d						
		Spring					
		0.13	3.47	6.18	1.42	1.85	0.190

	0.26	0.36	1.74	1.42	0.47	0.500
	0.50	5.26	2.49	1.42	1.90	0.185
Breeding						
	0.13	3.12	2.87	1.42	0.02	0.901
	0.26	5.87	5.31	1.42	0.08	0.782
	0.50	5.12	3.08	1.42	1.02	0.325
Post-breeding						
	0.13	0.75	3.11	1.42	1.38	0.256
	0.26	2.69	0.76	1.42	0.93	0.348
	0.50	0.38	3.77	1.42	2.86	0.108
Fall Migration						
	0.13	1.17	5.60	1.42	4.87	0.041
	0.26	6.11	2.31	1.42	3.56	0.075
	0.50	10.63	4.06	1.42	10.72	0.004
Carolina Wren		1.62	1.26	0.35	1.09	0.336
Hooded Warbler ^c						

	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 ^d						
	Spring					
	0.13	0.37	0.38	0.61	0.00	0.982
	0.26	0.00	0.00	0.61	0.00	1.000
	0.50	1.50	1.55	0.61	0.01	0.938
	Breeding					
	0.13	1.42	0.77	0.61	1.12	0.304
	0.26	2.23	1.13	0.61	3.20	0.090
	0.50	1.04	1.14	0.61	0.03	0.871
	Post-breeding					
	0.13	0.38	0.00	0.61	0.38	0.546
	0.26	1.15	0.00	0.61	3.54	0.076

Table 2 Continued

Tracey B. Champlin

		0.50	0.00	1.89	0.61	9.52	0.006
		Fall Migration					
		0.13	0.86	1.07	0.61	0.11	0.745
		0.26	1.67	1.75	0.61	0.02	0.894
		0.50	3.27	2.32	0.61	2.42	0.137
	Northern Parula		0.22	0.58	0.24	2.20	0.188
	Recaptures		3.17	2.55	0.62	0.95	0.368
2003	All Birds		7.48	7.36	1.48	0.01	0.942
	Insectivores		5.50	5.91	1.15	0.13	0.736
	Foliage Gleaners ^d						
		Spring					
		0.13	4.18	4.01	1.98	0.00	0.950
		0.26	4.83	3.96	1.98	0.10	0.758
		0.50	6.34	7.19	1.98	0.09	0.766
		Breeding					
		0.13	2.55	2.62	1.98	0.00	0.983

	0.26	3.13	3.87	1.98	0.07	0.796
	0.50	6.26	2.98	1.98	1.38	0.256
	Post-breeding					
	0.13	3.04	2.59	1.98	0.03	0.874
	0.26	3.31	4.38	1.98	0.15	0.706
	0.50	5.17	9.81	1.98	2.74	0.115
	Fall					
	0.13	6.23	2.03	1.98	2.25	0.151
	0.26	3.39	6.16	1.98	0.97	0.337
	0.50	1.95	9.92	1.98	8.09	0.011
Carolina Wren		0.75	0.70	0.14	0.12	0.750
Hooded Warbler		0.21	0.19	0.14	0.01	0.907
Common Yellowthroat		2.00	2.33	0.59	0.31	0.600
Northern Parula ^e						
	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		2.35	2.75	0.78	0.26	0.628

^a *P* values are from PROC MIXED ANOVA.

^b Gap size x treatment interaction; gap size analyzed separately.

^c Levels of the factor interacting with treatment (i.e., gap size or period) are given in this column.

^d Gap size x treatment x period interaction; gap size and treatment analyzed separately within period.

^e Treatment x period interaction; period analyzed separately.

Table 3. Foraging attack rates (attacks per minute) for each year in treated (arthropods removed) and control canopy gaps in South Carolina (2002 - 2003). Degrees of freedom for treatment effect are $F_{1,6}$ and for the treatment x period interaction is $F_{1,184}$.

Year	Variable	Control	Treated	SE	<i>F</i>	<i>P</i> ^a
2002	All Species*	3.78	2.75	0.68	2.33	0.178
2003	All Species**					
	Season ^b					
	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

^a *P* values are from PROC MIXED ANOVA.

^b Significant treatment x period interaction; seasons analyzed separately.

* All species for 2002 includes: Yellow-billed Cuckoo (*Coccyzus americanus*) - 4; Ruby-throated Hummingbird (*Archilochus colubris*) - 2; Eastern Wood-Pewee - 12; Acadian Flycatcher - 3; Great Crested Flycatcher - 7; White-eyed Vireo - 1; Yellow-throated Vireo - 4; Red-eyed Vireo - 4; Carolina Chickadee - 1; Tufted Titmouse - 7; White-breasted Nuthatch - 2; Carolina Wren - 10; Blue-gray Gnatcatcher - 10; Gray Catbird - 1; Northern Parula - 7; Magnolia Warbler - 1; Yellow-rumped Warbler - 1; Black-and-White Warbler - 1; American Redstart - 3; Common Yellowthroat - 38; Yellow-breasted Chat - 1; Summer Tanager - 11; Northern Cardinal - 6; Blue Grosbeak - 7; Indigo Bunting - 24; Unknown - 1.

** All species for 2003 includes: Yellow-billed Cuckoo - 6; Ruby-throated Hummingbird - 4; Eastern Wood-Pewee - 5; Acadian Flycatcher - 5; Eastern Phoebe - 1; Great Crested Flycatcher - 4; White-eyed Vireo - 2; Red-eyed Vireo - 1; Carolina Chickadee - 1; Carolina Wren - 6; House Wren - 1; Sedge Wren (*Cistothorus platensis*) - 1; Ruby-crowned Kinglet (*Regulus calendula*) - 1; Blue-gray Gnatcatcher - 9; Northern Parula - 10; Yellow-rumped Warbler - 2; American Redstart - 1; Northern Waterthrush - 1; Common Yellowthroat - 101; Hooded Warbler - 2; Summer Tanager - 6; Scarlet Tanager - 1; Swamp Sparrow (*Melospiza georgiana*) - 1; Northern Cardinal - 4; Indigo Bunting - 27.

Table 4. Percent vegetation cover and stem density in six treatment and six control canopy gaps at the Savannah River Site, South Carolina (2002 - 2003). Degrees of freedom are $F_{1,6}$ for all variables in both years.

