

TERRITORY AND NEST-SITE SELECTION OF CERULEAN WARBLERS IN EASTERN ONTARIO

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ABSTRACT.—We examined habitat selection by breeding Cerulean Warblers (*Dendroica cerulea*) at three spatial scales in eastern Ontario over three years (1997–1999). Territories were characterized by well-spaced large trees, with high canopies and dense foliage cover at heights between 12–18 m. Nesting habitat additionally was characterized by dense foliage cover above 18 m. The results of our nest-patch (0.04 ha circle around nest) and nest-site (0.01 ha circle) analyses indicate that male Cerulean Warblers may take active roles in nest-site selection when selecting territories. We conclude from our nest-patch and nest-site selection analyses that territories likely contain multiple nest patches and sites and that male Cerulean Warblers may defend areas with multiple nest patches or sites, which may attract females to settle with them. Whether or not Cerulean Warbler females use nest-site availability as a mate- or territory-choice cue remains unknown. We also tested the validity of a commonly made assumption that a random sampling of habitat by researchers is representative of the habitat actually available to birds and found that, in our study area, the assumption was invalid. Taken together, our results point toward the need to maintain sizeable stands of mature, deciduous forest to ensure the persistence of Cerulean Warblers in eastern Ontario. Population characteristics such as lower minimum area requirements and a resilience to habitat disturbance may make that an easier job in eastern Ontario than elsewhere in this species' breeding range. Received 25 February 2000, accepted 28 February 2001.

PREFERENCES FOR CERTAIN HABITATS are presumed to be adaptive (i.e. fitness is higher in selected habitats), yet few studies of avian habitat selection address fitness (Martin 1998, Clark and Shutler 1999). Those that do rarely focus on individual fitness despite the fact that detailing the potential fitness consequences of individual microhabitat choices (e.g. nest-sites) within habitat types may provide the best appreciation of the adaptive foundation of habitat-selection patterns (Martin 1986, 1998). It is equally important to recognize that habitat selection (including selection of microhabitats) is a hierarchical process, both in space and time (Johnson 1980, Wiens et al. 1987, Kotliar and Wiens 1990, Orians and Wittenberger 1991). For birds, habitat likely affects nest placement and success at two spatial scales: nest-patch (characteristics of the habitat surrounding the nest-site) and nest-site (characteristics in the immediate vicinity of the nest) (Martin and Roper 1988). For species that maintain all-purpose territories, those influences are felt after the selection of general breeding habitat, such as territory selection. Understanding the hierarchical processes leading to observed habitat

use patterns can help prevent critical management errors when dealing with species of conservation concern (Caughley 1994).

The focus of this study is the Cerulean Warbler (*Dendroica cerulea*). Data from the North American Breeding Bird Surveys indicate that this species is exhibiting severe local population declines (Robbins et al. 1992, Peterjohn et al. 1995, James et al. 1996). This species has been variously designated as threatened, rare, or of special concern in the United States and of special concern in Canada (Robbins et al. 1992, Committee of the Status of Endangered Wildlife in Canada 2000, Hamel 2000). In general, Cerulean Warblers are thought to require large tracts of mature, deciduous forest (Robbins et al. 1992); however, its small-scale habitat affinities are poorly understood beyond a general conclusion that large trees with dense canopies are preferred as nest habitat (Robbins et al. 1992, Oliarnyk 1996).

In this paper, we examine habitat selection by Cerulean Warblers at several spatial scales. First, we describe territory selection by males. Second, at two nest scales (nest patch and nest site), we test a commonly made assumption that a random sampling of habitat by researchers provides an accurate assessment of habitat

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available to the focal species. Third, using the results of these tests, we examine nest-site selection and the fitness consequences of selection patterns at both nest scales. Finally, we discuss the practical implications of our findings for Cerulean Warbler conservation.

