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AVIAN COMMUNITY AND MICROHABITAT ASSOCIATIONS OF CERULEAN WARBLERS IN ALABAMA

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ABSTRACT.—Cerulean Warblers (*Dendroica cerulea*) have experienced one of the highest population declines of any neotropical-Nearctic migratory species in North America. We performed point counts and habitat assessments in areas used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons to examine their avian associations and identify microhabitat features that best explained their occurrence. We detected on average ~50 Cerulean Warbler males (total) in three disjunct populations during each breeding season. Areas used by Cerulean Warblers were characterized by avian communities with significantly higher species richness, diversity, and abundance compared to areas where they were not detected. Correspondence analysis related Cerulean Warblers to inhabitants of riparian, bottomland deciduous forests (e.g., Kentucky Warbler [*Oporornis formosus*], Acadian Flycatcher [*Empidonax virescens*], and Northern Parula [*Parula americana*]) and two edge specialists (Blue-winged Warbler [*Vermivora cyanoptera*] and Indigo Bunting [*Passerina cyanea*]) suggesting Cerulean Warblers in our study areas may be tolerant of some habitat disturbance within an otherwise largely forested landscape. Information theoretic criteria and canonical correspondence analysis indicated Cerulean Warblers preferred bottomland forests containing tall (> 29 m), large diameter, well-spaced (> 27 m^2/ha) deciduous trees with greater canopy cover ($\geq 90\%$), closer (< 20 m) canopy gaps, fewer snags (≤ 25/ha), and a moderately complex canopy structure. *Received 5 March 2010. Accepted 22 December 2010.*

The Cerulean Warbler (*Dendroica cerulea*) has lost nearly 70% of its breeding population since 1966 (Rich et al. 2004) because of alterations in breeding, migratory, and wintering habitats compounded by the bird's dependency on extensive tracts of large deciduous trees in many parts of its range (Hamel 2000a). Northern Alabama historically represented a portion of the Cerulean Warbler's southern-most breeding range where they were described as common and even numerous in several counties throughout the state (Imhof 1976). This warbler is now rarely encountered in Alabama during the breeding season and was designated a Priority One species (highest conservation concern) by the Alabama Department of Conservation and Natural Resources (Mirarchi et al. 2004).

Selection of breeding territories by landbirds is heavily influenced by structure and composition of the surrounding habitat and avian community (MacArthur and MacArthur 1961, Wiens 1989). Thus, effectiveness of management initiatives is dependent upon not only identifying the habitat requirements of the species under investigation, but also the avian community with which it associates. Recent studies of Cerulean Warblers emphasize breeding habitat requirements (Robbins et al. 1992, Jones and Robertson 2001, Weakland and Wood 2005, Barg et al. 2006b), nesting behavior (Oliarnyk and Roberston 1996, Barg et al. 2006a, Rogers 2006, Roth and Islam 2008), and habitat management (Hamel 2005, Hamel et al. 2005b, Hamel and Rosenberg 2007), while information regarding avian associations of Cerulean Warblers remains scarce (Jones et al. 2004) and anecdotal (Lynch 1981, Hamel 2000b).

Recent discoveries of two small Cerulean Warbler populations in Alabama suggest habitat is available in this portion of the species range to support small breeding populations (Carpenter et al. 2005). This study was initiated in response to the Rosenberg et al. (2000) recommendation for additional Cerulean Warbler research in Alabama to provide more accurate population estimates and habitat requirements needed to effectively manage habitat for this species. Our objectives were to: (1) examine avian associations of the Cerulean Warbler to facilitate a better understanding of this species' habitat use and the bird community in which it breeds, and (2) identify microhabitat features that best explain Cerulean Warbler occurrence in the southern portion of its range where populations are in serious decline (Buehler et al. 2008).

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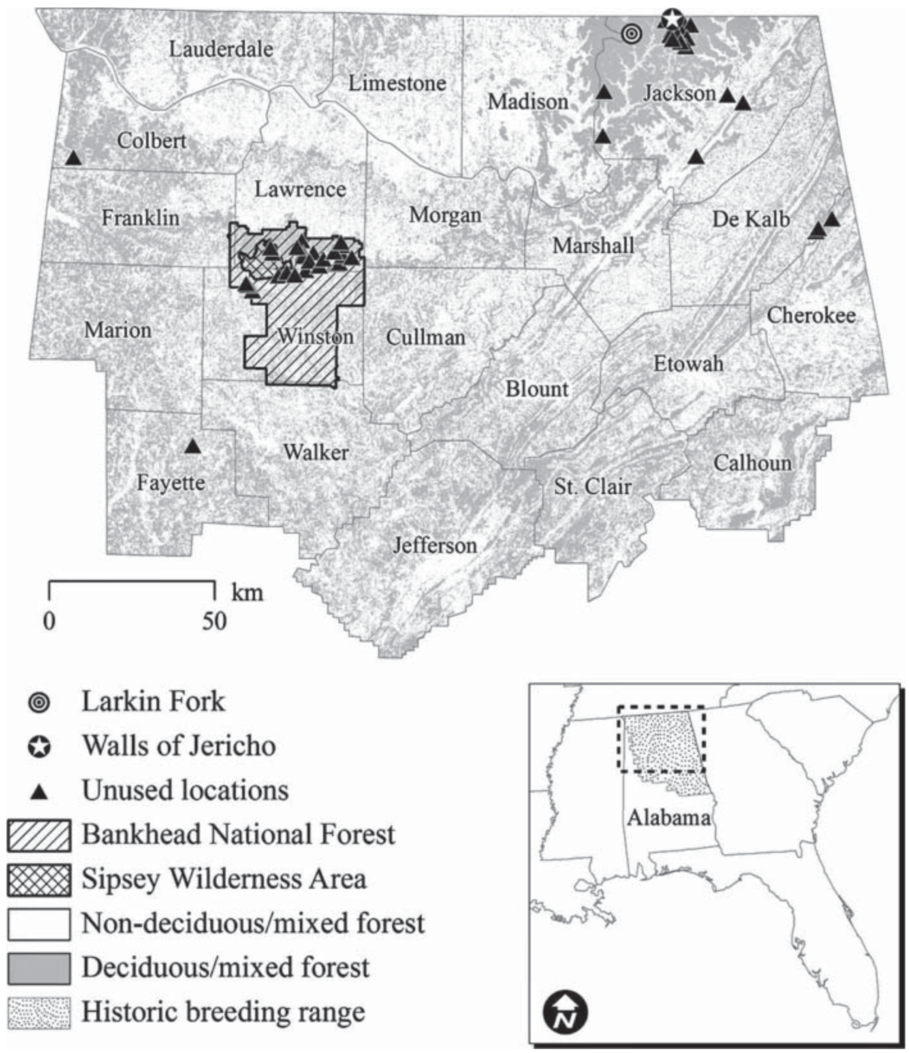

