

FRENCH:
Fauvette azurée,
Paruline azurée

SPANISH:
Bijirita azulosa (Cuba),
Verdín azulado,
Gorjeador ceruleo, Chipeceruléo (Mexico),
Reinita cerúlea (Venezuela)

Cerulean Warbler

Dendroica cerulea

This small, canopy-foraging insectivore breeds locally in mature and older deciduous forests with broken canopies across much of the eastern United States. Sky blue, sky high in the canopy, the Cerulean Warbler has been little studied; management actions to enhance its habitat have not yet been specified. Among *Dendroica*, this species forages and nests higher in the canopy, and migrates farther and earlier, than most others. Its social system remains poorly understood. Numerous interesting questions about wintering individuals in montane South American forests, where this species associates with others in mixed flocks of canopy insectivores, await investigation.

Although the Cerulean Warbler was formerly among the most abundant breeding warblers in the Ohio and Mississippi River valleys, its numbers plummeted in the 1900s.

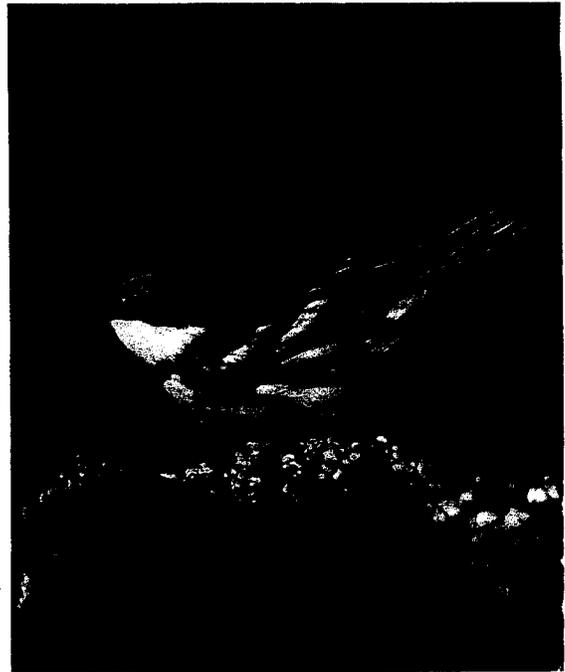
The Birds of North America

Life Histories for the 21st Century

Concern for the future of this species is warranted. Yet even in the face of these steep declines, some populations are currently expanding.

Several independent teams have investigated this warbler on its breeding grounds: in southern Illinois, by the Illinois

Natural History Survey, principally Scott Robinson (Vanderah and Robinson 1995); in the Cumberland Plateau, by the University of Tennessee (Knoxville), principally David Buehler and Charles Nicholson (Nicholson and Buehler 1998); southern Ontario, by scientists at



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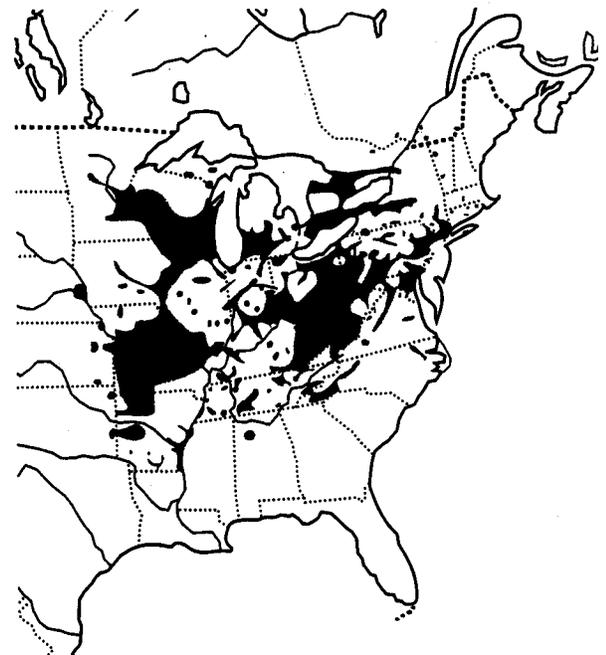


Figure 1. Breeding distribution of the Cerulean Warbler. This species winters in South America. See text for details. Adapted and modified from Dunn and Garrett 1997.

Queen's University, principally Raleigh Robertson (Oliarnyk 1996; Oliarnyk and Robertson 1996; Jones and Robertson 1997, 1998); and in the lower Mississippi Alluvial Valley, by scientists at the USDA Forest Service, Southern Hardwoods Lab, principally the author. Progress reports on the work of these groups were combined in a 1998 symposium (Hamel 1998a).

DISTINGUISHING CHARACTERISTICS

Small wood-warbler (11.5 cm, 8–10 g) with relatively long, pointed wings and short tail with long undertail-coverts. Adult male deep cerulean blue above, white below, with a narrow blue-black band across the throat. Adult female bluish green above, white washed with yellow below, with a distinct white or yellowish line over the eye. Both sexes in all plumages have 2 white wing-bars and white tail-spots. Males have streaked backs in all plumages; females do not. Seasonal variation in adult plumage is less than that among individuals. Some fall males show greenish edges to back feathers. First-fall (Basic I plumage) individuals are similar to adult female in general appearance, with upperparts gray-green to olive (female) or bluish to blue-gray washed with green (male), prominent pale superciliary stripe, dark ear-coverts, dull whitish underparts, and 2 white wing-bars. In first-fall males, streaking is present above but may be limited to sides of back, the adult breast band is lacking or restricted to the sides of the breast, and underparts have blurry streaking. The combination of a bluish crown, pale supercilium, blurred ventral streaking and wing-bars is fairly distinctive. In first-fall females (the most greenish and yellowish plumage), the upperparts are unstreaked and the underparts are only indistinctly streaked. First-fall individuals of both sexes are variably yellowish below, with females more extensively yellow than are males. First-spring (Alternate I plumage) individuals similar to adults but duller and not as boldly marked, with whitish supercilium present in males (Dunn and Garrett 1997, Pyle 1997).

Confusion with other species unlikely except for immature in its first fall, which is superficially similar to young female Blackburnian Warbler (*D. fusca*). Young Blackburnian appears to have a dark triangular auricular patch outlined by the lighter supercilium and pale side neck; Cerulean has only a light line over the eye. Young Blackburnian may appear buffy below, Cerulean white with pale or more intense yellow. Blackburnian in all plumages has pale streaking on the sides of the back, Cerulean never does (Dunn and Garrett 1997). Blackburnian also has longer tail. Immature Cerulean may also superficially resemble immature Black-throated Gray Warbler (*D. nigrescens*) but latter species is always gray above, never bluish or greenish.

DISTRIBUTION

THE AMERICAS

Breeding range. Following description based on Dunn and Garrett 1997, except as noted. Breeds mainly from central Minnesota, n. Wisconsin, the central Lower Peninsula of Michigan (locally in w.-central Upper Peninsula of Michigan), s. Ontario (north to about 44.30°N; Eagles 1987), New York (including Long I. but absent from Adirondack Mtn. region), Connecticut, and Rhode Island, south through nw. New Jersey, Pennsylvania, extreme n. Delaware, and the mountains of w. Virginia, w. North Carolina, and extreme ne. Georgia, and west to central Arkansas, Missouri, and e. and central Iowa. Within this area, not uniformly distributed; breeding more widespread within some areas (e.g., s. Missouri, s. Wisconsin, e. Kentucky, W. Virginia, e. Ohio), while extremely local in other areas (e.g., Illinois, n. Indiana, w. Tennessee, w. Kentucky). Local breeding also extends north to extreme s. Quebec (north to about 45.30°N; Bannon and Robert 1996), w. Vermont, central Massachusetts; east to e. Virginia and e. North Carolina; south to n. Alabama, s. Arkansas, and possibly n. Mississippi (Turcotte and Watts 1999); and west to easternmost portions of Oklahoma, Kansas, and Nebraska, and possibly se. South Dakota (Peterson 1995). May also breed in n. Louisiana and extreme nw. South Carolina. Populations in s. Ontario and central New York are increasing.

Winter range. Winter range (Dunn and Garrett 1997, cf. Am. Ornithol. Union 1998) in mountains of n. South America, on both east and west slopes of the Andes in Colombia, on east slopes in Venezuela, Ecuador, Peru, and n. Bolivia. Winter records exist also for the tablelands of e. Venezuela. Occasional records on west slopes of Andes in Ecuador (J. Lyons pers. comm.) and forested foothills as far as se. Brazil (Dunn and Garrett 1997).

A few individuals recorded wintering in Grand Cayman as nonbreeding residents (Raffaele et al. 1998). Dec, Jan, and Feb specimen records are confined to Venezuela, Colombia, Ecuador, and Peru (D. Pashley pers. comm.). Sight records of individuals in Pacific lowlands (< 500 m) of Costa Rica in Jan (D. Buehler pers. comm.).

Other records. Casual west to N. Dakota and sw. Manitoba, north to s.-central Ontario (North Bay), New Hampshire, Maine, Nova Scotia, and Newfoundland, and east to Bermuda, the Bahamas, and Greater Antilles. Also casually recorded in w. North America in Colorado, New Mexico, Arizona, Nevada, n. Baja California, and California (where at least 13 records). Of warblers with breeding ranges confined to e. North America, this species is among those least frequently recorded in w. North America and, despite increasing intensity of searching, records seem to have become less numerous since 1980. Roberson (1980) lists 9

California records prior to 1980; the number had increased only to 13 for the state in the mid-1990s (Dunn and Garrett 1997).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

Conspicuous and abundant species throughout the Ohio and Mississippi River valleys during nineteenth century (Audubon 1856, Brewster 1875, Coues 1878, Ridgway 1889, Widmann 1907); currently the species no longer breeds in some areas of former abundance, such as much of the Mississippi Alluvial Valley (Smith et al. 1996). While the overall geographic limits of the breeding range have changed little during recent history, the relative abundance of the species within the range has experienced considerable change (mostly declined) since the early 1900s (Hamel 2000). Some of the increase in area of the range in the northeast, e.g., in Quebec (Ouellet 1967) or Ontario (Eagles 1987), may represent an extension of the limits of the range, rather than a reoccupation of area from which the birds had been earlier extirpated.

FOSSIL HISTORY

No information.

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

No plumage variation documented; no subspecies recognized. Genetic variation is currently under study (Veit et al. 1998).

RELATED SPECIES

A hybrid *Dendroica cerulea* × *Mniotilta varia* (Cerulean × Black-and-white Warbler) was collected in 1954 (Parkes 1978).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Medium- to long-distance complete migrant; no resident populations. Migrates across Gulf of Mexico (Bonhote 1903, Bullis 1954, Crawford 1980). Migration occupies approximately 2 mo in spring, >4 mo in fall. Very southerly wintering areas give the species an extended migratory route (Averill 1920, Banks and Baird 1978). Pattern of arrivals indicates that individuals appear at known breeding locations 1 or even 2 wk earlier than as transients at same latitude. Fall migration begins very early, and individuals may arrive on South American wintering grounds as early as Aug (Dunn and Garrett 1997).

TIMING OF MIGRATION

A detailed summary of migration dates is presented in Hamel 2000.

Spring. Late Mar–mid-May, peaking in Apr along Gulf Coast and early May in Midwest and Northeast (Hamel 2000).

Florida records 23 Mar–21 May (Stevenson and Anderson 1994). In Louisiana (1988 study), first encountered 13 Apr at Cameron Parish (F. Moore pers. comm.). In Alabama, arrives late Mar in both coastal and mountain localities (Imhof 1976); migrants have left coastal situations by 21 Apr. Arrives Arkansas very late Mar, becoming more numerous in third–fourth week of Apr, widespread after that (James and Neal 1986).

