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SPATIAL VARIATION IN BREEDING HABITAT SELECTION BY CERULEAN WARBLERS (*SETOPHAGA CERULEA*) THROUGHOUT THE APPALACHIAN MOUNTAINS

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Abstract.—Studies of habitat selection are often of limited utility because they focus on small geographic areas, fail to examine behavior at multiple scales, or lack an assessment of the fitness consequences of habitat decisions. These limitations can hamper the identification of successful site-specific management strategies, which are urgently needed for severely declining species like Cerulean Warblers (*Setophaga cerulea*). We assessed how breeding habitat decisions made by Cerulean Warblers at multiple scales, and the subsequent effects of these decisions on nest survival, varied across the Appalachian Mountains. Selection for structural habitat features varied substantially among areas, particularly at the territory scale. Males within the least-forested landscapes selected microhabitat features that reflected more closed-canopy forest conditions, whereas males in highly forested landscapes favored features associated with canopy disturbance. Selection of nest-patch and nest-site attributes by females was more consistent across areas, with females selecting for increased tree size and understory cover and decreased basal area and midstory cover. Floristic preferences were similar across study areas: White Oak (*Quercus alba*), Cucumber-tree (*Magnolia acuminata*), and Sugar Maple (*Acer saccharum*) were preferred as nest trees, whereas red oak species (subgenus *Erythrobalanus*) and Red Maple (*A. rubrum*) were avoided. The habitat features that were related to nest survival also varied among study areas, and preferred features were negatively associated with nest survival at one area. Thus, our results indicate that large-scale spatial heterogeneity may influence local habitat-selection behavior and that it may be necessary to articulate site-specific management strategies for Cerulean Warblers. *Received 4 June 2012, accepted 9 November 2012.*

Key words: behavioral plasticity, breeding behavior, conservation biology, *Dendroica cerulea*, floristics, geographic variation, multiscale habitat selection, nonadaptive behavior, *Setophaga cerulea.*

Variación Espacial en la Selección del Hábitat Reproductivo de *Setophaga cerulea* en las Montañas Apalaches

Resumen.—La utilidad de los estudios de selección de hábitat por lo general es limitada porque se enfocan en áreas geográficas pequeñas, no examinan el comportamiento a múltiples escalas o carecen de una evaluación de las consecuencias que acarrean las decisiones de hábitat en términos de la aptitud. Estas limitaciones pueden impedir la identificación de estrategias exitosas de manejo específicas para cada sitio, las cuales se necesitan con urgencia para especies fuertemente amenazadas como *Setophaga cerulea*. Evaluamos cómo varían las decisiones de selección del hábitat reproductivo de *S. cerulea* y sus consecuencias para la supervivencia de los nidos a través de las montañas Apalaches. La selección de características estructurales del hábitat varió sustancialmente entre áreas,

particularmente a la escala de los territorios. Los machos de los hábitats menos boscosos seleccionaron características del microhábitat que reflejaban las condiciones de un dosel cerrado, mientras que los machos de hábitats más boscosos favorecieron características asociadas con disturbio en el dosel. La selección de los atributos del parche y el sitio de anidación por parte de las hembras fue más consistente entre áreas; las hembras seleccionaron lugares con árboles más grandes y mayor cobertura en el sotobosque, pero con menor área basal y menor cobertura en el estrato medio del bosque. Las preferencias florísticas fueron entre áreas de estudio: los árboles de las especies *Quercus alba, Magnolia acuminata* y *Acer saccarum* fueron preferidos para anidar, mientras que los del subgénero *Erythrobalanus* y de la especie *Acer rubrum* fueron evitados. Las características del hábitat que se relacionaron con la supervivencia de los nidos también variaron entre áreas de estudio, y las características preferidas estuvieron asociadas negativamente con la supervivencia de los nidos en una de las áreas. De este modo, nuestros resultados indican que la heterogeneidad espacial a gran escala podría afectar el comportamiento de selección de hábitat a nivel local, y que puede ser necesario articular estrategias de manejo de *S. cerulea* específicas para cada sitio.

Elucidating patterns in habitat selection by avian species has long been a central goal of ornithological research (e.g., MacArthur et al. 1962, Cody 1985). Habitat selection studies, however, often are limited in geographic scope, fail to examine habitat selection at multiple scales, and do not link habitat decisions with fitness consequences (Jones 2001, Schaub et al. 2011). These shortcomings can be problematic because habitat selection may be assumed to be a fixed adaptive behavior, whereas in reality it may be scale dependent (e.g., territory vs. nest selection; Johnson 1980, Deppe and Rotenberry 2008), region or site specific (Whittingham et al. 2007, Fortin et al. 2008, Bamford et al. 2009), or maladaptive (Battin 2004). These issues are particularly important for species of conservation concern because extrapolation of habitat associations to different scales and regions may result in inappropriate conservation strategies. Thus, spatially extensive, replicated studies with experimental habitat manipulations are necessary to help managers develop strategies to conserve high-priority avian species (e.g., Donovan et al. 2002).

Avian habitat selection usually occurs in a hierarchical manner (Johnson 1980, Orians and Wittenberg 1991, Gaillard et al. 2010) and, because proximate cues may differ at each step, evaluation of habitat selection at multiple scales is vital to understanding the overall behavioral process and to developing successful conservation strategies on behalf of a species. In Neotropic–Nearctic migrants during the breeding season, males typically arrive on breeding grounds first and select and defend territories (territory selection). Females arrive shortly after, assess males and territories, and select a patch within a territory appropriate for raising a brood (nest-patch selection). Females, occasionally with help from males, then select a specific location within that patch (in a single tree or grass patch) to build a nest and raise a brood (nest-site selection). In addition, at any point during this hierarchical process, context-dependent habitat selection may occur; for example, at the territory scale, features selected may not be consistent across all geographic (or landscape) contexts. Although many factors may play a role in this behavioral process, vegetation structure and composition (hereafter "floristics") are undoubtedly important and among the most amenable variables for management (MacArthur et al. 1962, Wiens and Rotenberry 1982, Scott et al. 2002).

In addition to documenting which habitat features birds select at multiple scales, it is valuable to understand how habitat selection behavior is related to fitness. If behaviors involved in habitat selection are subject to natural selection, individuals that breed in the most preferred habitats should experience the highest fitness (Williams and Nichols 1984). Maladaptive habitat selection is not uncommon, however, when birds use human-altered habitats (Battin 2004). Although lifetime fitness is determined by several components (e.g., fecundity and annual survival), reproductive measures such as nest success are likely to be greatly influenced by breeding habitat decisions. In addition, reproductive measures can be accurately estimated and compared with habitat selection patterns to infer the adaptiveness of behaviors.

The Cerulean Warbler (*Setophaga cerulea*) is an example of a species for which an understanding of the variability of habitat selection behavior and the relationship with reproduction is critically needed. Cerulean Warblers are among the fastest-declining passerines in North America (Ziolkowski et al. 2010). Populations of this migrant songbird declined by 3.2% year^{-1} from 1966 to 2003, and this trend worsened to a decline of 4.6% year^{-1} from 2003 to 2008 (Ziolkowski et al. 2010). Consequently, Cerulean Warblers are designated a "first-priority" species for conservation action by the U.S. Fish and Wildlife Service (USFWS) and Partners in Flight (USFWS 2008) and as "vulnerable" to extinction by BirdLife International (2010).

