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BREEDING BEHAVIOR AND REPRODUCTIVE SUCCESS OF CERULEAN WARBLERS IN SOUTHEASTERN ONTARIO

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ABSTRACT.—Little is known about the breeding biology of the Cerulean Warbler (*Dendroica cerulea*), a species declining throughout much of its range. However, life history information can provide important insight into the vulnerability of a rare species to habitat disturbance. We studied the breeding behavior of Cerulean Warblers at three different sites in southeastern Ontario through the breeding season, from early May to late July 1995, and at one of the above sites in 1994. Twenty-seven nests, including three renests, were located within 27 territories. Average territory size was 1.04 ha (N = 18). Although both males and females displayed at potential nest sites, building was performed only by females and took five to six days. Nest trees were predominantly sugar maple (*Acer saccharum*) or oak (*Ouercus spp.*), with an average height of 17.7 m and an average diameter at breast height (DBH) of 40.2 cm. Average nest height was 11.8 m. There were no incidents of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and nest loss due to predation was low (14%). Incubation, performed only by females, lasted 11 to 12 days. Clutch size ranged from two to five eggs, with a modal clutch size of 5 (N = 6). During the 10 to 11 day nestling period, both males and females fed the chicks equally. Reproductive success in this population was high in both years. Twenty of the 27 pairs successfully fledged young, with a mean of 3.2 fledglings per successful nest. Record increases, and the high reproductive success of Cerulean Warblers in the Frontenac Axis area of the Canadian Shield, may be the result of reforestation of agricultural lands abandoned at the turn of the century. *Received 28 Nov. 1995, accepted 15 April 1996.*

The Cerulean Warbler (*Dendroica cerulea*), like many other Neotropical migrants, is a species of conservation concern. Robbins et al. (1992) found that between 1966 and 1988, Cerulean Warblers declined at an average rate of 3.4% per year, the greatest decline for any species of warbler during that period. Currently listed as vulnerable in Canada (McCracken 1992), its dependence on large tracts of mature deciduous forest for successful breeding may make the Cerulean Warbler especially sensitive to continuing forest fragmentation and isolation (Adams and Barrett 1976, Temple 1986, Robbins et al. 1992, Parker 1994). Concurrent with this overall decline, several authors have suggested that Cerulean Warblers are undergoing a northeastern expansion of their range as agricultural lands abandoned at the turn of the century are allowed to succeed to mature forest (Ouellet 1967, Laughlin and Kibbe 1985, Andrle and Carroll 1988, Hamel 1992, Maurer 1994). This may be the case in Ontario.

The northernmost portion of the Cerulean Warbler's range occurs in

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the mixed deciduous forests from the Bruce Peninsula to eastern Ontario, Canada, with a concentration on the Frontenac axis, at the northeast tip of Lake Ontario (Cadman et al. 1987). Local records suggest a gradual increase in the number of Cerulean Warblers in the Kingston area. Since sporadic sightings began in the 1930s, the birds have been found annually since 1961 (Weir 1989).

While interest in the Cerulean Warbler appears to be growing, details of its life history, necessary for establishing management and conservation programs, are incomplete. In this paper, we provide descriptions of the breeding behavior, nesting chronology, habitat use, and breeding success of a population of Cerulean Warblers in southeastern Ontario.

METHODS

During the spring and summer of 1995, we monitored a population of Cerulean Warblers at three 9-ha study sites near the Queen's Univ. Biological Station (QUBS), Lake Opinicon, Leeds/Frontenac Counties, Ontario, Canada (44°30'N; 76°23'W). The sites were selected as areas where Cerulean Warblers had been recorded with greatest regularity and highest density based on breeding bird surveys (R. Weir, pers. comm.). In 1994, a less intensive, preliminary study was conducted at one of the sites. Nests located in 1994 are included in the results on nesting success and nest-tree species use; all other results are based on data collected in 1995 alone.

The physiography of the region around QUBS consists of shallow till soils with rock ridges and undulating topography (Chapman and Putnam 1984). The area was initially cleared for agriculture in the early 1800s, but the amount of forest cover has increased since the early settlement period, as a result of abandonment of farmland and reduction of timber harvesting (Keddy 1994). The forest at all three sites is now characterised by second-growth mixed deciduous forest, dominated by sugar maple, with components of ironwood, oak, elm, ash, hickory, basswood, and birch (see Table 1 for scientific names of trees).