Typically arrives Tennessee mid-Apr (Robinson 1990), with early dates of 29 Mar mid-state, 5 Apr in west, and 11 Apr in east. In se. Missouri, arrives early Apr, peak migration statewide in early May (Robbins and Easterla 1991). Numbers increase to late Apr in Illinois (Robinson 1996, Bohlen 1989), peak in Kentucky by 1 May (Mengel 1965). In Ohio, 25–30 Apr arrival, few migrants detected after 20 May (Peterjohn 1989). In Rhode Island, 55% of 58 records between 12–23 May (J. Ferren pers. comm.). Arrives s. Lower Peninsula of Michigan first or second week of May, less often late Apr, peaking about mid-May (R. J. Adams in Granlund et al. 1994). At Long Point Bird Observatory, Ontario, 27 of 28 records from 18 Apr to 25 May (J. McCracken pers. comm.). Earliest arrival in Quebec, 1 May (Cyr and Larivée 1995).

Fall. Few records; needs study. Latest Quebec departure 22 Aug (Cyr and Larivée 1995). In Michigan (Wood 1951, Adams 1991), apparent departure as early as late Jul, perhaps through Aug and into early Sep (R. J. Adams in Granlund et al. 1994). Rarely reported in fall in New York, but recorded as late as 8 Oct (Levine 1998). Four fall records for Rhode Island, 17 Aug–16 Sep (J. Ferren pers. comm.). Aug–early Sep peak in Ohio, ending usually by 25 Sep, perhaps as late as 9 Oct (Peterjohn 1989). Mid-Aug–early Sep departure from Missouri, with late dates 28 Sep 1897, 26 Sep 1968 (Robbins and Easterla 1991). Coastal Alabama records 18 Jul–16 Sep. Coastal Plain records to 24 Sep (Imhof 1976). Recorded in Florida 11 Jul–15 Oct, where Taylor and Anderson (1973) noted TV tower kills from late Aug to late Sep. Rare to sporadically common late Aug–mid-Oct on Caribbean lowlands and foothills of Costa Rica, usually to 500 m, sometimes to 1,500 m, with smaller numbers in central highlands and Pacific slope (Stiles and Skutch 1989). In Panama, late Aug–early Oct (Ridgely and Gwynne 1989). Very early arrival on wintering grounds is demonstrated by 2 records in Aug from Ecuador (Ridgely and Greenfield in press) and a Sep record from Peru (D. Pashley pers. comm.). Nevertheless, singing males recorded on breeding grounds as late as 21 Aug in Tennessee (C.

Woodson pers. comm.) and 28 Aug in Michigan (Brodkorb 1929). Latest North American record 2 Dec in Newfoundland, but late fall records of this species should be carefully evaluated because of possible confusion with Blackburnian Warbler (Lehman 1987).

Records from western North America. Casual during migration in w. North America (see Distribution: other records, above), where more often recorded in fall (2 Sep–27 Oct; $n = 13$ records) than spring (17 May–6 Jun; $n = 7$ records). Most western records from California ($n = 13$; Dunn and Garrett 1997).

MIGRATION ROUTES

Apparently from Andean wintering grounds to northern mountains of Colombia and Venezuela, thence perhaps nonstop flight over Panama to Maya Mtns. of Belize (Parker 1994), thence across Gulf of Mexico to n. Gulf Coast of U.S. and northeastward primarily through Mississippi and Ohio River valleys. Some may move north along coastal lowlands of Central America (Howell and Webb 1995). High concentrations noted at certain inland U.S. locations such as Kennesaw Mtn., GA (G. Beaton pers. comm.), and Sharps Ridge, TN (Robinson 1990). Fall routes presumably the reverse of spring (but few data), beginning in Jul and extending into Oct. Few data exist on concentrations in Central America in fall. Most records from w. North America and from Bermuda and the West Indies have occurred during fall (Dunn and Garrett 1997).

MIGRATORY BEHAVIOR

Nocturnal migrant (Bonhote 1903, Bullis 1954, Crawford 1980). Scant knowledge of stopover ecology is primarily from Parker (1994) in Belize, and G. Beaton (pers. comm.) in Georgia. Heavy fat loads in spring migrants that were killed by a tornado on northern Gulf Coast suggest need for extensive reserves for crossing Gulf of Mexico (Wiedenfeld and Wiedenfeld 1995).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Routinely identified with predominantly forested landscapes, mature forest, large and tall trees of broad-leaved, deciduous species (Wilson 1811) with an open understory; in wet bottomlands, or upland situations including mesic slopes, and mountains, from <30 to >1,000 m elevation. Historical accounts described species as especially abundant in old-

growth bottomland forests of the Mississippi Alluvial Valley (Widmann 1895a, 1895b, 1897); these forests no longer exist. Mesic upland forests of the type this species used are now scarce as well (replaced by farmland); occurrence in flood plains thus may be an artifact, rather than a preference.

Expanding populations in ne. North America now occupy landscapes formerly cleared for agriculture (Oliarnyk 1996). Thus, species will occupy second-growth as well as mature forest.

Usually considered an area-sensitive species. Minimum forest-tract size varies, e.g. from 20–30 ha in Ohio to 700 ha in the Middle Atlantic states and 1,600 ha in Mississippi Alluvial Valley of Tennessee (Robbins et al. 1989, 1992, Peterjohn and Rice 1991). Mueller et al. (1999) suggest tracts >8,000 ha may be required to support stable breeding populations in the Mississippi Alluvial Valley.

In Ontario, however, found breeding in tracts as small as 10 ha (J. Jones pers. comm.). Species response to habitat fragmentation may reflect factors that covary with fragment size, such as intensity of Brown-headed Cowbird (*Molothrus ater*) parasitism and of predation, rather than particular behavioral aversion to small fragment size or to edges (Robinson et al. 1995b, Hamel et al. 1998a). More research on this topic is needed.

No apparent preference for tree species or group for nesting and foraging (Hamel 2000), although certain species or trees of certain crown classes may be used frequently in particular localities (Vanderah 1993 and pers. comm.; Oliarnyk and Robertson 1996; and Hamel 2000 and unpubl.; *contra* Robbins et al. 1992).

Minimum habitat requirements of this species along the Roanoke River in N. Carolina: (1) a closed canopy; (2) presence of scattered, very tall, old-growth canopy trees; (3) distinct zonation of canopy, subcanopy, shrub, and ground-cover layers (Lynch 1981). Floodplain areas of even-aged timber with no old-growth trees contained few, if any, breeders in this region. In Tennessee study, Robbins et al. (1992) found Cerulean Warblers (1) to perch in trees whose diameters were significantly larger than average trees available to males in their territories, (2) to occupy territories containing trees with significantly larger diameters than average for the stands in which the territories were located, and (3) to occur in stands dominated by trees with larger diameters than the dominants of the average stand in the study region. In e. Tennessee and w. North Carolina, usually found in stands generally lacking in well-developed sapling or shrub layers (D. Buehler pers. comm.). Oliarnyk (1996: page i) noted: "Within a territory, habitat surrounding successful nests was significantly more likely to contain larger than average trees and a dense upper

canopy, while unsuccessful nests were associated with a dense understory." Hamel et al. (1994) indicated that while Cerulean Warblers occur in areas dominated by large trees, within those areas the locations at which individuals spend their time may not be predictable by tree diameters alone.

Bent (1953), Harrison (1984), Oliarnyk (1996), Oliarnyk and Robertson (1996), and others indicate that gaps in the canopy, or openings, are important for this species. In Missouri breeding habitats, canopy cover averaged 85%, minimum value 65% (Kahl et al. 1985). This species persisted in stands heavily damaged by Hurricane Opal on the Chattahoochee National Forest in Georgia (E. J. Williams pers. comm.). On a Mississippi Alluvial Valley site in Desha Co., AR, however, a severe ice storm was followed by a decline in the population (Hamel et al. 1998b).

Important habitat elements for this species thus appear to be large tracts with big deciduous trees in mature to older-growth forest with horizontal heterogeneity of the canopy. The pattern of vertical distribution of foliage in the canopy is also important.

SPRING AND FALL MIGRATION

Little information, particularly for South America. Chapman (1917) collected 2 specimens at 1,370 m on steep, heavily wooded slopes at the eastern edge of the Colombian llanos.

Fjeldså and Krabbe (1990) found this species in tropical and lower subtropical zones of the Andes, noting that during migration, individuals rarely occurred in the lower temperate zone.

WINTER RANGE

Limited observations indicate that wintering birds occupy canopy and borders of broad-leaved, evergreen forests and woodland at middle and lower elevations (approximately 500–1,500 m) on the east slopes of the Andes from Colombia to Peru and possibly Bolivia, as well as montane forests of Venezuela (Salvin and Godman 1879–1904, Allen 1907, Meyer de Schauensee 1966, Ridgely and Tudor 1989, Robbins et al. 1992, DeGraaf and Rappole 1995).

Some (Terborgh 1989, Robbins et al. 1992, DeGraaf and Rappole 1995) believe that this species is confined to areas of old-growth native forest and that primary forest is thus a habitat requirement. Others (P. Greenfield pers. comm., W. P. Smith and PBH unpubl.), however, have observed this warbler in areas of second-growth or disturbed forests within the same elevational band in Ecuador. In Merida and Balinas states, Venezuela, Jones and Robertson (1997) associated the species with shade-coffee plantations and second-growth forest. Brief reconnaissance of habitats in which the species is routinely seen at the Cascada de San Rafael, on Rio

Quijos, Prov. Oriente, Ecuador, found considerable variation in canopy structure at sites inhabited by this species (W. P. Smith and PBH unpubl.). It remains to be determined whether architecture of forest canopies in wintering areas is similar to, or differs from, that in breeding areas.

Generally occurs in mixed-species flocks of canopy-dwelling species, primarily tanagers. Winter habitat thus consists not only of geographical, elevational, and vegetational structure components, but may include specific avifaunal components as well. Little information published on occurrence of Cerulean Warblers with mixed-species flocks of tanagers (but see Robbins et al. 1992). The work of Jones and Robertson (1997) in Venezuela has indicated that >90% of Cerulean Warblers associate with mixed-species canopy flocks. Thus, this species may be an obligate flock follower in the nonbreeding season, but this needs study.

FOOD HABITS

FEEDING

Main foods taken. Primarily insectivorous, foraging on insects in foliage. Also eats small amounts of plant material, as small fatty masses attached to fruits of some tropical trees, during migration (R. Greenberg pers. comm.).

Microhabitat for foraging. Takes food from leaf bases and foliage in canopy of a great variety of trees (C. Woodson unpubl.). No tree species preferred. Foraging heights range from 2 to 3 to >45 m. Typically hops along twigs peering at upper and lower surfaces of leaves, petioles, and twigs. Male uses larger trees in more dominant canopy positions than does female, although the difficulty of observing silent birds in the dense canopy may complicate determination of preference for particular tree sizes (C. Woodson pers. comm.). Females in Mississippi Alluvial Valley sites forage in poison ivy (*Toxicodendron radicans*) vines extensively (PBH).

Food capture and consumption. Primary mode of foraging is gleaning insects from leaves. Species usually works from proximal portion of a twig toward distal, peering intently on upper and perhaps more often lower surfaces of leaves for prey. Male often forages in portions of tree canopies with particularly dense foliage. Often standing on twig at the base of a leaf petiole, an individual will stretch up, down, or out and pick a prey item from surface of a leaf. Females in Mississippi Alluvial Valley often glean leaves and inflorescences of poison ivy (*Toxicodendron radicans*) vines that encircle the boles of canopy trees, working in a spiral around tree. To a lesser extent, the species uses sallying and hover-gleaning to capture prey (PBH).

DIET

Major food items. Insects, especially homopterans and larval lepidopterans, during breeding season (Howell 1924, Sample et al. 1993). No study of diet from winter or migration seasons.