Our current knowledge of the spatial variability of habitat selection behavior in Cerulean Warblers at fine scales is minimal, but at broader scales, habitat selection by these birds varies substantially across their breeding range. For example, they use bottomland riparian forests in the Mississippi Alluvial Valley but prefer upland forests along ridgetops and upper slopes in the Appalachian Mountains (Hamel 2000, Weakland and Wood 2005). Within the Appalachian region, where >70% of the remaining population breeds (Hamel and Rosenberg 2007), little is known about the process or variability of multiscale habitat selection behavior, and what is known has been uncovered mostly in the past decade. For well over a century, this species was thought to breed exclusively in mature deciduous forests with predominantly closed canopies and open understories (Wilson 1811, Lynch 1981, Robbins et al. 1992). A growing body of evidence, however, suggests that in the Appalachians and at other locations, Cerulean Warblers often occupy mature forest characterized by diverse canopy structure and disturbance (Oliarnyk and Robertson 1996, Perkins 2006, Bakermans and Rodewald 2009) or by successional forest (Wood et al. 2005). Heterogeneous canopy conditions occur naturally in the Appalachians because of topography (e.g., steep slopes and knolls) and are enhanced by natural disturbances such as fire, wind or ice storms, insect outbreaks, and natural tree senescence, particularly in old-growth forests (Lorimer 1980). Because natural disturbances are often

rare in contemporary second-growth forests (Lorimer and Frelich 1994), appropriate forest structure can be created by using forest management techniques (such as partial timber harvesting or prescribed burning) where natural disturbance regimes have been disrupted (Bakermans and Rodewald 2009). However, information regarding the regional variability of habitat selection behaviors in Cerulean Warblers and the adaptive nature of habitat selection in such anthropogenically disturbed forests is lacking.

The goals of our study were threefold. At experimentally disturbed forests of the Appalachian Mountains, we sought to (1) determine the topographic, structural, and floristic features associated with habitat selection by Cerulean Warblers at multiple scales (territory, nest patch, and nest site); (2) evaluate whether, and how, habitat selection at each scale varied across six widely spaced study areas; and (3) assess the reproductive consequences of habitat decisions (across study areas). The information gained will help us better understand variability in the process of habitat selection and improve our ability to make appropriate local and regional management decisions for Cerulean Warbler conservation.

Methods

Study areas.—Our research was conducted during the breeding seasons of 2008–2010 at six widely spaced study areas in the Appalachian Mountains (Fig. 1), all within the Central Hardwood mixed-mesophytic forest region (Fralish 2003), which corresponds to the core of the Cerulean Warbler range. Study areas were on Royal Blue Wildlife Management Area, Tennessee (RB); Sundquist Wildlife Management Area, Tennessee (SQ); Raccoon Ecological Management Area, Ohio (REMA); Daniel Boone National Forest, Kentucky (DB); Lewis Wetzel Wildlife Management Area, West Virginia (LW); and a large, privately owned forest tract in Wyoming County, West Virginia (WYO). Our selection of study areas was based on the presence of known breeding Cerulean Warbler populations and the ability to implement partial timber harvests. All study areas were embedded within a matrix of mature forest; mean (± SE) percent forest cover within 10 km of study area centers was 83.0 ± 2.8% (range: 74–95%; 2001 National Land Cover Database). Mean elevation was 550 ± 80 m
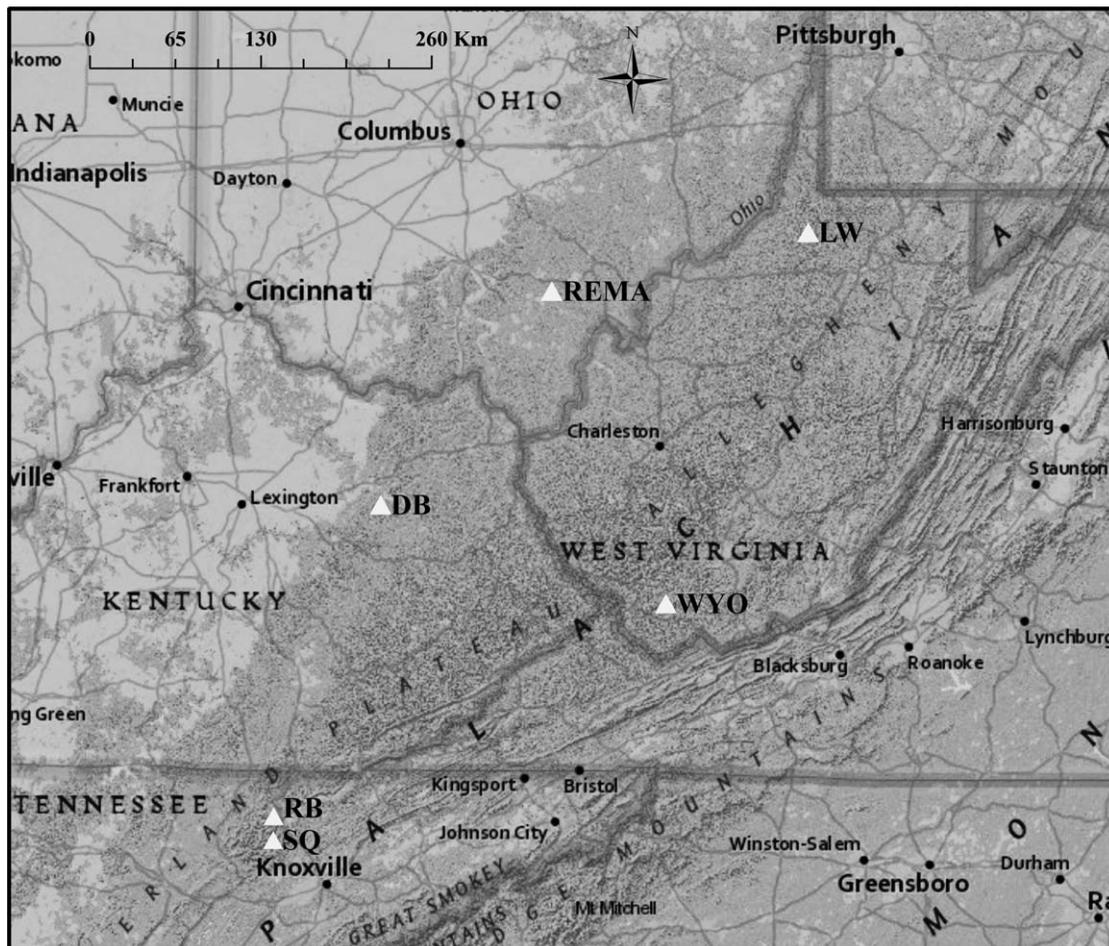
FIG. 1. Locations of study areas across the Appalachian Mountains, all within the core of the Cerulean Warbler breeding range. Study areas were on Royal Blue Wildlife Management Area, Tennessee (RB), Sundquist Wildlife Management Area, Tennessee (SQ), Raccoon Ecological Management Area, Ohio (REMA), Daniel Boone National Forest, Kentucky (DB), Lewis Wetzel Wildlife Management Area, West Virginia (LW), and a privately owned forest in Wyoming County, West Virginia (WYO).