All three sites were contained within a region of extensive forest cover interspersed with lakes, roads, and some small agricultural fields—an area which is more or less contiguous with extensive forests on the Canadian Shield to the north without significant interruptions of agriculture or urban development. Consequently, limits of forest patch size were not easily determinable either from topographic maps or aerial photos, and any attempt to define forest area would be arbitrary at best. Two of the sites were located about 500 m apart, while the third site was separated from the other two by approximately 15 km of forest and open water (Fig. 1). Because of small sample sizes, observations from all three sites were pooled for analyses.

To determine territory size, territorial boundaries were mapped in early May using playback (Falls 1981). We used a Sony Professional Walkman in combination with a single Sony SRS-77G, 25 watt speaker (audible to a distance of about 100 m) to broadcast the song of an unfamiliar conspecific to a territorial male. This method stimulates territorial males to sing, and draws them out to the boundaries of their territory. A boundary point is established either when the bird no longer approaches or a neighbor approaches the playback speaker. Each of the study plots consisted of a 6.25-ha grid marked with flagging tape every 25 m and represented only a sample of the total population in the area. Territories with boundaries at least 50% within a 6.25-ha grid were drawn on a map (Fig. 1). Territorial disputes, involving bouts of countersinging or fighting, were also mapped and used to con-

TABLE 1

CHARACTERISTICS OF NEST PLACEMENT FOR CERULEAN WARBLERS

Tree species	N	Tree height (m)	Nest height (m)	DBH (cm)	Dist. from trunk (m)	Dist. from canopy gap (m)
Sugar maple (*Acer saccharum*)	18	18.5 ± 0.64[a]	11.9 ± 0.53	44.6 ± 5.2	4.3 ± 0.39	35.8 ± 6.2
Burr oak (*Quercus macrocarpa*)	3	12.8 ± 1.6	9.1 ± 0.46	39.1 ± 15.8	2.6 ± 0.41	24.3 ± 13.1
White oak (*Q. alba*)	2	19.9 ± 1.9	14.7 ± 2.2	30.3 ± 0.25	2.0 ± 2.0	19.3 ± 6.4
Red oak (*Q. rubra*)	1	19.6	18.6	24.0	2.0	26.9
Ironwood (*Ostrya virginiana*)	1	9.5	7.0	11.2	1.8	79.0
Bitternut hickory (*Carya cordiformis*)	1	20.0	8.0	38.7	2.5	12.0
American elm (*Ulmus americana*)	1	16.0	14.0	32.9	3.0	29.7
Overall mean	27	17.7 ± 0.67	11.8 ± 0.56	40.2 ± 5.1	3.62 ± 0.33	33.4 ± 4.7

[a] Mean ± SE.

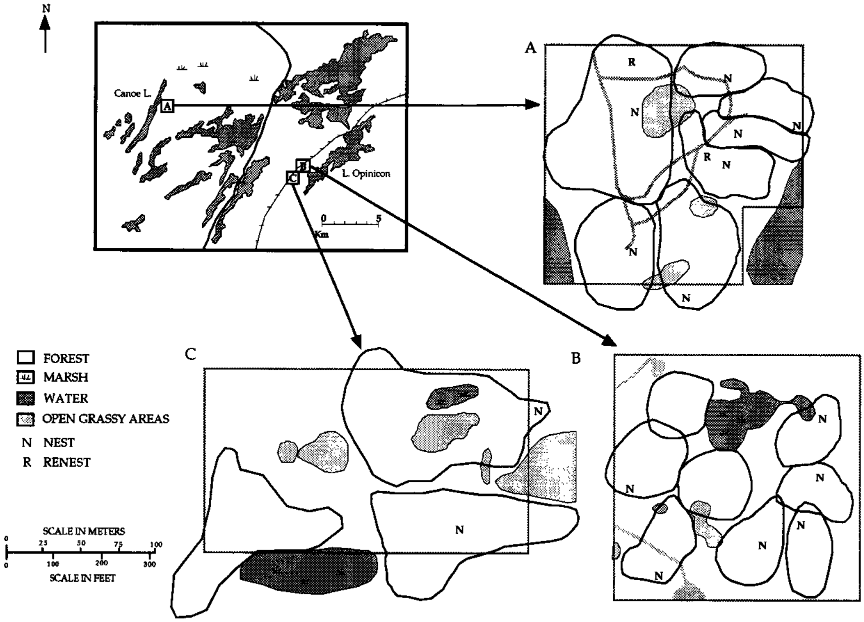

FIG. 1. Map of 18 Cerulean Warbler territories in 1995 at three sites (A = Hahn, B = Bedford Mills, and C = Lindsay Lake) near Lake Opinicon, Ontario (site A was studied in both 1994 and 1995). Outline shows the boundary of each 6.25-ha study site.

