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, SC. 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 from spring through fall, encompassing 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 affected by 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. However, we found few relationships between bird captures and the microclimate variables. Bird captures were inversely correlated with temperature during the breeding and post-breeding periods in 2002 and 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 conclude that variations in the local microclimate had minor influence on avian habitat use within gaps. Instead, habitat selection in relatively mild regions like the southeastern US is based primarily on vegetation structure, while other factors, including microclimate, are less important.

Introduction

Birds are often more abundant in and adjacent to gaps in forest canopies, especially larger gaps, than in adjacent mature forest (Kilgo et al. 1999, Moorman and Guynn 2001). However, the relative use of gaps by birds varies temporally from spring migration through fall migration (Bowen et al. 2007). For example, post-fledging dispersal of birds from natal areas 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 the breeding period. Higher food abundance (Blake and Hoppes 1986, Levey 1988), increased

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vegetative structure (Martin and Karr 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." Extremes in microclimate may have adverse effects on birds and their reproductive fitness (Martin and Ghalambor 1999, Wachob 1996a, Walsberg 1985). 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; Martin and Ghalambor 1999; Wachob 1996a, 1996b). 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, respond positively to light and negatively to shade (White 1984). Abundance and diversity of certain arthropod orders may be high in gaps because of high light intensity (Ulyshen et al. 2004).

Light, wind, temperature, radiation, humidity, and soil conditions define specific microclimates (Chen et al. 1999, Phillips and Shure 1990, Walsberg 1985). Whether natural or man-made, 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 (Chen et al. 1999, Phillips and Shure 1990, Saunders et al. 1991, Xu et al. 1997), in plant species composition and structure (Phillips and Shure 1990), and hence in resource availability (Levey 1988). These effects of microclimate on components of habitat quality may be important in influencing aspects of avian life history such as survival, reproduction, timing of breeding seasons, species dispersal, and habitat selection (McCollin 1998, Perrins 1965, Perry 1994).

Even within seemingly homogenous habitat patches, small-scale variability in microclimate may be important in habitat selection by birds (Sisk et al. 1997). Because microclimate metrics vary differentially with the type and size or length of edge (Chen et al. 1999, Saunders et al. 1991), gap size may similarly influence microclimate. For example, light intensity and air temperature increase 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.

Methods

Study site and design

We conducted the study during 2002 and 2003 at the US Department of Energy's Savannah River Site, a 78,000-ha National Environmental Research Park in the Upper Coastal Plain of South Carolina. The climate of the area is humid subtropical, with a mean annual temperature of 18 °C and mean annual precipitation of 122.5 cm (Blake et al. 2005). During April–October (our study period), long-term (1964–2001) mean monthly temperature ranged from 18.4 °C (April) to 28.1 °C (July), and mean relative humidity ranged from 56% (April) to 78% (August, September) (Blake et al. 2005).

Our 120-ha study site was located in a 70- to 100-year-old, seasonally flooded bottomland hardwood forest. The forest canopy of the study site included typical bottomland hardwood species: *Quercus falcata* var. *pagodaefolia* Elliot (Cherrybark Oak), *Q. laurifolia* Michaux (Laurel Oak), *Q. phellos* Linnaeus (Willow Oak), *Q. lyrata* Walter (Overcup Oak), *Q. michauxii* Nuttall (Swamp Chestnut Oak), *Liquidambar styraciflua* Linnaeus (Sweetgum), and *Pinus taeda* Linnaeus (Loblolly Pine). The understory was dominated by *Sabal minor* Persoon (Dwarf Palmetto) and *Arundinaria gigantea* Muhlenberg (Giant Switchcane), and a generally sparse midstory consisted primarily of *Ilex opaca* Aiton (American Holly), *Morus rubra* Linnaeus (Red Mulberry), and *Carpinus carolinianus* Walter (Ironwood).