FIG. 2. Proportions of trees by species located at random (i.e., available), territory, nest-patch, and nest-site (i.e., nest tree) points pooled across all study areas in the Appalachian 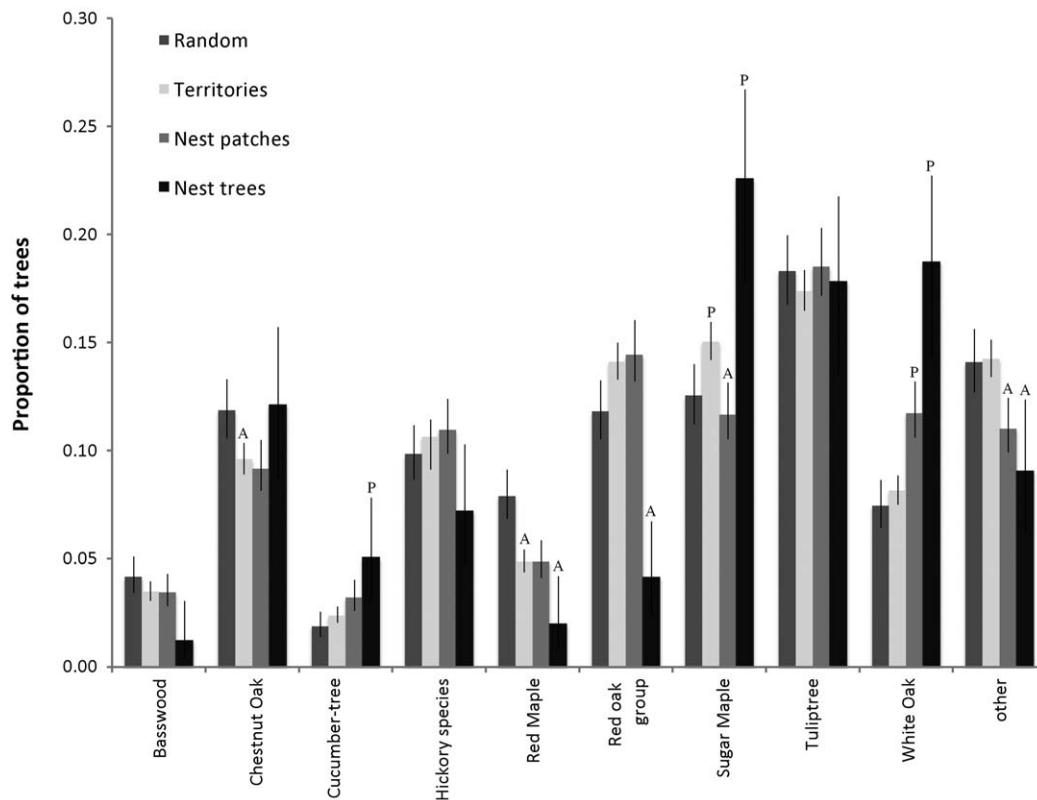Mountains, 2008–2010. The red oak group included Northern Red Oak (*Quercus rubra*), Black Oak (*Q. velutina*), and Scarlet Oak (*Q. coccinea*), and hickory species included Mockernut Hickory(*Carya tomentosa*), Bitternut Hickory (*C. cordiformis*), Pignut Hickory (*C. glabra*), and Shellbark Hickory (*C. laciniosa*). Error bars represent Goodman 95% multinomial confidence intervals (CIs; Goodman 1965). Selection for tree species at respective scales was evaluated by comparing 95% CIs of random points with those of territory points; territories with nest patches; and territories with nest trees. "P" indicates selection for a tree species (preference), and "A" indicates selection against (avoidance) at the respective scale of selection.

(range: 250–850 m). Plant composition differed slightly among study areas, but common overstory tree species included Tuliptree (*Liriodendron tulipifera*), Sugar Maple (*Acer saccharum*), Northern Red Oak (*Quercus rubra*), White Oak (*Q. alba*), Chestnut Oak (*Q. prinus*), and various hickories (*Carya* spp.; see random tree proportions in Fig. 2).

Habitat manipulations.—We implemented canopy disturbances of varying intensities on four forest plots at each study area using commercial harvesting techniques. These manipulations were designed to emulate natural processes that spanned the range of potential mature-forest disruptions and also represented common silvicultural practices. At each study area, three 10-ha stands were harvested at different intensities to meet predetermined ranges of residual basal area (BA) that we designated as light, intermediate, and heavy canopy disturbance. We also monitored Cerulean Warblers in 50 ha of undisturbed forest at each study area, which included a 20-ha reference plot and six 5-ha buffers, located on either side of each harvested plot (for a total coverage area of 80 ha at each study area). We left reference plots and buffers undisturbed throughout the duration of the study (BA = 27.7 ± 0.7 m² ha⁻¹; canopy cover [CC] = 73.2 ± 5.2%).

Light harvests mimicked mature forests with small treefall gaps typical of those caused by tree senescence, wind, etc., and were implemented using traditional single-tree selection methods. We reduced BA and overstory CC on these stands by approximately 20% (residual BA = 21.1 ± 1.2 m² ha⁻¹; residual CC = 60.9 ± 5.5%). Intermediate harvests mimicked more severe natural disturbances such as fire, blow-downs, or larger tree-fall gaps; we reduced BA and CC by approximately 40% (residual BA = 14.1 ± 1.2 m² ha⁻¹; residual CC = 45.5 ± 6.4%). Heavy harvests emulated even more severe natural disturbances such as large blow-downs, ice storms, landslides, or more intense fire; we reduced BA and CC by approximately 75% (residual BA = 6.5 ± 1.1 m² ha⁻¹; residual CC = 18.2 ± 4.3%). We also removed all understory and midstory stems >5 cm diameter at breast height (DBH) on the intermediate and heavy harvests. Overstory species composition was largely unchanged by harvests, and although most trees with economic value were removed, residual logging debris was scattered across the logged areas. Harvesting was performed in the fall of 2006 and early spring of 2007, more than 1 year before we began collecting data. This likely reduced the potential effects of site fidelity on habitat selection behavior, but it is not clear what effect residual philopatry may

have had on the resulting patterns of habitat selection. Although many avian species can be highly philopatric (Greenwood and Harvey 1982), Cerulean Warblers appear to be quite prone to dispersal between breeding seasons (Girvan et al. 2007). At our study areas, where a large number of males were marked, site fidelity was relatively low: <20% of marked individuals returned to their previous breeding territory (T. J. Boves unpubl. data).

Although we refer to harvest designations (e.g., intermediate harvest) for explanatory purposes here, we do not evaluate selection of the harvests per se, but rather identify relationships with the resulting continuous habitat features. Heterogeneity within and among harvests was high, which makes using continuous habitat features logical and, potentially, more biologically meaningful. Thus, we do not refer to these plots by harvest type again. All plots were located on north- or east-facing slopes to maximize potential for Cerulean Warbler presence (Buehler et al. 2006, Wood et al. 2006) and control for potential interactions between aspect and behavioral response.

Territory delineation.—We used three methods in combination to locate and delineate territories selected by male Cerulean Warblers. First, we spot mapped all plots at each study area on eight mornings between 15 May and 15 June (2008–2010), during which we recorded all locations of singing and countersinging males as well as other territorial behaviors (Bibby et al. 2000). Second, we intensively searched for nests on all plots and attempted to find all nests every year. Finally, we augmented our spot-mapping efforts by banding 122 males at five study areas (RB, SQ, LW, WYO, and REMA) using mist nets, a male Cerulean Warbler decoy, and territorial song-playback equipment. Each captured male was fitted with a unique combination of plastic color and numbered federal metal bands to permit individual identification in the field.

Nest searching and monitoring reproductive success.—During each breeding season (2008–2010), we searched for nests between 20 April and 10 July. We used behavioral cues of females during building and incubation and, to a lesser extent, male vocalizations and behavior, to locate nests. Because females and nests were easier to detect on harvested stands, we stratified our search efforts on each treatment to yield a similar proportion of nests (in relation to territory numbers) in each harvest type. We used female behavior to lead us to nests, and we believe that our sample of nests was representative of the population and not biased by visibility. We were unable to examine the contents of nests and, therefore, considered nests active only if we observed the female incubating, brooding, or feeding young, as has been standard in Cerulean Warbler breeding studies (D. A. Buehler pers. comm.). We monitored nests every 1–3 days until fledging or confirmed nest failure occurred. From nestling day 6 until fledging, we used spotting scopes to monitor nests for >45 min and attempted to find fledglings at nests that survived to the appropriate age to determine nest fate. We considered any nest that fledged ≥1 warbler young to be successful. Nests that fledged Brown-headed Cowbird (*Molothrus ater*) young were considered failures, but this occurred at only a small number of nests (<2% of nests were known to have been parasitized; <1% of nests produced cowbird young).