METHODS

Study Area.—This investigation was conducted at the Queen's University Biological Station (QUBS), Ontario, Canada (44°34'N, 76°20'W), within the Great Lakes–St. Lawrence mixed forest region. Our study area was restricted to ~2600 ha of research tracts managed by QUBS (Jones et al. 2000). All nest-searching activities were carried out in two study grids (11.4 and 6.4 ha) that were characterized as mature, secondary-growth, upland mixed deciduous forest with a canopy layer dominated by sugar maple (*Acer saccharum*), and to a lesser extent oak (*Quercus* spp.) and elm (*Ulmus* spp.). The landscape within which the study grids are imbedded is largely forested but is liberally interspersed with beaver meadows, abandoned farm fields, and dry, rocky ridges. The population studied in this research is located at the extreme northern edge of the breeding range of this species (Dunn and Garrett 1997).

Nest searching and territory mapping.—From May to June in 1998 and 1999, the two sites were searched for Cerulean Warbler nests. Nests were located by following females with nesting material or, for nests found at later stages, by following males delivering food to incubating females or by witnessing a feeding trip by either parent. Nests were checked every 2–3 days. Nests that fledged at least one young were considered successful. All failed nests, whether succumbing to predation, exposure, or abandonment, were lumped as unsuccessful because we were unable to ascertain the cause of nest failure in all cases. Also, we identified the species of each nest tree.

Territories of males were mapped using playback (Falls 1981) and by noting location of counter-singing bouts and aggressive interaction between neighboring males. Over two-thirds of the adult males in our study population were color-marked which simplified identification of territory boundaries.

Territory habitat sampling.—In 1998 and 1999, we sampled habitat in 115 territories throughout the study area (including the two study grids). For each territory, habitat was sampled in a single 5 m radius circle plot located within the territory boundaries. This location was selected by moving a random distance (restricted to ≤ 40 m) and direction (both generated by a random number generator) from the first detected location of the target male on the day of sampling. Within each of the plots, nine habitat variables were measured and calculated: number of saplings (SAPS; diameter at breast height [DBH] <3.0

cm), number of trees (TREE; diameter at breast height ≥ 3.0 cm), basal area of all trees (AREA), the ratio of AREA to TREE (ARAT), foliage cover in four height categories (<6 m, FC1; ≥ 6 –12 m, FC2; ≥ 12 –18 m, FC3; ≥ 18 m, FC4), and maximum tree height (MAX). Foliage cover was measured in a 1 m radius cylinder, centered within the 5 m radius plot, which was projected from the forest floor to the top of the canopy. Total cover and percentage cover of each species was estimated by eye in each height interval on a scale of 0 to 10 (0 = 0% cover, 10 = 100% cover). Foliage cover was estimated by the same observer in all years.

Identical habitat measurements were made at 111 nonterritory locations within the study area. Those locations were selected by moving a random distance and direction from the territory habitat sampling location and were restricted in two ways. Each 5 m radius circle could not contain water (e.g. not on a pond edge) and each point had to be at least 200 m away from the nearest singing male to limit the likelihood that the sampling point fell within a male's territory. No territories for which we had mapped boundaries exceeded 200 m in length or width (J. Jones et al. unpubl. data).

Nest-patch and nest-site habitat sampling.—The same habitat variables were measured for nest patch and nest-site analyses. Five 5 m radius plots were used; one plot was centered on the nest and the other 4 were centered on points 11.4 m away from the nest in each of the cardinal directions (cf. James and Shugart 1970). Measurements from all five plots were averaged for the nest-patch analyses, and only the central plot was used for the nest-site analyses (Fig. 1). In 1998, all foliage-cover estimates were made by the same two observers who standardized their estimates at the start of each season; one of these observers performed all foliage-cover estimates in 1999.

