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Cerulean Warblers in the Ozark region: habitat selection, breeding biology, survival, and space use

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ABSTRACT. Cerulean Warblers (*Setophaga cerulea*) are a species with declining populations that exhibit regional variation in habitat selection and demographic rates. The Ozark region of the south-central United States likely provides important habitat for Cerulean Warblers, but little is known about their breeding biology in that region. We studied Cerulean Warblers in riparian forests of the Ozarks of Arkansas from 2018 to 2020. We assessed multi-scale habitat selection for vegetative and topographic features, documented their breeding biology, estimated within-season and annual apparent survival, and estimated territory sizes. We found that Cerulean Warblers selected riparian habitat characterized by large-diameter trees across all spatial scales. Contrary to the results of previous studies, males appeared to avoid white oaks (*Quercus* spp., Section *Quercus*) at the territory scale, but this avoidance may reflect an underlying preference for riparian habitat. Our logistic-exposure estimate of nest survival (0.32; 85% confidence interval: 0.21–0.46) was similar to the median of estimates reported in previous studies. Our results indicate that maintaining riparian forests with large trees is important to provide suitable habitat for Cerulean Warblers in the Ozark region. Because of similarities in habitat selection among regions, some management practices from other populations, including retaining large trees and promoting a heterogeneous canopy structure, may be useful for managing for Cerulean Warblers in riparian areas of the Ozarks. However, selection for topography and tree species by Cerulean Warblers in our study also suggests that region-specific management strategies will be beneficial. Finally, our demographic rate estimates for this population should prove valuable in future full-annual-cycle population modeling efforts.

RESUMEN. **El chipe *Setophaga cerulea* de los Ozark: selección de hábitat, biología reproductiva, sobrevivencia y uso del espacio**

El chipe *Setophaga cerulea* es una especie con poblaciones en declive que muestra variación regional en selección de hábitat y tasas demográficas. La región de los Ozark en el sur-centro de los Estados Unidos probablemente provee hábitat importante para este chipe, aunque se sabe poco acerca de su biología reproductiva en la región. Estudiamos a *S. cerulea* en los bosques riparios de los Ozarks de Arkansas de 2018 a 2020. Determinamos su selección de hábitat a múltiples escalas según características de la vegetación y topografía, documentamos su biología reproductiva, estimamos sobrevivencia intra-estacional y aparente anual, y estimamos sus tamaños de territorio. Encontramos que estos chipes seleccionaron hábitats riparios caracterizados por árboles de diámetros gruesos en todas las escalas espaciales. Contrario a los resultados de estudios previos, los machos parecen evitar los robles blancos (*Quercus* spp., sección *Quercus*) a la escala de territorio, si bien dicha evasión podría reflejar una preferencia subyacente por hábitat ripario. Nuestra estimación de exposición logística de sobrevivencia de nido (0.32; 85% intervalo de confianza: 0.21–0.46) fue similar a la mediana de las estimaciones reportadas en estudios previos. Nuestros resultados indican que el mantenimiento de bosques riparios con grandes árboles es importante para proveer de hábitat adecuado para *S. cerulea* en la región de los Ozark. Dadas las similitudes en la selección de hábitat entre regiones, algunas prácticas de manejo de otras poblaciones, incluido el mantenimiento de grandes árboles y la promoción de una estructura heterogénea en el dosel, podrían ser útiles para el manejo de *S. cerulea* en áreas riparias de los Ozarks. Sin embargo, la selección de la topografía y especies de árboles por *S. cerulea* en nuestro estudio también sugiere que estas estrategias de manejo específicas a la región les serían benéficas. Finalmente, nuestras estimaciones de tasas demográficas de esta población deben ser valiosas en futuros esfuerzos de modelación de poblaciones de ciclo anual completo.

Key words: migratory songbird, nesting, population, return rate, riparian forest, *Setophaga cerulea*, territory

Cerulean Warblers (*Setophaga cerulea*) are Nearctic-Neotropical migrants with declining populations (Sauer et al. 2017). An estimated 73% of the overall population was lost between 1970 and 2014 (Rosenberg et al. 2016). Habitat loss and degradation across the full annual cycle are the broad underlying causes of this decline (U.S. Fish and Wildlife Service 2007), although specific causes are still in question. In their breeding areas in

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deciduous forests of the eastern United States and Canada, Cerulean Warblers have a patchy distribution, with variation in habitat selection within and among regions (Boves et al. 2013a, Buehler et al. 2020). At a broad scale, breeding habitats vary from upper mountain slopes to riparian bottomlands (Buehler et al. 2020). At a finer scale, Cerulean Warblers typically prefer forests with a heterogeneous canopy structure (Wood et al. 2013) and large trees (e.g., Robbins et al. 1992, Roth and Islam 2008, Carpenter et al. 2011, Boves et al. 2013a). Preferred tree species vary geographically, but Cerulean Warblers often select white oak (*Quercus alba*) (Buehler et al. 2020). These warblers also exhibit regional variation in reproductive success (Buehler et al. 2008, 2020) and population trends (Fig. 1A; Sauer et al. 2017). Because of this variation, understanding the biology of local populations will likely be important for effective conservation.