Habitat measurements.—We measured habitat characteristics annually at three point locations: random (R), territory (T),

and nest (N). Random points provided us with a measure of overall habitat availability from which males selected territories. We established 80 random points study area^{-1} year^{-1} (using ARCGIS, version 9.2; ESRI, Redlands, California), stratified so that there was an equal number of points in each harvest type and undisturbed forest (i.e., 1 point located within each hectare of forest). Because our study areas were all within deciduous forest with appropriate topography, elevation, and forest type, we considered all areas on our plots to be available for selection by males. We selected random points independently of Cerulean Warbler activity; thus, each point could have been located within or outside of territory boundaries. We placed territory points (1 point territory^{-1}) at either (1) a location of increased male foraging activity or, if this information was not available, (2) the geographic center of each mapped territory. We established nest points directly under each nest and recorded nest-patch and nest-site measurements from this location. Nest-patch and nest-site points differed by scale; patches were characterized by habitat features surrounding the nest (e.g., canopy cover in a 0.04-ha area surrounding the nest site), whereas nest sites were characterized by features based on the location of the nest itself (e.g., nest height). At all points, we measured habitat variables that we thought to be important proximate factors for habitat selection at one or more scales, based on previous literature and our understanding of Cerulean Warbler ecology. These variables included (1) topographic slope (in degrees using a clinometer), (2) aspect (transformed to reflect vegetative productivity following Beers et al. 1966), (3) BA (m^2 ha^{-1} using a 2.5× factor metric prism), (4) DBH (cm) of all trees >10 cm within BA prism plot, (5) distance (m) to nearest natural or artificial canopy gap within 100 m, (6) average canopy height within the prism plot (m, using a clinometer), and (7) percent understory (0.5–3 m), (8) midstory (3–12 m), and (9) overstory canopy cover (>18 m). We estimated canopy cover of the above strata within a 0.04-ha plot by recording foliage presence at 21 points (5 points along transects in each cardinal direction and 1 at point center) using an ocular tube. We also identified the species (or species group) of all trees within the BA prism plot. At each nest site, we also measured (1) nest tree DBH (cm), (2) nest tree height (m), (3) nest height (m), distance from nest to (4) bole and (5) outer edge of tree foliage (m), and (6) distance from nest to top of crown (m), and recorded (7) nest tree species.

Analytical methods: Regional variation in habitat features used.—We first used multivariate analyses of variance (MANOVAs) to assess variability of habitat characteristics of territories, nest patches, and nest sites, without regard to availability, among our six study areas. Study area was treated as a fixed effect and year as a random effect. The 10 habitat variables chosen *a priori* were related to physiognomy (mean and maximum DBH of trees in prism plot, BA, canopy height, distance to nearest canopy gap, and understory, midstory, and overstory cover) and topography (slope and Beers aspect). Prior to this MANOVA and all subsequent parametric tests, we examined data for collinearity, univariate and multivariate normality, and equality of covariances. We found little evidence of collinearity among variables (Pearson's $r < 0.5$), except a potential case between mean and maximum DBH ($r = 0.71$). To ensure that this relationship did not affect our conclusions, we performed separate MANOVAs with each variable and found no difference in our inferences (we therefore report only results with both

variables included). To meet assumptions, we arcsin-square-root transformed all canopy cover proportions and log-transformed distance to nearest gap; we added 0.5 m to distances of zero before calculating log transformations. After transformations, we still detected minor departures from multivariate normality and heteroscedasticity (Box's M-test, $P < 0.001$), so we evaluated significance for territory and nest-patch characteristics using Pillai's trace statistic, which is robust to violations of assumptions (Scheiner 2001). For nest-site characteristics, assumptions were met and we evaluated significance using Wilks' lambda. If we found significance in a MANOVA, we subsequently performed univariate ANOVAs to identify sources of variation. We considered geographic differences to exist when $P \leq 0.05$, but we recognize that multiple tests could result in inflated Type I error rates, so we also evaluated significance after controlling Type I error rate at 0.05 using the Dunn-Sidak method (Gotelli and Ellison 2004) where $k = 10$ for territory and nest-patch variables ($\alpha = 0.0052$) and 5 for nest-site variables ($\alpha = 0.01$).

Habitat selection.—For each study area, we performed two MANOVAs to test for habitat differences between (1) random and territory points (for territory selection) and (2) territory and nest-patch points (for nest-patch selection). We evaluated the same suite of habitat features as described above and treated point type as a fixed effect and year as a random effect. To assess and address potential violations of parametric assumptions, we also followed the same steps described above. When we found significance in a MANOVA, we subsequently performed univariate ANOVAs to identify sources of variation. We considered $P \leq 0.05$ as indication that selection for a habitat variable occurred and adjusted for multiple comparisons using the Dunn-Sidak method.

In addition to MANOVA, we conducted a meta-analysis to evaluate consistency of habitat selection across our study areas. We calculated raw mean differences (D) across study areas for each habitat variable at two orders of selection (for territories: territory minus random; for nest patches: nest patch minus territory). Thus, a positive D indicated selection for greater values of a habitat feature, and a negative D indicated selection for lesser values of a feature. We constructed confidence intervals around the average D using a random-effects model because we assumed effects to be heterogeneous across study areas, a likely scenario in ecological research (Gurevitch and Hedges 2001). We considered D to be significantly different from zero if 95% confidence intervals (CIs) did not include zero.

Selection for floristics.—We assessed multiscale selection for tree species, or tree groups in the case of hickory (*Carya* spp.) and red oak groups (subgenus *Erythrobalanus*), at each individual study area and all areas combined by comparing multinomial CIs. We included only tree species (or groups) that made up >4% of available trees (derived from random points) or >4% of nest trees. Species that comprised the remainder of trees were combined into a group designated as "other." The number of tree species or groups included varied by study area and ranged from 8 to 11. We compared tree composition at random points to tree composition at territory points (territory selection), and territories to nest patches (nest-patch selection) and nest trees (nest-site selection), by constructing and comparing CIs calculated using the Goodman method for deriving multinomial CIs, a method that controls the Type I family-wise error

rate (Goodman 1965, May and Johnson 1997). When CIs did not overlap (95% CI for all study areas combined, 90% for individual areas) at the respective scale of selection, we considered floristic selection to have occurred. We used 90% CIs for individual study areas because the Goodman method is sensitive to sample size, which was relatively low for nest trees at some study areas. We found that 90% CIs for trees at random points overlapped across all years (at each study area and overall). Therefore, we averaged annual random-point CIs to estimate availability. For territory, nest patch, and nest tree, we pooled trees across years. We performed all habitat selection analyses using NCSS, version 7.1.19 (NCSS, Kaysville, Utah), and SAS, version 9.2 (SAS Institute, Cary, North Carolina). For ease of interpretation, we report untransformed data in all text and tables and means ± SE unless otherwise noted.

Nest survival.—We analyzed daily nest survival rates (DSRs) of 413 Cerulean Warbler nests (6,384 nest exposure days) by comparing logistic exposure models in Program MARK to evaluate how habitat features were related to daily nest survival. This method uses a generalized linear model with binomial distribution for each day (nest fate = 0 if successful, 1 if failed) in relation to covariates that may be related to nest survival. To assess the relationship between habitat selection behavior and nest survival, and to limit the number of models evaluated, we applied a hierarchical approach to modeling nest survival based on *a priori* hypotheses derived from the habitat selection results (Dinsmore et al. 2002). We used Akaike's information criterion corrected for small sample size (AIC_c) to compare candidate model fit. Habitat selection differed among study areas (see below), so we analyzed the association of covariates with DSR at each study area independently. At each study area, we developed three suites of models; after evaluating each level, we carried all models that had a ΔAIC_c value < 2 (indicating equivalent support to the highest-ranked model; Burnham and Anderson 2002) over to the next suite of models. Our first suite included univariate models of habitat covariates that were significant in our analysis of territory selection (study-area-specific). Our second suite included univariate models that incorporated covariates significant at the scale of nest-patch selection (but not at the territory level), and our third suite incorporated nest-site covariates (for which we did not analyze habitat selection behavior) and up to two covariates representing nest tree species that were selected for or against. In this final suite, we also included a null model (constant survival) and a saturated additive model that included all covariates with $\Delta AIC_c < 2$. We evaluated the relationship between habitat selection behavior and nest survival by comparing the sign of the slope (β coefficient) and associated 95% CI of each univariate feature included in the final suite of models with the direction of habitat selection for that feature (e.g., if a feature was selected for and had a positive influence on DSR, with 95% CIs that did not include zero, we would consider that behavior adaptive). We used raw covariate values because standardization did not affect numerical optimization (Rotella 2007).

Results

We measured habitat characteristics at 1,437 random points, 936 territories, and 479 nests across all study areas from 2008 to 2010; measurements across all areas are summarized in Table 1.