All habitat variables were also measured at a random location (five, 5 m plots) for each nest site or patch, the randomly selected center representing a nest location. Random locations were selected by moving a randomly generated distance and direction from the focal nest. To test the assumption that a random sampling of habitat by researchers provides an accurate representation of the habitat actually available to a bird when making nest-site decisions, random locations were chosen in two ways. In the first set of analyses, only those random locations that fell within the territory boundaries of the focal male were accepted and measured. Those locations and analyses are referred to throughout the manuscript as "available" locations (Fig. 1); in this sense, habitat availability is defined by the behavior of the bird. In the second set of analyses, all random locations were accepted and measured, irrespective of territory boundaries; some random locations fell within territory boundaries. Those locations and analyses are

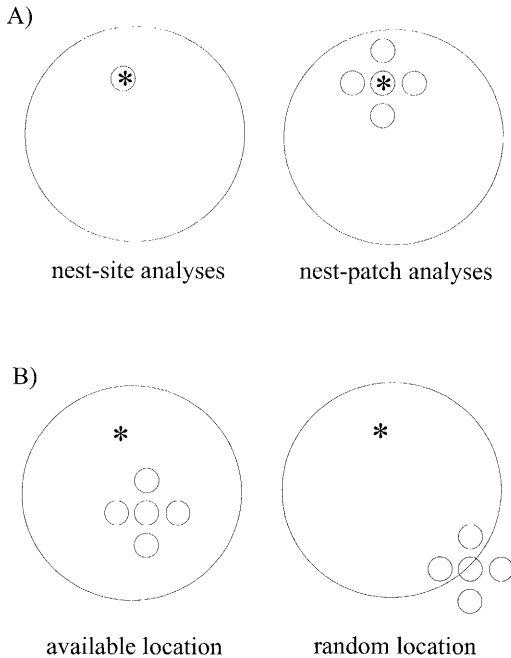


FIG. 1. Schematic diagram of nest patch and nest-site habitat sampling regime. Large circles represent hypothetical territory boundaries and asterisks denote nest locations. (A) Only the central 5 m radius plot at each location was included in the nest-site versus available-site or random-site analyses. All five 5 m radius plots were averaged for the nest-patch versus available-patch or random-patch analyses. The following habitat variables were measured in each 5 m radius plot: number of saplings, number of trees, basal area of all trees, a basal-area to stem ratio, foliage cover under 6 m, foliage cover between 6–12 m, foliage cover between 12–18 m, foliage cover above 18 m, and maximum tree height. (B) Both available and random locations are situated at a random distance and direction from the nest location. Available locations for nest patch and nest-site selection analyses fell within known territorial boundaries, whereas random locations were selected without reference to territorial boundaries although they were accepted if they fell wholly or partially within territory boundaries.

referred to throughout the manuscript as “random” locations (Fig. 1).

Analyses.—Statistical analyses were performed with JMP 3.2.1 (SAS Institute 1997). All habitat variables that were not normally distributed (as determined by Shapiro–Wilk tests) were transformed before using them in analyses (square-root transformations for SAPS in all analyses, square root transformation for TREE in territory analyses, square root transformation for AREA in territory

analyses, log transformation for ARAT in the territory analyses, square-root transformation for ARAT in the nest-site analyses). Bartlett’s tests for homogeneity of variances were performed on both the transformed and remaining untransformed variables, and no significant heteroscedasticity was detected. Means \pm SE of untransformed data are presented in the tables for ease of interpretation.

To test the assumption that *random* equals *available*, *t*-tests were performed on each of the habitat variables comparing between nest locations and random locations and between nest locations and available locations. Univariate analyses (*t*-tests) were also used to compare successful nest patches and nest sites with unsuccessful ones. We lumped all nests for these analyses due to within-year sample size constraints.

We also examined the differences in habitat variables between unsuccessful first nest-sites and successful re-nest sites in 1999 using Mann–Whitney *U*-tests due to sample size constraints. First nest-sites are defined as the first nest found for a given pair in a given territory; re-nests are any other nests found subsequently in the same territory, following failure of the first nest. We tested for nest tree selection for all years by comparing the nest tree species distribution against canopy tree availability determined from nest-site habitat plots using a Pearson chi-square test. Sequential Bonferroni corrections were applied where appropriate to control the group-wide Type I error rates (Rice 1989). Differences statistically significant before Bonferroni corrections were treated as suggestive.