The Ozark region of the south-central United States has a relatively large population of breeding Cerulean Warblers, and this species is of conservation concern in the region (Fowler and Anderson 2015, Missouri Department of Conservation 2015, Central Hardwoods Joint Venture 2021). Although most studies conducted in the Ozarks have focused on documenting distribution records in upland and riparian forests, investigators have provided some information about habitat types and tree species used (Robbins et al. 1998, 2009, 2010, Rosenberg et al. 2000, James et al. 2001, Thompson et al. 2012). In-depth information on habitat selection is lacking. Robbins et al. (2009) estimated territory sizes in Missouri Ozark riparian forests and reported that some males were unpaired. However, no information is available about either the breeding biology or demographic rates of Cerulean Warblers in the Ozarks.

Information on fine-scale habitat selection by Cerulean Warblers in the Ozarks is needed for effective local management. Forest management guidelines have been developed to benefit Cerulean Warblers in the Appalachian Mountains (Wood et al. 2013) and Mississippi Alluvial Valley (Hamel 2005). However, given the variation in habitat selection among and within regions, the extent to which these management guidelines are applicable to populations in the Ozarks is unclear. Basic biological information is, therefore, needed to inform potential management strategies for Cerulean Warblers in this region.

To help resolve these gaps in our knowledge, we studied Cerulean Warblers in the Ozarks of Arkansas. Specifically, our objectives were to (1) assess habitat selection at multiple spatial scales, (2) estimate rates of nest survival and describe their breeding biology, (3) estimate apparent within-season and

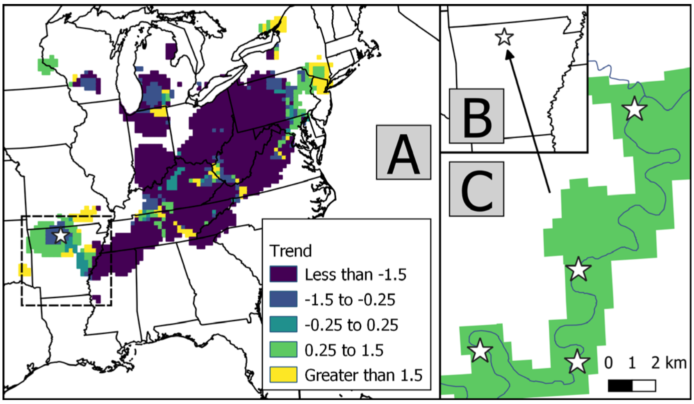

Fig. 1. (A) Population trends for Cerulean Warblers (percent change per year) from North American Breeding Bird Survey data, 1966–2015 (Sauer et al. 2017). (B) Location of our study area in Arkansas; the extent of this panel on map A is the dashed box. (C) Locations of our main study sites (stars) in the Buffalo National River corridor (shaded area); stars on panels A and B represent the overall location of our study area on those panels. Additional spatial data are from Natural Resources Canada et al. (2010), Arkansas Department of Environmental Quality (2015), and the U.S. National Park Service (2020). [Colour figure can be viewed at wileyonlinelibrary.com]

annual survival of males, and (4) estimate the size of territories.

METHODS

Our study was conducted in the Lower District of the Buffalo National River in northern Arkansas, USA (36.02°N–36.13°N, 92.53°W–92.64°W; Fig. 1B, C) from 2018 to 2020. The Buffalo National River comprises a protected corridor along the river. The area is a mostly forested gorge with steep slopes; non-forest areas include campgrounds, old fields, and managed hayfields. We selected study sites based on the known presence of Cerulean Warblers from previous studies (Raybuck et al. 2017, TJB, pers. observ.). In this area, these warblers are typically present along the Buffalo River (usually ≤ 300 m from the river), but rarely farther up adjacent forested slopes (JLW and TJB, pers. observ.). Abundant tree species in these riparian forests include boxelder (*Acer negundo*), elms (*Ulmus* spp.), hackberries (*Celtis* spp.), hickories (*Carya* spp.), American sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar styraciflua*), ashes (*Fraxinus* spp.), walnuts (*Juglans* spp.), and oaks (*Quercus* spp.), and abundant understory species include northern spicebush (*Lindera benzoin*) and giant cane (*Arundinaria gigantea*). We conducted field research from April to July 2018–2019. In 2020, we conducted a short field season focused on resighting previously banded males.