Quantitative analysis. Stomachs of 4 birds taken in Alabama in 1912 contained: Hymenoptera (42% of prey items); Lepidoptera (35%); and Coleoptera, including weevils (23%; Hamel 1992). Sample et al. (1993) reported on differences in diet of individuals ($n = 14$) taken during studies of gypsy moth (*Lymantria dispar*) invasion of W. Virginia forests. These birds had eaten Homoptera (52% of total biomass of gut contents); Lepidoptera, primarily larvae (37%); Coleoptera (7%); and small amounts of Hymenoptera, Diptera, Hemiptera, Araneae, and other arthropods. Study plots were treated with Diflubenzuron, an insecticide that interferes with molting of larval insects. Subsequent to treatment, Cerulean Warbler diets shifted from Lepidoptera toward Homoptera. Birds in control plots ate twice as much lepidopteran prey by weight as they did homopteran, while those in treatment plots ate 3 times as much homopteran as lepidopteran prey. The effect was most pronounced immediately after the treatment. Birds collected a month later all were eating more lepidopteran than homopteran prey again; Lepidoptera/Homoptera ratio in treatment plots was 1.4:1, and that in control plots 4:1.

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLET-CASTING, AND DEFECATION

No information.

SOUNDS

VOCALIZATIONS

Woodward (1997) documented vocalizations and vocal behavior in Ontario, the same population studied by Oliarnyk and Robertson (1996).

Development. Not documented.

Vocal array. Songs of the Cerulean Warbler have been studied (Woodward 1997), calls have not. Songs typically involve 3 sections, an introductory set of longer figures, a middle section of shorter figures, perhaps on a slightly higher pitch, and a final buzz. To the human ear, songs can be described as ZHEE ZHEE ZIZIZIZI zzzzeet (similar

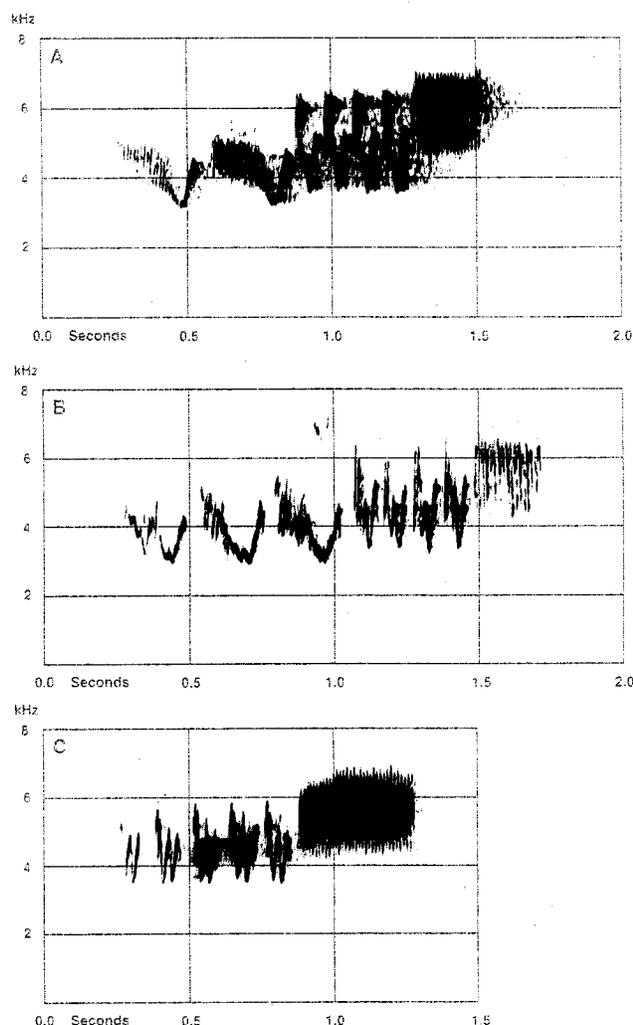


Figure 2. Three song types of the Cerulean Warbler. From recordings made by D. J. Borror in the collection of the Borror Laboratory of Bioacoustics (BLB), The Ohio State University (A: BLB no. 14843, recorded in Vinton Co., OH, 3 Jun 1978; B: BLB no. 3346, recorded in Franklin Co., OH, 8 May 1958; C: BLB no. 10544, recorded in Pike Co., OH, 9 May 1970). Prepared by the staff of BLB, using a Kay Elemetrics DSP 5500 Sona-Graph (with effective frequency resolution of 150 Hz and a 200-point FFT transform size). The songs appear to the author to correspond with those listed by Woodward (1997: 8–10) as follows: Fig. 2A “C”; Fig. 2B “F”; and Fig. 2C “F”.

to Fig. 2A), ZEE ZEE ZEE ZIZIZIZI zeeet (similar to Fig. 2B), or zz ZI ZI ZI zeeet (similar to Fig. 2C), where capitalization indicates more heavily stressed syllables.

Singing documented only in males. Woodward (1997) documented that the song type used by a male for his dawn song early in the season (“early” song, serving a mate-attraction function) was replaced by a different song type for dawn song later in the season (“late” song, primarily used in intrasexual communication). Mid-morning song bouts early in the season were predominantly “early” song, while those later in

the season alternated "early" and "late" songs. Songs of the species are not form encoded, in that individual songs are typically used for mate attraction or for male-male interaction. Nor are they strictly performance encoded, in which context can be used to determine the whether a song is an "early" or "late" song.

Phenology. Annual pattern of vocalizing has not been studied. Sexual differences have not been documented.

Daily pattern. Sings during much of daylight hours; for reasons not yet determined, individual male may or may not sing on any given day (PBH).

Places of vocalizing. Male sings from different locations in canopy of trees in the breeding territory; may or may not use fixed song perches from day to day, although frequently sings from same individual tree (PBH). Appears to sing from higher perch after having mated than before (Woodward 1997). Vocalizes throughout the day. Male sings while foraging and while preening, occasionally sings in flight, as well as while sitting on exposed perch (PBH).

Repertoire and delivery of songs. Geographic variation in songs studied by Woodward (1997) based on samples of songs from se. Ontario ($n = >33$), sw. Ontario ($n = 4$), and s. Illinois ($n = 28$). Among 33 males recorded in 1994, 8 different songs, combinations of syllables, recorded. Preliminary observations suggested that geographic variation in the form of songs was small. Individual males usually included 2, occasionally 3 (20% of males) songs in their repertoire. Males typically sang a single song-type in repeat mode early in the season, presumably for mate attraction, and another song type later in the season. For birds with >2 song types, late-season song bouts included 2 song types presented alternately.

Social context and presumed functions. Sings 2 different songs, 1 mostly for mate attraction, apparently, and the other primarily for territory defense. Similar pattern as in *Vermivora*, *Parula*, other *Dendroica*, *Mniotilta*, and *Setophaga* warblers (Spector 1992). The vocal repertoire is restricted structurally, however, compared to these other species. Differences between intrasexual and intersexual communication are primarily in the rate of delivery and pitch of the songs. Males sing at slower rate (7.1 songs/min daytime ± 0.6 SE, $n = 6$) and higher pitch (4.8 kHz ± 0.1 SE, $n = 17$) when the songs are associated with attraction of potential mates, and at higher rate (8.6 ± 0.6 songs/min daytime, $n = 6$) and lower pitch (4.3 ± 0.1 kHz, $n = 17$) when the songs are associated with territory defense. Males may or may not respond to tape-recorded playback with singing behavior. Indeed, when attempts are made to catch this species, lack of singing in response to playback is associated with higher probability of capture, suggesting that higher levels of aggressiveness do not involve vocalizing (PBH). Incubating females frequently call from the nest, apparently in response to a

song from their presumed mate (C. Woodson pers. comm., PBH). Countersinging by adjacent territory holders is common. Recognition of mates, neighbors, geographic variants, or other species has not been studied. Differences in responses to presumed mate attraction and territory defense singing in playback experiments suggested to Woodward (1997) that the different song types in males' repertoires serve these separate functions. More work is needed on geographic and seasonal variation in vocalizations.

NONVOCAL SOUNDS

Not documented.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Generally hops on small branches and twigs in the forest canopy, in lateral or slightly upward direction. Female often hops from vine to vine in poison ivy on tree boles in both upward and downward direction. Walking and climbing not observed (PBH). Robbins et al. (1992) indicated that in a sample of all behaviors taken from Tennessee, the Cerulean Warblers were found at an average height of 17 m in a tree of average height of 22 m. A much more extensive data set from Arkansas and Tennessee bottomland hardwood forests indicated an average perching and foraging height of 15 m in a tree of average height of 22 m (PBH).

Flight. Short, direct flights between trees, occasionally accompanied by fluttering or slow flapping and spread tail that makes the white patches in the tail and on the inner vanes of the primaries and secondaries obvious to the observer below (PBH). Longer flights also common.

Swimming and diving. Not known.

SELF-MAINTENANCE

No information.

AGONISTIC BEHAVIOR

Physical interactions. Breeders can be very aggressive (PBH). Males sometimes attack each other at canopy heights of ≥ 20 m, meeting in mid-air with audible collision. The birds grapple with each other with bills and feet as they fall, spiraling to the ground with spread wings and tails. Similar fights observed between females; when pairs interact aggressively at territory boundaries early in the season, intrasexual fights between males and between females may be occurring at the same time (PBH). Female sometimes flies directly at and hits male, sometimes known to be her mate, as male sits on a perch. Male occasionally does the same to female.

Communicative interactions. No information.

SPACING

Territoriality. Mean breeding territory size of 1.04 ha \pm 0.16 SE based on 18 Ontario territories that ranged in size from 0.38 to 2.4 ha (Oliarnyk 1996). Maximum breeding densities on published Breeding Bird Censuses (Robbins et al. 1992) suggest that territories smaller than these are possible.

Nature and extent of territory has not been studied in detail. Although most observers treat the species as exhibiting all-purpose territories, this topic deserves further study. Observers have frequently noted that the species occurs in aggregates, groups, or "colonies" during the breeding season. Bagg (1900) noted 25 individuals inhabiting a single patch of woods in New York; Peck and James (1987) used this information to infer that the species has a narrow habitat preference. Statistical determination of the clumped distribution of this species has not been made, however. Study of this topic will help to interpret how these birds use their habitats, as well as how they maintain their territories.

Male apparently establishes and maintains territory primarily by singing, with some physical combat involved (see Agonistic behavior, above).

Interspecific territoriality has not been determined, although frequent interspecific aggressive behavior has been observed between this and a number of other species, including Blue-gray Gnatcatcher (*Poliophtila caerulea*), American Redstart (*Setophaga ruticilla*), Northern Parula (*Parula americana*), and other species (Hamel 2000).

Winter territoriality not documented. Observations of Robbins et al. (1992) that mixed-species flocks contain at most a single individual (or pair, male and female; J. Jones pers. comm.) suggest need for additional study.

Dominance hierarchies have not been observed.
Individual distance. No information.

SEXUAL BEHAVIOR

Mating system and sex ratio. Apparently monogamous (Verner and Willson 1969); not yet studied with marked birds.

Pair bond. Duration of pair bond not demonstrated with marked individuals. Presumably, it exists for a single nesting attempt or perhaps breeding season. No published reports of polygamous matings. Courtship displays, mate-guarding, and pre- and post-copulatory displays have not been described.

Extra-pair copulations. No information.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Only speculation can be brought to bear on this issue: Association between wintering individuals and mixed-species flocks of canopy-inhabiting species suggests interspecific sociality to a degree. The often-noted tendency of this species to occur in "clumps" in breeding season has

not been distinguished from random distribution or habitat specificity.

Play. No information.

Nonpredatory interspecific interactions. Murray and Gill (1976) noted that Cerulean Warblers were attacked by both Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*). Fights between Cerulean Warbler females and female American Redstarts, and between Cerulean Warblers and Blue-gray Gnatcatchers observed in Mississippi Alluvial Valley study sites; individuals were contesting each other for nesting material, primarily spider webs (PBH). Aggressive interactions between Cerulean Warblers and American Redstarts, Least Flycatchers (*Empidonax minimus*), Red-eyed Vireos (*Vireo olivaceus*), and White-breasted Nuthatches (*Sitta carolinensis*) common in Ontario (J. Barg pers. comm.). Interactions between Cerulean Warblers and Red-eyed Vireos and Hooded Warblers (*Wilsonia citrina*) observed in Arkansas (C. Kellner pers. comm.), where the other species displaced the Cerulean Warblers.