Variable	Percent Vegetation Cover					Stem Density				
	Control	Treated	SE	<i>F</i>	<i>P</i>	Control	Treated	SE	<i>F</i>	<i>P</i>
TOTAL										
2002	45.21	47.76	4.56	0.31	0.597	40.71	49.90	5.80	2.52	0.166
2003	53.57	59.17	10.10	0.31	0.600	49.30	57.89	7.24	1.41	0.281
FORB										
2002	15.10	15.95	5.62	0.02	0.884	17.32	20.44	7.34	0.18	0.686
2003	12.43	13.21	3.55	0.05	0.832	9.47	11.11	3.27	0.25	0.635
GRASS										
2002	22.31	24.60	5.84	0.15	0.709	12.91	21.07	5.18	2.48	0.166
2003	23.69	31.83	7.61	1.15	0.326	26.41	38.04	6.78	2.95	0.137
VINE										
2002	3.19	2.36	1.57	0.28	0.616	6.67	3.61	3.37	0.67	0.444
2003	6.45	3.86	2.98	0.76	0.418	9.31	4.16	4.98	1.09	0.337
WOODY										
2002	4.62	4.86	1.67	0.02	0.891	3.81	4.79	0.84	1.37	0.287
2003	11.00	10.26	4.77	0.02	0.882	4.11	4.58	1.58	0.09	0.774

Figure Legends

Figure 1. Mean arthropod abundance in six treated and six control canopy gaps by year, at the Savannah River Site, South Carolina (2002 - 2003). Data transformation was used to obtain homogeneity of variance for arthropod abundance [$\text{Log}(x+1)$].

Figure 2. Foliage height profiles for (A) 0.13, (B) 0.26, and (C) 0.50-ha gaps in treatment and control gaps in a bottomland hardwood forest in South Carolina (2002 - 2003).

Vegetation measurements were collected in July and August in 2002 and 2003, respectively.

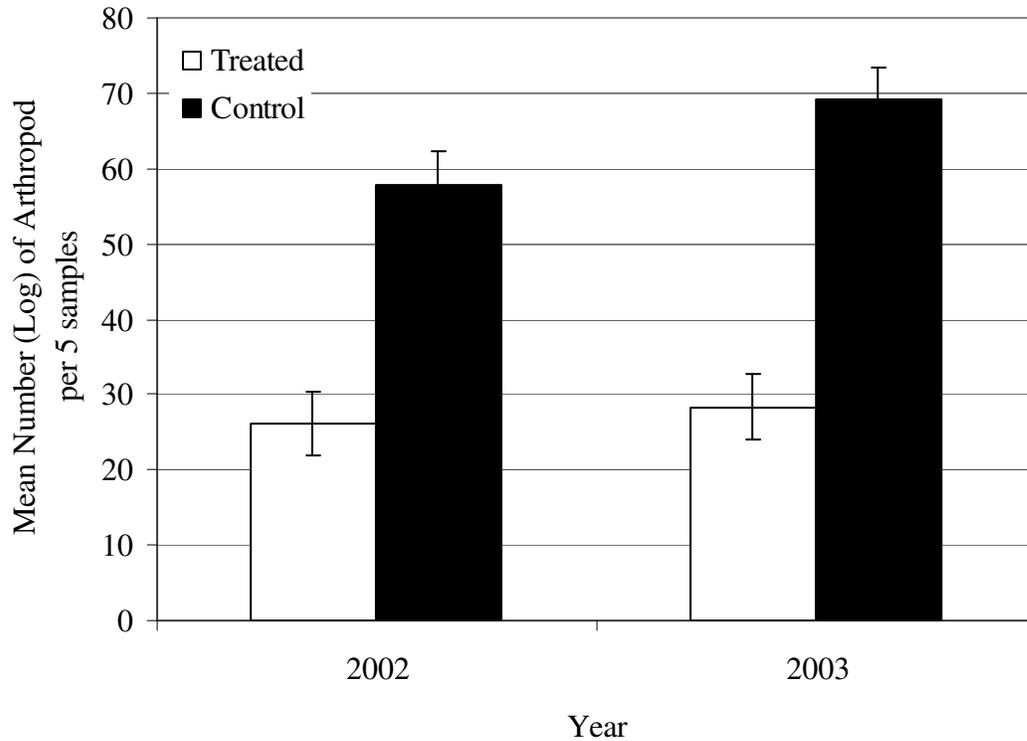


Figure 1. Mean arthropod abundance in six treated and six control canopy gaps by year, at the Savannah River Site, South Carolina (2002 - 2003). Data transformation was used to obtain homogeneity of variance for arthropod abundance [$\text{Log}(x+1)$].