Capture and resighting. After males established territories, we thoroughly searched sites to locate territorial males. We captured males using 6-m mist-nets (28-mm mesh). To lure males to nets, we used playback of conspecific vocalizations, supplemented by a wooden decoy. We banded males with a unique combination of plastic color bands, as well as a numbered U.S. Geological Survey aluminum band. Throughout each season in 2018 and 2019, we attempted to resight each male weekly to estimate apparent within-season survival. Territorial males are usually easily resighted because they are vocal and can often be heard from > 100 m away. Because we spent extensive time on our study sites while searching for and monitoring nests and mapping territories, we typically resighted banded males incidentally while engaged in other activities. If we did not resight males in this manner, we searched for each male for at least an additional 15 min per week, before 10:30 when possible, and used playback to lure nearby males into view. We continued resighting efforts for individuals until we either failed to resight them for three consecutive weeks or their young fledged. Fledglings can roam beyond territorial boundaries (Raybuck et al. 2020), making males difficult to detect. In 2019 and 2020, we attempted to resight returning banded males to estimate apparent annual survival. We verified the identity of all males present on our study sites and searched ≥ 500 m up and down river from the previous season's territory of each banded male and on both sides of the river when necessary. In 2019, we resighted banded males and covered our study sites throughout the field season. In 2020, we searched for returning banded males from 19 to 21 May and 4 to 6 June. We searched for each male at least three times, with two attempts during one time period and one during the other. We were unable to conduct resighting earlier in the 2020 breeding season because the Buffalo National River was closed to all access from 2 April to 14 May due to the COVID-19 pandemic.

Nest searching and monitoring. After females arrived each season, we searched for nests in known territories. We located most nests by observing bird behavior, especially female behavior (Martin and Geupel 1993, Boves and Buehler 2012). Once located, we monitored nests every 2 to 3 days using spotting scopes to determine nest activity and stage. Because nests were high in the canopy and we could not see nest contents until nestlings were visible above the rim of nests, we considered nests active when parental activity indicated the presence of eggs or nestlings (e.g., female incubating or parents bringing food). We counted nestlings when possible, but exact counts were often difficult because of the steep viewing angles to nests and because leaves obscured nest cups. When the anticipated fledging date neared (nestlings ≥ 8 days old), we monitored nests daily to attempt to observe fledging or otherwise accurately determine nest fate. If we did not directly observe fledging, we searched the vicinity of nests for fledglings. If we did not observe fledglings, we inferred nest fate based on nest stage, nest condition, and parental behavior. For example, young are not known to fledge earlier than nestling day eight. Damage to nest cups suggested that a nest had been predated. Additionally, on rare occasions when we were still unable to determine nest fate, we used playback of avian mobbing calls and assessed the response of the parents. We considered young to have fledged if parents responded aggressively; typically, if a nest failed, adults would not respond aggressively to mobbing calls.

Space use. To map space use, we visually followed banded males in 30–45-min sessions during which we marked male locations (≤ 30 locations per session) with a GPS unit at intervals of 1 min when possible. This interval is thought to be sufficient to allow males to traverse their entire territory and therefore allow for biologically independent data (Barg et al. 2005, Wood and Perkins 2012, Perkins and Wood 2014). If we lost contact with focal males during a session, we searched the territory until they were re-located, and then continued mapping. We conducted all sessions before 10:30. We ceased mapping of space use for males with fledged young (three of 16 males used in our territory size analysis) because they are generally not as active in territory defense.

Habitat selection. To assess habitat selection, we measured variables related to vegetation structure, vegetation species composition, and topography at paired used and random points. We assessed this at multiple spatial scales, including territory, within-territory (core area use), nest-patch, and nest-site scales. We designed our random points to sample areas available for habitat selection at each scale (i.e., random points were not constrained to unused areas; Jones 2001). We defined a territory as the area defended by a male, as estimated by our territory mapping, and a nest patch as the general area, within a territory, surrounding a nest. We ensured that paired used and random points did not overlap. All paired points at territory, within-territory, and nest-patch scales were ≥ 23 m apart, given that we measured canopy cover within an 11.3-m radius circle at each point. We constrained random points to forest habitat because Cerulean Warblers do not use other habitats.

At the territory scale, we compared used points in territories to random points that represent areas available for territory selection, and also to random points in territories. We first used Google Earth Pro 7.3 (Google 2017) to visualize locations where we had recorded males during territory mapping, and we identified clusters of points, or core areas of high use. Males had 1–3 core areas per territory. We then randomly selected one used point in each core area. We selected points either by using the “Create Random Points” tool in ArcMap 10.3 (ESRI 2015) or based on a random integer while visualizing points in QGIS 3.4.2 (QGIS.org 2018). We generated random integers via a true random number generator at www.random.org. We paired each used point with a random point located in a random direction and at a random distance between 50 to 300 m from the used point, and located points using Google Earth. We considered random points to represent habitat available for territory selection. The 300-m maximum distance ensured that we sampled nearby areas that males would likely have assessed when selecting a territory. To assess selection of habitat in core areas in territories (see below for methods of territory delineation), we paired each used point in a territory with a within-territory random point, selected using the “Create Random Points” tool in ArcMap or the “Random points inside polygons” tool in QGIS.