PREDATION

Kinds of predators. Little information. Blue Jays (*Cyanocitta cristata*) known to eat nestlings (J. Barg pers. comm.).

Manner of predation. No information.

Response to predators. Few specific observations of responses to potential predators. Mobbing snakes, giving alarm calls and "freezing" in response to presence of Mississippi Kites (*Ictinia mississippiensis*), suggest that the species recognizes these animals as predators (PBH).

BREEDING

PHENOLOGY

Pair formation. Males usually arrive before females on the breeding grounds, often by at least a week. Pair formation commences soon after arrival of females.

Nest-building. Only by the female; may last from a few days to as much as a week or more.

First/only brood per season. Generally raises a single brood to independence. Few published egg dates distinguish first from renestings. From 17 to 26 Apr in n. Texas (Pulich 1988); late Apr-early Jul in Mississippi Alluvial Valley of Arkansas and Tennessee, 50% of 25 nests initiated 9-21 May (PBH); late May-early Jul in Michigan (Wood 1951); 4-17 Jun in Ohio (Peterjohn and Rice 1991); 24 May-27 Jun ($n = 36$ nests), 7-14 Jun ($n = 18$) in Ontario (Peck and James 1987); late May-early Jul in Ontario (Oliarnyk 1996, J. Jones and J. Barg pers. comm.). No data on duration of laying first to last eggs in clutch, on hatching dates, or on when young depart from the nest.

Second/later brood per season. Can produce 2 broods in 1 season, but apparently does so rarely. In

the Mississippi Alluvial Valley, color-marked pairs have re-nested after losing first nests (even with large young) to predators (PBH).

NEST SITE

Selection process. Apparently both male and female help choose nesting location. Males and females observed together at locations where nests were later built; sometimes male went to location before the female (G. Vanderah pers. comm., PBH). Nests in a great variety of tree species, at least 11 named and 3 genera listed in publications (Hamel 2000). Another 13 species identified among 70 nests in Mississippi Alluvial Valley (PBH). It is not clear if they actually select certain species in greater frequency than the species occur in the environment.

Microhabitat. Nests usually placed on lateral limb of deciduous tree in mid-story or overstory canopy, usually concealed from above by clumps of live leaves on small twigs of the nest tree or by clumps of leaves or vines growing along the nest branch (Bent 1953, J. Jones pers. comm., PBH).

Nests often located over an open space (Bent 1953), which may be as small as 1 m between nest branch and a lower branch of the same tree. More often, however, open space may be 5–20 m from nest to nearest vegetation below (PBH). Variety of situations in which nests are located within the canopy makes characterization difficult. Needs study; would benefit conservation of this bird.

Site characteristics. Hamel (2000) summarized published nest height information. Rangewide, based upon 80 nests, mean nest height was 11.4 m \pm 0.41 SE, range 4.6–18.3 m; mean distance from bole 3.38 m \pm 0.37, range 0.9–7.3 m. Analysis of variance of nest height information indicates significant differences in mean nest height among localities. Hamel (2000) compared nest and vegetation heights from survey work in Ontario (Oliarnyk and Robertson 1996) and the Mississippi Alluvial Valley (PBH) to these historical data (rangewide values). All Mississippi Alluvial Valley nest measurements were significantly greater than values from Ontario and rangewide values from the literature. Ontario values exceeded rangewide values from literature for nest height, but not for distance from bole of tree. Differences among nest heights may relate to the general physiognomy of the vegetation at the breeding locality (Hamel 2000).

NEST

Construction process. Not described in detail. Constructed entirely by female (PBH). Length of time to build nest varies from perhaps 3 to >8 d (PBH).

Structure and composition matter. Not yet characterized. Bent (1953) quotes Kirkwood concerning materials in a single nest, which included brown bark fiber, fine grass stems, a few black horse hairs; fin-

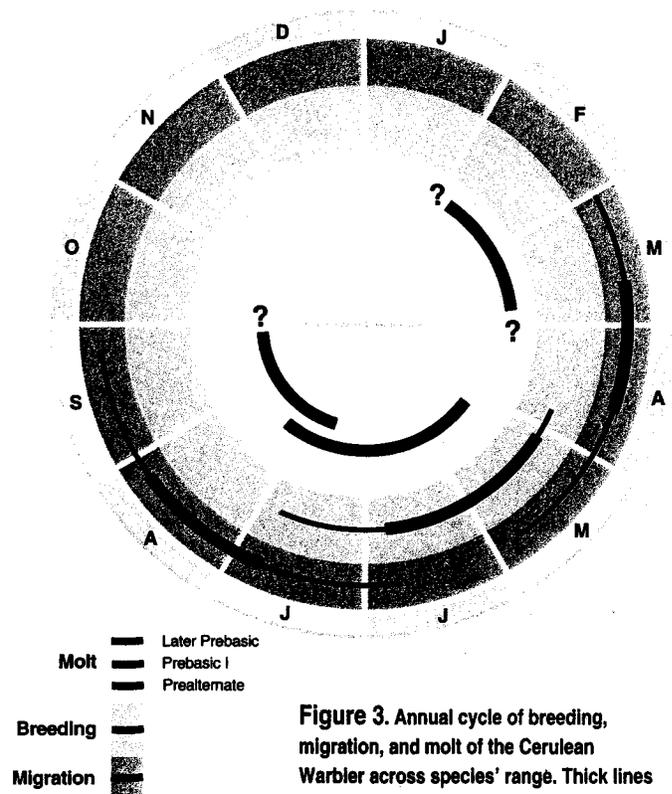


Figure 3. Annual cycle of breeding, migration, and molt of the Cerulean Warbler across species' range. Thick lines show peak activity; thin lines, off-peak.

ished with gray shreds of bark, spider web, and some water-soaked pieces of newspaper. Cerulean Warbler typically decorates outside of nest with some small gray or white materials; different materials serve the role in different parts of the range.

Dimensions. From Bent (1953): Outside diameter and height ($n = 3$ nests) based on 3 examples: 7 \times 4.5–5 cm. Inside diameter and depth (i.e., of nest cup), from the same nests: 3.4–4.5 \times 2.2–2.5 cm.

Microclimate. No information.

Maintenance or re-use of nests, alternate nests. From Oliarnyk and Robertson 1996, PBH. When re-nesting after nest failure, female routinely uses portions of old nest, probably caterpillar silk and spider webs used to attach outer part of the nest to supporting branch, in the construction of new nest. Fresh lining is apparently gathered for new nest.

Nonbreeding nests. Unknown.

EGGS

Shape. Ovate to short ovate (Bent 1953).

Size. Length and breadth of 50 eggs: 17 \times 13 mm (Bent 1953). From collections of Western Foundation for Vertebrate Zoology (WFVZ), length: 16.68 mm (range 15.28–18.93); breadth: 12.78 mm (range 11.89–13.59); mass of empty shell: 0.076 g (range 0.062–0.091; $n = 20$ clutches, 77 eggs; L. Kiff and R. Corado pers. comm.).

Mass. No information.

Color. "Grayish white, creamy white, or even very pale greenish white, and they are speckled, spotted or blotched with 'bay,' 'chestnut,' or 'auburn,' intermingled with spots of 'light brownish drab,' or 'brownish drab.'" (Bent 1953: 331).

Surface texture. "Slight luster" (Bent 1953: 331).

Eggshell thickness. No information.

Clutch size. In Ontario, clutches at 6 nests ranged from 2 to 5 eggs (mean 3.8 ± 0.2 SE; Oliarnyk 1996). In 36 Ontario nests, range 1 to 4 eggs, mode 4 eggs (Peck and James 1987). Twenty clutches in WFVZ collections averaged 3.85 (R. Corado and L. Kiff pers. comm.). Additional data indicate that clutch size is typically 3 or 4 eggs (Hamel 2000); mean of 40 clutches in literature 3.78 eggs ± 0.1 SE (range 2–5).

Egg-laying. No information.

INCUBATION

Onset of broodiness and incubation in relation to laying. No information.

Incubation patch. Only the female has a brood patch (Pyle 1997, PBH).

Incubation period. In Ontario, 11 ($n = 5$ nests) and 12 days ($n = 3$ nests; Oliarnyk 1996).

Parental behavior. Only female incubates (PBH). Male occasionally provisions his mate with food while she incubates (Oliarnyk and Robertson 1996, G. Vanderah pers. comm.); no data on rate at which this occurs. Incubation rhythm, duration of attentive periods not described. Several observers have noted a characteristic behavior of female when leaving the nest after an incubation or brooding bout: drops vertically from side of nest with closed wings for several meters through space below nest, opening her wings only when well below the nest (called "bungee-dropping"; G. Vanderah, J. Barg pers. comm.).

Hardiness of eggs against temperature stress; effect of egg neglect. No information.

HATCHING

No information.

YOUNG BIRDS

No information; no studies of growth.

PARENTAL CARE

Brooding. Almost entirely by the female. No information on brooding rhythm. Roles and behavior of parents not documented.

Feeding. Both parents feed young. Initially male provides most visits, later female increases her feedings as she devotes less time to brooding the young (G. Vanderah pers. comm., PBH). No published studies.

Nest sanitation. Both parents remove fecal sacs (PBH).

COOPERATIVE BREEDING

Not known in this species.

BROOD PARASITISM

Identity of parasitic species. Robbins et al. (1992) list nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) as an important factor in the decline of the species. Study of nest parasitism by Brown-headed Cowbird is part of the protocol in studies in Ontario (Oliarnyk 1996), Mississippi Alluvial Valley (PBH), Cumberland Plateau in Tennessee (D. Buehler pers. comm.), and Illinois (S. Vanderah pers. comm.). No other nest parasites have been observed.

Frequency of occurrence, seasonal or geographic variation. Friedmann's (1963, Friedmann et al. 1977) records of parasitism by Brown-headed Cowbirds are taken from virtually throughout the range of the Cerulean Warbler, suggesting that range overlap between the species has been of relatively long duration, and that the incidence of nest parasitism results from changes in habitat configuration brought about by human intervention rather than from changes in breeding ranges. Because Cerulean Warblers nest high in the canopy of forests, where their nests are difficult for humans to find, only detailed and intensive searches for nests can be expected to provide even minimal estimates of actual rates of parasitism experienced by populations of Cerulean Warblers in different habitats.

Parasitism rates differ in different parts of the breeding range. No parasitism by Brown-headed Cowbirds observed by Oliarnyk (1996) in Ontario. In another Ontario data set, Peck and James (1987) recorded 18% of 36 nests parasitized by Brown-headed Cowbirds. In the Cumberland Mtns. of Tennessee, 1 of 52 nests known to be parasitized (D. Buehler and C. Nicholson pers. comm.). In the Midwest and the Mississippi Alluvial Valley, where forest patches of all sizes are surrounded by a matrix of agricultural lands, most potential breeding habitats for Cerulean Warblers also support breeding Brown-headed Cowbirds, and parasitism of Cerulean Warbler nests has been observed in all study sites in the lower Mississippi Alluvial Valley (PBH). Cowbirds observed parasitizing Cerulean Warbler nests in continuous forest constructed over flooded bottomlands at least 1.6 km from upland habitats and as high as 25 m above the ground (PBH). Of 66 nests found in the Mississippi Alluvial Valley 1992–1997, at least 9 were parasitized by Brown-headed Cowbirds (Hamel 1998b).

Timing of laying in relation to host's laying. Unknown. One nest in Mississippi Alluvial Valley produced a Cerulean Warbler fledgling and a Brown-headed Cowbird fledgling a week apart (R. P. Ford unpubl.).

Response to parasitic mother, eggs, or nestlings. No information.