RESULTS

Territory selection.—Differences in mean habitat variables between territories and nonterritory sites were consistent in both 1998 and 1999 (Table 1). Territories had significantly higher mean basal areas (AREA), basal-area to stem ratios (ARAT), and foliage cover between 12–18 m (FC3) in both years. In 1998, the maximum tree height (MAX) was significantly higher in territories; in 1999, there was a suggestive difference in the same direction. Territories in 1998 also appeared to have fewer saplings than did nonterritory sites.

Univariate tests of nest-patch and nest-site selection.—In total, 71 nests were found in 1998–1999. At the nest-patch scale, no significant differences were found comparing nest patches to available patches although there were three suggestive differences (Table 2); 1999 nest patches tended to have fewer trees (TREE), more foliage cover above 18 m (FC4), and taller

TABLE 1. Comparison of habitat variables within and outside of occupied territories. Values shown are mean \pm SE of untransformed variables. *P*-values for the territory vs. nonterritory *t*-tests are given in parentheses. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05. Values significant before correction are italicized.

	Within territories		Nonterritories (<i>n</i> = 111)
	1998 (<i>n</i> = 67)	1999 (<i>n</i> = 48)	
No. of saplings (SAPS)	38.9 \pm 2.51 (0.016)	42.5 \pm 2.77 (0.221)	50.2 \pm 2.79
No. of trees (TREE)	15.9 \pm 0.80 (0.584)	15.2 \pm 0.93 (0.311)	16.6 \pm 0.83
Tree basal area (m ²) (AREA)	0.23 \pm 0.017 (0.0004)	0.23 \pm 0.024 (0.004)	0.17 \pm 0.014
AREA: TREE (m ² /stem) (ARAT)	0.02 \pm 0.002 (<0.0001)	0.02 \pm 0.003 (<0.0001)	0.01 \pm 0.001
Foliage cover below 6 m (FC1)	4.8 \pm 0.27 (0.231)	5.0 \pm 0.21 (0.532)	5.2 \pm 0.18
Foliage cover 6–12 m (FC2)	4.4 \pm 0.32 (0.137)	4.8 \pm 0.34 (0.745)	4.9 \pm 0.23
Foliage cover 12–18 m (FC3)	4.5 \pm 0.32 (0.0006)	4.4 \pm 0.38 (0.005)	3.0 \pm 0.28
Foliage cover over 18 m (FC4)	1.8 \pm 0.33 (0.053)	1.2 \pm 0.29 (0.733)	1.1 \pm 0.22
Maximum tree height (m) (MAX)	17.3 \pm 0.48 (<0.0001)	15.7 \pm 0.60 (0.015)	13.3 \pm 0.59

trees (MAX). Comparing nest patches to random patches uncovered two significant differences (Table 2); 1999 nest patches had fewer trees (TREE) and higher basal area to stem ra-

tios (ARAT). The comparison with random patches also hinted at several additional habitat differences (Table 2); 1998 nest patches tended to have fewer saplings (SAPS) and fewer trees

TABLE 2. Comparison of nest patches with available and random patches. Available patches were located within known territorial boundaries, whereas random patches were placed without reference to territory boundaries. Shown are means \pm SE of untransformed variables. *P*-values for nest vs. available or random *t*-tests are in parentheses. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05. Values significant before correction are italicized.