At nest-patch and nest-site scales, we paired each used point with one random point. For nest patches, we centered each used point on the nest location. We then located each paired random point at a random location in the territory using ArcMap or QGIS. To select random nest-patch points for nests of males whose territories we did not map (12 of 33 nests), we delineated a polygon in Google Earth for each male based on our observations of their space use. For each nest, we then generated a random point within the polygon approximating the territory. At the nest-site scale, we located the used point at the nest tree and the random point at the closest other tree to a point a random direction and a random distance from 1 to 11 m from the nest. We considered only trees with a diameter at breast height (DBH) ≥ 10 cm and a height ≥ 9 m as possible nest trees because nests are rarely in small trees (TJB, unpubl. data). Voucher photographs of all nest trees are archived on the community science website iNaturalist (https://www.inaturalist.org/projects/cerulean-warbler-nest-trees). When possible, we collected physical specimens, which are archived in the Arkansas State University Herbarium (STAR).

At each scale, we measured habitat variables that previous investigators have found to be important in habitat selection by Cerulean Warblers (Table 1). At the nest-site scale, we recorded only tree species, tree DBH, and tree height. At territory and nest-patch scales, we measured slope and Beers aspect (aspect transformed to reflect forest productivity; Beers et al. 1966). Additionally, at each plot, we estimated basal area and, for each tree in the basal area prism plot, identified the species or species group (for closely related species). For example, we included all species in the white oak group (Section *Quercus*) in one category. We also measured the DBH of all trees with a DBH $\geq$ 10 cm; Cerulean Warblers rarely use smaller trees so we did not consider them available. We used a prism plot for assessing tree DBH and species because of the importance of large trees for Cerulean Warblers. We also measured mean canopy height, distance to the nearest canopy gap (with diameter $\geq$ 5 m) within 100 m and whether it was natural or anthropogenic, and canopy cover at understory (0–4 m), mid-story (4–15 m), and overstory (> 15 m) levels. To consistently measure canopy cover at each plot, we visually determined if there was vegetative cover in each height class at each of five points along an 11.3-m radius in each cardinal direction and at the center of the plot. We used a rangefinder to aid in determining foliage heights. From these presence/absence values, we calculated proportions of cover in each canopy height class at each plot. We also calculated mean tree DBH for each plot. Because observations in this area suggested that proximity to the river was correlated with the presence of Cerulean Warblers, we also calculated the distance between the river and each territory or nest-patch plot. We delineated a polygon of the relevant section of the Buffalo River in Google Earth and calculated the distance between each sampling point and the river using the software package geosphere (Hijmans 2019) in R 3.6.1 (R Core Team 2019).

Data analyses. We estimated nest survival using logistic-exposure models (Shaffer 2004, Shaffer and Thompson 2007) in R. We used a 25-d duration of the laying, incubation, and nestling stages for calculating the overall survival estimate from the daily survival rate from the model (Buehler et al. 2008, Boves and Buehler 2012). We analyzed male apparent survival data using Cormack-Jolly-Seber open population models in Program MARK 9.0 (White and Burnham 1999). Apparent survival estimates from Cormack-Jolly-Seber models differ from return rates because they include a recapture parameter to improve survival estimates. We report estimates from null (ϕ.p.) models because of small sample sizes. For apparent weekly within-season survival, we excluded from our analysis five males only present early in the season, two males never re-located after banding, and one male that was not reliably re-located because his territory spanned the river. We used only the first nine weeks of resighting data, which included the time period from the third week of April until the second week of June. We did not include resighting data from later in our 2018 and 2019 field seasons (which lasted until the first week of July) because most males had finished nesting and became difficult to detect. For apparent annual survival, we built a model with three yearly sampling occasions. Importantly, apparent survival estimates represent minimum estimates because they cannot account for individuals that may have dispersed elsewhere after capture (e.g., Cilimburg et al. 2002).

We estimated territory sizes as the 95% contour of the kernel density estimate of each male's utilization distribution using the package adehabitatHR 0.4.16 (Calenge 2006) in R. We used the bivariate normal kernel with the default grid extent split into 100 intervals. When we generated preliminary estimates to inform placement of habitat sampling plots, we used the reference bandwidth for the smoothing parameter (h). Later, for males where the reference bandwidth over-smoothed the territory estimate, we improved estimates by manually setting h. We visually assessed the results of a range of h values to achieve an appropriate amount of smoothing to best reproduce observed space use patterns. Additionally, for males with territories adjacent to non-forest (unavailable) areas like the Buffalo River or open fields, we used the method of

Table 1. Habitat features measured, method of measurement, and justification for why we hypothesized that the feature may be important to habitat selection by Cerulean Warblers along the Buffalo National River in the Ozarks of Arkansas, USA.