Effects of parasitism on host. No data.

Success of parasite with this host. No data. Study needed to ascertain whether cowbird parasitism is a threat, whether it is exacerbated by forest fragmentation, and how its impact varies across the range of

the Cerulean Warbler; see Demography and populations: reproductive success, below.

FLEDGLING STAGE

Departure from nest. Little information. Nestling period in Ontario between 10 ($n = 6$ nests) and 11 d ($n = 4$ nests; Oliarnyk 1996). At fledging, some fledglings can fly weakly from the edge of the nest to an adjacent tree (R. Ford and C. Woodson unpubl.).

Growth. No information.

Association with parents or other young. Audubon (1856) noted that adults often take their fledglings to areas with extensive tangles of grape vines (*Vitis* sp.). Same behavior noted in the Mississippi Alluvial Valley (PBH). Usually, where >1 fledgling is produced, adult male will attend some fledglings and the adult female the rest (C. Woodson unpubl.).

Ability to get around, feed, and care for self. No information.

IMMATURE STAGE

No information.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Can breed successfully when 1 yr old (PBH); annually thereafter.

Clutch. Hamel (2000) summarized clutch sizes from published sources, as well as Cornell Nest Record Card Program and collections of WFVZ. Ontario: 3.8 eggs \pm 0.2 SE (range 2–5, $n = 6$ nests; Oliarnyk 1996), mean 3.25, median 4 eggs (range 1–4, $n = 36$ nests; Peck and James 1987); Pennsylvania: 3.82 eggs \pm 0.12 SE (range 3–4, $n = 11$ nests); Michigan: 4.33 eggs \pm 0.21 SE (range 4–5, $n = 6$ nests); New York: 3.58 eggs \pm 0.15 SE (range 3–4, $n = 12$ nests). Number of clutches/breeding season usually 1; 2 or possibly even 3 may be laid if earlier ones are lost (PBH). No published reports of re-nesting after successful fledging of first brood.

Annual reproductive success. For 27 nests found in 1994 ($n = 10$) or 1995 ($n = 17$) on 3 study sites in Ontario, 18 (67%) produced fledglings which, together with observations of fledglings in territories where no nests were found, represented 20 of 27 pairs successfully fledging young over the 2 yr (Oliarnyk 1996).

Oliarnyk (1996) reported 3.0–3.5 fledglings per nesting attempt on 3 Ontario sites in 1995; when these were converted to fledglings/successful nest, the mean value was 4.6 fledglings/successful nest. In 3 Mississippi Alluvial Valley sites monitored from 1992 to 1997, by contrast, 21 of 66 nests produced 37 fledglings, a mean value of 1.7–1.9 fledglings/successful nest. Mayfield daily success was 0.9402 ± 0.01 ($n = 51$ nests; Hamel 1998b).

Number of broods normally reared per season. Usually 1. Sufficient time is available in the southern part of the breeding range for a pair to raise 2 broods successfully, but this has not been observed.

Proportion of total females that rear at least one brood to nest-leaving or independence. In Ontario, 74% of pairs in 1 study produced young that fledged (Oliarnyk 1996).

LIFE SPAN AND SURVIVORSHIP

Total of 1,399 Cerulean Warblers (data through Aug 1999; K. Klimkiewicz pers. comm.) have been banded in 35 states ($n = 1,245$), 2 Canadian provinces ($n = 129$), and 6 countries on the migration and winter grounds ($n = 25$). Majority of bandings in North America have taken place on breeding grounds, May–Jul ($n = 957$); in s. U.S., majority of bandings occurred during spring migration, Mar–Apr. Only 1 individual has been banded during Dec, Jan, or Feb. Longevity record is 6-yr-old male (E. and J. Peartree pers. comm.). Another male was at least 5 yr old when recaptured in 1998 (PBH). Only 1 of 1,399 (through 1999) banded birds has been recaptured or recovered away from the banding locale (Leberman and Clench 1975). No published studies of survivorship.

DISEASE AND BODY PARASITES

No information.

CAUSES OF MORTALITY

No information.

RANGE

Initial dispersal from natal site. No information.

Fidelity to breeding site and winter home range. Individual color-banded birds have returned to breeding sites in Ontario (C. Oliarnyk unpubl.) and in the Mississippi Alluvial Valley (PBH) for at least 2 consecutive years. Numbers of returning individuals are at present too small to estimate return rates. No reports of proportions of returning birds have been made. No winter returns have been published.

Dispersal from breeding site or colony. Distances moved by color-banded individuals (likely underestimates average distances moved by individuals) generally <1 km (PBH).

Home range. No information.

POPULATION STATUS

Numbers. Species recorded on 332 Breeding Bird Censuses (BBC; J. Lowe pers. comm., B. Hoover pers. comm.). These spot-map censuses represent studies of 133 plots in 15 states and provinces. Studies of individual plots continued from 1 to 49 yr between 1932 and 1993. Mean density did not differ significantly by state. Mean recorded density was 43 pairs (± 42 SD)/100 ha. Hamel (1992) reported a mean den-

sity of 24.2 ± 3.5 pairs/100 ha from a more restricted data set. Robbins et al. (1992) reported maximal densities of 82–290 pairs/100 ha from 11 different BBC plots, 8 in W. Virginia and 1 each in Indiana, Michigan, and Ohio. These BBCs were conducted between 1949 and 1971, and most were conducted on upland sites.

Fourteen BBC plots were each censused at least 5 times, representing 141 censuses from 5 states; no changes from year to year were found in analysis of variance after the effect of plot was removed. Significant differences did exist in density among the plots (PBH). One Ohio plot was censused 47 times between 1940 and 1991. When grouped into 10-yr periods, analysis of variance revealed significant differences in density among decades, indicating that density on that plot was lowest in the 1940s (16 pairs ± 7 SD/100 ha) and highest in the 1960s (36 pairs ± 2 SD/100 ha).

No population or density estimates are available from the winter grounds.

Trends. Breeding Bird Survey (BBS) data show populations declining significantly during the years 1966–1996. Mean relative abundance for the continent was 0.41 birds/route over the entire survey period. Sauer (1993) indicated that, while sufficient sampling intensity in the BBS existed to detect a 50% decline in population of the species over a 25-yr period with probability 0.9, low relative abundance of this species mandated caution in interpretation of trend results.

The BBS estimate of the average annual trend 1966–1996, $-3.7\%/yr$ (95% confidence interval -2.5 to -5.0), is based on 236 routes. Trend for 1966–1979 ($-5.5\%/yr$, $n = 113$) indicates a significant decline over the first half of the survey period. That for the remainder of the period, 1980–1996 ($-0.4\%/yr$, $n = 183$), is not significant. These trend estimates suggest that the population declined most dramatically prior to 1980. Whether this represents the primary period of decline or perhaps indicates that, by 1980, populations were reduced to the point that the BBS became a less useful monitoring tool rangewide is not clear. In some parts of the range where the birds were formerly numerous, such as the Mississippi Alluvial Valley, BBS trend estimates can no longer be calculated with any statistical confidence (Smith et al. 1996). Trend estimates in other areas, particularly the Northeast, may not reflect adequately the apparently increasing populations there.

The adequacy of the BBS as a method to monitor forest birds such as Cerulean Warblers has been questioned (Peterjohn et al. 1995, James et al. 1996). Concerns focus on changes in habitat along roadside routes, which would reduce detectability of the birds potentially more than their numbers, and the fact that because BBS routes are along roadsides to begin with, BBS coverage may be biased against forest birds like Cerulean Warblers.

Villard and Maurer (1996: 63, see also Maurer 1994) conducted a separate geostatistical analysis

of BBS data to assess changes in Cerulean Warbler numbers over the period of the BBS. Their analysis was not based on the physiographic strata, but on the entire range of the birds. They concluded that "spatial pattern of variation in Cerulean Warbler abundance thus appears to be characterized by declines concentrated in the areas of high abundance within the breeding range."

These trends are cause for concern (Robbins et al. 1992). See Conservation and management: effects of human activity, below, for some potential causes of these population declines.

POPULATION REGULATION

Not studied specifically. See Conservation and management: effects of human activity, below, for how changes in habitat have affected populations of this species.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Not an issue with this species.

Pesticides and other contaminants/toxics. No data.

Collisions with stationary/moving structures or objects. As many as 141 casualties documented in 25 yr at Florida TV towers (Stevenson and Anderson 1994).

Degradation of habitat: breeding and wintering. Land-use changes brought about by increasing human populations in the breeding, migratory, and winter ranges of this species appear to be the underlying cause of the population decline of the bird in this century; see Trends, above. Humans have cleared habitats for other land uses. Such forest fragmentation is most obvious in western and southwestern parts of the breeding range (e.g., Mississippi Alluvial Valley, Indiana, Illinois; Moseley 1947, Robbins et al. 1992, papers in Hagan and Johnston 1992). How fragmentation of habitats affects populations, especially in nonbreeding periods, is not precisely known (Robinson et al. 1995a, 1995b). How the populations of this species fluctuated in response to wholesale logging of large portions of the mountainous areas of the East during the period 1880–1930 has not been documented.

BREEDING HABITAT. Robbins et al. (1992) listed 6 breeding-season constraints. Four of them relate to habitat; they are:

(1) Loss of mature deciduous forest, especially along stream valleys. This is clearly the most serious long-term problem facing the species on its breeding grounds. Large areas of potential breeding terrain are not currently inhabitable by this warbler because they lie in urban areas or because they have been converted to agriculture. Forests managed with long

rotations, however, represent potential habitat for the species. Recent range extensions in the north and east (e.g., Ontario, New York; see Distribution: historical changes, above) indicate that the Cerulean Warbler is capable of reoccupying areas when suitable habitat structure develops.

(2) Fragmentation and increasing isolation of remaining mature deciduous forest. Perhaps more than most North American birds, the Cerulean Warbler is sensitive to landscape-level changes in habitat. Minimum tract size in the western part of the breeding range is apparently larger than that in the eastern portion (Robbins et al. 1989, Oliarnyk 1996, Hamel et al. 1998a). Occupied forest patches in the Mississippi Alluvial Valley had lower proportions of surrounding cropland at distances of 2.4–8 km from breeding habitat than did patches on which Cerulean Warblers did not occur (Hamel et al. 1998a).

The threat of habitat destruction may be related to the proportion of the landscape that is forested. In largely forested areas (see percolation theory, Milne 1991), forest-harvest activities appear not to affect the birds (Oliarnyk 1996). In primarily agricultural landscapes, forest clearing may present a serious threat to the species (Hamel et al. 1998a). Research is needed: (a) to identify at what point a landscape becomes too fragmented for these birds (see Hamel et al. 1998a, Hamel 1998b); (b) to compare reproductive success and other demographic parameters in areas of the range representing different levels of fragmentation; and (c) to determine land-management activities compatible with producing source populations (those that can colonize new areas).

(3) Change to shorter rotation periods and even-aged management, so that less deciduous forest habitat reaches maturity. As land uses become more competitive with each other on a regional scale, pressure to achieve particular rates of return on investment increases. Such pressure has caused many forest landowners to intensify their management activities by shortening rotations. Management practices that do not include some large sawtimber production as part of the later structural stages of stand development will not provide habitats for Cerulean Warblers.

(4) Loss of key tree species, especially oaks from oak wilt and gypsy moths, sycamores from a fungus, elms from Dutch elm disease, and American chestnuts from chestnut blight. The wide variety of habitats in which Cerulean Warblers breed, and the high densities apparently present in the past in the Mississippi Alluvial Valley on flat terrain at low elevation and Cumberland Mtns. at considerably higher elevation and steeper terrain indicates that this species can use a great variety of tree species for its breeding habitats (see Oliarnyk 1996, Hamel 2000).

