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LANDSCAPE-LEVEL FOREST COVER IS A PREDICTOR OF CERULEAN WARBLER ABUNDANCE

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ABSTRACT.—We examined support for the hypothesis that abundance of Cerulean Warblers (*Setophaga cerulea*) increases with percentage of bottomland and upland forest, and decreases with percentage of developed land at a local-habitat scale (within a 250-m buffer) and increases with percentage of all forest at a landscape scale (within a 10-km buffer). We conducted surveys along 16 rivers in Missouri and Arkansas from 1999 to 2006 and related habitat and landscape factors to counts of Cerulean Warblers in 123 5-km segments on these rivers. We detected 576 singing male Cerulean Warblers and found support for both local and landscape effects on Cerulean Warbler abundance. Model fit was good with an average correlation of 0.841 between predicted and observed values based on an eight-fold cross-validation procedure. The abundance of Cerulean Warblers increased 390.7, 8.7, and 4.1 times across the observed range of forest within 10 km, bottomland forest within 250 m, and upland forest within 250 m, respectively. Conservation and research need to address large-scale forest patterns in addition to local habitat for Cerulean Warblers. Further research is needed on abundance patterns across riparian and upland forests and demographic rates in this part of their range. *Received 17 April 2012. Accepted 19 June 2012.*

There is great conservation concern for the Cerulean Warbler (*Setophaga cerulea*) (Hamel et al. 2004), largely the result of range-wide declines in their abundance (Sauer et al. 2011). Loss or alteration of breeding habitat has commonly been assumed to be a cause of declines; however, little is known about their wintering range and threats during the non-breeding season (Hamel 2000). Recent demographic analyses indicated increasing overwinter survival would have the greatest effect on population growth and that increases in the amount of forest cover in agricultural-dominated landscapes may be required to increase fecundity (Buehler et al. 2008).

Local habitat characteristics associated with Cerulean Warblers include mature deciduous forest with large trees and heterogeneous canopies (Hamel 2000, Jones and Robertson 2001, Roth and Islam 2008, Bakermans and Rodewald 2009, Hartman et al. 2009). Heterogeneous canopies used by Cerulean Warblers have been associated with riparian or bottomland forests (Hamel et al. 2004, Carpenter et al. 2011), upland forest and ridgetops (Dettmers and Bart 1999, Weakland and Wood 2005, Buehler et al. 2006, Newell and Rodewald 2011), and timber harvest (Oliarnyk and Robertson 1996, Rodewald and Yahner 2000, Bakermans and Rodewald 2009, Newell and Rodewald 2012). Cerulean Warblers generally prefer heavily forested landscapes and are considered area sensitive. Landscape effects include positive effects of percent forest or forested wetlands in a 1- to 8-km radius and negative effects of edge and open or agricultural land (Hamel et al. 1998, Dettmers and Bart 1999, Thogmartin et al. 2004, Weakland and Wood 2005, Buehler et al. 2006, Wood et al. 2006). Landscape requirements may vary across the breeding range and Cerulean Warblers may require larger patches in more fragmented landscapes with less forest (Hamel 2000).

Understanding how habitat and landscape factors affect abundance of Cerulean Warblers across their breeding range remains a research priority (Hamel 2000; Hamel et al. 2004, 2006; Hamel and Rosenberg 2007). Local or landscape factors affecting abundance of Cerulean Warblers remain largely unstudied in Missouri. This state is the western terminus of the both the Cerulean Warbler's range and the central hardwoods forest region, the most important forest region for the Cerulean Warbler (Hamel 2000). Past studies have spanned micro-habitat to landscape scales, but none has directly compared support for the importance of local habitat versus landscape forest composition. A large proportion of Cerulean Warblers breed in riparian forest in portions of this species' range such as Missouri and Arkansas, which have been poorly sampled using conventional survey methods (Jacobs and Wilson 1997,

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Robbins et al. 1998). The latter (1998, 2010) conducted river-based surveys in 1999–2006 in Missouri and northern Arkansas to address this lack of data and document occurrence of some species of concern, including Cerulean Warblers, in riparian habitats across the state. These surveys are not a representative sample of forest in the state but they do represent forests where Cerulean Warblers are known to occur and reach modest densities (Reidy et al. 2011). The study design provided an opportunity to assess how local-versus landscape-scale habitat composition affects abundance in this previously unstudied region.