firm borders between neighboring males. To increase confidence in the boundaries, five males were banded with a Canadian Wildlife Service metal band and two color bands in early June (at least one per site). Males were captured using aerial mist nets raised to a level of approximately 10 m, accompanied by playback and model presentation. All subsequent observations of these males occurred within the previously recorded boundaries.

Territories were visited at least twice a week for periods of 30 to 60 minutes to search for nests for the duration of the breeding period, or until the nest was located. If a nest failed, the territory was monitored for renesting. Nests were monitored every second day to determine the length of the nest building, incubation, and nestling periods. Incubation period was considered to be the time between the first prolonged visit to the nest by the female (≥20 min) and the first observed feeding visit. Behavior at the nest, such as feeding rates and duration of parental visits, was recorded during 60-min nest watches between 07:00 and 08:00 EST on days 3, 7, 10, 14, 17, and 20 of the nesting cycle. On the estimated day of fledging, nests were monitored starting at 05:00 EST in order to count the number of chicks leaving the nest. For nests that were not clearly observable from the ground, in addition to monitoring the nest on the day of fledging, the nest tree was climbed on day 7 or 8 of the nestling period to give a maximum estimate of the number of young likely to fledge. In 1994, six trees were climbed during the incubation period, and this information was used to determine clutch size. Trees were climbed using ropes, a leather climbing belt, and occasionally, climbing spurs. Once the observer was at nest height, nest contents were examined using an extendible mirror pole to determine brood size and degree of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*).

Parasitism by Brown-headed Cowbirds has been implicated in reducing reproductive success in certain forest songbirds (Brittingham and Temple 1983), including Cerulean Warblers in northwestern Ohio (Mayfield 1977). To determine the density of cowbirds in the area of the study sites, we recorded each visual or acoustic identification of Brown-headed Cowbirds throughout the breeding season.

We recorded nest-tree species and measured five characteristics at each nest: tree height, nest height, diameter at breast height (DBH), distance of nest from the trunk, and distance of nest tree to the nearest canopy gap. We defined a canopy gap as an area where the height of the vegetation changed abruptly from average canopy height to ground level, such as a dirt road, rock outcrop, field, or open water. Heights were measured using a rangefinder and DBH was measured using a diameter tape.

RESULTS

Territorial behavior and pair formation.—Males began to arrive in the area during the first week of May. Before pairing, males moved around their territories singing from high, often exposed, perches. The male song has been described as *zray, zray, zray, zree* with the final *zree* syllable sliding upwards slightly in pitch (Peterson 1980). Variations of this song occurred between individuals (R. Woodward, unpubl. data). Females did not sing, but both males and females used a soft, high-pitched, metallic "chip" note which is used as a contact and alarm call. The chip note of the male was shown on a sonagram to be slightly lower in frequency than that of the female, but the difference is difficult to distinguish by ear (C. Oliarnyk, unpubl. data).

Territories ranged from 0.38 ha to 2.4 ha, with a mean size (±SE) of 1.04 ± 0.16 ha (N = 18). Territories covered most of the area of the study grids, and boundaries of several territories abutted one another (Fig. 1). Males defended territories with bouts of counter-singing with neighboring males at the boundaries of their territory. Eight times, physical disputes were observed between males, in which one male would either supplant another from a perch (N = 6) or make contact in mid-air (N = 2).

Females arrived the second week of May, and pairs spent the first couple of days foraging close together. During this courtship period, several pairs were observed in short chase flights initiated by the male. Females were also sometimes involved in disputes between neighboring pairs (N = 5).

Nest construction.—Nest-site selection and construction began one to two days after the arrival of the female on a territory. Both males and females were seen displaying at potential nest sites by spreading their wings and fanning their tails in combination with nest-shaping motions. This behavior was usually performed with the mate nearby, and often the observing mate would replace the displaying individual and repeat the display (N = 5). Only two copulations were observed, one at a nest, the other about 75 m from a nest.