FIG. 1. Sampling locations unused by Cerulean Warblers and Cerulean Warbler populations (Walls of Jericho, Larkin Fork, and Sipsey Wilderness) sampled in northern Alabama during the 2005 and 2006 breeding seasons. Historic range from Imhof (1976).

METHODS

*Study Areas.—*We studied Cerulean Warblers at three sites in northern Alabama during the 2005 and 2006 breeding seasons (Fig. 1). The most recently discovered Cerulean Warbler populations are in Jackson County along Hurricane Creek in the Walls of Jericho tract of Skyline Wildlife Management Area (WMA) (34° 58′ N, 86° 6′ W) and on private property along Larkin Fork (34° 57′ N, 86° 13′ W). Both Jackson County populations breed in bottomland hardwood forest of the Mid-Cumberland Plateau where vegetation is dominated by mature (80+ year-old) forest categorized as oak and oak-hickory (*Quercus* spp.-*Carya* spp.) with mixed mesophytic communities restricted to valleys and coves (Braun 1950). Additional canopy species include box elder (*Acer negundo*), elm (*Ulmus* spp.), hackberry (*Celtis occidentalis*), tulip poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern sycamore (*Platanus occidentalis*), and black walnut (*Juglans nigra*). Several maintained fields averaging

2 ha in size occur throughout the floodplains of these sites. A third Cerulean population is in Lawrence County within the 71,600-ha Bankhead National Forest (34° 20′ N, 87° 22′ W). Bankhead National Forest (BNF) is along the southern Cumberland Plateau and is characterized by dissected sloping ridges and rock bluffs dominated by loblolly pine (*Pinus taeda*), upland hardwood, and mixed hardwood-pine with additional canopy species similar to those at the Jackson County sites (USDA Forest Service 2004). Cerulean Warblers are concentrated in BNF along the floodplain forests of the 4,200-ha Sipsey Wilderness Area.

Bird Surveys.—We surveyed Cerulean Warblers from May to June during the breeding seasons of 2005 and 2006 by walking the floodplains and adjacent slopes of Hurricane Creek and Larkin Fork, and along Flannigan and Borden creeks in Bankhead National Forest. We mapped male Cerulean territories on multiple visits using radiotelemetry, repeated observations of color-banded males, and by distinguishing song variability between neighbors (Woodward 1997). Ten-minute, fixed-radius point counts ($n = 53$) were performed within a territory and centered under individual, singing male Cerulean Warblers. All counts were conducted once at each location prior to 1030 hrs EST following Hamel et al. (1996) by a single observer to eliminate multiple surveyor bias (Sauer et al. 1994).

Point counts were also performed once at 47 additional locations from May to June 2005 and 2006 in an effort to locate new breeding populations (Fig. 1). We concentrated our sampling effort in Skyline WMA and Bankhead NF to reduce spatial variability; however, our only requirements for these locations were that they must occur in deciduous/mixed forest and the Cerulean Warbler's historic breeding range in Alabama (Imhof 1976). We used the ArcGIS (Version 9.1, ESRI 2005) extension Hawth's Tools (Beyer 2004) to generate 26 random points: 12 in Skyline WMA, six in Bankhead NF, and eight in state parks and nature preserves. An additional 19 locations were selected from 122 pre-existing point count stations in Bankhead NF (USDA Forest Service 1995). The remaining two locations were based on Cerulean Warbler observations from Alabama Breeding Bird Atlas surveys in 1999 and 2001 (R. L. West, pers. comm.) in an effort to verify the continued existence of breeding Cerulean Warblers. Playback of a conspecific song was broadcast for 5 min at the conclusion of these counts to ensure that no Cerulean Warblers were present.

Microhabitat Characteristics.—We compared microhabitat from used habitat ($n = 52$) centered at point counts conducted under Cerulean Warbler males, and in unused habitat ($n = 47$) defined as point count locations where Cerulean Warblers were not detected. Habitat measurements for one used point count were not collected due to logistic constraints. The median distance between used locations in the year of sampling was 192.9 m (interquartile range = 112.4–383.6) and 2.1 km (interquartile range = 1.0–2.8) between unused locations. Vegetation was measured by one observer within 0.04-ha (11.3-m radius) circular plots following James and Shugart (1970) and Noon (1981). Plot measurements included basal area, total live stems $\geq$3-cm diameter at breast height (DBH), total snags $\geq$8-cm DBH, tree height, slope, aspect, understory density, and distance to and size of nearest canopy gap. Percent canopy cover was estimated from 40 $\pm$ vertical readings along transects in the cardinal directions using an ocular densitometer tube. Each reading was assigned one of four height intervals ($<$ 5, 5–15, $>$ 15–25, $\geq$ 25 m, or no cover) to estimate canopy structure complexity. Slope was measured in degrees using a clinometer and aspect was transformed to a value ranging from 0.0 to 2.0 (Beers et al. 1966). This distinguished less productive, southwest facing slopes (value = 0.0) from more productive, mesic northeast slopes (value = 2.0) (van Manen et al. 2005). We assigned flat plots a neutral value of 1.0. Distance to and size of the nearest canopy gap $<$50 m from plot center and $\geq$10 m^2 were measured following Runkle (1992).