	1998			1999		
	Nest (<i>n</i> = 43)	Available (<i>n</i> = 24)	Random (<i>n</i> = 42)	Nest (<i>n</i> = 28)	Available (<i>n</i> = 20)	Random (<i>n</i> = 35)
SAPS	36.3 \pm 1.9	38.2 \pm 3.9 (0.79)	44.6 \pm 3.1 (0.034)	41.9 \pm 2.7	38.2 \pm 2.4 (0.37)	45.3 \pm 2.6 (0.39)
TREE	15.3 \pm 0.8	14.2 \pm 1.0 (0.35)	16.2 \pm 0.9 (0.034)	12.9 \pm 0.8	15.6 \pm 0.9 (0.02)	17.1 \pm 0.8 (0.0003)
AREA (m ²)	0.20 \pm 0.01	0.22 \pm 0.02 (0.52)	0.19 \pm 0.01 (0.071)	0.21 \pm 0.01	0.22 \pm 0.02 (0.29)	0.18 \pm 0.01 (0.03)
ARAT (m ² /stem)	0.02 \pm 0.001	0.02 \pm 0.002 (0.90)	0.01 \pm 0.001 (0.074)	0.02 \pm 0.002	0.02 \pm 0.001 (0.12)	0.01 \pm 0.001 (<0.0001)
FC1	4.9 \pm 0.2	4.6 \pm 0.2 (0.23)	4.9 \pm 0.1 (0.86)	5.3 \pm 0.2	5.0 \pm 0.2 (0.25)	5.1 \pm 0.1 (0.57)
FC2	4.1 \pm 0.2	3.9 \pm 0.3 (0.53)	4.6 \pm 0.2 (0.11)	4.3 \pm 0.2	4.5 \pm 0.3 (0.69)	5.0 \pm 0.2 (0.03)
FC3	3.5 \pm 0.2	3.5 \pm 0.3 (0.83)	3.4 \pm 0.2 (0.86)	3.4 \pm 0.3	2.6 \pm 0.4 (0.09)	2.9 \pm 0.3 (0.21)
FC4	1.6 \pm 0.3	1.1 \pm 0.3 (0.13)	1.1 \pm 0.2 (0.083)	0.9 \pm 0.2	0.3 \pm 0.1 (0.01)	0.7 \pm 0.02 (0.54)
MAX (m)	16.6 \pm 0.6	15.5 \pm 0.7 (0.62)	14.9 \pm 0.6 (0.17)	14.8 \pm 0.4	12.8 \pm 0.7 (0.01)	13.4 \pm 0.5 (0.06)

TABLE 3. Comparison of nest-sites with available sites and random sites. Available sites were located within known territorial boundaries, whereas random sites were placed without reference to territory boundaries. Values shown are means \pm SE of untransformed variables. *P*-values for nest vs. available or random *t*-tests are in parentheses. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05. Values significant before correction are italicized.

	1998			1999		
	Nest (<i>n</i> = 43)	Available (<i>n</i> = 24)	Random (<i>n</i> = 42)	Nest (<i>n</i> = 28)	Available (<i>n</i> = 20)	Random (<i>n</i> = 35)
SAPS	36.2 \pm 1.9	38.2 \pm 3.9 (0.79)	43.0 \pm 3.3 (0.14)	43.2 \pm 3.9	41.5 \pm 3.9 (0.84)	45.2 \pm 3.3 (0.67)
TREE	15.3 \pm 0.8	14.2 \pm 1.0 (0.35)	14.3 \pm 1.0 (0.29)	13.3 \pm 1.2	17.8 \pm 1.3 (0.01)	16.2 \pm 1.1 (0.09)
AREA (m ²)	0.22 \pm 0.01	0.21 \pm 0.02 (0.37)	0.17 \pm 0.02 (0.004)	0.22 \pm 0.03	0.25 \pm 0.04 (0.60)	0.19 \pm 0.03 (0.25)
ARAT (m ² /stem)	0.02 \pm 0.001	0.02 \pm 0.002 (0.87)	0.01 \pm 0.002 (0.003)	0.02 \pm 0.004	0.01 \pm 0.002 (0.33)	0.01 \pm 0.002 (0.02)
FC1	4.8 \pm 0.2	4.6 \pm 0.2 (0.23)	4.9 \pm 0.3 (0.97)	5.1 \pm 2.8	4.9 \pm 0.3 (0.70)	5.1 \pm 0.3 (0.97)
FC2	4.1 \pm 0.2	3.9 \pm 0.3 (0.53)	3.8 \pm 0.4 (0.47)	4.8 \pm 4.6	4.9 \pm 0.5 (0.93)	4.3 \pm 0.5 (0.48)
FC3	3.5 \pm 0.2	3.5 \pm 0.3 (0.83)	2.9 \pm 0.4 (0.17)	5.7 \pm 0.3	2.6 \pm 0.6 (<0.0001)	2.3 \pm 0.4 (<0.0001)
FC4	1.7 \pm 0.3	1.1 \pm 0.3 (0.13)	0.93 \pm 0.2 (0.03)	0.2 \pm 0.4	0.1 \pm 0.1 (0.001)	0.4 \pm 0.2 (0.001)
MAX (m)	16.0 \pm 0.6	15.5 \pm 0.7 (0.62)	13.0 \pm 0.9 (0.01)	17.8 \pm 0.4	12.7 \pm 1.0 (<0.0001)	11.3 \pm 0.8 (<0.0001)

(TREE) whereas 1999 nest patches tended to have higher basal area (AREA).