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, and 0.50 ha) were harvested, with the boundary of each gap at least 150 m from the nearest adjacent gap. Because arthropod abundance was manipulated in six of the gaps, herein we consider only data from the six unmanipulated control gaps (two of each size). 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), *Eupatorium capillifolium* (Lam.)

Small (Dogfennel), Dwarf Palmetto, Giant Switchcane, and some woody stump sprout regenerative growth.

Mist-netting

We determined the relationship between bird use of various sized gaps and their microenvironments during four periods: spring migration (1 Apr–12 May), breeding (13 May–7 Jul), post-breeding (8 Jul–31 Aug), and fall migration (1 Sep–18 Oct). Dates for these periods were based on previous research in the area (Kilgo et. al 1999, Moorman and Guynn 2001). Mist-netting and microclimate measurements (see below) were conducted simultaneously, 5 days per week during all periods. Because vegetation structure was generally similar among our gaps and was <3 m tall (the height of our mist nets), we felt that biases typically associated with mist-net sampling were minimized (Remsen and Good 1996). 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 hrs 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). Numbers of captures were standardized to captures per 100 net hours. Our sample size was too small to conduct analyses at the species level.

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). Because most gap vegetation occurred within 3 m of the ground, we sampled only the lowest 3 m of vegetation. 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 7 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, and 2–3 m. 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 the 2–3-m height interval, we sighted along the pole and recorded the presence or absence of vegetation. We grouped all height intervals to calculate % cover for each of the four vegetation types (GRASS, FORB, WOODY, and VINE), and a gap's total % cover (COVER) was calculated as the sum of % cover for the four vegetation types.

Microclimate data collection

We measured temperature, light intensity, and relative humidity. We selected these variables because they were easily measured and have been used commonly in other studies of bird response to microclimate. We could

not measure the effects of wind because we could not sample bird response in windy conditions with mist nets. We used Four-channel HOBO[®] H-8 data loggers (Onset Computer Corporation, Bourne, MA) that had an accuracy and collection range for temperature, light intensity, and relative humidity of ± 0.70 °C over -20 – 70 °C, ± 21.5 lumens/m² ($\pm 20\%$ of reading) over 22 – 6458 lumens/m², and $\pm 5\%$ over 5 – 50 °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 hr, 37 min (1985 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 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.

Data analysis

Only those mist-net captures that had corresponding microclimate data 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. Because of substantial differences in rainfall between sampling years, with drought in 2002 and the presence of surface water in spring 2003, we analyzed years separately. All data were tested for normality.

We used a linear mixed model (PROC MIXED, SAS Institute 2001) 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 were collected once per year, this model did not include period.

We used a linear mixed model (PROC MIXED, SAS Institute 2001) 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.

We analyzed bird response to microclimate separately for each bird-use period. We used a linear mixed model (PROC MIXED; SAS institute 2001)

to test avian response to the effects of temperature ($^{\circ}\text{C}$), light intensity (lumens/ m^2), and relative humidity (%). 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

Mist-net captures

In 2002, we operated mist nests for 3842 net hours, during which time we obtained microclimate data and captured 263 individual birds (excluding recaptures) representing 41 species. In 2003, we operated mist nets for 4107 net hours and captured 282 individuals representing 33 species. However, six species comprised 70% of the captures: *Baeolophus bicolor* Linnaeus (Tufted Titmouse, 6%); *Thryothorus ludovicianus* Latham (Carolina Wren, 17%); *Parula americana* Linnaeus (Northern Parula, 7%), *Geothlypis trichas* Linnaeus (Common Yellowthroat, 22%), *Cardinalis cardinalis* Linnaeus (Northern Cardinal, 6%), and *Passerina cyanea* Linnaeus (Indigo Bunting, 12%).