Analysis of Point Counts.—All nocturnal, colonial, and raptor species including birds with restricted vocalizations (e.g., hummingbirds), were excluded from the analysis because of the difficulty of reliably detecting them during diurnal point counts (Bibby et al. 2000). Species richness was calculated as the total number of species detected during each count, and total number of individuals counted at each location was used as bird abundance. Species diversity was estimated with the Shannon-Weiner index using the Microsoft ® Office Excel (Microsoft Inc. 2003) macro Biological Tools Version 0.2 (Hanks 1995). We constructed a conservation concern value using designations developed by the Alabama Nongame

Wildlife Division (Mirarchi et al. 2004), and summed the number of species designated moderate or higher detected at each count. We pooled data from both seasons to increase sample size because multivariate analysis of variance (MANOVA) tests suggested there was no interaction or the trend was consistent between year and type of survey (used vs. unused) for habitat variables (Philai's Trace = 0.11, $F = 0.51$, df = 18 and 78, $P = 0.95$) and for avian community variables (e.g., abundance, richness and diversity index, Philai's Trace = 0.08, $F = 2.10$, df = 4 and 93, $P = 0.09$). Independent sample *t*-tests were used to test for differences between used and unused plots in bird species richness, abundance, diversity, and conservation concern values, as well as abundance of Brown-headed Cowbirds (*Molothrus ater*) and three common nest predators: American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and Red-bellied Woodpecker (*Melanerpes carolinus*).

Analysis of Avian Community Associations.—Detrended correspondence analysis (DCA) was used with bird abundance to help explain the structure of the sampled avian community (Hill and Gauch 1980). We chose nonlinear scaling and detrended the axes using second-order polynomials following Jongman et al. (1995) to avoid the limitations inherent in DCA, including distorted gradient structure and a lack of robustness (Minchin 1987). Rare species were down-weighted and ordination scores were obtained with biplot scaling focused on inter-species distances using CANOCO 4.54 (ter Braak and Šmilauer 2006). We referenced Birds of North America accounts (Poole 2005) for general habitat preferences of each species to assist in interpretation of DCA axis, and excluded species detected at less than three locations to reduce the effect of transient or accidental species (Wakeley et al. 2007).

Analyses of Microhabitat Characteristics.—We attempted to correct any variables with non-normal distributions using Shapiro-Wilk tests and square root or logarithmic transformations. Independent sample *t*-tests were used to compare mean measurements of vegetation from used habitat plots with unused plots, and two-sample Mann-Whitney *U*-tests for variables that violated normality or equal variance assumptions. Canopy structure complexity was estimated with the Shannon-Weiner diversity index expressed as a proportion of the maximum possible diversity using the number of readings assigned to each height interval (Zar 1999).

Analysis of Microhabitat and Avian Community.—We used principal components analysis (PCA) to reduce the dimensionality of the original microhabitat variables. All components had variance inflation factors <1.1 and were considered to be unique contributors to the analysis (Lepš and Šmilauer 2003). Canonical correspondence analysis (CCA) was used to expose patterns of variation in avian community composition and species abundance related to PCA variables (ter Braak 1986), and to guide selection of habitat characteristics for modeling Cerulean Warbler microhabitat. The length of the longest gradient (i.e., ordination axis) was 3.68, and we considered unimodal ordination methods (e.g., CCA) more appropriate than linear methods (e.g., redundancy analysis) (Lepš and Šmilauer 2003). We used bird abundance and confined the CCA to those species detected at three or more locations within 50 m of plot center using CANOCO 4.54. This is preferable to analyzing all bird detections, which assumes vegetative measures within our plots are an adequate representation of habitats used by birds that were detected farther away where microhabitat characteristics are likely to vary. We used randomized Monte Carlo tests ($n = 499$) to evaluate significance of CCA axes.

Analysis of Microhabitat Models.—We used logistic regression to examine the relationship between Cerulean Warbler occurrence and habitat variables with the binary dependent variable representing used and unused habitat plots. We established 20 models *a priori* and compared them using the information-theoretic approach of Burnham and Anderson (2004). Variable selection was based on Cerulean Warbler literature (Hamel 2000a), as well as habitat plot comparisons, CCA, and field observations from this study. We performed a second-order bias correction (AIC_c) because $n/K < 40$ and calculated evidence ratios based on Akaike weights (w_i) as an indication of model strength in comparison to other models considered (Burnham and Anderson 2004). We examined a variable's beta coefficient to identify its relationship (positive or negative) to Cerulean Warbler presence. Variables present in the model with the highest w_i were considered the best predictors for Cerulean Warbler occurrence.