Habitat feature	Method of measurement	Justification from other studies of Cerulean Warblers	References (not exhaustive)
Basal area	Cruising prism	Selection for basal area / tree density	Jones and Robertson (2001), Boves et al. (2013a)
Beers aspect	Compass	Preference for mesic, productive aspects	Boves et al. (2013a), Nemes and Islam (2017)
Canopy cover	Visually	Preference for complex canopy structure	Boves et al. (2013a), Wood et al. (2013)
Distance to nearest canopy gap within 100 m	Measuring tape or GPS	Association with canopy gaps	Boves et al. (2013a), Perkins and Wood (2014)
Distance to river	Calculated from coordinates in R	Preference for riparian habitat at our study sites	JLW and TJB, personal observations
Mean canopy height	Clinometer and rangefinder or measuring tape	Selection of areas with tall trees	Jones and Robertson (2001), Nemes and Islam (2017)
Slope	Clinometer	Use of forested slopes	Wood et al. (2013), Nemes and Islam (2017)
Tree diameter at breast height (DBH)	DBH tape	Selection of large trees in territories and for nesting	Bakermans and Rodewald (2009), Boves et al. (2013a)
Tree species identity	Visually	Selection of specific tree species (e.g., white oaks)	Boves et al. (2013a), Nareff et al. (2019)

Benhamou and Cornélis (2010) as implemented in adehabitatHR to exclude these areas from territory estimates. This method requires manually setting h. Finally, when estimating the areas used by males, we included only males where we recorded ≥ 50 locations.

To assess habitat selection for all habitat features except tree species composition, we first assessed collinearity by calculating all pairwise correlations. We used Spearman's rank correlation (r_s) because Shapiro–Wilk tests showed that some habitat variables were not normally distributed. Correlated variables ($|r_s| > 0.7$) included mean and maximum DBH, and tree DBH and tree height at the nest-site scale. We included mean DBH in analyses because it is based on more data than maximum DBH and, therefore, likely better describes habitat. At the nest-site scale, we included tree DBH instead of tree height because tree DBH is a more accurate measurement. At the territory scale, we built generalized linear mixed models in the package lme4 1.1-21 (Bates et al. 2015) in R. We included habitat variables as fixed effects and the used or random status of the point was the binary response variable. We included bird identity as a random intercept to prevent pseudoreplication because the number of habitat plots differed among males due to differences in the number of core areas. For nest-site and nest-patch scales, we built generalized linear models in R. At territory and nest-patch scales, we built and compared all univariate and bivariate models. We compared models independently at each scale on the basis of Akaike's Information Criterion corrected for small sample size (AIC_c) using the R package AICcmodavg (Mazerolle 2019). We also included an intercept-only (null) model and models that consisted of all combinations of variables included in any model with $\Delta AIC_c \leq 2$ of the top model. We considered any model with $\Delta AIC_c \leq 2$ of the top model to be equivalent. We calculated 85% confidence intervals (CIs) of β estimates in top models to screen for uninformative parameters with CIs overlapping zero. This level of confidence is compatible with AIC_c

model selection (Arnold 2010). No variables in top models had CIs that overlapped zero. We examined the sign (+/-) of β estimates to assess the directionality of selection.

To assess selection of tree species, we generated 85% multinomial CIs around frequencies of tree species or species groups at used and random points at each spatial scale and considered selection to be occurring if CIs did not overlap between used and random points at a scale. To calculate CIs, we used the Goodman method (Goodman 1965) in the package DescTools (Signorell 2019) in R. We pooled species that made up < 4% of trees at each scale as "other" (Boves et al. 2013a).

Finally, to assess the relationship between habitat and nest survival, we built logistic-exposure models in R featuring fixed effects of habitat variables at territory, nest-patch, and nest-site scales. For territory and nest-patch scales, we built univariate models and models with all bivariate combinations of habitat variables. We then compared these models, and the intercept-only null model, independently at each scale via AIC_c. Except where otherwise noted, we report results as means ± SE.

RESULTS

Habitat selection. At each spatial scale, Cerulean Warblers preferred areas with larger trees (i.e., larger DBH; Fig. 2, Table 2). At the territory scale, males preferred areas closer to the river with greater overstory cover. Within territories, males also preferred areas closer to canopy gaps and characterized by greater basal area and understory cover. At the nest-patch scale, Cerulean Warblers preferred areas with greater understory cover. Table 2 summarizes β estimates and 85% CIs of fixed effects from top models, as well as the means of these habitat variables at used and random points (see also Table S1, which lists top models). Males preferred areas with fewer white oaks at the territory scale (85% CI for used points: 0.004 to 0.064, for random points: 0.084 to 0.215; Fig. 3). No other selection for tree species existed at any scale; all other paired 85% CIs overlapped.