Vegetation

Total % 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 % cover (COVER) and % 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, resulting in 7949 logger-hours. This produced 2,384,700 12-sec readings (7949 logger-hours x 60 min/hr x 5 readings/min) for each microclimate variable over the 2-yr study. During daylight hours (06:00–13:00), mean air temperature in canopy gaps averaged 22.56 ± 1.98 $^{\circ}\text{C}$ in 2002 and 22.08 ± 2.76 $^{\circ}\text{C}$ in 2003. Mean light intensity averaged 5884 ± 1173 lumens/ m^2 in 2002 and 5679 ± 1157 lumens/ m^2 in 2003. Mean relative humidity averaged $81.99 \pm 6.94\%$ in 2002 and $76.90 \pm 8.71\%$ in 2003.

We detected few effects of gap size on microclimate. 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).

Temperature and relative humidity differed among net locations in all seasons of both years except during the 2002 post-breeding period (Table 3).

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 (Table 3).

Avian response to microclimate

Bird captures decreased with temperature increases during the breeding and post-breeding periods in 2002 and increased with temperature increases during spring 2003 (Table 4). Bird captures were lowest where light intensity was highest during the breeding period in 2002 (Table 4). Bird captures and relative humidity were positively correlated during the post-breeding period in 2002 and negatively correlated during spring migration in 2003 (Table 4). During the fall migration period, no relationships between captures and microclimate were detected (Table 4).

Table 1. Percent vegetation cover in three gap sizes (ha) and at five net locations in canopy gaps at the Savannah River Site, SC (2002–2003).

a. Gap size

Variable	0.13 ha	0.26 ha	0.50 ha	SE	$F_{2,3}$	P
COVER						
2002	45.93	46.64	43.07	9.73	0.08	0.929
2003	53.79	48.14	58.79	11.23	0.45	0.675
FORB						
2002	13.64	18.43	13.21	6.65	0.38	0.714
2003	12.50	12.21	12.57	3.42	0.01	0.994
GRASS						
2002	22.57	24.79	19.57	5.89	0.40	0.704
2003	23.21	27.71	20.14	4.49	1.44	0.365
VINE						
2002	4.93	1.07	3.57	3.21	0.74	0.547
2003	7.79	3.00	8.57	6.04	0.50	0.650
WOODY						
2002	4.79	6.07	6.71	3.06	1.02	0.459
2003	10.29	5.21	17.50	7.53	1.35	0.383

b. Net location

Variable	North	South	East	West	Center	SE	$F_{4,12}$	P
COVER								
2002	22.50	23.21	61.07	54.88	64.40	7.52	15.16	0.001
2003	24.17	34.29	65.12	64.40	79.88	5.99	30.33	<0.001
FORB								
2002	2.50	1.55	27.02	17.74	26.67	5.64	9.82	0.001
2003	3.57	2.14	19.88	13.57	22.98	3.37	15.55	0.001
GRASS								
2002	15.00	11.79	23.57	30.48	30.71	5.62	4.79	0.015
2003	11.90	16.19	24.40	32.50	33.45	5.49	6.11	0.006
VINE								
2002	0.60	4.05	6.19	2.38	2.74	2.32	1.61	0.236
2003	1.79	7.98	9.05	6.67	6.79	3.40	1.34	0.311
WOODY								
2002	4.40	5.83	4.29	4.29	4.29	2.11	0.21	0.929
2003	6.90	7.98	11.79	11.67	16.67	5.11	1.13	0.388

Discussion

Microclimate varied much more within gaps than among gaps of different sizes. This within-gap variation was likely a result of differential shading or distance to mature trees. The progression of light entering a gap as the sun rose influenced the microclimate gradients in the gap. For example, the west nets were first to receive light as the sun penetrated the interior of gaps, 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. Temperature generally corresponded to light intensity with a slight time lag, because temperature usually increases as light intensity increases (Ritter 2006). As gaps warmed, relative humidity changed inversely with air temperature. Relative humidity, the ratio of the amount of water vapor in the

Table 2. Microclimate variation by gap size (ha) in six canopy gaps at the Savannah River Site, SC (2002–2003).