Our objective was to evaluate the relative support for the hypotheses that percentage of bottomland and upland forest had a positive effect, and developed land a negative effect on abundance of Cerulean Warblers in Missouri and Arkansas. We compared support for effects at: (1) a local-habitat scale (within a 250-m buffer), (2) a landscape scale (within a 10-km buffer), or (3) a combination of local-habitat and landscape scales.

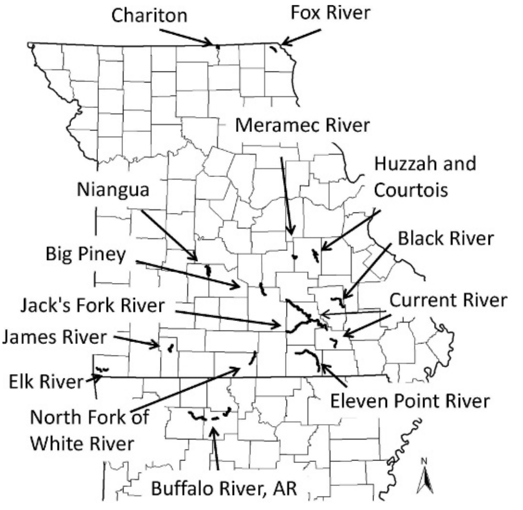

FIG. 1. Portions of rivers along which we measured effects of habitat and landscape factors on the number of singing Cerulean Warblers in Missouri and Arkansas, 1999–2006.

METHODS

Study Area.—We conducted surveys along 16 rivers in Missouri and northern Arkansas (Fig. 1).We selected rivers that had at least some riparian forest along them, occurred across the region and along a gradient of landscapes from mostly forested to minimally forested, and were accessible by canoe to allow us to conduct surveys across public and private land. Rivers in southern Missouri and northern Arkansas occurred in landscapes of rolling hills covered primarily with hardwood forests interspersed with glades and woodlands and dissected by deep river valleys. The two rivers in northern Missouri occurred in landscapes dominated by cropland and pasture with narrow corridors of riparian forest. Forests in the river floodplains included oaks (*Quercus* spp.), hickories (*Carya* spp.), ash (*Fraxinus* spp.), maples (*Acer* spp.), hackberry or sugarberry (*Celtis* spp.), and American Sycamore (*Plantanus occidentalis*). Forests in the uplands in southern Missouri and northern Arkansas were dominated by oaks, hickories, and shortleaf pine (*Pinus echinata*).

Bird Surveys.—We conducted surveys during 0500–1000 hrs (CST) from a canoe with little to no paddling at average ($\pm$ SD) flow rates of 4.0 $\pm$ 0.5 km/hr. We did not survey birds during river flow extremes (i.e., after heavy rains which increased flow and noise, or during low water levels) and only under conditions of no precipitation and no or very light wind. We surveyed river sections that did not exceed 20 km, with few exceptions, to ensure surveys were completed by ~1000 hrs. River width was generally <50 m (maximum 90 m) and birds on both sides of the river could be heard. Robbins et al. (2010) estimated that Cerulean Warblers could be heard ~100 m in width on each side of the river bank. Each Cerulean Warbler was heard singing at least twice before being recorded to ensure it was not confused with Type B (= Song Type II), (Moldenhauer and Regelski 1996) of Northern Parula (*S. americana*). We calculated coordinates of each singing Cerulean Warbler by estimating the direction and shortest perpendicular distance to a bird from our position on the river with a laser rangefinder; we measured our position on the river with a global positioning system unit (Garmin 12, Map Datum WGS 84). Observations were directly marked on topographic maps on a limited number of surveys. Four observers conducted surveys but the same observer conducted all surveys on a river to eliminate multiple surveyor bias (Sauer et al. 1994).

Habitat and Landscape Measurements.—We partitioned rivers into 5-km segments and created 250-m and 10-km flat-ended buffers around each segment in a geographic information system so there was no overlap in buffered areas between segments. We partitioned rivers into segments to account for variation in land cover along the rivers and 5-km was sufficiently large to capture variation in numbers of birds. We calculated the number of singing Cerulean Warblers in each segment. We created maps of selected land cover types for the two different buffer sizes around each river from Version 7-21-2000 of the National Land Cover Data (NLCD; http://www.mrlc.gov/). We compared 2000 and 2006 versions of the NLCD since surveys spanned 1999–2006 and there was $<1\%$ decline in forest cover. Thus, we used the 2000 NLCD for all analyses to avoid having to address potential compatibility issues between classifications. We mapped upland forest as all forested upland classes from the NLCD, bottomland forest as the woody wetland class from the NLCD, developed land as all developed classes from the NLCD, and forest as bottomland and upland forest combined. We intersected each buffered river segment with the land cover map in a geographic information system and calculated percent coverage of each land cover.