An *alpha* level of 0.1 was selected for all tests of significance due to the conservation status of the Cerulean Warbler (Askins et al. 1990). All statistical analyses, unless previously described, were performed using SPSS ® Version 15.0 (SPSS

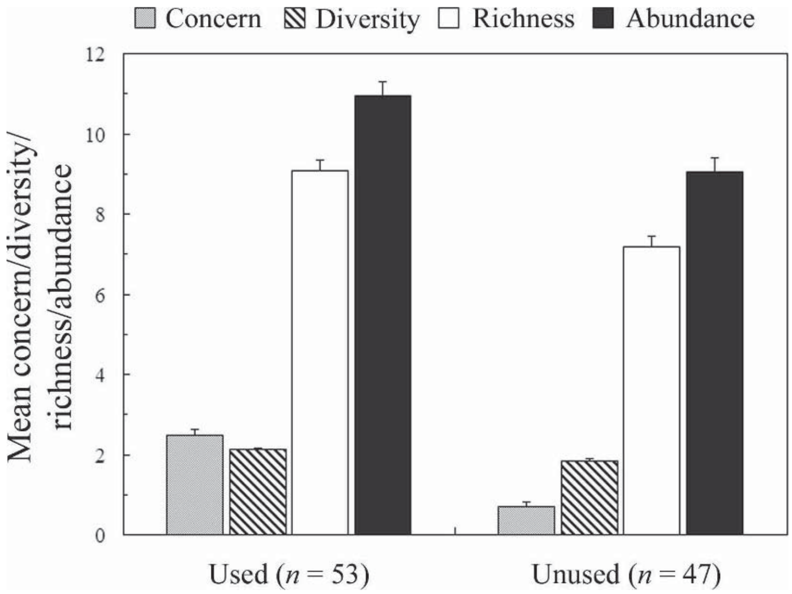

FIG. 2. Mean species richness, diversity index, bird abundance, and number of species of conservation concern detected at point counts conducted in areas used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. All values were significantly higher ($P < 0.01$) at used locations. Error bars are + SE.

Inc. 2006). Means ± standard error (SE) are presented unless noted elsewhere.

RESULTS

Bird Surveys.—Approximately 50 Cerulean Warbler males were detected in northern Alabama during each of the 2005 and 2006 breeding seasons. Cerulean Warblers were found only in Jackson County along Larkin Fork and Hurricane and Mill creeks in Walls of Jericho, and Lawrence County in Bankhead National Forest along Borden, Flannigan, and Horse creeks. No Cerulean Warblers were encountered at unused points or during additional target searches throughout Jackson County or BNF. Walls of Jericho had the highest number of detections with 20 males followed by 15 territorial males in Bankhead National Forest and Larkin Fork.

Bird species richness ($t = 4.91$, df = 98, $P < 0.01$), abundance ($t = 3.85$, df = 98, $P < 0.01$), diversity ($t = 4.99$, df = 98, $P < 0.01$), and conservation concern values ($t = 9.06$, df = 98, $P < 0.01$) were significantly higher in areas where Cerulean Warblers were detected compared to areas where they were not found (Fig. 2). We detected no difference in abundance of Brown-headed Cowbird ($t = 1.06$, df = 98, $P < 0.29$), American Crow ($t = -0.63$, df = 98, $P < 0.52$), Blue Jay ($t = -1.01$, df = 98, $P < 0.31$), or Red-bellied Woodpecker ($t = 0.85$, df = 98, $P < 0.40$) between used and unused locations.

Avian Community Associations.—The proportion of variance explained by the DCA ordination was 23.7% with the first two axes accounting for greater than half of the variability (13.5%). Species most closely associated with Cerulean Warblers were Kentucky Warbler (*Oporornis formosus*), Northern Parula (*Parula americana*), Acadian Flycatcher (*Empidonax virescens*), Blue-winged Warbler (*Vermivora cyanoptera*), Louisiana Waterthrush (*Parkesia motacilla*), American Redstart (*Setophaga ruticilla*), Belted Kingfisher (*Megaceryle alcyon*), and Indigo Bunting (*Passerina cyanea*) (Fig. 3). Bird community associations revealed by the DCA suggested Axis 1 represented a gradient from xeric upland to mesic bottomlands, while Axis 2 distinguished interior deciduous forest from edge and mixed forest habitat.

Microhabitat Characteristics.—Used plots, when compared to unused habitat, had significantly fewer live trees ≥3 cm DBH ($t = -4.01$, df = 97, $P < 0.01$, Table 1), higher ratio of basal area to number of stems ($t = 3.56$, df = 97, $P < 0.01$), greater percentage of deciduous basal area ($Z = -4.5$, df = 97, $P < 0.01$), taller lower,