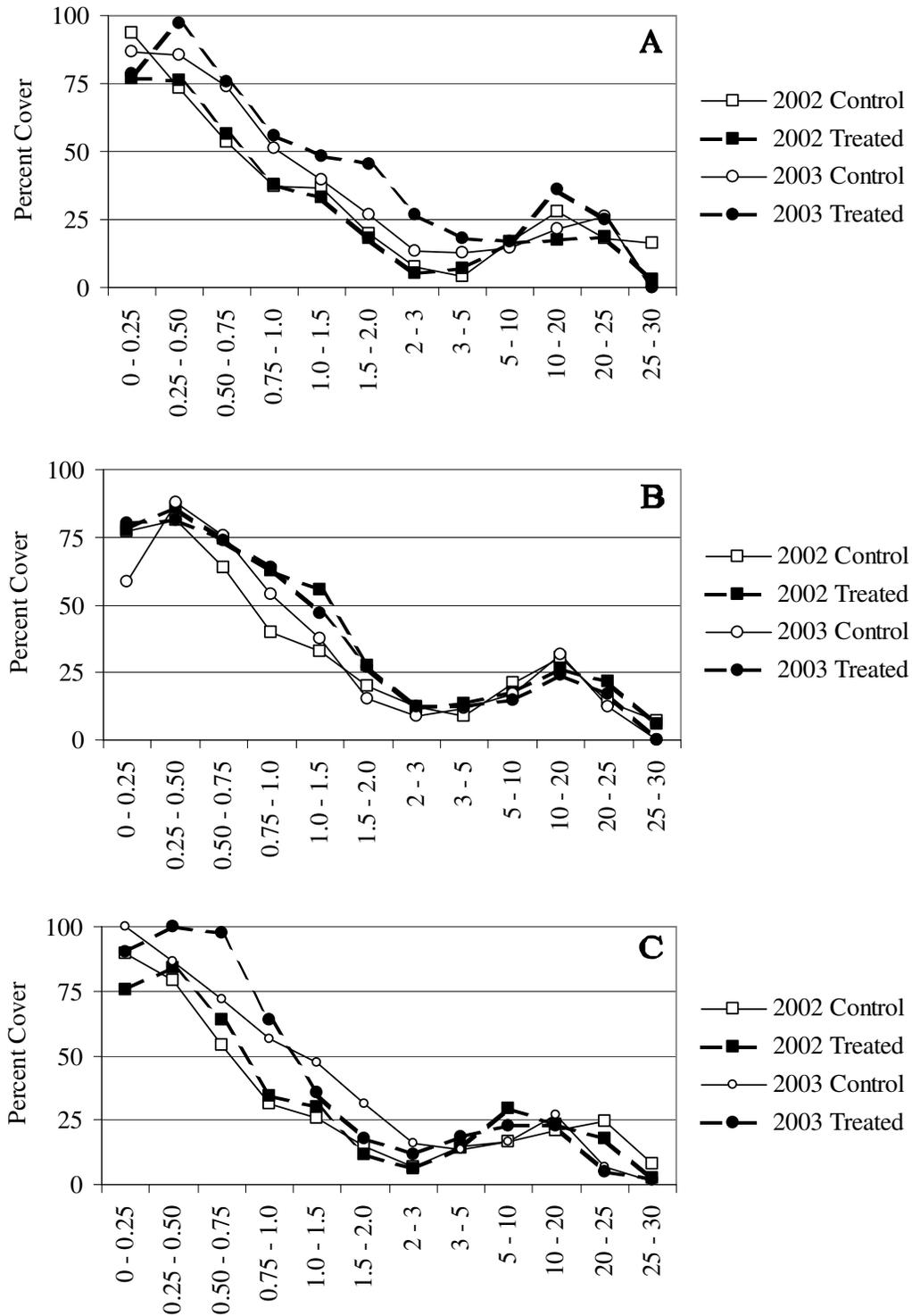


Figure 2. Foliage height profiles for (A) 0.13, (B) 0.26, and (C) 0.50-ha gaps in treatment and control gaps in a bottomland hardwood forest in South Carolina (2002 - 2003). Vegetation measurements were collected in July and August in 2002 and 2003, respectively.

APPENDICES

Appendix 1. Species captured in experimental canopy gaps in South Carolina (2002-2003).

Scientific names follow AOU (2005). Recaptures not included.

Species	Scientific Name	2002	2003
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	3	0
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	3	0
Downy Woodpecker	<i>Picoides pubescens</i>	1	2
Hairy Woodpecker	<i>Picoides villosus</i>	1	1
Eastern Wood-Pewee	<i>Contopus virens</i>	10	0
Acadian Flycatcher	<i>Empidonax virescens</i>	10	10
Eastern Phoebe	<i>Sayornis phoebe</i>	5	3
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	4	1
White-eyed Vireo	<i>Vireo griseus</i>	5	15
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0	1
Red-eyed Vireo	<i>Vireo olivaceus</i>	3	9
Carolina Chickadee	<i>Poecile carolinensis</i>	3	6
Tufted Titmouse	<i>Baeolophus bicolor</i>	40	12
White-breasted Nuthatch	<i>Sitta carolinensis</i>	1	0
Carolina Wren	<i>Thryothorus ludovicianus</i>	106	68
House Wren	<i>Troglodytes aedon</i>	2	3
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	10	5
Veery	<i>Catharus fuscescens</i>	2	2
Gray-cheeked Thrush	<i>Catharus minimus</i>	2	1
Swainson's Thrush	<i>Catharus ustulatus</i>	1	2

Hermit Thrush	<i>Catharus guttatus</i>	1	0
Wood Thrush	<i>Hylocichla mustelina</i>	0	4
Gray Catbird	<i>Dumetella carolinensis</i>	7	8
Northern Mockingbird	<i>Mimus polyglottos</i>	1	0
Brown Thrasher	<i>Toxostoma rufum</i>	3	1
Tennessee Warbler	<i>Vermivora peregrina</i>	2	1
Northern Parula	<i>Parula americana</i>	31	70
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	1	3
Magnolia Warbler	<i>Dendroica magnolia</i>	7	1
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	5	4
Yellow-rumped Warbler	<i>Dendroica coronata</i>	2	0
Blackburnian Warbler	<i>Dendroica fusca</i>	1	0
Yellow-throated Warbler	<i>Dendroica dominica</i>	0	1
Pine Warbler	<i>Dendroica pinus</i>	5	0
Palm Warbler	<i>Dendroica palmarum</i>	2	0
Black-and-white Warbler	<i>Mniotilta varia</i>	2	2
American Redstart	<i>Setophaga ruticilla</i>	7	6
Prothonotary Warbler	<i>Protonotaria citrea</i>	0	4
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	2	1
Ovenbird	<i>Seiurus aurocapilla</i>	4	2
Northern Waterthrush	<i>Seiurus noveboracensis</i>	1	33
Kentucky Warbler	<i>Oporornis formosus</i>	3	2
Common Yellowthroat	<i>Geothlypis trichas</i>	87	176

Hooded Warbler	<i>Wilsonia citrina</i>	29	16
Yellow-breasted Chat	<i>Icteria virens</i>	4	2
Summer Tanager	<i>Piranga rubra</i>	18	10
Scarlet Tanager	<i>Piranga olivacea</i>	0	1
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	3	1
Northern Cardinal	<i>Cardinalis cardinalis</i>	47	17
Blue Grosbeak	<i>Passerina caerulea</i>	8	5
Indigo Bunting	<i>Passerina cyanea</i>	66	78
Painted Bunting	<i>Passerina ciris</i>	1	1
Total		562	591

Appendix 2. Number of arthropods collected per gap in treatment and control canopy gaps in a bottomland hardwood forest in South Carolina (2002 - 2003).

Order	Number of Individuals											
	2002						2003					
	Control			Treatment			Control			Treatment		
	0.13	0.26	0.50	0.13	0.26	0.50	0.13	0.26	0.50	0.13	0.26	0.50
Acari	6	50	0	1	0	0	1	3	1	0	0	0
Araneae	243	192	188	93	59	53	845	1260	598	140	57	75
Coleoptera	165	975	477	462	43	83	98	148	178	27	20	38
Collembola	9	1	10	11	7	12	20	19	8	0	1	0
Diptera	1167	1085	967	434	477	504	2232	2852	2210	792	1230	801
Geophila	1	0	0	0	0	0	30	66	16	36	35	11
Hemiptera	33	116	23	1	6	9	47	51	82	7	8	1
Homoptera	351	380	317	15	36	24	768	711	656	57	55	102
Hymenoptera	240	176	195	133	126	119	231	316	168	74	57	91
Lepidoptera	67	66	44	3	3	3	78	27	42	2	7	5
Odonata	0	0	0	0	0	0	7	6	3	1	7	8
Orthoptera	199	693	54	24	13	10	25	38	33	4	3	3
Siphoniulida	10	0	3	0	0	0	1	0	0	0	0	0
Neuroptera	5	1	0	0	0	0	2	5	1	0	0	0
Thysanoptera	2	2	1	0	0	0	0	0	0	0	0	0
Unknown	7	5	9	1	0	2	15	43	10	2	22	2
Total	2505	3742	2288	1178	770	819	4400	5545	4006	1142	1502	1137