At the level of the nest site, differences were also detected between analyses using random and available locations (Table 3) although those differences were not the same ones detected at the level of the nest patch. The nest versus available comparisons uncovered three significant differences (Table 3); 1999 nest sites had higher foliage cover at 12–18 m (FC3), higher foliage cover above 18 m (FC4), and taller trees (MAX), and they tended to have fewer trees (TREE). The nest versus random comparisons highlighted five significant differences (Table 3); 1998 nest sites had higher basal area (AREA)

and higher basal-area to stem ratios (ARAT) whereas 1999 nest sites had higher foliage cover at 12–18 m (FC3), lower foliage cover above 18 m (FC4), and taller trees (MAX). Several additional differences were suggestive; 1998 nest sites tended to have higher foliage cover above 18 m (FC4) and taller trees (MAX) whereas 1999 nest sites tended to have higher basal-area to stem ratios (ARAT).

Very few habitat characteristics were linked to nest success. At the scale of the nest patch, no significant habitat differences were detected in the univariate analyses of successful and unsuccessful patches (Table 4). The only significant difference detected between successful

TABLE 4. Comparison of successful and unsuccessful nest-patches (successful = 12, unsuccessful = 59, *df* = 69). Shown are means \pm SE of untransformed variables and results of *t*-tests.

	Successful	Unsuccessful	<i>t</i> (<i>P</i>)
SAPS	39.3 \pm 3.7	38.2 \pm 1.8	0.304 (0.762)
TREE	14.1 \pm 1.3	14.4 \pm 0.6	-0.213 (0.832)
AREA (m ²)	0.25 \pm 0.01	0.22 \pm 0.01	1.687 (0.096)
ARAT (m ² /stem)	0.02 \pm 0.002	0.02 \pm 0.001	1.627 (0.108)
FC1	5.4 \pm 0.3	5.0 \pm 0.1	1.425 (0.159)
FC2	4.4 \pm 0.2	4.2 \pm 0.2	0.659 (0.512)
FC3	3.8 \pm 0.4	3.4 \pm 0.2	1.145 (0.256)
FC4	1.6 \pm 0.3	1.3 \pm 0.2	0.723 (0.472)
MAX (m)	16.0 \pm 0.8	15.4 \pm 0.4	0.632 (0.530)

TABLE 5. Comparison of successful and unsuccessful nest-sites in 1998 and 1999 (successful = 12, unsuccessful = 59, $df = 69$). Shown are means \pm SE of untransformed variables and results of t -tests. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05. Values significant before correction are italicized.

	Successful	Unsuccessful	t (P)
SAPS	38.3 \pm 4.1	39.1 \pm 2.20	-0.085 (0.932)
TREE	14.7 \pm 2.0	14.5 \pm 0.71	-0.080 (0.936)
AREA (m ²)	0.28 \pm 0.045	0.21 \pm 0.096	1.928 (0.058)
ARAT (m ² /stem)	0.02 \pm 0.004	0.02 \pm 0.002	1.599 (0.115)
FC1	5.2 \pm 0.36	4.9 \pm 0.16	1.069 (0.298)
FC2	5.9 \pm 0.49	4.1 \pm 0.22	3.383 (0.001)
FC3	5.1 \pm 0.60	4.2 \pm 0.23	1.555 (0.125)
FC4	2.9 \pm 0.57	1.6 \pm 0.24	<i>2.121 (0.038)</i>
MAX (m)	18.1 \pm 0.84	16.4 \pm 0.43	1.604 (0.113)

and unsuccessful nest sites was higher foliage cover between 6–12m (FC3) for successful nest sites although there was a suggestion that foliage cover above 18 m (FC4) was higher at successful nest sites (Table 5).