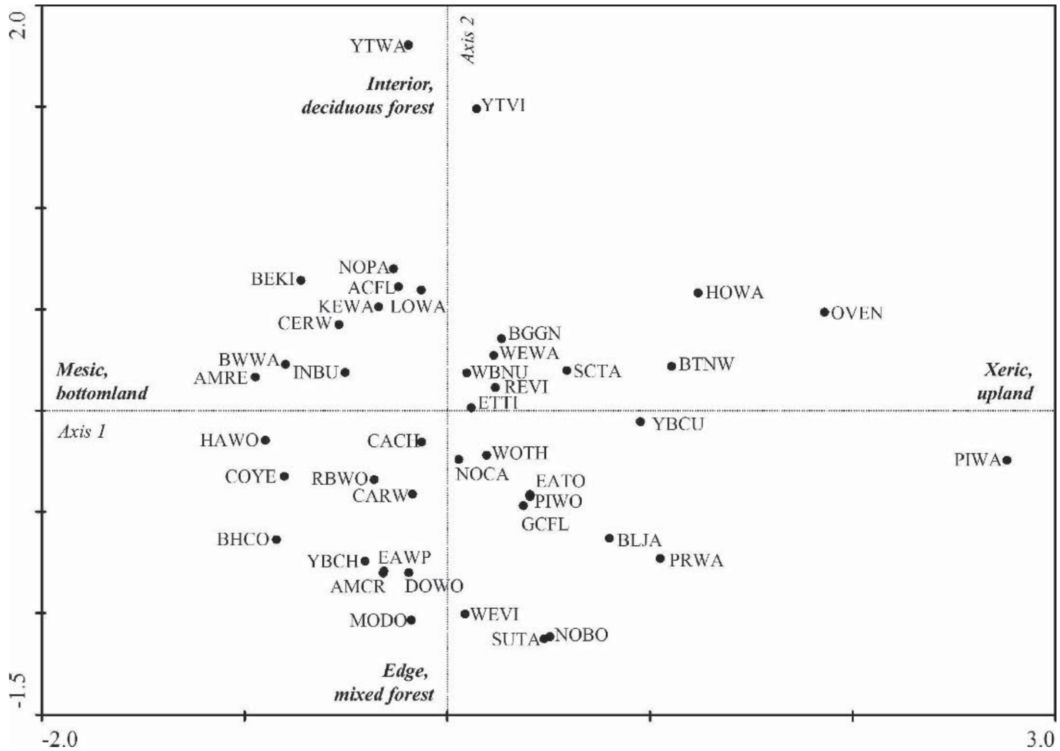

FIG. 3. Plot based on detrended correspondence analysis of bird abundance from locations used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. Axis gradients represent general habitat preferences (Poole 2005). ACFL (Acadian Flycatcher), AMCR (American Crow), AMRE (American Redstart), BEKI (Belted Kingfisher), BGGN (Blue-gray Gnatcatcher, *Polioptila caerulea*), BHCO (Brown-headed Cowbird), BLJA (Blue Jay), BTNW (Black-throated Green Warbler, *Dendroica virens*), BWWA (Blue-winged Warbler), CACH (Carolina Chickadee, *Poecile carolinensis*), CARW (Carolina Wren, *Thryothorus ludovicianus*), CERW (Cerulean Warbler), COYE (Common Yellowthroat, *Geothlypis trichas*), DOWO (Downy Woodpecker, *Picoides pubescens*), EAPH (Eastern Phoebe, *Sayornis phoebe*), EATO (Eastern Towhee, *Pipilo erythrophthalmus*), EAWP (Eastern Wood-Pewee, *Contopus virens*), ETTI (Tufted Titmouse, *Baeolophus bicolor*), GCFL (Great Crested Flycatcher, *Myiarchus crinitus*), HAWO (Hairy Woodpecker, *Picoides villosus*), HOWA (Hooded Warbler, *Wilsonia citrina*), INBU (Indigo Bunting), KEWA (Kentucky Warbler), LOWA (Louisiana Waterthrush), NOBO (Northern Bobwhite, *Colinus virginianus*), NOCA (Northern Cardinal, *Cardinalis cardinalis*), NOPA (Northern Parula), OVEN (Ovenbird, *Seiurus aurocapilla*), PIWA (Pine Warbler, *Dendroica pinus*), PIWO (Pileated Woodpecker, *Dryocopus pileatus*), PRAW (Prairie Warbler, *Dendroica discolor*), RBWO (Red-bellied Woodpecker), REVI (Red-eyed Vireo, *Vireo olivaceus*), SCTA (Scarlet Tanager, *Piranga olivacea*), SUTA (Summer Tanager, *P. rubra*), WBNU (White-breasted Nuthatch, *Sitta carolinensis*), WEVI (White-eyed Vireo, *Vireo griseus*), WEWA (Worm-eating Warbler, *Helmitheros vermivorus*), WOTH (Wood Thrush, *Hylocichla mustelina*), YBCH (Yellow-breasted Chat, *Icteria virens*), YBCU (Yellow-billed Cuckoo, *Coccyzus americanus*), YTVI (Yellow-throated Vireo, *Vireo flavifrons*), YTWA (Yellow-throated Warbler, *Dendroica dominica*).

middle, and upper canopy heights (t = 1.69, df = 97, $P < 0.10$; t = 2.58, df = 97, $P < 0.01$; Z = −1.68, df = 97, $P < 0.09$), greater canopy cover (Z = −3.48, df = 97, $P < 0.01$), larger diameter trees near plot center (t = 5.49, df = 97, $P <$ 0.01), and larger canopy gaps (Z = −1.69, df = 97, $P < 0.09$). They also occurred in areas with less complex canopy structure (t = −1.64, df = 97, $P < 0.10$) and fewer seedlings/shrubs (t = −3.23, df = 97, $P < 0.01$).

We extracted six components from the PCA, which accounted for 67.4% of the cumulative variance (Table 2). Canonical correspondence analysis produced four significant axes (F = 1.46, $P < 0.01$) that explained 83.8% of the total variance with the first two axes accounting for greater than half of the variability (53.9%). Cerulean Warblers displayed the strongest relationships with the principal component representing high percent deciduous basal area, fewer trees

TABLE 1. Microhabitat characteristic comparisons for Cerulean Warbler study plots in northern Alabama during the 2005 and 2006 breeding seasons. Values are means (± SE) for *t*-tests and median (interquartile range) for Mann-Whitney *U*-tests of untransformed variables. Bold type denotes significant differences, $P < 0.1$.