CHAPTER 2

Avian response to microclimate

AVIAN RESPONSE TO MICROCLIMATE IN CANOPY GAPS IN A BOTTOMLAND HARDWOOD FOREST

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Abstract

Microclimate may influence use of early successional habitat by birds. We assessed the relationships between avian habitat use and microclimate (temperature, light intensity, and relative humidity) in experimentally created canopy gaps in a bottomland hardwood forest on the Savannah River Site, South Carolina. Gaps were 2- to 3-year-old group-selection timber harvest openings of three sizes (0.13, 0.26, 0.50 ha). Our study was conducted during four bird-use periods (spring migration, breeding, post-breeding, and fall migration) in 2002 and 2003. We used mist netting and simultaneously recorded microclimate variables to determine the influence of microclimate on bird habitat use. Microclimate was strongly correlated with net location within canopy gaps in both years. Temperature generally was higher on the west side of gaps, light intensity was greater in gap centers, and relative humidity was higher on the east side of gaps. Relationships between bird captures and the microclimate variables were inconsistent. Bird captures were inversely correlated to temperature during the breeding and post-breeding periods in 2002 and captures were positively correlated with temperature during spring 2003. Captures were high where humidity was high during post-breeding 2002 and captures were low where humidity was high during spring 2003. We suggest variations in the local microclimate had minor influence on avian habitat use. Instead, habitat selection is based primarily on vegetation structure, while other factors, including microclimate, play lesser roles.

Key Words: canopy gaps, forest birds, habitat use, light intensity, microclimate, relative humidity, temperature.

INTRODUCTION

Birds may be more abundant in and adjacent to canopy gaps, especially larger ones, than adjacent mature forest (Kilgo 1999, Moorman and Guynn 2001). Bird use of gaps may vary temporally from spring migration through fall migration (Bowen et al. 2007). For example, post-fledging dispersal of birds from their natal habitats in mature forest with high canopy cover tends to be towards large openings or patches of early successional habitat with little to no canopy and a dense understory (Anders et al. 1998, Vega Rivera et al. 1998), thus yielding greater abundance there during the post-breeding period than in the breeding period. Higher food abundance, increased vegetative structure (Blake and Hoppes 1986), or higher temperature (Karr and Freemark 1983) may explain the greater use of gaps by birds. However, few studies have addressed the roles these habitat components play in temporal or spatial changes in bird use of early successional habitat.

Karr and Freemark (1983) suggested the importance of microclimate as a factor in determining avian “physiological comfort.” Microclimate may have adverse effects on birds and their reproductive fitness (Walsberg 1985, Wachob 1996a, Martin and Ghalambor 1999). Conversely, selection for particular microclimatic conditions may minimize foraging costs in relation to benefits. Feeding in open areas such as forest canopy gaps, where the incoming solar radiation and air temperature is greater than the adjacent forest (Chen et al. 1993), energetically reduces foraging costs (DeWoskin 1980). Most microclimate studies have focused on fixed points in time or space, such as single seasons, nest sites, roost sites, or breeding or wintering grounds (Calder 1973, Wachob 1996a, 1996b, Martin and Ghalambor 1999). Less is known about the effects of microclimatic factors on diurnal activities of birds across a spatial and temporal gradient, although microclimate studies have been conducted in

clearcuts where air temperature dramatically increases during the day relative to forest interiors (Chen et al. 1993). Birds may respond directly to microclimate changes or indirectly to changes in food or cover resulting from microclimate changes. For example, many arthropods, which constitute an important food resource for birds, exhibit a positive response to light and a negative response to shade (White 1984). Additionally, gaps are an important determinant of arthropod abundance and diversity because of high light intensity (Ulyshen et al. 2004).

Light, wind, temperature, radiation, humidity, and soil conditions define specific microclimates (Walsberg 1985, Phillips and Shure 1990, Chen et al. 1999). Whether natural or manmade, changes in forest structure affect the local microclimate (Minckler et al. 1973, Phillips and Shure 1990, Saunders et al. 1991). The creation of a canopy gap results in spatial and temporal differences in the microclimate (Phillips and Shure 1990, Saunders et al. 1991, Xu et al. 1997, Chen et al. 1999), and in plant species composition and structure (Phillips and Shure 1990), and hence resource availability (Levey 1988). These changes to components of habitat quality may be important in influencing biological processes such as survival, reproduction, species dispersal, and habitat selection (Perry 1994, McCollin 1998). Temperature also can influence the timing of breeding seasons (Perrins 1965).

Within seemingly homogenous habitat patches, small-scale variability in microclimate may be important in habitat selection by birds (Chen et al. 1993, 1995, Matlack 1993, Sisk et al. 1997). Because microclimate metrics vary differentially with the type and size or length of edge (Saunders et al. 1991, Chen et al. 1999), gap size may similarly influence microclimate. For example, light intensity and air temperature increases from mature to successional forests (Chen et al. 1995, Sisk et al. 1997). Similarly, particular

locations within a canopy gap likely have unique microclimates that may influence bird activity because of shading or distance to forest.

The degree to which birds respond to microclimatic variation within canopy gaps and among gaps of different size is unknown. We assessed the relationships between avian use of gaps and microclimate measures (temperature, light intensity, and relative humidity) in experimentally created forest canopy gaps of three sizes in a bottomland hardwood forest on the Savannah River Site in South Carolina. We hypothesized that mist-net captures of birds would vary with temperature, light intensity, or relative humidity.

STUDY SITE

We conducted the study during 2002 and 2003 at the Department of Energy's Savannah River Site, a 78 000-ha National Environmental Research Park in the Upper Coastal Plain of South Carolina. The 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 generally sparse midstory consisted primarily of American holly (*Ilex opaca*), red mulberry (*Morus rubra*), and ironwood (*Carpinus carolinianus*). The 57-year (1948-2004) mean temperature for the months of April - October ranged from 10.06-33.56 °C (mean = 22.96 °C), and mean monthly rainfall ranged from 70.1-125.5 mm (mean = 105.2 mm; SERCC 2005).