Statistical Analysis.—We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate our three hypotheses concerning factors affecting Cerulean Warbler abundance. We constructed a set of three candidate models representing our three hypotheses plus a null model consisting of only an intercept term representing constant abundance. We included percent cover of upland forest, bottomland forest, and developed land in the 250-m buffer as fixed effects in the model for hypothesis # 1 (local effects). We included percent cover of upland forest, bottomland forest, and developed land in the 10-km buffer for hypothesis # 2 (landscape effects). We included percent cover of bottomland forest and developed land in the 250-m buffer and percent forest in the 10-km buffer for hypothesis # 3 (local and landscape effects). We combined forest types in the 10-km buffer to reduce cross scale correlation with bottomland forest in the 250-m buffer; tolerance values were >0.48 for all variables in the model indicating no substantial multicollinearity (Allison 1999). We used percent forest cover in a 10-km buffer as a metric of habitat availability and fragmentation (*sensu* Robinson et al. 1995) because other fragmentation statistics are highly correlated with percent forest cover in Midwestern landscapes (Robinson et al. 1995, Thompson et al. 2002). Percent forest cover best explains variation in nest predation (Lloyd et al. 2005), and is a strong predictor of Brown-headed Cowbird (*Molothrus ater*) abundance and parasitism (Donovan et al. 2000, Chace et al. 2005, Lloyd et al. 2005).

We compared support for the models by ranking models from most to least supported using Akaike's Information Criterion for small sample sizes (AIC*c*; Burnham and Anderson 2002). We evaluated the goodness-of-fit of the selected model using a *k*-fold cross validation procedure (Boyce et al. 2002). We sequentially removed 15 randomly-selected observations without replacement and evaluated how well predictions from a model fit to the remaining observations, compared to observed values for the 15 observations, eight times and calculated the Pearson correlations between observed and predicted values. We plotted predicted counts of Cerulean Warblers for $\sim$10 values across the range of each supported covariate that had biologically meaningful effects while holding other covariates at their mean.

We fit a generalized Poisson model with random intercepts by maximum likelihood (Proc GLIMIX; SAS Institute Inc, Cary, NC, USA). We initially fit both a standard Poisson and generalized Poisson model (Joe and Zhu 2005) to our global model and, since the generalized Poisson had a lower AIC_C and overdisperion parameter ($\hat{c}$), we used it for all candidate models. We specified rivers as the subject for the random effect which allowed the intercept to vary among rivers. A river was surveyed in 1 year by the same observer and in a narrow range of dates; this model allowed us to accommodate year, observer, and date effects on detection probability. This model also acknowledges the likely correlated abundances of Cerulean Warblers among segments on the same river. Counts estimated by this model are an index of relative abundance, but the random intercepts can account for difference in detection among rivers (and hence observers) when estimating the fixed effects. We acknowledge the desirability and benefits of methods that directly consider the probability of detection (Rosenstock et al. 2002); however, survey designs that cannot estimate detection probability may still provide useful indices of abundance (Johnson 2008).

RESULTS

We conducted surveys along 16 rivers from 1999 to 2006 that we subsequently divided into 123 5-km segments. We detected 576 singing male Cerulean Warblers with an average of 4.7 singing males per 5-km segment. Land cover varied among rivers ranging from 30.7% forest in

TABLE 1. Descriptive statistics for variables used in models to estimate the number of singing male Cerulean Warblers along 5-km river segments in Missouri, 1999–2006. Habitat variables represent the percent of the area defined by the 250-m or 10-km buffer represented by that vegetation type.

Variable	Mean ± SD	Min	Max
Number singing males	4.7 ± 5.66	0.0	18.0
Bottomland forest in 250 m	6.07 ± 8.05	0.0	36.5
Developed land in 250 m	0.27 ± 0.45	0.0	3.2
Upland forest in 250 m	68.57 ± 18.92	11.5	96.0
Bottomland forest in 10 km	0.67 ± 1.19	0.0	6.6
Developed land in 10 km	0.27 ± 0.34	0.0	1.5
Upland forest in 10 km	80.27 ± 16.13	25.8	96.8
Forest in 10 km	80.87 ± 15.35	30.7	97.3

a 10-km buffer in north Missouri to 97.3% forest in southeastern Missouri (Table 1).