TABLE 1. Cerulean Warbler habitat measurements (means ± SE) at random (R), territory (T), and nest-patch (N) points pooled across six study areas in the Appalachian Mountains, 2008–2010 (see text for description of habitat variables; DBH = diameter at breast height).

Habitat variable	R (n = 1,437)	T (n = 931)	N (n = 479)
Average DBH (cm)	39.23 ± 0.26	41.50 ± 0.31	43.58 ± 0.43
Maximum DBH (cm)	62.90 ± 0.47	63.97 ± 0.50	65.07 ± 0.69
Basal area (m² ha⁻¹)	22.04 ± 0.27	21.56 ± 0.32	20.69 ± 0.44
Understory canopy cover (%)	0.38 ± 0.01	0.39 ± 0.01	0.47 ± 0.01
Midstory canopy cover (%)	0.52 ± 0.01	0.47 ± 0.01	0.45 ± 0.01
Overstory canopy cover (%)	0.64 ± 0.01	0.66 ± 0.01	0.69 ± 0.01
Distance to gap (m)	21.20 ± 0.66	12.29 ± 0.49	14.18 ± 1.02
Canopy height (m)	28.02 ± 0.15	29.11 ± 0.19	29.54 ± 0.25
Slope (°)	23.14 ± 0.24	22.37 ± 0.31	23.18 ± 0.44
Beers aspect	1.31 ± 0.02	1.46 ± 0.02	1.46 ± 0.03

Regional variation of habitat features used.—Without accounting for availability, habitat characteristics at territories varied among study areas (Pillai's trace = 1.06, F = 24.71, df = 50 and 4,615, P < 0.0001), and all individual habitat features differed (all P < 0.0001; see Table 2). Characteristics of nest patches also varied among study areas (Pillai's trace = 1.25, F = 15.51, df = 50 and 2,335, P < 0.0001), and all individual habitat features differed (all P < 0.0001; see Table 2). Nest-site characteristics also varied among study areas (Wilks' λ = 0.67, F = 6.40, df = 30 and 1,874, P < 0.0001). Nest height, distance from nest to foliage edge, and distance from nest to top of crown differed among areas (all P < 0.003; Table 3), whereas nest-tree DBH and distance from bole to nest did not differ (P > 0.05).

Territory selection: Habitat structure.—Multivariate habitat selection occurred at the territory scale at all six study areas (Pillai's trace, all P < 0.05). One or more habitat features influenced territory selection at each study area, but the combination of selected features differed among areas (Table 2). Direction of selection for four habitat features (mean DBH, BA, overstory canopy cover, and canopy height) also differed among study areas. Territories were characterized by large-diameter trees at four study areas (RB, REMA, LW, and WYO), whereas at SQ, mean diameter of trees in territories was less than at random points. Territories at RB and SQ had less BA than random points, whereas territories at DB and REMA had greater BA than random points. At three study areas (DB, REMA, and LW), territories had greater overstory canopy cover than at random points, but at SQ the pattern was reversed. And at three study areas (REMA, LW, and WYO), territories had higher canopies than at random points, whereas at SQ, males selected territories with lower canopies than at random. Males at REMA and SQ selected habitat characteristics in contradictory manners more often than at any other pair of study areas, with opposing selection patterns for all four variables. By contrast, males at REMA and DB and at RB and LW selected territory characteristics more similarly than males at any other pairs of study areas, with consistent selection for three variables.

Based on the meta-analysis, Beers aspect had a positive effect and distance to nearest gap had a negative effect on territory selection across study areas (Table 4). Thus, males consistently selected territories that were relatively closer to gaps and located on slopes that were (presumably) more productive (northeast aspects).

Nest-patch selection: Habitat structure.—Females demonstrated multivariate habitat selection at the nest-patch scale at all study areas except for WYO (Pillai's trace, all P < 0.05). The habitat features selected at this scale differed among study areas, but the direction of selection differed for only one feature: canopy height (Table 2). Females chose nest patches with higher canopies (than available territory points) at DB and SQ, whereas at REMA and LW they selected nest patches with lower canopies.

Meta-analysis also showed nest-patch selection to be more consistent than territory selection. Four variables had significant effects on nest-patch selection across study areas: mean DBH, BA, midstory cover, and understory cover. Mean DBH and understory cover had positive effects, and BA and midstory cover had negative effects (Table 4). Thus, females consistently selected nest patches characterized by relatively fewer but larger-diameter trees with a relatively high amount of understory cover and a relatively low amount of midstory cover.

Floristics.—At any given scale, selection for tree species exhibited little variation among study areas; the only exception was at the territory scale, where Tuliptrees were more common than expected at DB and less common at RB (Table 5). With all study areas combined, species composition in territories differed from random in that Red Maples and Chestnut Oaks were less common than expected and Sugar Maples were more common than expected (Fig. 2). At nest patches, with all study areas combined, White Oaks were more common than expected and Sugar Maples were less common than expected (Fig. 2). At two study areas, Tuliptrees were also more common than expected in nest patches (Table 5). With all study areas combined, White Oaks, Sugar Maples, and Cucumber-trees (*Magnolia acuminata*) were all used more often as nest trees than expected, whereas red oak species and Red Maples were used less than expected (Fig. 2).

Relationship between habitat features and nest survival.—The habitat features most strongly related to nest DSR differed by study area and mainly involved features selected at the territorial scale (Table 6). At three study areas (RB, DB, LW), we found weak evidence, given that 95% CIs of β included zero, that features preferred at the territorial scale were related to a decrease in nest survival; by contrast, at SQ we found weak evidence that preferred territorial features were related to an increase in nest survival (Table 6). At only one study area, REMA, did habitat selection

Table 2. Cerulean Warbler habitat measurements (means ± SE) at random (R), territory (T), and nest-patch (N) points on six study areas in the Appalachian Mountains, 2008–2010 (see text for description of habitat variables; DBH = diameter at breast height). To evaluate habitat selection, we compared T with R for territories and N with T for nests. Significance of point type (MANOVA, Pillai's trace statistic) was <0.05 at all study areas (at both scales of selection, except for nest patch at WYO). Significance of selection for individual variables is indicated by bold; + indicates that selection for the variable was positive, and – indicates that selection for the variable was negative. Significance at α = 0.05 is indicated by a single + or –; significance at α = 0.0052 (following Dunn-Sidak adjustment) is indicated by ++ or – –.

Habitat variable	Royal Blue, Tennessee (RB)			Sundquist, Tennessee (SQ)			REMA, Ohio (REMA)		
	R (n = 242)	T (n = 253)	N (n = 187)	R (n = 240)	T (n = 89)	N (n = 51)	R (n = 246)	T (n = 89)	N (n = 88)
Average DBH (cm)	41.65 ± 0.55	**44.47 ± 0.54 (++)**	**46.56 ± 0.69 (+)**	39.76 ± 0.47	**36.21 ± 0.92 (– –)**	37.80 ± 0.96	39.65 ± 0.51	**42.31 ± 0.84 (+)**	42.55 ± 0.79
Maximum DBH (cm)	66.31 ± 0.98	67.06 ± 0.96	68.30 ± 1.06	62.46 ± 0.99	**52.77 ± 1.56 (– –)**	54.69 ± 2.19	63.78 ± 0.96	66.78 ± 1.47	66.15 ± 1.31
Basal area (m² ha⁻¹)	24.07 ± 0.61	**21.70 ± 0.64 (–)**	20.99 ± 0.77	24.51 ± 0.67	**20.26 ± 1.05 (– –)**	21.25 ± 1.51	22.55 ± 0.66	**25.99 ± 1.09 (++)**	25.06 ± 0.79
Understory canopy cover	0.48 ± 0.02	**0.57 ± 0.02 (++)**	0.59 ± 0.02	0.54 ± 0.01	0.58 ± 0.03	0.59 ± 0.03	0.33 ± 0.02	0.34 ± 0.02	0.37 ± 0.03
Midstory canopy cover	0.56 ± 0.02	**0.48 ± 0.02 (– –)**	**0.43 ± 0.02 (–)**	0.62 ± 0.02	0.65 ± 0.03	0.58 ± 0.04	0.48 ± 0.02	0.51 ± 0.03	**0.57 ± 0.03 (+)**
Overstory canopy cover	0.77 ± 0.02	0.74 ± 0.02	0.78 ± 0.01	0.83 ± 0.02	**0.75 ± 0.03 (– –)**	0.75 ± 0.03	0.63 ± 0.02	**0.71 ± 0.03 (++)**	0.74 ± 0.02
Distance to gap (m)	19.68 ± 1.52	**13.53 ± 1.01 (– –)**	13.71 ± 1.36	20.40 ± 1.40	**9.03 ± 2.64 (–)**	10.46 ± 0.92	20.49 ± 1.60	20.49 ± 2.56	33.34 ± 3.62
Canopy height (m)	30.43 ± 0.29	30.67 ± 0.27	31.06 ± 0.32	30.68 ± 0.36	**28.92 ± 0.72 (–)**	**32.00 ± 0.92 (+)**	25.13 ± 0.20	**27.21 ± 0.38 (+)**	26.19 ± 0.32
Slope (°)	24.14 ± 0.45	23.34 ± 0.40	23.7 ± 0.50	24.10 ± 0.44	23.40 ± 0.88	24.92 ± 1.18	15.36 ± 0.56	16.79 ± 0.97	**18.58 ± 1.04 (+)**
Beers aspect	1.68 ± 0.03	1.68 ± 0.02	1.71 ± 0.03	1.70 ± 0.02	1.69 ± 0.05	**1.55 ± 0.08 (–)**	0.93 ± 0.05	**1.14 ± 0.08 (+)**	1.31 ± 0.07