METHODS

As part of a larger study examining bird-arthropod relations in canopy gaps (Champlin 2007), we created 12 experimental canopy openings (hereafter gaps) via group-selection timber harvest in August 2000. Four replicates of three sizes (0.13, 0.26, 0.50 ha) were harvested, with the boundary of each gap at least 150 meters from the nearest adjacent gap. Because arthropod abundance was manipulated in six of the gaps, herein we consider only data from six (two of each size) unmanipulated control gaps. Gaps were circular in shape and were defined to include all of the cleared area within the circumference delineated by the boles of trees left standing at the gap perimeter. During our study, which occurred during the second and third growing seasons post-harvest, gaps mainly contained 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.

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 mist 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 meters. Vegetation touches were recorded along a 2-cm x 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 vegetation types (GRASS, FORB, WOODY, and VINE) because most gap vegetation occurred within 3 m of the ground and nets we sampled only the lowest 3m of vegetation. A gap's total percent cover (COVER) was calculated by averaging the four vegetation types.

MICROCLIMATE DATA COLLECTION.

We used Four-channel HOBO[®] H-8 data loggers (Onset Computer Corporation, Bourne, MA) to measure temperature, light intensity, and relative humidity. These data loggers had an accuracy and collection range for temperature, light intensity, and relative humidity of $\pm 0.70^{\circ}\text{C}$ over -20°C to $+70^{\circ}\text{C}$, ± 2 lumens/ m^2 ($\pm 20\%$ of reading) over 2 to 600 lumens/ ft^2 , and $\pm 5\%$ over $+5^{\circ}\text{C}$ to $+50^{\circ}\text{C}$, respectively.

Data loggers were placed each day at fixed positions at the midpoint of each mist net (see Avian Response below), 1 m from the cleared net lane and 1 m above the ground (Sisk et al. 1997). North and south nets measured conditions at the gap edges, though data loggers were placed within the gap. East, west, and center nets measured conditions in the gap. Loggers were affixed to the top of a 1-m cane pole with Velcro[®] to minimize contact surface area that might influence the environmental readings. HOBO[®] logger data collection intervals were set to once every 12-sec, for a maximum collection time of 6 hrs, 37 minutes (1 985 data points per logger). We assumed that birds in the net at the time of extraction were caught within the climate recording hour interval (synonymous with mist-net checks every hour). Loggers were not deployed when conditions were foggy (i.e., visible water vapor in the air) to prevent damage to the humidity sensor (Onset Computer Corporation, Bourne, MA), and were removed if rain was threatening. We calculated the mean for each

microclimate variable by averaging the values from points taken within the net-check hour each day for each logger.

AVIAN RESPONSE.

We determined the relationship between bird use of various sized gaps and their microenvironments during four periods: spring migration (Apr 1 – May 12), breeding (May 13 – Jul 7), post-breeding (Jul 8 – Aug 31), and fall migration (Sep 1 – Oct 18). Mist netting and microclimate measurements were conducted simultaneously, 5 days per week during all periods. Five nets (4-panel, 30-mm mesh) were deployed in each gap: one at center, one each on and perpendicular to the north and south edges, and two halfway to the east and west gap edges. Nets were operated in three gaps (one of each size) each day from daylight until approximately 3-5 hours post sunrise, depending on weather conditions. Captured birds were identified to species, banded with a metal federal band, aged, sexed, measured, and released (Pyle 1997). Only those captures that had corresponding microclimate readings were used in analyses. For example, if a data logger was removed early because of the threat of rain, any subsequent captures were not included in the analyses. Numbers of captures were standardized to captures per 100 net hours. Our sample size was too small to conduct analyses at the species level.

DATA ANALYSIS.

Because of extreme differences in environmental conditions between sampling years, with drought in 2002 and flooding in 2003, we analyzed years separately.

Vegetation.—We used a linear mixed model (PROC MIXED, SAS Institute 1990) to analyze the effects of gap size and net location on vegetation. We considered gaps as the replicate whole plot units, gap size as the whole plot factor, and net location as the subplot

factor. Because vegetation data was collected once per year, this model did not include period.

Microclimate.—We used a linear mixed model (PROC MIXED, SAS Institute 1990) to compare mean temperature, light intensity, and relative humidity among periods, gap sizes, and net locations in each year. All microclimate measures were highly correlated ($r > 0.9$), so each microclimate parameter was analyzed in a separate model. We considered gaps as the replicate whole plot units, gap size and period as the whole plot factors, and net as the subplot factor.

Avian response.—We analyzed bird response to microclimate separately for each bird use period. We used a linear mixed model (PROC MIXED, SAS institute 1990) to test avian response to the effects of temperature ($^{\circ}\text{C}$), light intensity (lumens/ ft^2), and relative humidity (Rh)%. We considered gaps as the replicate whole plot units, gap size as the whole plot factor, and net location as the subplot factor. Birds considered winter residents (Hamel 1992), present only in early spring or late fall, and hummingbirds were not included in analyses. Only initial captures were used in analyses to minimize effects of autocorrelation. We could not test for daily response because the number of bird captures each day was small.

RESULTS

VEGETATION.

Total percent cover of vegetation (COVER) and the four categories of vegetation cover (GRASS, FORB, VINE, WOODY) did not differ among gap sizes (Table 1). In both years, total percent cover (COVER) and percent cover of FORB and GRASS were highest at center nets and lowest at the north and south edge nets (Table 1).

MICROCLIMATE.

We deployed Hobo[®] data loggers 108 days in 2002 and 119 days in 2003. This resulted in 9 807 minutes of data (2 941 981 12-second readings) for each microclimate variable over the 2-year study.

During daylight hours (0600-1300 hours), mean air temperature in canopy gaps averaged $22.56 \pm 1.98^{\circ}\text{C}$ in 2002 and $22.08 \pm 2.76^{\circ}\text{C}$ in 2003. Mean light intensity averaged 543.61 ± 108.99 lumens/ft² in 2002 and 527.62 ± 107.49 lumens/ft² in 2003. Mean relative humidity averaged $81.99 \pm 6.94\%$ in 2002 and $76.90 \pm 8.71\%$ in 2003

Gap size.—Relative humidity was highest in 0.13-ha gaps during the breeding period in 2003, and light intensity was highest in 0.50-ha gaps during the breeding, post-breeding, and fall migration periods in 2003 (Table 2).

Net location.—Temperature and relative humidity differed among net locations in all seasons of both years except during the 2002 post-breeding period (Table 2). Light intensity differed among net locations in every period of 2002 except for fall migration, but differed among net locations only during the breeding period and fall migration in 2003.

AVIAN RESPONSE.