We found support for both local and landscape effects on Cerulean Warbler abundance. The model with both landscape and local effects had overwhelming support (w_i = 0.984; Table 2). Model fit was good based on the *k*-fold validation procedure with a mean Pearson correlation of 0.84 (range = 0.67–0.96) between predicted and observed values and the overdispersion parameter was close to 1 ($\hat{c}$ = 0.83). Abundance of Cerulean Warblers increased 390.7, 8.7, and 4.1 times over the observed range of forest within 10 km, bottomland forest within 250 m, and upland forest within 250 m, respectively (Fig. 2). The 95% confidence intervals for the effects, bottomland and upland forest within 250 m, overlapped zero (Table 3), which indicated some uncertainty in these effects. However, the weight of evidence for the most supported model with the effects, bottomland and upland forest, was 61.5 times that of the second most supported model without those effects (w_1/w_2; Table 3). The model coefficient for the percent of developed land within 250 m was relatively large and negative compared to other coefficients (Table 3) but, because percent developed land only ranged from 0 to 1.5%, the overall effect on density was smaller than other effects and the confidence interval was large.

DISCUSSION

We found strong support for our hypothesis that abundance was affected by both local and landscape-scale habitat composition. The greatest effect on abundance was the amount of forest within a 10-km buffer, followed by the effect of riparian forest and upland forest within a 250-m buffer. The strength of the effect for the amount of forest in the landscape emphasizes the importance of extensive forest areas for the Cerulean Warbler and the potential negative effects of fragmentation, edge, or interspersion of non-forest land uses. Counts of Cerulean Warbler were predicted

TABLE 2. Model description, number of parameters (K), $-2 \times$ log likelihood, Akaike's Information Criteria adjusted for small samples (AICc), difference in AICc from the most supported model (Δ), Akaike weights (w_i), and overdispersion parameter ($\hat{c}$) for models estimating the number of singing male Cerulean Warblers in 5-km river segments in Missouri, 1999–2006.

Model[a]	K	−2log	AICc	Δ	w_i	$\hat{c}$
Intercept + developed 250 m + bottomland forest 250 m + upland forest 250 m + forest 10 km	7	520.34	535.32	0.00	0.984	0.83
Intercept + developed 10 km + bottomland forest 10 km + upland forest 10 km	6	530.85	543.58	8.26	0.016	0.73
Intercept + developed 250 m + bottomland forest 250 m + upland forest 250 m	6	560.42	573.14	37.82	0.000	0.55
Intercept	3	578.61	584.81	49.49	0.000	0.50

[a] Developed 250 m, bottomland forest 250 m , upland forest 250 m = the percent of area in a 250-m buffer around the river segment that was developed land, bottomland forest, and upland deciduous forest, respectively. Forest 10 km, developed 10 km, bottomland forest 10 km, upland forest 10 km = the percent of area in a 10-km buffer around the river segment that was forest (all types pooled), developed land, bottomland forest, and upland deciduous forest, respectively.