Once a nest site was selected, interactions between males and females were infrequent. Usually they were seen together less than once every half hour. Nest building was performed entirely by the female, and lasted 5–6 days, not including the egg-laying period. The range of dates for initiation of construction for known first brood nests was 18 May to 24 May (N = 12) and for renests was 31 May to 4 June (N = 3).

Nests were open, shallow cups resembling a knot on a branch when viewed from the ground. The exteriors were formed from bark strips, grasses, and other plant fibres. Linings were made of spider webs, fine bark strips and soft plant material. Lichen and birch bark "shingles" usually covered parts of the exterior of the nest. Five nests were collected and measured and had the following dimensions (mean ± SE): outside diameter 6.5 ± 1.2 cm, inside diameter 5.0 ± 0.6 cm, outside depth 3.3 ± 0.7 cm, and inside depth 3.0 ± 0.9 cm.

Nest location.—In 1995, 17 nests, including two renests, were located in 15 of the 18 mapped territories. Adults were observed feeding fledglings in two of the three territories where nest sites were not determined. Therefore, we assume that nesting efforts were made in most, if not all, of the 18 territories. One female abandoned her first nest during the early part of the incubation period, possibly due to the presence of an Eastern Wood-Pewee (*Contopus virens*) nest 1.7 m from it in the same tree. In 1994, ten nests were located, one of which was a renest. In all three instances of renesting, the second nest was constructed using material from the previous nest which was carried to the new site. No second broods were found in either 1994 or 1995.

Seventy percent of nests were located within ten meters of a territorial boundary, and over half (59%) were within thirty meters (mean distance ± SE = 33.4 ± 4.7 m, N = 27) of a canopy gap (see Fig. 1). In a random sample of points taken from within a territory, only 23% were within 30 m of a gap. It should be noted that in only one case did a nest occur near a gap between differing, adjacent habitat types. Most were contained within patches of otherwise continuous forest. The majority of nests were found in the lower third of the canopy (71%), had no other vegetation between the nest and ground cover (understory gap) (59%), and were found on the outer edge of a lateral branch (77%). The most commonly used tree species for nesting were those with the greatest overall basal area; sugar maple (N = 18) and oak spp. (N = 6) (Table 1). Sugar maple was the dominant species in all three sites, and oaks were the second most abundant species group with mean total basal areas of 199.58 $m^2 \cdot ha^{-1}$ and 128.71 $m^2 \cdot ha^{-1}$ respectively.

Clutch size.—Clutch size ranged from two to five eggs (mean ± SE = 3.8 ± 0.22, N = 6), with five being the modal clutch size. We found no Brown-headed Cowbird eggs in any of the six nests examined before hatching, and no cowbird chicks being fed either during the nestling period or after fledging. Cowbirds were recorded only two or three times at each of the three sites and only during the period between 12 May and 12 June.

Incubation.—Incubation was performed by the female and lasted between 11 (N = 5) and 12 (N = 3) days. The first incubating female was found on 30 May, and the last day of observed incubation was 23 June. The mean (±SE) total incubation time per hour was 50 ± 5.3 min (N = 18 h, 9 nests). Males were twice observed feeding females on the nest during incubation (N = 20 h, 9 nests). Contact was maintained by call notes from incubating females in response to their mate's song. Females also sometimes gave call notes when they left the nest.

Nestlings.—The nestling period lasted between 10 (N = 6) and 11 (N = 4) days. Female attentiveness remained high for the first one to three days after hatching, with the female spending a mean (±SE) of 49.2 ± 4.7 (N = 5 h, 5 nests) min per hour brooding the nestlings. Time spent at the nest by the female declined progressively as the nestlings matured (Fig. 2), with females spending less time brooding the nestlings and more time standing near, or on, the edge of the nest. Males spent minimal time at the nest, usually just long enough to feed the young. Both males and females fed the young as soon as they hatched, with males and females feeding approximately equally (mean feedings/h ± SE; males = 3.5 ± 1.8, females = 3.5 ± 3.7, N = 17 h, 8 nests).