Breeding biology. We observed nesting on our study sites from 23 April (earliest construction date) to 25 June (latest fledging date). We located 33 nests, with 25 becoming active (i.e., known to have had eggs). We located 15 nests (12 active) in 2018 and 18 nests (13 active) in 2019. The constant-survival logistic-exposure model best explained patterns of nest survival, so no habitat features we measured appeared to be related to nest survival. From this model, the daily survival rate was 0.956 (85% CI: 0.939–0.969), and the 25-d entire-period survival estimate was 0.32 (85% CI: 0.21–0.46). Apparent nest survival was eight of 25 nests, or 32%. Four nests were successful during each year of our study. For six nests where we could see well enough to confidently count nestlings, brood sizes were three.

Adult apparent survival and space use. In total, we monitored 41 banded males. In 2018, three males banded in a previous study in 2017 returned to our sites. We banded 28 males and three incidentally captured females in 2018. In 2019, we banded 10 males. We estimated apparent within-season survival from 42 encounter histories (we monitored some males in both 2018 and 2019) and apparent annual survival for 41

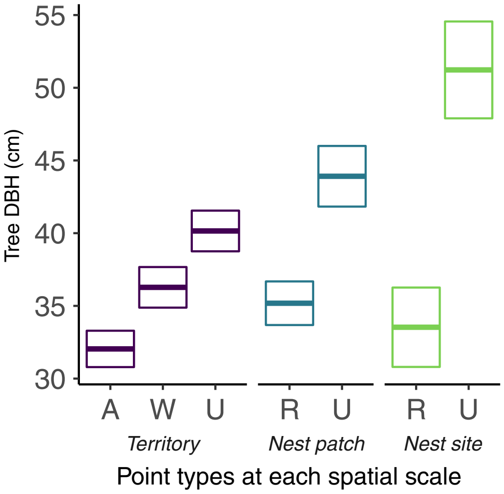

Fig. 2. Selection of trees of relatively large diameter at breast height (DBH) at territory, nest-patch, and nest-site spatial scales by Cerulean Warblers along the Buffalo National River in the Ozarks of Arkansas, USA. A: available random points at the scale of male territories, W: random points in male territories, U: used points, R: random points at nest-patch or nest-site scale. Values are means ± SE. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Habitat variables from top models of Cerulean Warbler habitat selection along the Buffalo National River in the Ozarks of Arkansas, USA[a].

Spatial scale of habitat selection	Number of used/random plots	Habitat variable	β estimate	85% confidence interval	Used points		Random (available) points	
					Mean	SE	Mean	SE
Territory	45	Distance to river (m)	−0.02	−0.03 to −0.01	49.40	4.61	132.85	13.77
		Mean tree diameter at breast height (DBH) (cm)	0.06	0.01 to 0.11	40.15	1.40	32.04	1.25
		Proportion overstory	1.83	0.06 to 3.69	0.80	0.03	0.75	0.04
Within-territory	45	Basal area (m^2/ha)	0.09	0.04 to 0.14	25.28	0.99	21.87	1.37
		Distance to nearest canopy gap (m)	−0.04	−0.08 to −0.01	12.09	1.34	15.61	2.52
		Mean tree DBH (cm)	0.06	0.02 to 0.10	40.15	1.40	36.27	1.40
		Proportion understory	2.13	0.29 to 4.07	0.66	0.03	0.58	0.03
Nest patch	33	Mean tree DBH (cm)	0.11	0.06 to 0.17	43.91	2.08	35.18	1.50
		Proportion understory	3.27	1.30 to 5.43	0.64	0.04	0.53	0.04
Nest site	33	Tree DBH (cm)	0.06	0.03 to 0.08	51.23	3.33	33.53	2.73

[a] We compared models using Akaike's Information Criterion corrected for small sample size (AIC_c). Models are binomial generalized linear mixed models (territory and within-territory scales) and generalized linear models (nest-patch and nest-site scales). If a spatial scale had more than one model in the top model set, we report estimates from the model that contained all variables that were in the top model set (see also Table S1).

males. For apparent within-season survival, the weekly apparent survival estimate was 0.95 (85% CI: 0.92–0.97). From 2018 to 2019, return rate was 29% (nine males of 31 returned). From 2019 to 2020, 11% of males (two of 19) returned. The Cormack-Jolly-Seber null model estimate of overall apparent annual survival was 0.22, which is equal to the raw value of 11/50 because the recapture probability parameter estimate was 1. No individuals were observed in 2018, not observed in 2019, and then observed in 2020, which would have allowed us to estimate a recapture probability < 1. Four returning males occupied the same approximate territory each year; two of these males returned over both yearly intervals. Two returning males shifted their territories slightly (up to a few hundred meters). Three males that returned appeared to be transients or floaters in one or two years, during which we did not detect them for much of the breeding season despite their subsequent or previous presence. Nest sites of a female banded in 2018 and also observed in 2019 were 6.64 km apart. Mean territory size was 1.14 ± 0.12 ha ($N = 16$, range = 0.33–2.03 ha), and territory sizes were normally distributed.