Habitat variable	Daniel Boone, Kentucky (DB)			Lewis Wetzel, West Virginia (LW)			Wyoming County, West Virginia (WYO)		
	R (n = 238)	T (n = 231)	N (n = 48)	R (n = 237)	T (n = 193)	N (n = 63)	R (n = 234)	T (n = 76)	N (n = 43)
Average DBH (cm)	36.88 ± 0.67	36.90 ± 0.50	38.64 ± 1.26	43.35 ± 0.67	**46.31 ± 0.72 (++)**	47.80 ± 1.00	33.98 ± 0.76	**38.63 ± 0.92 (++)**	38.90 ± 1.51
Maximum DBH (cm)	57.80 ± 1.12	59.54 ± 0.89	59.57 ± 1.89	68.48 ± 1.23	69.83 ± 1.05	70.95 ± 1.91	58.44 ± 1.39	61.94 ± 1.54	58.62 ± 2.31
Basal area (m² ha⁻¹)	18.93 ± 0.57	**22.47 ± 0.57 (++)**	20.36 ± 1.23	20.45 ± 0.67	19.64 ± 0.68	**16.82 ± 0.94 (–)**	21.63 ± 0.66	19.26 ± 0.91	**15.83 ± 1.08 (–)**
Understory canopy cover	0.19 ± 0.01	0.18 ± 0.01	0.19 ± 0.03	0.34 ± 0.02	0.36 ± 0.02	0.42 ± 0.03	0.38 ± 0.01	0.39 ± 0.02	0.50 ± 0.04
Midstory canopy cover	0.46 ± 0.02	0.43 ± 0.01	**0.37 ± 0.03 (–)**	0.49 ± 0.02	**0.41 ± 0.02 (–)**	**0.33 ± 0.03 (–)**	0.48 ± 0.01	0.50 ± 0.02	**0.40 ± 0.04 (– –)**
Overstory canopy cover	0.51 ± 0.03	**0.62 ± 0.02 (++)**	**0.55 ± 0.01 (–)**	0.51 ± 0.02	**0.59 ± 0.02 (++)**	**0.53 ± 0.02 (–)**	0.57 ± 0.02	0.58 ± 0.03	0.49 ± 0.03
Distance to gap (m)	17.21 ± 1.49	13.40 ± 1.14	**8.55 ± 0.68 (– –)**	16.32 ± 1.29	**7.67 ± 0.87 (– –)**	**2.57 ± 0.56 (– –)**	32.91 ± 2.31	**9.23 ± 1.68 (– –)**	**3.60 ± 0.96 (–)**
Canopy height (m)	27.87 ± 0.84	27.85 ± 0.39	**30.28 ± 0.36 (++)**	26.39 ± 0.30	**28.88 ± 0.50 (++)**	**26.29 ± 0.72 (– –)**	27.61 ± 0.49	**30.86 ± 0.75 (++)**	30.77 ± 1.05
Slope (°)	22.16 ± 0.70	**19.93 ± 0.62 (–)**	20.21 ± 1.54	23.27 ± 0.38	22.66 ± 0.68	22.42 ± 1.15	30.18 ± 0.58	31.53 ± 1.46	32.74 ± 2.03
Beers aspect	1.22 ± 0.05	**1.44 ± 0.04 (++)**	1.50 ± 0.09	1.15 ± 0.04	**1.31 ± 0.45 (+)**	**1.01 ± 0.08 (– –)**	1.14 ± 0.04	1.24 ± 0.08	1.19 ± 0.11

Table 3. Cerulean Warbler nest-site characteristics at random (R), territory (T), and nest-patch (N) points on six study areas in the Appalachian Mountains, 2008–2010 (for names of study areas, see Table 2; for description of habitat variables, see text). Nest-site locations varied among study areas (MANOVA, Wilks' $\lambda = 0.68$, $P < 0.0001$) and nest height, distance to top of crown, and distance to foliage edge varied individually (ANOVA, all $P < 0.003$). We detected no difference in nest tree diameter at breast height (DBH) and distance from nest to bole among study areas (ANOVA, $P > 0.05$).

Study area	n	Nest tree DBH (cm)				Nest height (m)				Distance to top of crown (m)				Distance to bole (m)				Distance to foliage edge (m)			
		Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max
DB	48	42.56	2.54	14.60	80.00	18.51	0.81	10.40	30.50	9.64	0.72	1.00	24.40	3.44	0.27	0.65	7.90	2.05	0.16	0.40	5.40
LW	63	43.92	1.89	10.10	85.30	18.80	0.76	6.10	32.54	9.67	0.70	0.40	22.00	3.90	0.30	0.50	12.00	2.25	0.17	0.40	6.00
RB	187	44.04	1.12	12.10	95.50	19.32	0.37	7.60	35.00	9.82	0.32	0.00	25.00	3.80	0.11	0.50	9.00	2.38	0.10	0.10	9.80
REMA	87	45.55	1.49	19.00	90.00	19.78	0.55	5.00	32.00	6.23	0.39	0.50	17.00	3.52	0.17	0.00	8.00	1.67	0.12	0.00	6.00
SQ	51	43.36	1.79	20.60	62.10	23.40	1.01	9.00	35.00	8.80	0.85	1.50	36.25	4.38	0.27	1.00	10.00	2.13	0.15	0.50	5.80
WYO	43	43.01	1.94	20.32	62.50	20.61	0.99	8.84	35.36	13.28	1.07	2.14	33.55	3.61	0.26	0.75	9.00	2.29	0.30	0.00	11.00
All	479	43.99	0.67	10.10	95.50	19.80	0.26	5.00	35.36	9.33	0.24	0.00	36.25	3.77	0.08	0.00	12.00	2.17	0.06	0.00	11.00

behavior appear to be maladaptive (or adaptive for that matter); the use of preferred White Oak as a nest tree was negatively related to DSR (and CI did not include zero). At WYO, the only model with $\Delta AIC_c < 2$ was the distance to the edge of nest-tree foliage (and DSR was positively related), a nest-site feature for which we did not assess habitat selection, so we are unable to evaluate the adaptive nature of this behavior.

Discussion

Our results demonstrate that male and female Cerulean Warblers select for a variety of topographic, structural, and floristic habitat features on their breeding grounds in the Appalachian Mountains. Patterns of habitat selection for specific features, however, varied by scale (territory vs. nest patch) within some study areas, and within scales among study areas. Habitat selection by males at the territory scale was more spatially variable than habitat selection by females at the scale of nest patch and nest site. Habitat selection based on floristics occurred predominantly at the nest-site scale and was largely consistent across study areas. Also importantly, we found regional variation in the relationship between preferred habitat features and nest survival, which raises the possibility of heterogeneity in the adaptive value of behaviors involved in habitat selection. Because heterogeneity in habitat selection behavior, and associated reproductive consequences, can result in inappropriate conservation strategies when they are assumed to be similar at multiple scales and across broad areas, these results have important conservation and management implications.