On the day of fledging, activity and noise from the parents and chicks were high, with both the male and female chipping rapidly and continuously, and the chicks begging for food. Several pairs also showed alarm at our presence for the first time on fledging day. This activity made locating already fledged chicks relatively easy, however, direct observation of the chicks after the day of fledging was difficult. Fledglings used all parts of the canopy, were often hidden under leaves, and their call was very difficult to isolate. In addition, chicks responded quickly to parental alarm calls. On two occasions, when a male gave a chip note, nestlings ceased all begging calls and movement and did not resume until the male began to sing again. In begging behavior the fledgling crouched down low on the branch, fluttered its wings, and gave high-pitched, burry call notes. All young had fledged by 4 July. One pair was observed feeding young 19 days after fledging. Adults were observed feeding chicks within territorial boundaries at least 10 days after fledging in 50% of the successful territories. If parents were observed feeding fledged young within

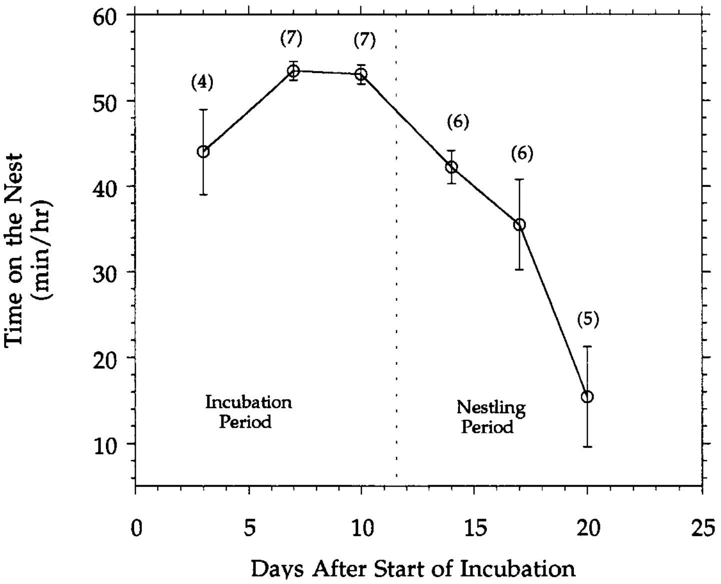

FIG. 2. Time (mean ± SE) spent at the nest by female Cerulean Warblers during the nesting cycle, based on 35 one-hour watches at nine different nests. Time 0 is the start of incubation and vertical dotted line indicates the start of the nestling period. Sample size is indicated in brackets above each point.

the bounds of a territory, they were assumed to belong to the territorial pair; however, family groups are likely quite vagile. For example, one banded male was observed feeding a fledgling approximately 100 m from the edge of his territory, within the territory of an unpaired male.

Nesting success.—Twenty of 27 pairs successfully fledged young over the two years of the study. No significant difference in reproductive success (successful fledging of at least one chick) existed between years (Fisher Exact Test, $P = 0.65$, df = 1). The mean (±SE) number of young in nests examined before fledging was 3.6 ± 0.2 (N = 8). This is slightly higher than the number based on observations of fledging from the ground 3.2 ± 0.2 (N = 20).

Nine nests failed (five in 1995, four in 1994). Four nests were likely depredated. Two of these nests failed during the nestling stage and although no evidence of nestlings was found, almost the entire bottom of both nests was torn out, suggesting predation. The other two nests failed early in the incubation stage. In all cases of suspected predation the female was probably preyed on as well. No subsequent observations of females were recorded on these territories from the time of nest failure to the end of the breeding season in mid-July. Males on these territories also resumed behavior characteristic of unpaired males, such as continuous singing from high, exposed perches for extended periods of time. It is not known what preyed on these nestlings and females, but Blue Jays (*Cyanocitta cristata*) and Red-shouldered hawks (*Buteo lineatus*) were sometimes heard in the area. Gray squirrels (*Sciurius carolinensis*) were observed in trees containing nests—at nest height. On one occasion a black rat snake (*Elaphe obsoleta*) was observed in a nest tree above nest height, approximately one hour after the nestlings had fledged.

The reason for the abandonment of the other five failed nests is unknown although, as mentioned earlier, interspecific interference may have played a role. Females from three of these territories renested, but the status of the other two was not determined.

DISCUSSION

Despite increasing data demonstrating declining trends in Cerulean Warbler numbers, this local population appears to be relatively successful. Low instances of nest predation and brood parasitism suggest that, in this area at least, Cerulean Warbler numbers are not limited by poor reproductive success.