WINTER HABITAT. Winter-habitat destruction is an important concern as well. Present understanding of habitat modification in the montane subtropical forest

where Cerulean Warbler winters suggests that conversion of primarily forested landscapes to pastures and farms is proceeding rapidly (Terborgh 1989, Robbins et al. 1992). Further conversion of primary forest lands to other uses is inevitable; e.g., Cerulean Warblers occur in winter at the same elevation where coca is grown; coca production is increasing in response to increase in demand for cocaine and crack among North American and European populations. As coca production increases, land-use changes to support its cultivation are inevitable. These probably will have a detrimental effect on Cerulean Warbler habitat. As attempts to eradicate coca plants are employed, they will also have detrimental effects on forests and mixed-species flocks in Cerulean Warbler winter habitats (Robinson et al. 1988). Information on Cerulean Warblers in winter is limited and contradictory, but suggests that: (1) these birds do not persist when the great majority of their limited winter habitat has been converted to other land uses (Robbins et al. 1992), and (2) they can use shade-coffee plantations, allowing them to persist in some agricultural areas (Jones and Robertson 1998).

MIGRATORY-STOPOVER HABITAT. The extent to which the species is limited by migratory-stopover habitats is unclear. Resting locations close to the coast may provide the measure of difference in survivorship for inexperienced migrants or for more experienced birds that encounter adverse weather while crossing the Gulf of Mexico (Moore and Simon 1992).

Disturbance at nest and roost sites. Unknown.

Direct human/research impacts. Unknown.

MANAGEMENT

Conservation status. Hamel (2000) summarized legal status of the species. On its breeding grounds, not considered Endangered in any region; listed as Threatened in 2 states; considered in need of some less restrictive protection in 13 states and 1 Canadian province.

Measures proposed and taken. Current activities for Cerulean Warblers include planning projects that use estimates of minimum tract size for the species as criteria for habitat acquisition and protection (Mueller et al. 1999); land protection and acquisition projects managed by the Tennessee Wildlife Resources Agency and Partners in Flight (Southeastern Working Group) that are designed to increase the amount of forest in certain areas such as the Interior Low Plateaus and Coastal Plain of Tennessee (R. P. Ford pers. comm.); and the Cerulean Warbler Atlas Project, an information-gathering project managed by scientists at the Cornell Laboratory of Ornithology (Barker and Rosenberg 1997).

SILVICULTURE OF BREEDING HABITAT. No specific experimentation on silviculture for the species has been attempted. Current work in the Mississippi Alluvial Valley, the Cumberland Mtns. of Tennessee, and

Ontario is likely to result in some management suggestions. Some guidelines for land managers on effective silviculture of breeding habitat have been suggested by Kahl et al. (1985), Hands et al. (1989), Hamel (1992), Robbins et al. (1992), and Flaspohler (1993).

Simple protection and silviculture of breeding habitats are the primary tools available to an individual land manager. For Cerulean Warblers, silviculture of breeding habitat means management for premium quality sawtimber products, involving long rotations with intermediate treatments directed toward fostering long boles, large diameters, and full canopies of dominant trees. It likely means strategies to produce a varied 3-dimensional stand with extensive development of vertical diversity, such as tall canopies of dominants and canopy emergents towering above midstory or intermediate trees. Conditions such as these can be produced by uneven-aged management of extensive stands, and by old-growth or wilderness management techniques that foster an extensive network of canopy gaps. Other strategies, including even-aged management with long rotations, may also be effective.

Landscape context of the managed stands is an important silvicultural consideration because the species is area-sensitive, found only in the large tracts. Future policy and land-use planning decisions that favor the existence of large tracts of forest, or landscapes that are primarily forested, will aid these birds (Mueller et al. 1999). Where these landscapes can be self-sustaining, i.e., maintained by their own production, Cerulean Warblers will likely prosper. Where extensive economic subsidy is required to maintain the landscape in primarily forested condition, the future of the species would seem more tenuous.

Forest stand-management techniques that result in "ideal" or even "high quality" Cerulean Warbler habitat cannot yet be stated. When developed and tested, they will include parameters like length of rotations, average height, diameter and density of canopy trees, tree-species composition, extent of ground and mid-story vegetative cover, minimum forest-tract size, and amount of canopy closure. Kahl et al. (1985) have made specific proposals, applicable in Missouri. Because of the variety of deciduous-forest habitats occupied by Cerulean Warblers, it is premature to assume that the correlates of occurrence found by Kahl et al. (1985) in Missouri apply to the habitats of this bird throughout its range or that these are the values that will provide habitat in which the species reproduces most successfully. Specific manipulative research on habitats is necessary to make such determinations with assurance.

WINTER-HABITAT MANAGEMENT. Little known; needs study. Suggestions that only primary forest is adequate for this warbler (Robbins et al. 1992), if correct, mean that only protection of intact ecosystems will assure the future of the species. Intense pressure

from growing human populations limits the extent of such forest on the winter grounds. Cerulean Warblers have been found in other habitats (D. Buehler pers. comm.). Consequently, efforts to reforest now and in the future will likely be required to maintain nonbreeding habitats for Ceruleans. Encouragement of economically viable crops from primary or "altered" primary forest may offer a means to maintain forest cover useful to this species. Such an approach has been successful in maintaining habitats for other species elsewhere in the tropics, e.g., where Brazil nuts, shade coffee, or other crops have been grown.

Effectiveness of measures. No published results describe the response of Cerulean Warblers to purposefully conducted management activities.

APPEARANCE

In addition to distinct Juvenal, First Basic, First Alternate, and later, Definitive Basic and Alternate plumages (Dunn and Garrett 1997), it is possible that Second Basic and Second Alternate Plumages also could be described. However, the necessary material of known age does not currently exist. Distinct variation in plumage with age cannot be distinguished as yet from individual variation in plumage. Color terminology in the following is from Smithe (1975), and molt and plumage descriptions follow Dunn and Garrett (1997), Dwight (1900) and Pyle (1997), unless otherwise stated.

MOLTS AND PLUMAGES

Hatchlings. Hatchlings have light mouse gray to light drab natal down; bill, legs and feet pinkish buff (Oberholser and Kincaid 1974).

Juvenal plumage. Prejuvenal molt complete, begins in the nest, completed shortly after fledgling. This plumage is described by Oberholser and Kincaid (1974: 756), as "upper surface hair brown, very slightly washed with olive, broad median stripe on pileum dull brownish; sides of head buffy white, long post-ocular streak hair brown . . . lower surface dull buffy white."

Following description comes primarily from 2 U.S. National Museum specimens, no. 89243, Wabash, IL, 20 May 1878, labeled male juvenile; and no. 82940, Mt. Carmel, IL, 27 Jul 1875, no sex or age listed on the label. The latter specimen is molting from the Juvenal to Basic I plumage. Juvenal plumage is a buffy gray color corresponding to dark Drab or grayish horn above. Below paler and whitish, the plumage has a slight drab gray cast (no. 89243) or yellowish cast (no. 82940). The gray color is darkest on the crown and wings and tail. Each specimen has a median crown stripe that extends from the bill to the nape, a pale superciliary line, and 2 buffy wing-bars. Remiges are Sepia, Hair Brown, or Vandyke Brown. Inner margins

of remiges are white as in older individuals. Leading edge of flight feathers, including alula, of 1 specimen (no. 89243) appears variously as Pratt's Payne's Gray or Light Sky Blue or as Citrine or Smoke Gray, depending on light. Edge of flight feathers, including alula, of the other specimen (no. 89240) appears Citrine or Smoke Gray, depending on the light. This plumage is replaced by Basic I plumage soon after the birds leave the nest Pyle (1997) provides useful criteria for aging and sexing the young birds.

Basic I plumage. Prebasic I molt partial; includes body-feathers, usually all median and greater wing-coverts, and often the greater alula, but no remiges or rectrices (Pyle 1997). Prebasic I molt occurs very shortly after the fledglings leave the nest and is complete by Jul or Aug of their natal year. This plumage may be acquired before the fledglings become independent of their parents, which is earlier than Dwight (1900) believed. Unique characteristics of this plumage are well described by Pyle (1997).

MALE. Remiges Vandyke Brown edged grayish-green, rectrices Dusky Brown with pale Sky Blue cast to the leading edges. Alula and primary-coverts brownish with little to no blue edging. Upperparts greenish (Olive Yellow, Lime Green, or Parrot Green) washed with blue or bluish (Pratt's Payne's Gray) with a greenish wash. One very bluish individual (USNM no. 340979) had Sky Blue back feathers with edges that appeared Lime Green, Bunting Green, Paris Green, or Apple Green. Usually the crown is more greenish and the rump less so than the back. The rump may be Sky Blue. Some blackish streaking on the back extending to the back of the crown. This is variable among individuals. Some individuals have only 1 or 2 streaked feathers, others are prominently streaked. Underparts white with variable amount of yellowish cast (Olive-Yellow or Sulphur Yellow), more pronounced in first than in later Basic plumages. Breast band absent or restricted to sides of breast. Two white wing-bars. White patches in 5 outer rectrices. Some blurry dusky streaks on the sides and flanks. Superciliary line whitish washed with Sulphur Yellow. Usually more extensive and prominent behind the eye, the extent of this line is variable; in some individuals, the portion anterior to the eye is much more prominent than in others. The appearance of the leading edge of the remiges is also quite variable. All edges in some individuals appear quite greenish (Citrine). In others the edges of the inner primaries are greenish and those of the outer 2 or 3 primaries almost Sky Blue. Others have base of the edges Sky Blue with greenish tips. Others have primarily Sky Blue edges. Edges of remiges of each bird further vary depending upon the angle of the light in which they are examined.

FEMALE. The most greenish and yellowish plumage, with little if any bluish. Remiges Hair Brown or Vandyke Brown, edged greenish yellow or Citrine, alula brownish, sometimes with buff edging. Primary-

coverts brown, edged greenish. Two white wing-bars. Rectrices Sepia or Dark Neutral Gray. Upperparts uniformly Bunting Green, with no blue cast, and without streaking. Crown and back are unstreaked, and usually the same color; when they contrast with each other, the crown is darker, almost Paris Green. Underparts variably yellowish (Olive-Yellow, Sulphur Yellow, Straw Yellow), or dull whitish washed pale yellowish, especially on sides of throat, breast, and flanks. Flanks diffusely streaked Grayish Olive. Superciliary line yellowish. Postocular stripe grayish and ear-coverts pale grayish, washed yellow. Variable amount of white on inner webs of rectrices.

Alternate I plumage. Prealternate I molt takes place on the winter grounds, probably during Feb and Mar, and includes most of the head and body plumage, but not the remiges. Pyle (1997) indicates that occasionally 1 or 2 central rectrices are replaced in this and later Prealternate molts. Virtually all the birds in a sample of nearly 100 birds captured in the breeding season in Tennessee and Arkansas have fresh rectrices, indicating that these feathers were replaced during spring (PBH).

MALE. Sky Blue above with some black streaks on the back and uppertail-coverts, and concealed black patches on the sides of the crown. A white superciliary line is present behind, and often reaching anterior to, the eye. Auricular patch is Medium Plumbeous or Medium Neutral Gray. Underparts are white with a narrow black or Blue Black band across the throat and black streaks along the sides of the breast and flanks. Undertail-coverts extend beneath the tail virtually as far, in the closed tail, as the white patches in the 5 outer rectrices. Remiges Vandyke Brown and rectrices Dusky Brown with greenish outer edges. Remiges contrast noticeably with the blacker tertials and scapulars. Remiges have extensive white patches on the inner webs. White, more or less squarish sub-terminal spots on inner webs of all but the central rectrices; the latter may have white edges to inner webs (Oberholser and Kincaid 1974). Spots decrease in size from outer to inner rectrices and are smaller in this plumage than in later ones (PBH). Primary-coverts contrast noticeably with the secondary-coverts; they are entirely dusky or, when a contrasting color is present on the leading edge, it is greenish. Greater and median wing-coverts tipped white, forming 2 white wing-bars.