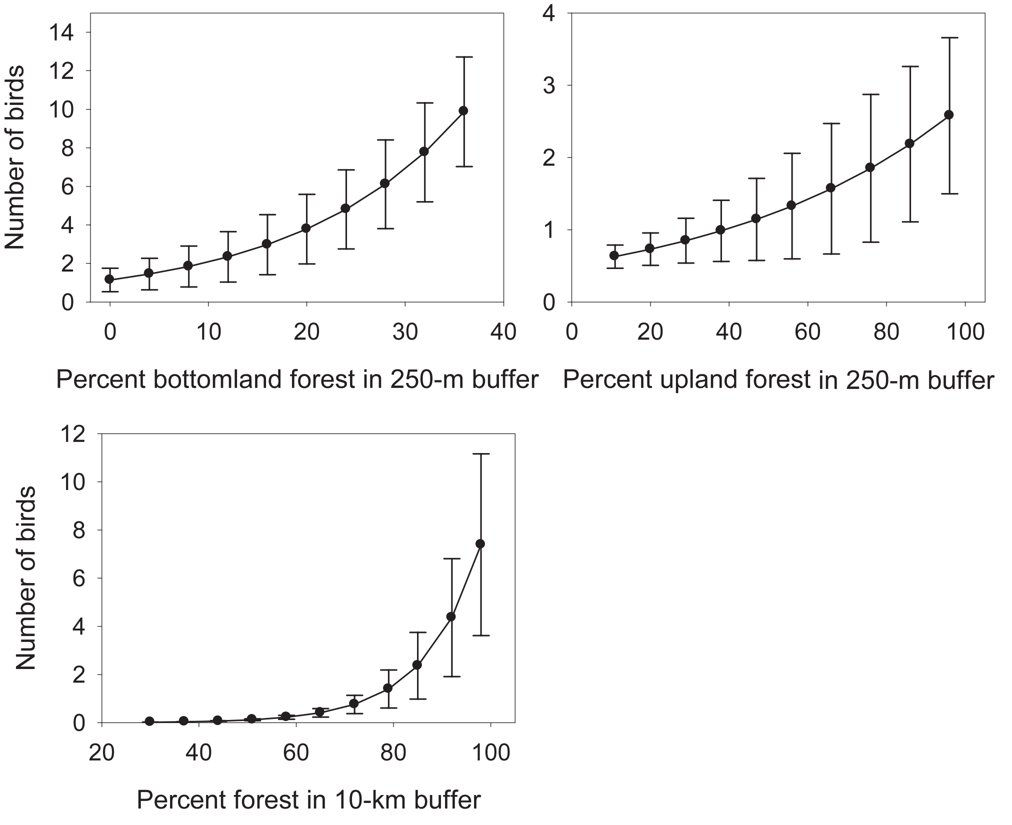

FIG. 2. Effects of forest composition at a local and landscape scale on the number of singing Cerulean Warblers along rivers in Missouri and Arkansas, 1999–2006.

to be essentially zero below 50% forest cover in the 10-km buffer (Fig. 2). Other studies of forest songbirds have found support for landscape versus patch or habitat effects but the strength of these effects varies considerably (McGarigal and McComb 1995, Howell et al. 2000, Hagan and Meehan 2002, Lichstein et al. 2002, Betts et al. 2006). Landscape may have had a larger effect on abundance than habitat factors because our sampling was constrained to riparian areas where forest is generally suitable for Cerulean Warblers. The importance of landscape is also consistent with the theory that habitat selection is hierarchical and landscape provides an important proximate cue (Hilden 1965). Potential ultimate factors affecting selection of more forested landscapes in this region include lower nest predation and brood parasitism (Robinson et al. 1995, Thompson et al. 2002).

Our finding that Cerulean Warbler abundance was greater in extensively forested landscapes is consistent with results elsewhere in their range.

TABLE 3. Parameter estimates for the most supported generalized Poisson model used to model habitat effects on the number of singing male Cerulean Warblers along 5-km river segments in Missouri, 1999–2006.

Effect	Estimate	SE	95% CL
Intercept	−7.999	1.495	−11.187, −4.812
Developed in 250 m	−0.642	0.494	−1.622, 0.339
Upland forest in 250 m	0.017	0.011	−0.006, 0.040
Bottomland forest in 250 m	0.060	0.019	−0.021, 0.099
Forest in 10 km	0.088	0.016	0.056, 0.119

Occurrence in the Lower Mississippi Alluvial Valley is positively related to the amount of forest cover within 4–8 km and negatively related to the amount of agricultural land (Hamel et al. 1998). Abundance in West Virginia is positively related to the amount of forest cover in a 3-km radius and negatively related to edge density (Wood et al. 2006) and distance to edge (Weakland and Wood 2005). Our finding that the amount of bottomland and upland deciduous forest at a local-habitat scale positively affected abundance is also consistent with patterns elsewhere in their range. Cerulean Warbler abundance is positively related to the percentage of forested wetlands and patch size in a 1-km buffer around North American Breeding Bird Survey routes in the upper Midwest (Thogmartin et al. 2004).

We surveyed riparian areas because they could be easily accessed by canoe and previous experience indicated Cerulean Warblers were rare in upland forests in Missouri. Occurrence or abundance in other parts of their range, especially the Appalachian region, is associated with upper slopes and ridges (Dettmers and Bart 1999, Weakland and Wood 2005, Buehler et al. 2006) but, in the southwestern part of their range, Cerulean Warblers are more common in bottomland or riparian forest (Hamel et al. 2004, Carpenter et al. 2011). Cerulean Warblers in Missouri appear to select landscapes and habitat similarly to elsewhere in their range. The magnitude of the landscape effect we observed reiterates the need for research and conservation to consider landscape effects (e.g., Buehler et al. 2008). We believe additional research is needed in this part of the Cerulean Warbler's range to better examine abundance patterns across riparian and upland habitats and to address key demographic parameters such as fecundity and survival.

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