DISCUSSION

Habitat selection. Several of our habitat selection results were similar to those of studies from other regions, indicating some consistency in habitat selection. Most importantly, selection of habitat characterized by relatively large trees (based on DBH), which we found at all spatial scales, is consistent with results from previous studies

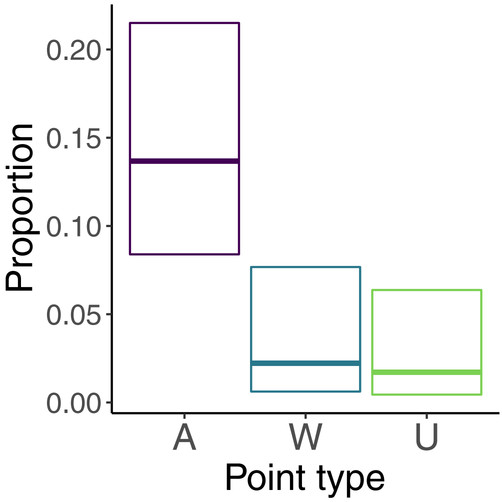

Fig. 3. Cerulean Warblers appeared to avoid white oaks (*Quercus* spp., Section *Quercus*) at the territory scale along the Buffalo National River in the Ozarks of Arkansas, USA. Values shown are 85% multinomial confidence intervals on proportions of white oaks in habitat plots at various point types. A: available random points at the scale of male territories, W: random points in male territories, U: used points in male territories. [Colour figure can be viewed at wileyonlinelibrary.com]

(Buehler et al. 2020). We also found that males selected core areas close to canopy gaps, as also reported in studies conducted in other regions (e.g., Perkins and Wood 2014). Possible benefits of canopy gaps for songbirds include improved song transmission (Perkins and Wood 2014) and increased prey abundance (Blake and Hoppes 1986). At the nest-patch scale, we observed selection for greater understory cover, which was also documented elsewhere (Boves et al. 2013a). Although Cerulean Warblers usually use the upper forest canopy, females in particular sometimes forage and collect nesting material in understory vegetation, and fledglings sometimes use understory vegetation immediately after leaving nests (Wood et al. 2013, JLW and TJB, pers. observ.). Understory cover also may be associated with other preferred factors like canopy gaps.

Despite these similarities with other studies, habitat selection by Cerulean Warblers in the Ozarks also differed from patterns elsewhere. First, Cerulean Warblers in other regions have often been found to prefer white oaks (Section *Quercus*), especially *Quercus alba*, at territory and nest scales (e.g., Boves et al. 2013a, Nemes and Islam 2017), but males in our study appeared to avoid white oaks at the territory scale. Selection of tree species by Cerulean Warblers is clearly geographically variable (Buehler et al. 2020), so this result may reflect the tree species preferences of males in the Ozark population. However, in our study area, white oaks are more abundant farther from the Buffalo River, so a preference for riparian habitat by Cerulean Warblers in our study could drive this apparent avoidance of white oaks. Future studies of tree species selection should aim to disentangle tree species composition from such gradients in habitat type. Second, investigators in studies elsewhere have considered slope and aspect to be important predictors of habitat selection by Cerulean Warblers because of a preference for mesic, productive, northeast-facing aspects, and steep slopes (e.g., Roth and Islam 2008, Boves et al. 2013a, Nemes and Islam 2017). However, slope and aspect did not appear to be important in our study, suggesting that males may select riparian habitat without regard to topography. Riparian habitats may promote forest conditions similar to those on mesic upland slopes through different mechanisms. Similarly, Nareff et al. (2019) found that forest management can positively affect densities of Cerulean Warblers at a variety of slope positions and aspects.

Breeding biology. Our entire-period nest survival estimate of 0.32 is intermediate relative to those reported in previous studies conducted in other regions (Buehler et al. 2008, 2020, Nemes and Islam 2017). Our estimate is similar to the median of 0.334 for estimates presented by Buehler et al. (2008) from five regions (range = 0.079–0.768). That our estimate was not lower is encouraging, but this estimate may still indicate localized population decline, based on previous population models for Cerulean Warblers (Buehler et al. 2008, Boves et al. 2013b). We were unable to identify causes of nest failure with much certainty, but some nests appeared to have been predated based on damage to nest cups.