FEMALE. Remiges Hair Brown or Vandyke Brown, edged Citrine or greenish yellow, alula brown. Upperparts Bunting Green. Crown (appears Paris Green, Emerald Green, Cyan, Turquoise Green, or Peacock Green depending on the light) contrasts with nape and back more than in Basic I plumage; however, individual variation in this feature is great. Females in all plumages lack the black centers on the feathers of the back and of the side of the crown possessed by the males. Underparts whitish with variable amount of yellowish (Sulphur Yellow), with suffused streaks

on flanks. Superciliary line white. Auriculars Olive-Gray or Smoke Gray. Two white wing-bars. White spots in rectrices as in male, but are smaller on each feather, and may occur only on outer 4 rectrices. Overall similar to Definitive Alternate female except often more yellowish below and more greenish above, but considerable variation, with some appearing as bluish above as adults. Best distinguished from adults by duller, more worn flight feathers, and by primary-coverts without blue-green edges.

Definitive Basic plumage. Definitive Prebasic molt complete, occurs after breeding during summer, presumably in Jul-Aug, depending on the individual and its breeding success that season.

MALE. Later Basic plumages of males are generally similar to Alternate plumages in color and pattern. Accurately aged individuals in older than Basic I plumage have not been examined, so the complete sequence of plumages cannot yet be described. However, second and subsequent Basic plumages appear to be more variable than second and subsequent Alternate plumages. Males in second and subsequent Basic plumages may or may not have extensive white superciliary lines, and the number of feathers on the back with black streaks is also variable. Usually, birds in Basic plumage have a narrower breast band than do those in subsequent Alternate plumages (band often partly veiled by white feather tips). Nape is slightly grayer than the crown or the back, and the back is slightly grayer than the rump. In some fall specimens in older than Basic I plumage, some of the blue feathers on the back are edged with pale greenish (Bunting Green, Lime Green, Paris Green or Apple Green), reminiscent of the greenish backs of the birds in their Basic I plumage.

FEMALE. Remiges Hair Brown, rectrices Sepia, edged with Sky Blue or Light Sky Blue. Alula Dusky Brown or Raw Umber with bluish edges. Upperparts greenish, unstreaked, with Cyan cast, especially on the rump. Crown and back contrast less than in corresponding Alternate plumages, but this is very variable. Underparts yellowish. Supercilium white. Two white wing-bars. White in tail probably more extensive than in Basic I, but this is variable. Overall similar to Definitive Alternate female except often more yellowish below and more greenish above.

Definitive Alternate plumage. Definitive Prealternate molt partial; occurs on the winter grounds probably during Feb and Mar, and includes most of the head and body plumage, but not the remiges. See Alternate I plumage.

MALE. Top of head (down to and including submustachial region) bluish, becoming bright Cerulean Blue on forehead and crown, and Sky Blue on remaining upperparts and rump; ear-coverts grayish, darker than in Alternate I. Loes and eye-line slaty and sides of crown (occasionally mid-crown) indistinctly and variably streaked with black. Some old males have two

distinct black patches on the side of the crown thus almost creating a Cerulean Blue median crown stripe bordered by black and the black bordered by a Cerulean Blue supercilium. Occasionally shows white feathering in postocular region. Back heavily streaked with black, and uppertail-coverts with broad black centers. Considerable variation in brightness of blue on crown and upperparts. Chin and throat white. Narrow Black or Blue Black band (width variable) across upper breast often slightly veiled whitish. Remaining underparts white with bold deep blue-gray to blackish streaking (may be veiled whitish) on sides and flanks. Lesser wing-coverts bluish; median and greater wing-coverts blackish edged blue-gray on outer web and tipped white, forming 2 wing-bars. Primary-coverts and remiges Sepia or blackish narrowly edged Sky Blue or Light Sky Blue on outer web, with tertials margined blue-gray and edged white. Rectrices Blackish Neutral Gray narrowly edged blue-gray with white subterminal patches on inner webs of outer 5 pairs.

Males in later, probably Definitive Alternate, plumage differ from those in Alternate I plumage as follows. The white superciliary line is typically not present, although a small number of white-tipped feathers may occur posterior to the eye. These are usually visible only in the hand. The auricular patch is darker, blackish rather than Medium Plumbeous or Medium Neutral Gray. The throat band is darker, including black and Blue Black feathers, and may possibly be wider. Remiges and rectrices are blackish and do not contrast noticeably with the scapulars. These feathers are edged with Sky Blue or Light Sky Blue, not greenish as in the younger, second-year (SY) birds. Primary-coverts are blackish and may have blue edges. In either case, they do not contrast with the secondary-coverts.

It is uncertain to what extent additional differences between SY and after-second-year (ASY) individuals exist, although the amount of white in the tail, as well as the intensity of the blue in the upperparts, may increase with age.

FEMALE. Crown Cyan with slightly greenish (Paris Green) tinge. Remaining upperparts Parrot Green to Cyan with slight greenish tinge and unstreaked. Supercilium (prominent behind eye) whitish or with slight Sulphur Yellow tinge. White arc under eye. Loes and indistinct eye-line gray. Ear-coverts pale Olive-Gray or Smoke Gray. Underparts dull whitish with variable Sulphur Yellow wash on sides of throat and upper breast. Blurred grayish or gray-green streaking on sides and flanks. Remiges Dusky Brown to Raw Umber and primary-coverts similar, edged Sky Blue on outer web. Median and greater wing-coverts tipped white, forming 2 wing-bars. Rectrices Sepia, narrowly edged Cyan on outer web and with white subterminal patches on inner webs of outer 4 or 5 pairs.

Crown contrasts with the back more strongly in Definitive Alternate female than in Alternate I.

Upperparts have a more Cyan cast than in younger birds, but variation among individual females is very great. Upperparts in Alternate plumages are more bluish than in corresponding Basic plumages. Underparts vary from white to yellowish white. Because underparts coloration appears to vary distinctly with light conditions, it is very difficult to age a female Cerulean accurately in the field. In the hand, age differences parallel those of the male, primarily involving the remiges and rectrices, which are browner and more dusky in SY birds in Alternate I plumage than in ASY birds, and possess more greenish edges in SY birds and bluish white (Light Sky Blue) edges in older individuals.

BARE PARTS

Bill. Adult males: bill black with varying amounts of Plumbeous or Pratt's Payne's Gray on the lower mandible; adult females: bill dusky with some brown on the lower mandible (PBH). Fledglings: dull brown; hatchlings: pinkish buff (Oberholser and Kincaid 1974).

Iris. Breeding adults: brown or reddish brown (PBH). Fledglings: dark brown; hatchlings: black (Oberholser and Kincaid 1974).

Legs and feet. Breeding adults: black, slaty, or dark horn, with soles of breeding males either buffy gray or pale Plumbeous or Pratt's Payne's Gray (PBH). Fledglings: dull brown; hatchlings: pinkish buff (Oberholser and Kincaid 1974).

MEASUREMENTS

LINEAR

Linear measurements (see Table 1) are presented by Hamel (2000). Sexes differ ($p < 0.001$) in wing-chord and tail length. Values for other measures are similar between the sexes.

MASS

Mass is summarized in relation to fat class in Hamel 2000. Among migrants of unspecified fat class at the University of Southern Mississippi banding station, 33 females averaged $8.04 \text{ g} \pm 0.16 \text{ SE}$, similar to the mass of 36 males which averaged $8.35 \text{ g} \pm 0.19$ (J. Clark pers. comm.). Among birds of unspecified fat class captured at Powdermill Nature Reserve Banding Station, in w. Pennsylvania, 34 females averaged $8.83 \text{ g} \pm 0.10 \text{ SE}$, significantly less than 47 males, which averaged $9.28 \text{ g} \pm 0.09 \text{ SE}$ (M. Niedermeier pers. comm.).

PRIORITIES FOR FUTURE RESEARCH

Numerous biologically interesting and relevant questions remain about the species. Hamel (2000), suggesting that conservation and management research

Table 1. Linear measurements (mm) of the Cerulean Warbler, from specimens in the U.S. National Museum. Data given as mean \pm SE. From Hamel 2000.

	Male $n = 23$	Female $n = 22$
Wing-chord	64.5 ± 1.26	62.3 ± 0.29
Tail length	42.4 ± 0.25	40.9 ± 0.27
Exposed culmen	9.62 ± 0.13	9.56 ± 0.10
Bill width	3.62 ± 0.03	3.57 ± 0.06
Bill height	3.43 ± 0.04	3.52 ± 0.04
Diagonal of tarsus	15.7 ± 0.14	14.8 ± 0.20
Middle toe	11.5 ± 0.38	11.1

needs be addressed first, grouped needed research activities on this species into 3 priority categories.

High-priority activities.

(1) Determine winter survivorship, habitat distribution, and relative abundance by habitat in forests on the east slope of the Andes and elsewhere in northern South America.

(2) Determine demography or population dynamics of the species in different parts of its range and under different silvicultural treatments of breeding habitats.

(3) Identify landscape characteristics of Cerulean Warbler occurrence, area-sensitivity, and distribution in relationship to forest fragmentation.

(4) Identify preferred vegetation structure within habitats.

(5) Determine response of populations to land-management activities.

Moderate-priority activities.

(6) Determine silvicultural activities that create good habitat for Cerulean Warblers.

(7) Test applicability of habitat models developed in 1 area to Cerulean Warbler habitats in other parts of the breeding or winter range.

(8) Test hypothesis that Cerulean Warblers are better censused by off-road than roadside counts.

(9) Develop survey techniques applicable in different physiographic situations.

(10) Summarize existing Breeding Bird Census data set.

Lower-priority activities.

(11) Determine migratory movements, stopover sites, stopover biology, and timing of migration.

(12) Determine breeding social system and local distribution of individuals.

(13) Clarify historical distribution of known breeding habitats.