Year	Period/variable	0.13 ha	0.26 ha	0.50 ha	SE	$F_{2,3}$	P
2002	Spring						
	Temp °C	20.74	22.57	21.92	1.11	0.69	0.566
	Light ^A	5656	6398	6802	475	1.50	0.354
	Humidity ^B	78.68	76.34	71.52	2.72	1.80	0.306
	Breeding						
	Temp °C	21.17	21.03	21.67	1.06	0.10	0.907
	Light	5169	5696	6458	464	1.95	0.286
	Humidity	85.00	82.50	80.58	3.00	0.55	0.627
	Post-breeding						
	Temp °C	23.78	23.92	24.39	0.62	0.27	0.780
	Light	4663	5437	6316	636	1.69	0.323
	Humidity	89.53	89.85	87.75	1.62	0.49	0.655
	Fall						
	Temp °C	22.57	23.04	23.92	0.82	0.70	0.564
	Light	5229	5838	6555	829	0.64	0.586
	Humidity	82.64	81.39	78.04	1.93	1.52	0.350
2003	Spring						
	Temp °C	20.92	21.79	20.56	1.29	0.24	0.801
	Light	5500	6488	6498	257	4.96	0.112
	Humidity	82.84	76.21	74.78	4.46	0.93	0.485
	Breeding						
	Temp °C	20.95	22.03	22.23	0.54	1.65	0.329
	Light	4778	5768	6406	262	9.81	0.048
	Humidity	85.25	82.58	76.55	1.10	16.29	0.025
	Post-breeding						
	Temp °C	24.28	25.29	26.42	0.41	6.96	0.075
	Light	4567	6009	6653	266	16.07	0.025
	Humidity	67.76	66.98	66.52	2.27	7.78	0.065
	Fall						
	Temp °C	18.19	20.32	22.04	0.78	6.09	0.088
	Light	4158	5479	5848	233	14.50	0.029
	Humidity	67.76	66.98	66.52	2.27	0.08	0.929

^ALight = lumens/m².

^BHumidity = relative humidity (%).

air to the amount of water vapor the air can hold for a given temperature, is dependent on air temperature (Critchfield 1983). The east side of gaps 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 gaps 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.

We found few relationships between bird captures and microclimate variables. Birds apparently were attracted to lower temperatures and higher humidity during the warmer seasons (breeding and post-breeding periods) of 2002, and they tracked higher temperatures and lower humidity during

Table 3. Microclimate variation by net location in six canopy gaps at the Savannah River Site, SC (2002–2003). N = north, S = south, E = east, W = west, and C = center.

Year	Period/variable	N	S	E	W	C	SE	$F_{4,12}$	P
2002	Spring								
	Temp °C	21.93	20.04	19.90	24.20	22.65	0.68	52.59	<0.001
	Light ^A	5404	5789	6385	6949	6900	305	20.58	<0.001
	Humidity ^B	74.64	79.48	80.99	68.73	73.73	1.69	50.03	<0.001
	Breeding								
	Temp °C	20.52	20.84	20.50	22.91	21.69	0.66	15.20	<0.001
	Light	4534	5286	6083	6289	6681	314	22.13	<0.001
	Humidity	84.10	83.12	86.29	77.77	82.20	1.91	11.97	0.001
	Post-breeding								
	Temp °C	23.93	23.81	23.37	24.94	24.10	0.47	2.97	0.064
	Light	4857	5734	5102	5510	6157	439	3.68	0.035
	Humidity	88.28	89.26	91.53	86.23	89.92	1.40	2.82	0.074
	Fall								
	Temp °C	24.18	21.73	22.43	23.82	23.72	0.56	9.66	0.001
	Light	5798	5752	5780	5998	6041	536	0.25	0.904
	Humidity	77.15	83.95	83.94	78.49	79.91	1.51	7.57	0.003
2003	Spring								
	Temp °C	21.40	19.39	19.42	22.49	22.74	0.80	25.23	<0.001
	Light	5420	5844	6205	6407	6934	332	2.97	0.064
	Humidity	77.60	81.76	83.16	73.13	74.07	2.69	26.96	<0.001
	Breeding								
	Temp °C	21.13	21.07	20.62	23.13	22.71	0.38	21.34	<0.001
	Light	4564	6004	5742	5739	6203	338	3.56	0.039
	Humidity	82.34	82.33	84.59	77.98	80.07	0.92	11.67	<0.001
	Post-breeding								
	Temp °C	24.92	24.56	24.36	26.77	26.04	0.36	11.74	0.001
	Light	5028	5510	6021	6224	5932	301	2.72	0.081
	Humidity	65.04	68.50	75.46	62.10	64.34	2.18	5.34	0.011
	Fall								
	Temp °C	20.91	18.41	18.81	21.75	21.05	0.61	10.53	0.001
	Light	4725	4639	5113	5967	5364	301	3.18	0.053
	Humidity	65.04	68.50	75.46	62.10	64.34	2.18	7.22	0.003