The variability of selection at the territory scale suggests that habitat selection behavior by males is quite plastic. This flexibility might be expected, given that Cerulean Warblers can disperse widely between breeding seasons (Girvan et al. 2007), potentially between habitat types even more diverse than those evaluated in our study (e.g., bottomland vs. ridgetop forest). However, even within relatively homogeneous Appalachian forests, it appears that rather than simply relying on information provided by local (or microhabitat) features, males may also use landscape-level information to make decisions about finer-scale territory selection. At REMA and DB, study areas located in the two least-forested landscapes (74% and 75% forest cover, respectively, within 10 km), males selected habitat features normally associated with closed-canopy, undisturbed mature forest (greater BA and greater overstory cover). At other study areas, where surrounding forest cover was greater, attraction to habitat attributes enhanced by disturbance was more evident: males selected territories with lower BA, greater understory cover, and greater proximity to canopy gaps. Thus, landscape structure, with an unknown threshold of "patchiness" or fragmentation, may partly govern the decision strategies that Cerulean Warblers use to select habitat at the territory scale. It should be noted that at DB, apparent selection for features related to decreased canopy disturbance may have partially been a function of the availability of habitat features, given that the overall forest structure at this study area was more open (see random points in Table 2). However, territory characteristics differed among study areas regardless of availability, and males at DB occupied territories with the lowest understory-cover component and the second-highest BA (behind only REMA), which suggests that males at DB still selected for relatively closed-canopy conditions.

Table 4. Meta-analysis results of Cerulean Warbler habitat selection on six study areas in the Appalachian Mountains, 2008–2010 (for description of habitat variables, see text; DBH = diameter at breast height). We report average D (raw mean difference) and 95% confidence intervals (CI) at two scales of selection: territory and nest patch. Significant effects are in bold.

Habitat variable	Territory selection		Nest-patch selection	
	D	95% CI	D	95% CI
Average DBH (cm)	1.55	−0.66 to 3.75	**1.41**	**0.44 to 2.37**
Maximum DBH (cm)	0.07	−3.47 to 3.63	0.35	−1.27 to 1.97
Basal area (m² ha⁻¹)	−0.44	−3.06 to 2.18	**−1.56**	**−2.69 to 0.42**
Understory canopy cover (%)	2.40	−0.65 to 5.51	**3.2**	**0.60 to 5.73**
Midstory canopy cover (%)	−2.42	−6.41 to 1.64	**−4.69**	**−9.03 to 0.31**
Overstory canopy cover (%)	2.83	−3.47 to 9.11	−1.8	−6.32 to 2.76
Canopy height (m)	1.02	−0.24 to 2.27	0.28	−1.11 to 1.67
Distance to gap (m)	**−8.19**	**−12.40 to −3.98**	−1.27	−4.91 to 2.37
Slope (°)	−0.47	−1.41 to 0.47	0.58	−0.33 to 1.49
Beers aspect	**0.10**	**0.01 to 0.19**	−0.042	−0.68 to 0.08

Spatial variation in habitat selection strategies may reflect differences in predation (Chalfoun et al. 2002), brood parasitism (Young and Hutto 1999), or interspecific competition among study areas (Martin and Martin 2001). Ecological conditions at our two most disparate areas, SQ and REMA, likely differed in terms of predator community (e.g., Blue Jays [*Cyanocitta cristata*] were more common at REMA, whereas most raptors and flying squirrels [*Glaucomys* spp.] were more common at SQ), potential for brood parasitism by Brown-headed Cowbirds or fragmentation-related predation risk (because REMA was surrounded by agricultural lands and SQ was located in a more highly forested setting), and interspecific competition and aggression (Eastern Wood-Pewees [*Contopus virens*] were abundant potential competitors and Black-throated Green Warblers [*S. virens*] were absent at REMA, whereas at SQ the latter were abundant potential competitors and the former were nearly absent).

Although variability in territory selection behavior among study areas was apparent, we also observed some similarities. Males, regardless of study area, selected territories closer to canopy openings than expected, which is consistent with the results of previous studies (Oliarnyk and Robertson 1996, Bakermans and Rodewald 2009). More productive, mesic slopes (i.e., more northeast-facing; Fekedulegn et al. 2003) were also preferred consistently. Indeed, aspect appears to be among the most important features associated with territory selection across the species' Appalachian range (Buehler et al. 2006, Wood et al. 2006). Although aspect is not likely the ultimate habitat feature of interest, this topographic feature is often correlated with other important habitat attributes and may be a useful cue early in the season, when foliage expansion is limited. Preference for more productive exposures may be related to differences in food availability (Tolbert 1975), tree growth and floristics (Doolittle 1958, Fekedulegn et al. 2003), or microclimate (Rosenberg et al. 1983).

Table 5. Multiscale habitat selection by Cerulean Warblers in relation to floristics at six study areas in the Appalachian Mountains, 2008–2010 (for names of study areas, see Table 2). Tree species (or tree groups) that made up >4% of either available or nest trees at a study area were included in the analysis. Selection determination was based on comparison of 90% Goodman multinomial confidence intervals between available and selected points (at each respective scale). "A" indicates avoidance of a species (dark gray fill), "P" indicates preference for a species (light gray fill), "=" no selection for the species, and "x" indicates that a species did not meet the proportional threshold at a study area.

	Territory						Nest patch						Nest site					
	DB	REMA	RB	SQ	LW	WYO	DB	REMA	RB	SQ	LW	WYO	DB	REMA	RB	SQ	LW	WYO
Ash species[a]	A	x	x	x	x	x	=	x	x	x	x	x	=	x	x	x	x	x
Basswood[a]	x	x	=	=	=	x	x	x	=	=	=	x	x	x	=	=	=	x
Black Cherry[a]	x	x	=	x	x	x	x	x	=	x	x	x	x	x	A	x	x	x
Black Locust[a]	x	x	x	=	x	x	x	x	x	=	x	x	x	x	x	=	x	x
Chestnut Oak	=	=	=	A	=	=	=	=	=	=	=	=	=	=	=	=	=	=
Cucumber-tree	x	x	=	x	x	=	x	x	=	x	x	=	x	x	P	x	x	=
Hickory species	=	=	=	=	=	=	=	=	=	=	=	=	=	=	A	=	=	=
Red Maple	x	=	=	=	=	=	x	=	=	=	=	=	x	=	=	=	=	=
Red oak group	=	=	=	=	P	=	=	=	=	=	=	=	A	A	A	=	=	=
Sugar Maple	=	=	=	=	=	=	=	=	=	=	A	=	=	=	P	=	=	=
Tuliptree	P	=	A	=	=	=	P	P	=	=	=	=	=	P	=	=	=	=
White Oak	=	=	=	x	=	=	=	=	=	x	P	=	P	P	P	x	P	=

[a] Ash species (*Fraxinus* spp.), Basswood (*Tilia americana*), Black Cherry (*Prunus serotina*), and Black Locust (*Robinia pseudoacacia*).

TABLE 6. Final candidate models from Cerulean Warbler nest survival analysis at individual study areas in the Appalachian Mountains, 2008–2010 (for names of study areas, see Table 2). Variables included were based on site-specific habitat selection patterns, and only models with substantial support (ΔAIC$_c$ < 2) are displayed. Beta indicates the direction of influence of a feature on nest survival (e.g., + β indicates positive influence). Scale of selection refers to the scale at which a feature was selected for (T = territory, NP = nest patch, NS = nest site). Adaptive status was inferred by comparing the direction of selection of a feature with its influence on daily nest survival rate. Maladaptive status indicates that the direction of selection for the feature was opposite the influence on survival. Neutral status indicates that the 95% confidence interval (CI) of β included zero, and the sign indicates whether selection behavior for that feature trended toward adaptive (+) or maladaptive (–). Nest-site structural characteristics were not tested for selection, so adaptiveness with respect to these variables was not evaluated.