Based on results from our study plots, Cerulean Warbler density in this area may be as high as 96 $\text{prs}\cdot\text{km}^{-2}$, assuming uniform conditions. Across Ontario, Cerulean Warblers were recorded in only 6% of the 10 × 10 km breeding bird atlas squares (Cadman et al. 1987). In areas where Ceruleans did occur, 80% of abundance estimates are of fewer than 11 pairs per atlas square. Based on these results, the density of birds around Kingston appears to be much higher than in the rest of Ontario. This may be related to the higher proportion of forested land in the area around Kingston relative to the more southerly parts of Ontario. However, it should be noted that an inconspicuous, forest interior bird such as the Cerulean Warbler may occur over a greater range or at a higher density than is indicated by breeding bird surveys (Cadman et al. 1987, Terborgh 1989). The density of birds, and consequently territory size, differed between the three sites; 1.12 $\text{prs}\cdot\text{ha}^{-1}$, 1.28 $\text{prs}\cdot\text{ha}^{-1}$, and 0.48 $\text{prs}\cdot\text{ha}^{-1}$ at sites A, B, and C respectively. Hamel (unpubl. data) has suggested that Cerulean Warblers seem to breed in loose "colonies". Since all three sites are the same forest type, the difference in density between the adjacent sites, B and C, may reflect this colonial nature, with site C acting as a spillover area for the more saturated site B.

The mean nest height of 11.8 m falls within the 5 to 18 m range of nest heights cited in the literature (Saunders 1900, Harrison 1984). Maple, oak, and elm were the three most commonly cited species of nest tree across the range of the Cerulean Warbler (Saunders 1900, Bent 1963 and references therein, Ouellet 1967, Bull 1976, Laughlin and Kibbe 1985, Peck and James 1987, Andrle and Caroll 1988). In this study, nests were most often located in sugar maple and oak spp., the dominant tree species at all three sites. Since insufficient information is provided on dominant tree species in the literature, it is not possible to determine whether Ceruleans use trees in proportion to occurrence, throughout their range.

The high proportion of nests associated with understory and canopy gaps, has also been noted by other authors (Bent 1963, Harrison 1984, Peck and James 1987). These apparent associations with gaps may be an important component of Cerulean Warbler nest-site selection. Examination of Fig. 1, and a comparison of nest location versus random locations within a territory, suggests that nests may be associated with gaps such as water, paths, or open areas in greater proportion than their availability within the territory. It is unlikely that this result is due to observer bias in locating easily observable nests associated with gaps, since nests were located in 83% of the territories. However, detailed analyses of habitat data are necessary before any definitive conclusions can be made about the role of gaps in nest-site selection.

The mean clutch size of four is the same as the mean clutch size of nests located in southern Ontario (N = 36) (Peck and James 1987). The modal clutch size of five, however, is a new record for Ontario (Peck and James 1987). In 35 nests in New York state, the average clutch size was again four eggs (51%), with nests also containing three eggs (26%) and five eggs (23%) (Bull 1976). The lack of brood parasitism by Brown-headed Cowbirds was noteworthy for the Ontario range. In southwestern Ontario, the incidence of Brown-headed Cowbird parasitism of Cerulean Warbler nests is as high as 17.9% (Peck and James 1987).

The incubation period of 11 to 12 days determined in this study is similar to Harrison's (1975) speculation that the incubation period is 12 to 13 days.

Cerulean Warbler habitat has been described as mature, riparian forest (Bull 1976, Lynch 1981, Laughlin and Kibbe 1985). The area of maturing second-growth forest, dotted with numerous lakes and streams, north of Kingston approaches this description. Forests in this area are also compositionally similar to forests present before extensive post-settlement alteration (Keddy 1994); therefore, the recorded northeastern expansion of the species may be a reoccupation of habitat within the species range prior to European settlement. Unfortunately, no records of Cerulean Warblers in this area exist prior to 1930 to confirm this theory.

The establishment and success of this northern population of Cerulean Warblers over the past two decades is likely the result of reforestation of areas rendered unsuitable by European colonization in the northern range of the Cerulean Warbler. With forested areas continuing to be cleared and maintained for agriculture, and local populations being eliminated in the southern portion of its breeding range, maturing second-growth forest in the north may provide an important source area for Cerulean Warbler populations in the future.

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