Microhabitat characteristic				*t*-test/*U*-test		
Variable code	Variable description	Used (n = 52)	Unused (n = 47)	df	*t/Z*	*P*
BA	Basal area of live trees (m^2/ha)	27.8 ± 1.5	25.6 ± 1.2	97	1.13 (*t*)	0.26
NTREE[a]	Number of live trees (ha)	840.4 ± 45.6	1,305.3 ± 121.1	97	−4.01 (*t*)	**0.01**
RBATR[a]	BA:NTREE	0.04 ± 0.003	0.03 ± 0.003	97	3.56 (*t*)	**0.01**
NSNAG	Number of snags (ha)	25.0 (25.0–68.8)	50.0 (25.0–100.0)	97	−1.51 (*Z*)	0.13
SNAGBA	Basal area of snags (m^2/ha)	0.6 (0.1–1.9)	1.0 (0.3–2.4)	97	−1.12 (*Z*)	0.26
RBASNAG	SNAGBA:NSNAG	0.01 (0.01–0.03)	0.02 (0.03)	97	−0.51 (*Z*)	0.61
DECBA	Deciduous tree BA (%)	100.0 (100.0–100.0)	96.2 (77.8–100.0)	97	−4.50 (*Z*)	**0.01**
TRDBH[a]	Diameter nearest tree (cm)	22.0 ± 1.6	13.5 ± 1.1	97	5.49 (*t*)	**0.01**
LOWHT[a]	Lower canopy height (m)	5.8 ± 0.2	5.2 ± 0.2	97	1.69 (*t*)	**0.10**
MIDHT	Mid canopy height (m)	17.0 ± 0.4	15.5 ± 0.5	97	2.58 (*t*)	**0.01**
UPHT	Upper canopy height (m)	29.4 (24.9–31.6)	26.2 (22.4–31.2)	97	−1.68 (*Z*)	**0.09**
CCVR	Canopy cover (%)	90.0 (83.1–95.0)	82.5 (77.5–90.0)	97	−3.48 (*Z*)	**0.01**
CSTRC[b]	Canopy structure	0.72 ± 0.02	0.75 ± 0.01	97	−1.64 (*t*)	**0.10**
GAPDIST[c]	Distance to nearest gap	2.0 (1.0–3.0)	2.0 (1.0–5.0)	97	−0.71 (*Z*)	0.48
GAPSZ[d]	Size of nearest gap	3.0 (1.0–4.0)	1.0 (1.0–4.0)	97	−1.69 (*Z*)	**0.09**
UNDSTRY[a]	Understory density (stems/ha)	771.6 ± 90.4	1,132.4 ± 92.4	97	−3.23 (*t*)	**0.01**
SLOPE	Slope (degree)	8.0 (0.0–21.4)	8.5 (0.0–14.0)	97	−0.64 (*Z*)	0.52
ASPECT[e]	Aspect	1.0 (1.0–1.3)	1.0 (0.9–1.5)	97	–0.19 (*Z*)	0.84

[a] Logarithmic or square root transformation.
[b] Shannon-Wiener diversity index.
[c] Relative size: 1 (< 10), 2 (10.1–20), 3 (20.1–30), 4 (30.1–40), 5 (40.1–50), 6 (> 50 m).
[d] Relative size: 1 (10–20), 2 (21–30), 3 (31–40), 4 (> 40 m^2).
[e] Transformed: $A' = \cos(45 - A) + 1$ (Beers et al. 1966).

TABLE 2. Principal components analysis of microhabitat characteristics from plots used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. Factor loadings < 0.25 not displayed.

	Rotated factor loadings[a]					
Original variables	PCAI	PCAII	PCAIII	PCAIV	PCAV	PCAVI
RBATR	0.88					
BA	0.80					
TRDBH	0.70					
UPHT	0.61	0.30				0.42
LOWHT	0.48					
MIDHT	0.45	0.39		0.30		0.37
GAPSZ		0.83				
GAPDIST		−0.82				
SNAGBA			0.94			
RBASNAG			0.85			
NSNAG			0.53		−0.31	−0.29
DECBA				0.76		
NTREE	−0.38			−0.71	0.36	
UNDSTRY		−0.28		−0.62	−0.28	0.31
CSTRC					−0.81	
CCVR	0.38				0.63	
ASPECT						0.79
SLOPE		0.44			0.35	0.47
Cumulative variance (%)	17.2	28.9	40.4	50.3	59.1	67.4

[a] Rotation method: varimax with Kaiser normalization.

≥3 cm diameter, and sparse understory (Fig. 4). Positive yet weaker affiliations existed with components describing canopy cover and structure, tree size (i.e., height, DBH, basal area) and density (i.e., basal area: number of stems), and snag density. The components derived from gap size and proximity to gaps, as well as aspect and slope, had strong negative associations with Cerulean Warbler presence.

The best-supported model relating Cerulean Warbler occurrence to microhabitat variables had an Akaike weight (w_i) of 0.87 (Table 3). Cerulean Warblers preferred flat bottomlands containing large, well-spaced deciduous trees, a moderately complex canopy structure, closer canopy gaps, and many smaller snags.

DISCUSSION

The closest associates of Cerulean Warblers were neotropical migratory species that breed near streams (Louisiana Waterthrush and Northern Parula, but also Belted Kingfisher) in moist woodlands and deciduous bottomland forests (Kentucky Warbler, American Redstart, and Acadian Flycatcher). Cerulean Warblers were not related to species that typically favor xeric

TABLE 3. Best supported logistic regression models for predicting occurrence of Cerulean Warblers. Akaike Information Criterion (AIC) values calculated using −2log-likelihood values (*L*) and *K* (total number of parameters +1). Akaike weights (w_i) derived from each model's likelihood (ML) divided by the sum of all ML values. Beta coefficients signify a variable's relationship (+, −, or ±) to Cerulean Warbler presence.