In 2002, we operated mist nests for 3 842 net-hours and captured 263 individuals representing 41 species. In 2003, mist nets were operated for 4 107 net hours and 282 individuals representing 33 species were captured. Bird captures decreased with temperature increases during the breeding and post-breeding periods in 2002 and increased with temperature increases in spring 2003 (Table 3). Bird captures were lowest where light intensity was highest in the breeding period in 2002 (Table 3). Bird captures and relative humidity were positively correlated during the post-breeding period in 2002 and negatively

correlated during spring migration in 2003 (Table 3). During the fall migration period, no relationships between captures and microclimate were detected (Table 3).

DISCUSSION

Relationships between bird captures and microclimate variables generally were inconsistent. Birds were attracted to lower temperatures and higher humidity during the warmer phases of the breeding and post-breeding periods and tracked higher temperatures and lower humidity during the cooler weeks of spring migration. Birds avoided areas of the greatest light intensity in gaps in all seasons and both years, though only the negative relationship during the breeding period in 2002 was significant. Nets with the highest light intensity likely were most visible to birds. Also, mist-net captures were lowest later in the morning when light intensity was highest. In general, the relationships between avian habitat use and microclimate were weak.

Microclimate varied among net locations in both years, likely as a result of differential shading or distance to forest. The progression of light entering a gap as the sun rises influences the microclimate gradients in the gap. For example, the west nets were first to receive light as the sun penetrated a gap's interior, thus beginning to warm the gaps from the west and progressing east. As the sun's angle increased, the temperature within a gap increased from west to east. As a gap warmed, relative humidity changed inversely with air temperature (Critchfield 1983). A gap's east side generally had cooler temperatures and thus experienced higher relative humidity. When the sun reached its zenith, the temperature differential across a gap abated.

Variations in microclimate within gap openings were fairly consistent. In nearly every season in both years, temperature was higher at the west nets, light intensity was

greater at the center nets, and relative humidity was higher at the east nets. Relative humidity is dependent on air temperature and is the ratio of the amount of water vapor in the air to the amount of water vapor the air can hold for a given temperature (Critchfield 1983). East nets, which tended to have the highest relative humidity, also had the lowest temperatures. Temperature generally corresponded to light intensity with a slight time lag; temperature increases as light intensity increases (Ritter 2006).

Several studies have demonstrated the influence of microclimate on animal habitat use and behavior. In a Mediterranean montane forest, Huertas and Dias (2001) determined that avian abundance and species richness could be predicted by the amount of solar radiation. Additionally, birds select roosting sites based on microclimate (Wolf et al. 1996). Petit et al. (1985) reported that relative humidity was positively correlated with avian species richness during the breeding season. Small passerines in the lowland tropics respond to high humidity and high temperatures by avoiding these conditions when foraging (Weathers 1997). Conversely, Albano (1992) found little evidence that microclimate played a significant role in reproductive success of Carolina Chickadees during the breeding season. Similarly, Buehler et al. (1991) also found little to suggest that microclimate was an important factor in roost-site selection.

Avian use of habitats may be equally related to temperature and humidity. Both temperature and humidity are controlling factors on the environment and may be considered as vital to the organisms within that environment (Twomey 1936). The rate at which a bird (and other animals) loses or gains heat to or from its surroundings is directly influenced by each of these environmental factors (Porter et. al. 2000). The most significant ambient factor which affects internal temperature and ultimately "physiological comfort" is air temperature,

affecting the rate of heat loss or gain by convection (Webb and Rogers 1988). Aside from wind (which we did not measure), humidity must also be in the equation. Humidity affects the rate at which the body loses heat by evaporation. During high temperatures, high humidity makes evaporative cooling more difficult (Webb and Rogers 1988). Variations in humidity can cause significant differences in heat loss by birds at higher temperatures, even if the birds are not heat stressed (Webb and Rogers 1988).

Although microclimate does not appear to be a primary determinant of habitat use in our study, it may be important in some seasons or conditions. Birds were attracted to lower temperatures and higher relative humidity during warmer periods and tracked higher temperature and lower relative humidity during the cooler weeks of spring migration. These within patch shifts in avian habitat use during various seasons suggest that some birds tracked microclimate for "physiologic comfort" (Karr and Freemark 1983). In more extreme environments, Phainopeplas shifted to cooler microclimates to balance thermoregulatory demands (Walsberg 1985), and Mountain Chickadees preferentially selected warmer foraging sites (Wachob 1996b). Avian habitat selection via microclimate may be less important at our study site because of the relatively mild climate there. The Southeast generally lacks environmental extremes. This less extreme climate may favor selection of habitats by birds via factors other than microclimate, except perhaps on the coldest and warmest days.

The lack of consistent relationships between bird captures and microclimate may be evidence that vegetation structure has more influence on avian use of canopy gaps than microclimate. Bowen (2004) and Champlin (2007) concluded that avian use of forest canopy gaps was in response to complex vegetation structure rather than arthropod prey availability.

Birds may select the dense vegetation in forest canopy gaps during migration and post-breeding dispersal, periods of increased mobility and vulnerability to predators. During the post-breeding period, molting adults and newly fledged young may seek out gaps for the protective cover they offer (Anders et al. 1998, Vega Rivera et al 1998).

We conclude that microclimate variability is not the primary determinant of gap habitat selection by birds in bottomland forests of the relatively mild southeastern U.S. Rather, habitat selection likely is based primarily on vegetation structure, while other factors, including microclimate, play lesser roles.

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LITERATURE CITED

- Anders, A. D., J. Faaborg, and Thompson F. R. III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349-358.
- Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103:328-340.
- Bowen, L. T. 2004. Seasonal relationships between birds and arthropods in bottomland forest canopy gaps. Ph.D. dissertation, North Carolina State University, Raleigh, NC.
- Bowen, L. T., C. E. Moorman, and J. C. Kilgo. 2007. Seasonal bird use of canopy gaps in a bottomland forest. *The Wilson Journal of Ornithology* 119:77-88.
- Calder, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology* 54:127-134.
- Champlin, T. B. 2007. Do food availability and microclimate determine bird use of forest canopy gaps? MS Thesis, North Carolina State University, Raleigh, NC.
- Chen J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219-237.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimate gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5:74-86.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288-297.
- DeWoskin, R. 1980. Heat exchange influence on foraging behavior in *Zonotrichia* flocks. *Ecology* 61:30-36.