In the comparison of unsuccessful nests and successful re-nests at the nest-site scale, successful re-nests had significantly higher foliage cover at 6–12 m (FC2) than failed first nests (Table 6). Foliage cover above 18 m (FC4) also appeared to be higher at successful re-nests (Table 6).

Most nests were located in maples (56%, 40 of 71 nests), followed by elms (17%, 12 of 71) and bitternut hickory (*Carya cordiformis*; 13%, 9 of 71). The distribution of nest tree species did not differ from the overall distribution of available canopy trees (Pearson's $\chi^2 = 0.16$, $df = 7$, $P = 0.99$).

DISCUSSION

The forest at QUBS is not saturated with Cerulean Warblers and, every year, apparently

suitable habitat goes unoccupied. However, the core areas of occupancy do not change appreciably between years (J. Jones et al. unpubl. data). Within those core areas, territory selection by male Cerulean Warblers at QUBS was influenced by the size (i.e. girth) of trees in an area, the foliage cover in the midstory, and the canopy height. Male Cerulean Warblers generally selected territories characterized by large, well-spaced trees with dense, high canopies. Territory selection by males was consistent between 1998 and 1999 with the exception of foliage cover below 6 m. Because that height stratum is infrequently used by Cerulean Warblers (J. Jones pers. obs.), this discrepancy is likely not ecologically significant to this species. Despite only sampling a single point per territory, we believe that the large number of territories sampled provided an accurate picture of the habitat structure within Cerulean Warbler territories.

The general lack of concordance between the nest versus random and nest versus available

TABLE 6. Nest-site comparisons between failed first nests and successful re-nests for 1999. Shown are mean \pm SE values of untransformed variables and results of Mann-Whitney U comparisons. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05. Values significant before correction are italicized.

	Failed first nests ($n = 10$)	Successful re-nests ($n = 5$)	U (P)
SAPS	43.7 \pm 5.5	33.2 \pm 9.2	1.22 (0.270)
TREE	10.9 \pm 1.4	13.4 \pm 2.9	0.98 (0.322)
AREA (m ²)	0.21 \pm 0.05	0.28 \pm 0.08	0.46 (0.500)
AREA (m ² /stem)	0.03 \pm 0.01	0.02 \pm 0.01	0.18 (0.668)
FC1	4.6 \pm 0.4	5.2 \pm 0.7	0.27 (0.602)
FC2	3.7 \pm 0.6	7.2 \pm 0.4	7.53 (0.006)
FC3	6.0 \pm 0.5	7.0 \pm 0.3	1.44 (0.230)
FC4	2.0 \pm 0.8	4.4 \pm 0.5	<i>4.56 (0.33)</i>
Max (m)	18.2 \pm 0.6	19.9 \pm 0.3	3.62 (0.057)

analyses highlight the need to test, in the field, the assumption that a random sampling of habitats by researchers generates an accurate representation of habitat availability (Aebischer et al. 1993, Jones 2001). Wherever possible, the selection of habitat sampling methodology ought to be informed by the natural history of the focal species (e.g. Ramsay et al. 1999). Given the evidence for territory selection by Cerulean Warblers in that region, it comes as no surprise that using sampling points outside of territory boundaries might provide an inaccurate representation of nest-site selection. In terms of determining which habitat variables are important in nest-patch and nest-site selection in this species, we believe that comparisons with random locations located within the males' territory boundaries (i.e. available locations) are more meaningful than comparisons with random locations not so constrained. The magnitude of the differences between available and random analyses also likely depends on the number of random locations that actually fall within territory boundaries; the greater the overlap, the fewer the differences. This degree of overlap will be influenced by the sociality of the study species. For species that tend to have densely packed territories, such as the Cerulean Warbler (Hamel 2000, J. Jones and R. J. Robertson unpubl. data), the likelihood that a random location will fall within a territory boundary is higher than for more solitary species, such as the Scarlet Tanager (*Piranga olivacea*).