Model	*L*	*K*	AIC	ΔAIC_c	ML	w_i
DECBA(+), ASPECT(−), CSTRC(−), GAPDIST(−), RBASNG(−), RBATR(+), TRDBH(+)	69.77	8	108.00	0.00	1.00	0.87
RBATR(−), BA(+), TRDBH(+), UPHT(−), LOWHT(+), MIDHT(−), DECBA(+), NTREE(−), UNDSTRY(±), CSTRC(−), CCVR(+)	66.12	12	112.00	5.81	0.05	0.05
RBATR(−), DECBA(+), CCVR(+), TRDBH(+), GAPSZ(+), MIDHT(+)	78.70	7	107.00	6.65	0.04	0.03
RBATR(+), RBASNG(−), DECBA(+), GAPSZ(+), GAPDIST(−), CCVR(−), CSTRC(−), TRDBH(+), UNDSTRY(±), UPHT(+)	69.47	11	111.00	6.75	0.03	0.03
BA(−), DECBA(+), CCVR(+), ASPECT(−), TRDBH(+), UPHT(−)	81.36	7	107.00	9.31	0.01	0.01
CCVR(+), TRDBH(+), UNDSTRY(±), UPHT(−), RBATR(+), DECBA(+)	81.70	7	107.00	9.65	0.01	0.01
DECBA(+), NTREE(−), UNDSTRY(±), CSTRC(−), CCVR(+)	85.63	6	106.00	11.32	0.00	0.00
NTREE(−), DECBA(+), GAPSZ(+), GAPDIST(−), CCVR(+)	86.48	6	106.00	12.17	0.00	0.00
RBATR(−), BA(+), TRDBH(+), UPHT(−), LOWHT(+), MIDHT(−), DECBA(+), NTREE(−), UNDSTRY(±)	78.98	10	110.00	13.88	0.00	0.00
DECBA(+), NTREE(−), UNDSTRY(−)	92.69	4	104.00	13.97	0.00	0.00

upland, mixed forests, and edge habitats; however, Indigo Buntings and Blue-winged Warblers, two species common in shrub and edge habitats, were closely associated with Cerulean Warblers. These patterns suggest Cerulean Warblers may be tolerant of small-scale disturbances within the otherwise large, contiguous forest tracts in which they are found (Hunter et al. 2001, Jones et al. 2001, Hamel et al. 2005a, Wood et al. 2005).

We observed Northern Parulas and Red-eyed Vireos reacting aggressively to Cerulean Warbler playback and engage in direct physical contact with Cerulean Warbler males on several occasions (JPC, pers. obs.; Jones et al. 2007). Both of these species are common canopy-dwellers in bottomland deciduous forests whose resource selection likely overlaps that of Cerulean Warblers. We detected no difference between counts of common nest predators and Brown-headed Cowbird abundance; however, the latter species was plotted near Cerulean Warblers along one axis of our ordination and may be attracted to the same edge habitat Blue-winged Warblers and Indigo Buntings are using. We did not examine these relationships in detail but acknowledge that more research is needed to learn if abundance and behavior of competing, predatory, and brood parasitic species are limiting productivity of Cerulean Warblers in Alabama.

We found Cerulean Warblers breeding in communities with more individuals and species, higher species diversity, and a greater number of species of conservation concern compared to areas where they were absent. Bird species richness and abundance increase as habitat patches increase in area and heterogeneity (Freemark and Merriam 1986, Blake and Karr 1987), which is characteristic of the forested landscapes surrounding our Cerulean Warbler populations (Carpenter 2007). Cerulean Warblers were not effective bio-indicators for overall species diversity in Ontario, but were suited as an umbrella species for similar, canopy-dwelling birds (Jones et al. 2004). Our results also suggest managing forests for Cerulean Warbler habitat may create habitat and improve conservation prospects for several additional species.

Many of our results mirror findings from similar studies throughout the Cerulean Warbler's range and agree with the general assumptions of Cerulean Warbler selection of microhabitat characteristics, including large diameter trees, less dense understory, and taller upper canopy (Lynch 1981, Jones and Robertson 2001, Wood et al. 2006). However, some