- Hamel, P. B. 1992. Land Manager's Guide to the Birds of the South. The Nature Conservancy, Chapel Hill, NC; USDA Forest Service, Southern Region, Atlanta, GA.
- Huertas, D. L., and J. A. Diaz. 2001. Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. *Canadian Journal of Zoology* 79:279-284.
- Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs* 41:130-148.
- Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64:1481-1494.
- Kilgo, J. C., K. V. Miller, and W. P. Smith. 1999. Effects of group selection timber harvest in bottomland hardwoods on fall migrant birds. *Journal of Field Ornithology* 70:404-413.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and Plants. *Ecology* 69:1076-1089.
- Martin, T. E., and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? *The American Naturalist* 153:131-139.
- Matlack, G. R. 1993. Microenvironment variation within and among deciduous forest edge sites in eastern United States. *Biological Conservation* 66:185-194.
- McCollin D. 1998. Forest edge and habitat selection in birds: a functional approach. *Ecography* 21:247-260.
- Minckler, Leon S., Woerheide, John D., and Richard C. Schlesinger. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. Research Paper NC-89, USDA Forest Service, North Central Experimental Station, St. Paul, MN. 6 p.

- Moorman, C. E. and D. C. Guynn, Jr. 2001. Effects of group selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11:1680-1691.
- SERCC, Southeastern Regional Climate Center. 2005. <http://cirrus.dnr.state.sc.us>. 11/2005.
- Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major* L. *Journal of Animal Ecology* 34:601-647.
- Perry, D. A. 1994. *Forest ecosystems*. Baltimore: Johns Hopkins University Press.
- Petit, D. R., K. E. Petit, and T. C. Grubb, Jr. 1985. On atmospheric moisture as a factor influencing distribution of breeding birds in temperate deciduous forest. *Wilson Bulletin* 97:88-96.
- Petit, D. R. 2000. Habitat use by landbirds along nearctic-neotropical migration routes: Implications for conservation and stopover habitats. Pages 15-33 *in* *Stopover Ecology of Nearctic-Neotropical Migrants: Habitat Relations and Conservation Implications*. (F. R. Moore ed.). *Studies in Avian Biology* No. 20.
- Phillips, D. L. and D. J. Shure 1990. Patch-size effects on early succession in southern Appalachian forests. *Ecology* 71:204-212.
- Porter, W. P., S. Budaraju, W. E. Stewart, and N. Ramankutty. 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist* 40:597-630.
- Pyle, P. 1997. *Identification Guide to North American Birds*. Slate Creek Press, Bolinas, CA.
- Ritter, Michael, E. 2006. *The Physical Environment: an Introduction to Physical Geography*. 10/29/06. http://www.uwsp.edu/geo/faculty/ritter/geog101/textbook/title_page.html.
- Saunders, D. A., R. J. Hobbs, C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.

- Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62:938-945.
- Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* 7:1170-1180.
- Twomey, A. C. 1936. Climographic studies of certain introduced and migratory birds. *Ecology* 17:122-132.
- Ulyshen, M. D., J. L. Hanula, S. Horn, J. C. Kilgo, and C. E. Moorman. 2004. Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. *Forest Ecology and Management* 199:259-272.
- Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. S. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69-78.
- Wachob, D. G. 1996a. A microclimate analysis of nest-site selection by mountain chickadees. *Journal of Field Ornithology* 67:525-533.
- Wachob, D. G. 1996b. The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *Condor* 98:114-122.
- Walsberg, G. E. 1985. Physiological consequences of microhabitat selection. *In* *Habitat Selection in Birds* (Cody, M. L. ed.), pp. 389-413. Academic Press, London and New York.
- Weathers, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. *Auk* 114:341-353.
- Webb, D. R. and C. M. Rogers. 1988. Nocturnal energy expenditure of Dark-eyed Juncos roosting in Indiana during winter. *Condor* 90:107-112.
- White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stress food plants. *Oecologia* 63:90-105.

Wolf, B. O., K. M. Wooden, and G. E. Walsberg. 1996. The use of thermal refugia by two small desert birds. *Condor* 98:424-428.

Xu M., Chen J., and Brookshire B. L. 1997. Temperature and its variability in the oak forests of southeast Missouri's Ozarks. *Climate Research* 8:209-223.

Table 1. Percent vegetation cover in canopy gaps of three sizes and at five net locations at the Savannah River Site, South Carolina (2002 - 2003).

Variable	Gap Size						Net Location								
	0.13	0.26	0.50	SE	$F_{2,3}$	P	North	South	East	West	Center	SE	$F_{4,12}$	P	
COVER															
2002	45.93	46.64	43.07	9.73	0.08	0.929	22.50	23.21	61.07	54.88	64.40	7.52	15.16	0.001	
2003	53.79	48.14	58.79	11.23	0.45	0.675	24.17	34.29	65.12	64.40	79.88	5.99	30.33	< 0.001	
FORB															
2002	13.64	18.43	13.21	6.65	0.38	0.714	2.50	1.55	27.02	17.74	26.67	5.64	9.82	0.001	
2003	12.50	12.21	12.57	3.42	0.01	0.994	3.57	2.14	19.88	13.57	22.98	3.37	15.55	0.001	
GRASS															
2002	22.57	24.79	19.57	5.89	0.40	0.704	15.00	11.79	23.57	30.48	30.71	5.62	4.79	0.015	
2003	23.21	27.71	20.14	4.49	1.44	0.365	11.90	16.19	24.40	32.50	33.45	5.49	6.11	0.006	
VINE															
2002	4.93	1.07	3.57	3.21	0.74	0.547	0.60	4.05	6.19	2.38	2.74	2.32	1.61	0.236	
2003	7.79	3.00	8.57	6.04	0.50	0.650	1.79	7.98	9.05	6.67	6.79	3.40	1.34	0.311	

WOODY

2002	4.79	6.07	6.71	3.06	1.02	0.459	4.40	5.83	4.29	4.29	4.29	2.11	0.21	0.929
2003	10.29	5.21	17.50	7.53	1.35	0.383	6.90	7.98	11.79	11.67	16.67	5.11	1.13	0.388

Table 2. Microclimate variation by gap size and net location in canopy gaps (n=6) in South Carolina, USA, 2002-2003.