The low number of detected differences between nest locations and available locations, at both nest scales, may indicate that important nest-patch and nest-site selection decisions were made when males chose their territories. Because females likely make the final nest-patch and site selection decisions in our study area, male Cerulean Warblers may try to defend areas with multiple nest patches or sites in order to maximize the probability that females settle with them. The importance of nest-site availability as a mate- or territory-choice cue for females has been hypothesized for other species (Leonard and Picman 1987, Martin 1988, Sedgwick and Knopf 1990, Steele 1993). Whether or not that is the case for Cerulean Warblers remains untested. Multiple nest patches or sites within a territory may be attractive for several reasons. One reason is that

multiple nest patches or sites may provide insurance sites in case of nest failure. A second reason is that nesting in an area with many potential nest patches or sites may act to lower nest predation pressures by increasing number of potential locations a predator must examine (Martin and Roper 1988). The presence of multiple nest patches or sites within a single territory would affect our ability to detect differences between nest sites or patches and available habitat if the "available" sampling point fell near a suitable but unused nest site or patch. The results of this portion of the study highlight the need to be aware that habitat selection is a hierarchical process and that, if the scale of study and analysis is inappropriate, key influences on habitat selection may be missed by the research (Orians and Wittenberger 1991, Aebischer et al. 1993).

Limiting the discussion to differences between nest habitat and available habitat, Cerulean Warblers prefer to nest in areas with a few large trees with dense foliage cover above 12 m. Within those sites, successful nests were in areas of highest cover above 18 m with additional cover between 6–12 m. These results are confirmed by the re-nest comparisons where we see evidence of individuals shifting towards areas of high canopy cover and high midstory cover.

There are several ecological and physical factors that may hamper our ability to detect consistent and significant habitat patterns in our population. First, as discussed, males may be selecting territories with multiple suitable nest sites within each territory. Second, the study population is relatively young, with the first nest record for the region from 1963 (Quilliam 1973), and is on the leading edge of a northward range expansion for this species (Robbins et al. 1992). The young age of the study population may contribute to the apparent lack of habitat saturation resulting in suitable Cerulean Warbler habitat going unused, which may confound efforts to consistently distinguish differences between used and available habitats (Wiens 1986, Wiens et al. 1987).

Third, nest-site selection in that region is possibly driven by current selection pressures that may have been recently altered by the ice storm in the winter of 1998, which drastically reduced the amount of foliage volume in the forest canopy (Jones et al. 2001). In fact, Ceru-

lean Warblers in our study area appear to have already altered certain aspects of their nest location preferences, such as distance to nearest canopy gap, following the ice storm (Jones et al. 2001). Large scale disturbances such as the ice storm can play major roles in altering selection pressures and can have major effects on habitat-selection patterns exhibited by bird populations (Brokaw and Grear 1991, Thurber et al. 1994, Paine et al. 1998).

Although it remains to be seen how applicable our results are to Cerulean Warblers across the extent of their breeding range (given the peripheral nature of the study population, the existence of unsaturated suitable habitat, and the potential confounding effects of the ice storm disturbance), our results do allow us to make a general recommendation aimed at supporting healthy Cerulean Warbler populations in eastern Ontario. The maintenance of sizeable stands of mature, deciduous forest that is characterized by large, well-spaced trees with dense, high canopies is critical to the continued survival of this species in eastern Ontario. Fortunately, Cerulean Warblers in eastern Ontario display two characteristics that will make that objective easier to attain. First, the minimum area requirements for this species are not as great in our region as has been reported in the literature for other areas (J. Jones unpubl. data, Robbins et al. 1992) although the reasons for that are unclear. Second, the apparent resilience of this species to certain forms of disturbance allows them to persist in forests that are actively managed; for example, Cerulean Warblers are abundant and breed successfully in forests managed for maple syrup (J. Jones and R. J. Robertson unpubl. data). That provides the potential for the development of a multiple-use land-management plan that will allow the maintenance of Cerulean Warbler habitat in eastern Ontario while maintaining economic integrity.

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