Although we found no relationship between habitat characteristics and nest survival, the results of previous studies have revealed evidence for both adaptive and maladaptive habitat selection by Cerulean Warblers (Bakermans and Rodewald 2009, Boves et al. 2013a,b, Nemes and Islam 2017). However, the apparent lack of association between habitat selection and fitness is common, and potential methodological and ecological explanations are numerous and beyond the scope of this discussion (reviewed by Chalfoun and Schmidt 2012). Further studies will be necessary to better understand which, if any, factors promote successful nesting by Cerulean Warblers in the Ozarks. In our study, brood size was within the range typical of Cerulean Warblers (typically three or four young; Buehler et al. 2020). As also reported in previous studies (Rogers 2006, Robbins et al. 2009), we observed putatively unpaired males on our study sites, suggesting that this population might be female-limited. Male-biased sex ratios are common across bird species, especially in small populations and species of conservation concern (Donald 2007, Morrison et al. 2016). Pairing success did not appear consistent in territories between years so male quality, rather than habitat quality, may partly explain the probability of pairing.

Adult apparent survival and space use. Our apparent within-season weekly survival estimate of 0.95 was lower than previous estimates (compared to 0.97, Raybuck et al. 2017; ~ 0.99, Jones et al. 2004), but our estimate could reflect movements rather than reduced survival. Several putatively unpaired males seemed to abandon their territories by about the end of May, which could have resulted in a survival estimate biased low. Our return rate estimates of 29% and 11% are lower than estimates reported in some studies (35% in Pennsylvania and the Ozarks, Raybuck et al. 2017; 40–43% in Michigan, Rogers 2013). However, the results of a recent study of Cerulean Warblers conducted in areas encompassing 10 states revealed return rates similar to those in our study (D. W. Raybuck, pers. comm.). Only one of seven banded males confirmed to have bred successfully in our study returned the next year. In contrast, other investigators have documented a positive relationship between reproductive success and return rates for several species of songbirds (Haas 1998, Hoover 2003).

Our estimate of mean territory size (1.14 ha) was relatively large compared to those reported in previous studies. Most investigators have reported mean territory sizes < 1 ha (Nemes and Islam 2017, Buehler et al. 2020), although others have reported mean estimates > 1 ha (Oliarnyk and Robertson 1996, Jones et al. 2001). Habitat characteristics, presumably related to habitat quality, could explain, at least in part, variation in territory sizes (Leonard et al. 2008, Anich et al. 2010). However, habitat quality is difficult to quantify (Johnson 2007). Additionally, differences among studies in field and size estimation methods make comparisons of territory size estimates difficult (Buehler et al. 2020). For example, choices such as the estimator used can influence estimates of space use (Barg et al. 2005). For kernel estimators, the choice of smoothing parameter can affect space use estimates. Some investigators in previous studies of Cerulean Warblers used least-squares cross-validation to estimate the smoothing parameter (Barg et al. 2005, Perkins and Wood 2014), but, in our study, this method did not delineate territories accurately compared to our field observations of space use by each male so we used a different smoothing method to estimate space use more accurately.

Management and conservation implications. At the local scale, our data suggest that maintaining riparian forests with large trees will be important in providing habitat for Cerulean Warblers along the Buffalo River and potentially in other areas in the Ozarks, such as along the Eleven Point and Current rivers in Missouri (Rosenberg et al 2000, Robbins et al. 2009). Our results suggest that habitat management guidelines from other regions may be compatible with populations of Cerulean Warblers in riparian areas in the Ozarks, as far as a focus on managing forests with large trees and heterogeneous canopy structure. However, in contrast to current management recommendations for the Appalachian region (with the exception of the recent findings of Nareff et al. 2019), we found that slope and aspect did not appear to be important in habitat selection by Cerulean Warblers in riparian forests in the Ozarks. Future studies in the Ozarks should also focus on upland sites, where habitat features selected by Cerulean Warblers may differ from those in riparian areas.

The effects of forest management on Cerulean Warblers can be complex (Boves et al. 2013b), so careful study is necessary before implementing management strategies. Additionally, management may be most effective in areas with low densities of Cerulean Warblers (Wood et al. 2013). To better understand geographic variation in the breeding biology of Cerulean Warblers, future studies across regions should be conducted in a coordinated manner and using consistent methods. The uncertainty of our return rate estimates also highlights the importance of developing methods for quantifying long-distance movements and dispersal by Cerulean Warblers and other small songbirds. Finally, at the global scale, our demographic rate estimates provide critical inputs for full-annual-cycle population models that require parameters specific to each population.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Top models from model selection of binomial generalized linear mixed models (territory and within-territory scales) and generalized linear models (nest-patch and nest-site scales) of Cerulean Warbler habitat selection along the Buffalo National River in the Ozarks of Arkansas, USA.