Year Period/Variable	Gap Size						Net Location								
	0.13	0.26	0.5	SE	$F_{2,3}$	P	N	S	E	W	C	SE	$F_{4,12}$	P	
2002 Spring															
Temp °C	20.74	22.57	21.92	1.11	0.69	0.566	21.93	20.04	19.90	24.20	22.65	0.68	52.59	<0.001	
Light ^a	525.45	594.37	631.94	44.12	1.50	0.354	502.02	537.83	593.14	645.56	641.04	28.35	20.58	<0.001	
Humidity ^b	78.68	76.34	71.52	2.72	1.80	0.306	74.64	79.48	80.99	68.73	73.73	1.69	50.03	<0.001	
Breeding															
Temp °C	21.17	21.03	21.67	1.06	0.10	0.907	20.52	20.84	20.50	22.91	21.69	0.66	15.20	<0.001	
Light ^a	480.19	529.18	599.98	43.08	1.95	0.286	421.18	491.11	565.09	584.24	620.64	29.14	22.13	<0.001	
Humidity ^b	85.00	82.50	80.58	3.00	0.55	0.627	84.10	83.12	86.29	77.77	82.20	1.91	11.97	0.001	
Post-breeding															
Temp °C	23.78	23.92	24.39	0.62	0.27	0.780	23.93	23.81	23.37	24.94	24.10	0.47	2.97	0.064	
Light ^a	433.16	505.15	586.74	59.11	1.69	0.323	451.18	532.74	473.95	511.92	571.97	40.74	3.68	0.035	
Humidity ^b	89.53	89.85	87.75	1.62	0.49	0.655	88.28	89.26	91.53	86.23	89.92	1.40	2.82	0.074	
Fall															

Table 2 Continued

Tracey B. Champlin

Temp °C	22.57	23.04	23.92	0.82	0.70	0.564	24.18	21.73	22.43	23.82	23.72	0.56	9.66	0.001
Light ^a	485.79	542.39	608.96	76.99	0.64	0.586	538.68	534.39	536.98	557.27	561.26	49.80	0.25	0.904
Humidity ^b	82.64	81.39	78.04	1.93	1.52	0.350	77.15	83.95	83.94	78.49	79.91	1.51	7.57	0.003
2003 Spring														
Temp °C	20.92	21.79	20.56	1.29	0.24	0.801	21.40	19.39	19.42	22.49	22.74	0.80	25.23	<0.001
Light ^a	510.96	602.73	603.72	23.91	4.96	0.112	503.53	542.91	576.45	595.26	644.20	30.87	2.97	0.064
Humidity ^b	82.84	76.21	74.78	4.46	0.93	0.485	77.60	81.76	83.16	73.13	74.07	2.69	26.96	<0.001
Breeding														
Temp °C	20.95	22.03	22.23	0.54	1.65	0.329	21.13	21.07	20.62	23.13	22.71	0.38	21.34	<0.001
Light ^a	443.85	535.85	595.12	24.34	9.81	0.048	424.02	557.83	533.41	533.14	576.29	31.42	3.56	0.039
Humidity ^b	85.25	82.58	76.55	1.10	16.29	0.025	82.34	82.33	84.59	77.98	80.07	0.92	11.67	<0.001
Post-breeding														
Temp °C	24.28	25.29	26.42	0.41	6.96	0.075	24.92	24.56	24.36	26.77	26.04	0.36	11.74	0.001
Light ^a	424.30	558.24	618.08	24.75	16.07	0.025	467.08	511.85	559.41	578.21	551.13	27.98	2.72	0.081
Humidity ^b	67.76	66.98	66.52	2.27	7.78	0.065	65.04	68.50	75.46	62.10	64.34	2.18	5.34	0.011
Fall														

Temp °C	18.19	20.32	22.04	0.78	6.09	0.088	20.91	18.41	18.81	21.75	21.05	0.61	10.53	0.001
Light ^a	386.33	508.99	543.30	21.68	14.50	0.029	438.99	431.02	475.00	554.34	498.36	27.98	3.18	0.053
Humidity ^b	67.76	66.98	66.52	2.27	0.08	0.929	65.04	68.50	75.46	62.10	64.34	2.18	7.22	0.003

^a Light = lumens/ft²

^b Humidity = (Rh)%.

Table 3. Slopes of the lines describing the relationships between microclimate variables and bird activity in six canopy gaps in South Carolina, USA (2002-2003). Also presented are the effects of gap size and net location, included in the ANOVA model to control variance contributed by these effects.

Year	Period/Variable	Slope	SE	$F_{1,11}$	P	Gap Size		Net	
						$F_{2,3}$	P	$F_{4,11}$	P
2002	Spring								
	Temp °C	-0.0619	0.208	0.09	0.771	2.03	0.277	0.78	0.560
	Light	-0.0059	0.004	1.87	0.199	3.86	0.148	1.24	0.351
	Humidity	0.1327	0.068	3.78	0.078	5.23	0.105	1.66	0.228
	Breeding								
	Temp °C	-0.3207	0.131	5.98	0.033	3.73	0.153	2.90	0.073
	Light	-0.0070	0.003	7.18	0.021	8.13	0.062	2.74	0.083
	Humidity	0.1017	0.054	3.57	0.085	3.12	0.185	2.94	0.070
	Post-breeding								
	Temp °C	-0.5613	0.246	5.20	0.044	0.96	0.477	2.84	0.077
	Light	-0.0041	0.003	1.57	0.237	1.20	0.414	1.71	0.218
	Humidity	0.1729	0.075	5.28	0.042	0.67	0.575	2.62	0.093
	Fall								
	Temp °C	-0.1566	0.153	1.05	0.328	22.37	0.016	3.69	0.038
	Light	-0.0013	0.002	0.57	0.467	20.67	0.018	3.72	0.038
	Humidity	0.0384	0.058	0.44	0.520	18.24	0.021	3.03	0.066
2003	Spring								

Temp °C	0.4391	0.142	9.62	0.010	3.04	0.190	5.38	0.012
Light	-0.0044	0.003	2.68	0.130	0.31	0.754	5.93	0.009
Humidity	-0.1393	0.047	8.85	0.013	2.30	0.248	5.15	0.014
Breeding								
Temp °C	0.2938	0.263	1.25	0.288	2.76	0.209	0.88	0.509
Light	-0.0019	0.003	0.32	0.582	3.27	0.176	1.88	0.184
Humidity	-0.0215	0.118	0.03	0.859	0.52	0.638	1.05	0.424
Post-breeding								
Temp °C	-0.4362	0.331	1.74	0.214	2.85	0.202	1.02	0.441
Light	-0.0061	0.004	2.45	0.146	4.15	0.137	1.27	0.341
Humidity	0.1176	0.055	4.61	0.055	6.30	0.084	1.63	0.236
Fall								
Temp °C	0.0451	0.178	0.06	0.805	0.42	0.693	0.38	0.821
Light	-0.0004	0.004	0.01	0.971	0.24	0.802	0.33	0.854
Humidity	0.0031	0.050	0.00	0.951	0.77	0.539	0.37	0.823