^ALight = lumens/m².

^BHumidity = relative humidity (%).

the cooler weeks of spring migration 2003. However, in most seasons, relationships were not significant. Birds avoided areas of the greatest light intensity during the breeding period in 2002, but nets with the highest light intensity probably were most visible to birds. Also, mist-net captures were lowest later in the morning when light intensity was highest. In general, relationships between avian habitat use and microclimate were weak.

Two factors that may have limited our ability to detect avian-microclimate relationships include the necessity of pooling all species and the scale of investigation. Pooling species may have obscured any species-specific responses. However, because our sample was dominated by shrub-scrub

Table 4. Slopes of the lines describing the relationships between microclimate variables and mist-net captures in six canopy gaps at the Savannah River Site, SC (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	Mist-net Captures		Gap size		Net	
				$F_{1,11}$	P	$F_{2,3}$	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 ^A	-0.0059	0.004	1.87	0.199	3.86	0.148	1.24	0.351
	Humidity ^B	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
2003	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
	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

^ALight = lumens/m².

^BHumidity = relative humidity (%).

species, we suspect that these species likely had similar tolerances for the microclimatic conditions of the early successional habitat in our gaps, and thus might have responded in similar ways. Likewise, the fact that we sampled only in gaps, and not in adjacent mature forest, prevented us from detecting birds that may have left gaps completely for potentially more desirable microclimates in nearby forested areas. Although we did not sample forested areas because our focus was on within-gap habitat use, we may have detected more consistent patterns in avian habitat use had we encompassed a broader range of microclimatic conditions.

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. During some warmer seasons, captures were greater in areas of lower temperatures and higher relative humidity, whereas during some cooler seasons, captures were greater in areas of higher temperature and lower relative humidity. These within-patch shifts in avian habitat use during various seasons suggest that birds occasionally tracked microclimate for physiologic comfort (Karr and Freemark 1983), even if these patterns were not consistent throughout the study. Similarly, *Phainopepla nitens* Swainson (*Phainopepla*) in the southwestern US shifted to cooler microclimates to balance thermoregulatory demands during summer (Walsberg 1985), and *Poecile gambeli* Ridgway (Mountain Chickadee) in Wyoming preferentially selected warmer foraging sites during winter (Wachob 1996b). Both of these studies were conducted in more extreme environments than ours. The influence of microclimate on avian habitat selection may be less important at our study site because of the relatively mild climate there. Despite the occurrence of both high and low rainfall conditions between the two years of our study, the microclimate variables we measured were within long-term norms for the area (Blake et al. 2005). The Southeast generally lacks environmental extremes, and this milder 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 the complex vegetation structure there 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 US. Rather, habitat selection is most likely based primarily on vegetation structure, with microclimate being less important.

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