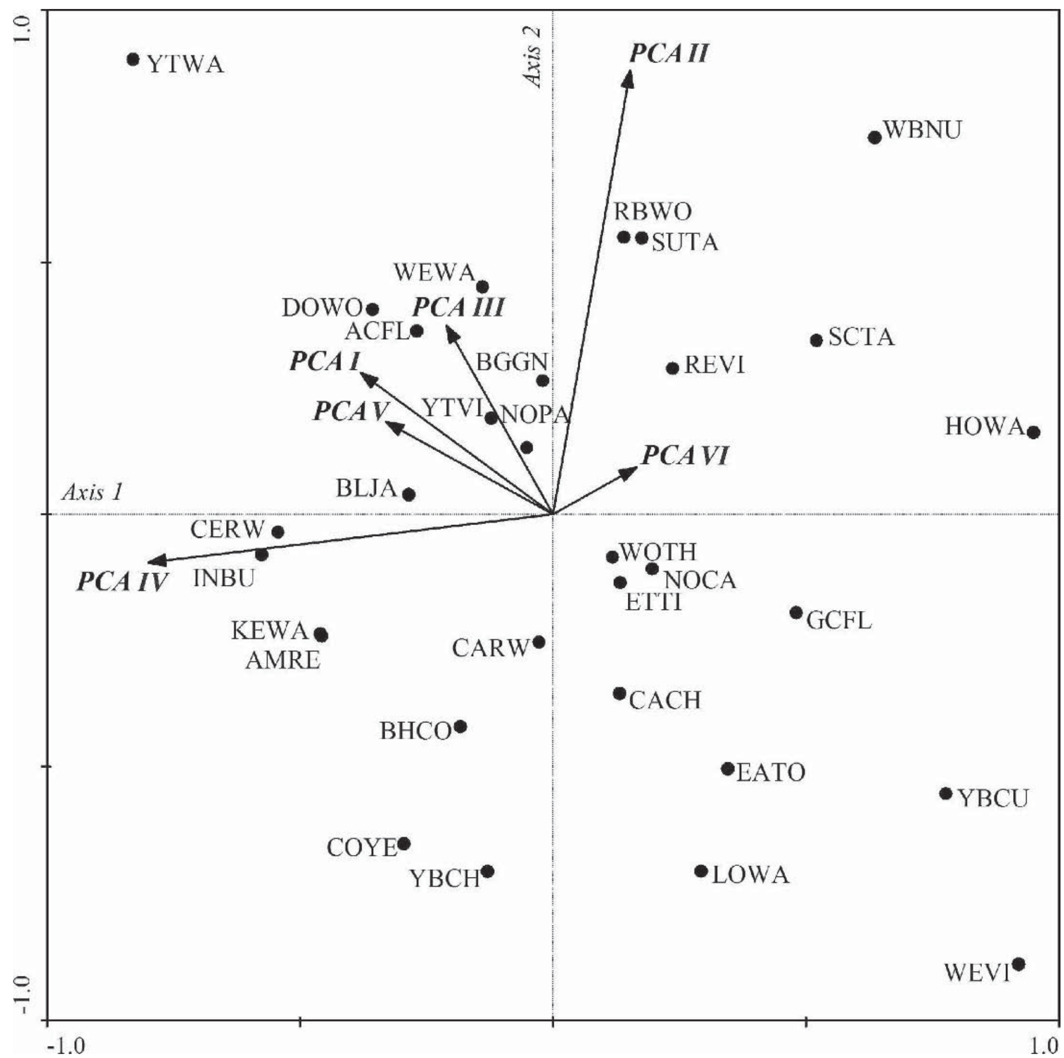

FIG. 4. Biplot based on canonical correspondence analysis of bird detections and principal components of habitat variables from locations used and unused by Cerulean Warblers in northern Alabama during the 2005 and 2006 breeding seasons. Habitat components are in bold italics. The longer an arrow and the closer a species to its tip, the stronger their correlation.

differences were evident as environmental conditions near the edge of a species' distribution can vary from those within the core of its range (Lawton 1993, Brown et al. 1995).

Over one-third of our plots (38.5%) were in flat bottomlands, and Cerulean Warblers displayed a strong negative relation to increasing slope and aspect. Cerulean Warblers are cited as inhabiting ridge tops throughout Appalachia, but this trend diminishes toward the peripheries of its distribution (Rosenberg et al. 2000). The apparent preference for floodplain forests in Alabama may be in response to extensive logging practices of the early 20th century in the Cumberland Mountains (Smalley 1984), which typically focused activity along ridge tops and may have forced Cerulean Warblers to lower elevations (Hamel 2000a). However, all three populations were in highly dissected areas, and the surrounding topography may still have an important role in a Cerulean Warbler's hierarchical process of selecting breeding habitat in Alabama.

Canopy complexity has received considerable attention in Cerulean Warbler habitat studies

(Hamel 2000b, Jones and Robertson 2001, Jones et al. 2001, Hamel 2005). Our average Shannon-Weiner index for used plots was 0.72 ± 0.01 (maximum 1.0) and indicates a moderately complex canopy structure. The disparity between our used and unused plots may be due to use of crude interval measurements which did not accurately distinguish finer complexities at a significance level of 0.1. This may also clarify why Cerulean Warbler presence was negatively related to canopy structure in our modeling. A more complex canopy structure at unused plots does not necessarily indicate an abundance of suitable habitat is available elsewhere in Alabama for Cerulean Warblers. The unused plots' lack of other microhabitat characteristics (e.g., high percent deciduous basal area and fewer but well-spaced, large diameter trees) identified as important to Cerulean Warblers will likely prevent these areas from supporting future populations, if current conditions persist.

The importance of canopy gaps to Cerulean Warbler territory and nest site selection has been supported by some studies (Oliarnyk and Robertson 1996, Nicholson 2004) and questioned by others (Jones et al. 2001, Hamel 2005, Barg et al. 2006b). Used plots had significantly larger canopy gaps compared to unused plots, and our top model indicated Cerulean Warbler presence increased as distance to a canopy gap decreased. Cerulean Warblers in our study may be exploiting these openings as supplemental foraging areas throughout the breeding season and during post-breeding dispersal (Blake and Hoppes 1986, Vitz and Rodewald 2006), and to increase vocal deliverance and recognition of neighboring conspecifics (Barg et al. 2006b). Cerulean Warblers may also be using openings <10 m^2 created by smaller snags, another variable present in our best supported model, which may be contributing to forest heterogeneity and canopy complexity (Oliarnyk and Robertson 1996, Wood et al. 2006; but see Barg et al. 2006b). Our ordination, however, contradicts these findings by disassociating the principal component representing canopy gaps with Cerulean Warblers. A plausible explanation is the cleared fields maintained within the heavily forested landscape of the Jackson County populations possibly influenced comparison with the more fragmented landscape surrounding unused locations (Carpenter 2007). The appropriate size, quantity, and distribution of canopy gaps and other small-scale disturbances, as well as evidence of whether or not Cerulean Warblers are using them, remains unclear in Alabama.

Our results help clarify the roles of avian species assemblages and vegetative characteristics in habitat used by Cerulean Warblers. This dynamic relationship is further complicated by resource availability, predation, competition with other organisms, and habitat alteration; none of which was accounted for in our study. Future Cerulean Warbler research in Alabama and elsewhere will benefit by addressing these issues in more detail.

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