Study area	Model	AIC$_c$	ΔAIC$_c$	k	β	Lower 95%	Upper 95%	Scale of selection	Adaptive status
RB	S(BA)	489.52	0.00	1	0.020	−0.006	0.05	T	Neutral (−)
	S(Dist nest to crown)	489.65	0.13	2	0.044	−0.02	0.10		
	S(Dist to gap)	489.67	0.15	2	0.012	−0.006	0.03	T	Neutral (−)
	S(Null)	489.91	0.39	2					
	S(Avg DBH)	491.06	1.54	2	−0.01	−0.04	0.01	T	Neutral (−)
	S(Dist nest to foliage edge)	491.13	1.62	2	−0.08	−0.25	0.09		
	S(Mid cover)	491.40	1.89	2	0.35	−0.62	1.32	T	Neutral (−)
								NP	Neutral (−)
	S(Nest ht)	491.51	1.99	2	−0.02	−0.07	0.03		
SQ	S(Canopy ht)	138.82	0.00	2	−0.06	−0.14	0.02	T	Neutral (+)
								NP	Neutral (−)
	S(Dist nest to foliage edge)	138.85	0.03	2	−0.32	−0.70	0.05		
	S(Nest ht)	138.98	0.17	2	−0.06	−0.14	0.02		
	S(Null)	139.25	0.43	1					
	S(Nest tree DBH)	139.55	0.73	2	−0.03	−0.07	0.01		
	S(Over cover)	139.60	0.78	2	−1.56	−4.11	0.99	T	Neutral (+)
	S(Avg DBH)	140.44	1.62	2	−0.03	−0.11	0.04	T	Neutral (+)
	S(BA)	140.45	1.63	2	−0.02	−0.08	0.03	T	Neutral (+)
LW	S(Nest ht)	256.42	0.00	2	0.059	−0.0001	0.12		
	S(Canopy ht)	257.64	1.22	2	0.048	−0.007	0.10	T	Neutral (−)
								NP	Neutral (+)
WYO	S(Dist nest to foliage edge)	195.35	0.00	2	0.27	−0.02	0.56		
REMA	S(Nest tree preferred)	249.92	0.00	2	−0.90	−1.72	−0.07	NS	Maladaptive
DB	S(Aspect)	186.40	0.00	2	−0.61	−1.38	0.16	T	Neutral (−)
	S(Null)	187.29	0.89	1					

In contrast to territory selection, there was a lack of variability in selection for habitat attributes at nest-patch and nest-site scales. This might be expected because nest-site choice likely has more direct effects on fitness than territory selection and is often evolutionarily conservative (Martin and Roper 1988, Martin 1993; but see Eggers et al. 2006, Lomáscolo et al. 2010). Across all study areas, females chose nest patches with relatively large, well-spaced trees, increased understory cover, decreased midstory cover, a relatively high proportion of White Oaks, and a relatively low proportion of Sugar Maples (when compared with available habitat). These habitat conditions would generally be found within or near the edges of small-scale canopy disruptions in mature forests. From a behavioral perspective, incubating and brooding female Cerulean Warblers will often drop vertically from nests before flying horizontally away from the nest, presumably to mislead predators as to their nest location (Jones and Robertson 2001); this behavior may be an adaptation for nest sites located where overstory and midstory cover is relatively sparse.

Unlike structural features, we found very little variability in patterns of selection related to floristics at any scale. The spatially consistent selection for nest-tree species suggests that fitness benefits have been historically linked to the use of specific tree species in the Appalachians. The pattern of floristic selection was also striking because of two unexpected patterns: (1) the avoidance of Sugar Maples at the nest patch, but preference for the species at territory and nest-tree scales; and (2) the preference for White Oaks and Sugar Maples, and avoidance of their congeneric counterparts, red oaks and Red Maples, as nest trees. The inconsistency of selection for Sugar Maples at different scales may reflect a preference for a mosaic of disturbed and undisturbed mature-forest habitat by Cerulean Warblers. Sugar Maples are disturbance-averse, shade-adapted trees that can become dominant in the overstory in undisturbed, closed-canopy forests. However, if disturbances are localized and undisturbed forest is adjacent, conditions may exist in which Sugar Maples do not dominate but are still present

on protected microsites at the edge of canopy disruptions (God-man 1965, Trimble 1973). At these edges, females may prefer Sugar Maples as nest trees because of their phenology (earlier leaf emergence; Lopez et al. 2008) and foliage profile (they produce leaves in thick bunches, increasing nest concealment and potentially improving stability; T. J. Boves pers. obs.). Moreover, overstories dominated by Sugar Maples will often suppress midstory development (Godman 1965), another component of preferred habitat by breeding females.

The conflicting selection of congeneric oak and maple species as nest trees suggests that it would be inappropriate to assume that congeneric trees have similar ecological values. Birds may select one closely related tree species over another on the basis of subtle differences. In this case, floristic selection patterns may be related to differences in bark or foliage structure (Blakeslee and Jarvis 1972), which may affect suitability for nest attachment or concealment, or differences in leaf chemistry, which may affect insect availability (Nicol et al. 1997, Forkner et al. 2004). George (2009) found a similar pattern in a foraging study of Cerulean Warblers; White Oaks were preferred as foraging substrates whereas red oaks were avoided.

The diversity of habitat features related to nest survival may help explain why habitat selection patterns differed spatially. As birds are subjected to different selective pressures across their range, they may modify their behavior to respond to the specific pressures present at a location, assuming that they have the genetic capacity to do so (Lima 2009). Adaptive habitat selection, which we did not find strong evidence for at any study area, would be expected if selective pressures associated with environmental cues from an ecologically relevant period are still linked in a similar fashion. Conversely, nonadaptive habitat selection, which appeared to occur at three study areas, would be more likely if environmental cues that were once consistently coupled with fitness are no longer as tightly linked. Even a broadly selected habitat feature was related to a decrease in nest survival at REMA, where nests placed in White Oaks (consistently preferred nest tree) were more likely to fail. These results suggest that sustaining Cerulean Warblers in these contemporary landscapes may be complicated by potentially nonadaptive, or more severe, maladaptive, habitat decisions. There are two important caveats to these conclusions. First, by pooling across years, we may have masked some temporal variability in the adaptive nature of habitat selection; patterns of this behavior may be driven by conditions that are present only in certain years. Second, we were unable to measure lifetime fitness, and the adaptive nature of habitat selection behavior may be related to fitness components other than nest survival (such as postfledging or annual survival). However, even if carryover effects of breeding habitat decisions occur (e.g., Harrison et al. 2011), we would still expect this behavior to influence current reproduction at least as much as (or more than) these future components of fitness. Indeed, on our study areas within-season adult survival was virtually 100% (T. J. Boves unpubl. data), and newly fledged young and parents often dispersed outside the confines of their territories soon after the nesting cycle was completed (T. J. Boves pers. obs.). Nonetheless, future studies designed to estimate other fitness components across various habitat conditions would be informative, but also very challenging, for this species.

Conservation and management implications.—Our results provide evidence that a variety of habitat attributes related to topography, vegetation structure, and overstory species composition may influence habitat selection by Cerulean Warblers in the Appalachian Mountains. However, our data suggest that a "one size fits all" management strategy across the Appalachians will likely be unsuccessful at sustaining Cerulean Warblers. Instead, land managers will need to account for local conditions when managing for the species, possibly in relation to landscape configuration. In addition, the paradox for conservation is that in some contemporary landscapes, habitat selection behavior may not be adaptive, and managing for preferred habitat features may result in decreased reproductive success. It is possible that these results may only be temporary or may be offset by a positive effect on adult or postfledging survival, but this is currently unknown. Conversely, habitat features that lead to increased nest survival do not appear to be as attractive for territory establishment. Our findings also highlight the importance of spatial replication in ecological studies. If this study were performed at only a single study area, as is often the case, the results might have been assumed, incorrectly, to be transferable to the entire Appalachian breeding range of Cerulean Warblers.

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