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REFERENCES

- Adams, R. J., Jr. 1991. Cerulean Warbler *Dendroica cerulea*. Pp. 424–425 in The atlas of breeding birds of Michigan (R. Brewer, G. A. McPeck, and R. J. Adams, Jr., eds.). Michigan State Univ. Press, East Lansing.
- Allen, J. A. 1907. Berlepsch and Stolzmann on birds from Peru. *Auk* 24: 361.
- American Ornithologists' Union. 1998. Check-list of North American birds. 7th ed. Am. Ornithol. Union, Washington, D.C.
- Audubon, J. J. 1856. The birds of America. Vol. II. V. G. Audubon, New York.
- Averill, C. K. 1920. Migration and physical proportions: a preliminary study. *Auk* 37: 572–579.
- Bagg, E. 1900. Bird news from central New York. *Auk* 17: 177–178.
- Banks, R. C., and J. Baird. 1978. A new hybrid warbler combination. *Wilson Bull.* 90: 143–144.
- Bannon, P., and M. Robert. 1996. Cerulean Warbler. Pp. 910–911 in The breeding birds of Quebec: atlas of the breeding birds of southern Québec (J. Gauthier and Y. Aubry, eds.). Assoc. québécoise des groupes d'ornithologues, Prov. of Québec Soc. for the protection of birds, Can. Wildl. Serv., Environ. Canada, Québec Region, Montréal.
- Barker, S., and K. Rosenberg. 1997. Cerulean Warbler atlas project (CEWAP). Cornell Lab. of Ornithol., Ithaca, NY.
- Bent, A. C. 1953. Life histories of North American wood warblers. Pt. 1. *U.S. Natl. Mus. Bull.* 203.
- Bohlen, H. D. 1989. The birds of Illinois. Indiana Univ. Press, Bloomington.
- Bonhote, J. L. 1903. Bird migration at some of the Bahama lighthouses. *Auk* 20: 169–179.
- Brewster, W. 1875. Some observations on the birds of Ritchie County, West Virginia. *Ann. Lyc. Nat. Hist. New York* 11: 129–146.
- Brodkorb, P. 1929. Notes from Berrien County, Michigan. *Auk* 46: 397–398.
- Bullis, H. R., Jr. 1954. Trans-Gulf migration, spring 1952. *Auk* 71: 298–305.
- Chapman, F. M. 1917. The distribution of birdlife in Colombia: a contribution to a biological survey of South America. *Bull. Am. Mus. Nat. Hist.* 36: 1–729.
- Coues, E. 1878. Birds of the Colorado valley. *U.S. Geol. Surv. Territ. Misc. Publ.* 11.
- Crawford, R. L. 1980. Wind direction and the species composition of autumn TV tower kills in northwest Florida. *Auk* 97: 892–895.
- Cyr, A., and J. Larivée. 1995. Atlas saisonnier des oiseaux du Québec. Société de Loisir ornithologique de l'Estrie, Univ. of Sherbrooke Press, Sherbrooke, Québec.
- Eagles, P. F. J. 1987. Atlas of the breeding birds of Ontario (M. D. Cadman, P. F. J. Eagles, and F. M. Helleiner, eds.). Univ. of Waterloo Press, Waterloo, ON.
- DeGraaf, R. M., and J. H. Rappole. 1995. Neotropical migratory birds: natural history, distribution, and population change. Comstock Publ. Assoc., Ithaca, NY.
- Dunn, J. L., and K. L. Garrett. 1997. A field guide to warblers of North America. Houghton-Mifflin Co., Boston, MA.
- Dwight, J., Jr. 1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. N.Y. Acad. Sci.* 13: 73–360.
- Fjeldså, J., and N. Krabbe. 1990. Birds of the high Andes. *Zool. Mus., Univ. of Copenhagen and Apollo Books, Svendborg, Denmark.*
- Flaspholer, D. 1993. Wisconsin Cerulean Warbler recovery plan. Wisconsin Endangered Resour. Rep. 101. Wisconsin Dep. of Nat. Resour., Madison.
- Friedmann, H. 1963. Host relations of the parasitic cowbirds. *U.S. Natl. Mus. Bull.* 233.
- Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. *Smithson. Contrib. Zool.* no. 235.
- Granlund, J., G. A. McPeck, R. J. Adams, P. C. Chu, J. Reinoehl, et al. 1994. The birds of Michigan. Indiana Univ. Press, Bloomington.
- Gray, G. W. 1924. The Cerulean Warbler in Dutchess County, NY. *Auk* 41: 161–162.
- Hagan, J. M., III, and D. W. Johnston, eds. 1992. Ecology and conservation of Neotropical migrant landbirds. *Smithson. Inst. Press, Washington, D.C.*
- Hamel, P. B. 1992. Cerulean warbler, *Dendroica cerulea*. Pp. 385–400 in Migratory nongame birds of management concern in the Northeast (K. J. Schneider and D. M. Pence, eds.). U.S. Fish Wildl. Serv., Newton Corner, MA.
- Hamel, P. B. 1998a. Rangewide variation in Cerulean Warbler ecology. Symposium, N. Am. Ornithol. Conference, St. Louis, MO, 6–12 Apr 1998.
- Hamel, P. B. 1998b. Landscape and habitat distribution of the Cerulean Warbler *Dendroica cerulea* in extensively fragmented Mississippi alluvial valley, USA. Abstract of poster, 22nd Int. Ornithol. Congr., Durban, South Africa, 16–22 Aug 1998. *Ostrich* 69: 286.
- Hamel, P. B. 2000. Cerulean Warbler status assessment. U.S. Fish Wildl. Serv., Minneapolis, MN.
- Hamel, P. B., R. J. Cooper, and W. P. Smith. 1998a. The uncertain future of Cerulean Warblers in the Mississippi Alluvial Valley. Pp. 95–108 in Proceedings of the Delta Conference, 13–16 Aug 1996, Memphis, TN. U.S. Dep. Agric., Nat. Resour. Conservation Serv., Madison, MS.
- Hamel, P. B., W. P. Smith, R. J. Cooper, and C. A. Woodson. 1994. Empirical prediction of habitat variables of cerulean warblers in bottomland hardwood forests. Abstract. Paper presented at First N. Am. Ornithol. Conference, Missoula, MT, Jun 1994.
- Hamel, P. B., C. A. Woodson, and M. Staten. 1998b. Weather-caused population decline of Cerulean Warblers in Desha County, Arkansas. N. Am. Ornithol. Conference, St. Louis, MO, 6–12 Apr 1998.
- Hands, H. M., R. D. Drobney, and M. R. Ryan. 1989. Status of the Cerulean Warbler in the north-central United States. *U.S. Fish Wildl. Serv., Twin Cities, MN.*
- Harrison, H. H. 1984. Wood warblers' world. Simon and Schuster, New York.
- Howell, A. H. 1924. Birds of Alabama. *Dep. Game Fish. of Alabama, Montgomery.*
- Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford Univ. Press, New York.
- Imhof, T. A. 1976. Alabama birds. 2nd ed. Univ. of Alabama Press, University.
- Jackson, J. A., ed. 1981. The "Mid-South bird notes" of Ben B. Coffey, Jr. *Spec. Publ. no. 1, Mississippi Ornithol. Soc., Mississippi State.*
- James, D. A., and J. C. Neal. 1986. Arkansas birds: their distribution and abundance. Univ. of Arkansas Press, Fayetteville.
- James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. *Ecology* 77: 13–27.
- Jones, J., and R. J. Robertson. 1997. Abstract 75: Winter ecology of the Cerulean Warbler in modified Venezuelan landscapes. Presented to the 115th stated meeting of the Am. Ornithol. Union, 13–16 Aug 1997. Minneapolis-St. Paul, MN.
- Jones, J., and R. J. Robertson. 1998. Cerulean Warblers in Venezuela: winter ecology and habitat use patterns. N. Am. Ornithol. Conference, St. Louis, MO, 6–12 Apr 1998.
- Kahl, R. B., T. S. Baskett, J. A. Ellis, and J. N. Burroughs. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. *Univ. Missouri-Columbia Agric. Exp. Stn. Res. Bull.* 1056.
- Leberman, R. C., and M. H. Clench. 1975. Bird-banding at Powdermill, 1974. Powdermill Nat. Reserve, Res. Rep. no. 35.
- Lehman, P. 1987. Immature Blackburnian and Cerulean warblers: a cautionary note. *Birding* 19: 22–23.
- Levine, E., ed. 1998. Bull's birds of New York State. Cornell Univ. Press, Ithaca, NY.
- Lynch, J. M. 1981. Status of the Cerulean Warbler in the Roanoke River basin of North Carolina. *Chat* 45: 29–35.
- Maurer, B. A. 1994. Geographical population analysis: tools for the analysis of biodiversity. Blackwell Scientific Publ., Oxford.
- Mengel, R. M. 1965. The birds of Kentucky. *Am. Ornithol. Union, Ornithol. Monogr.* 3.

- Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. Acad. of Nat. Sci. of Phila., Philadelphia, PA.
- Milne, B. T. 1991. Chapter 9. Lessons from applying fractal models to landscape patterns. Pp. 199-235 in *Quantitative methods in landscape ecology* (M. G. Turner and R. H. Gardner, eds.). Springer-Verlag, New York.
- Moore, F. R., and T. R. Simon. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pp. 345-355 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, eds.). Smithsonian Inst. Press, Washington, D.C.
- Moseley, E. L. 1947. Variations in the bird population of the north-central states due to climatic and other changes. *Auk* 64: 15-35.
- Mueller, A. J., C. R. Loesch, and D. J. Twedt. 1999. Development of management objectives for breeding birds in the Mississippi Alluvial Valley. Proc. Partners in Flight International Workshop, Cape May, NJ, 1-5 Oct 1995.
- Murray, B. G., Jr., and F. B. Gill. 1976. Behavioral interactions of Blue-winged and Golden-winged warblers. *Wilson Bull.* 88: 231-254.
- Nicholson, C. P., and D. A. Buehler. 1998. Nesting ecology of the Cerulean Warbler in the Cumberland Mountains of Tennessee. *N. Am. Ornithol. Conference*, St. Louis, MO, 6-12 Apr 1998.
- Oberholser, H. C., E. B. Kincaid, Jr. 1974. *The bird life of Texas*. Vol. 2. Univ. of Texas Press, Austin.
- Oliarnyk, C. J. 1996. Habitat selection and reproductive success in a population of Cerulean Warblers in southeastern Ontario. Master's thesis, Queen's Univ., Kingston, ON.
- Oliarnyk, C. J., and R. J. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. *Wilson Bull.* 108: 673-684.
- Ouellet, H. 1967. The distribution of the Cerulean Warbler in the province of Quebec, Canada. *Auk* 84: 272-274.
- Parker, T. A., III. 1994. Habitat, behavior, and spring migration of Cerulean Warbler in Belize. *Am. Birds* 48: 70-75.
- Parkes, K. C. 1978. Still another parulid intergeneric hybrid (*Mniotilta* × *Dendroica*) and its taxonomic and evolutionary implications. *Auk* 95: 682-690.
- Peck, G., and R. James. 1987. Breeding birds of Ontario: nidology and distribution. Vol. 2: Passerines. *R. Ontario Mus. Life Sci. Misc. Publ.*, Toronto.
- Peterjohn, B. G. 1989. *The birds of Ohio*. Indiana Univ. Press, Bloomington.
- Peterjohn, B. G., and D. L. Rice. 1991. *The Ohio breeding bird atlas*. Ohio Dep. Nat. Res., Columbus.
- Peterjohn, B. G., J. R. Sauer, and C. S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pp. 3-39 in *Ecology and management of Neotropical migratory birds* (T. E. Martin and D. M. Finch, eds.). Oxford Univ. Press, New York.
- Peterson, R. A. 1995. *The South Dakota breeding bird atlas*. S. Dakota Ornithol. Union, Aberdeen.
- Pulich, W. M. 1988. *The birds of north central Texas*. Texas A&M Univ. Press, College Station.
- Pyle, P. 1997. *Identification guide to North American birds*. Part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. *A guide to the birds of the West Indies*. Princeton Univ. Press, Princeton, NJ.
- Ridgely, R. S., and P. J. Greenfield. In press. *The birds of Ecuador*. Vol. 1: status, distribution and taxonomy. Cornell Univ. Press, Ithaca, NY.
- Ridgely, R. S., and J. A. Gwynne, Jr. 1989. *A guide to the birds of Panama, with Costa Rica, Nicaragua, and Honduras*. 2nd ed. Princeton Univ. Press, Princeton, NJ.
- Ridgely, R. S., and G. Tudor. 1989. *The birds of South America*. Vol. 1: the oscine passerines. Univ. of Texas Press, Austin.
- Ridgway, R. R. 1889. *The ornithology of Illinois*. Pt. 1: descriptive catalogue. State Lab. of Nat. Hist., Nat. Hist. Surv. of Illinois, Springfield.
- Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. *Wildl. Monogr.* 103.
- Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pp. 549-562 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III, and D. W. Johnston, eds.). Smithsonian Inst. Press, Washington, D.C.
- Robbins, M. B., and D. A. Easterla. 1991. *Birds of Missouri: their distribution and abundance*. Univ. of Missouri Press, Columbia.
- Roberson, D. 1980. *Rare birds of the west coast of North America*. Woodstock Publ., Pacific Grove, CA.
- Robinson, J. C. 1990. *An annotated checklist of the birds of Tennessee*. Univ. of Tennessee Press, Knoxville.
- Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995a. Chapter 15. Ecology and behavior of cowbirds and their impact on host populations. Pp. 428-460 in *Ecology and management of Neotropical migratory birds* (T. E. Martin and D. M. Finch, eds.). Oxford Univ. Press, New York.
- Robinson, S. K., J. Terborgh, and J. W. Fitzpatrick. 1988. Habitat selection and relative abundance of migrants in southeastern Peru. Pp. 2298-2307 in *Acta XIX Congress. Int. Ornithol.* (H. Ouellet, ed.). Univ. of Ottawa Press, Ottawa, ON.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995b. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Robinson, W. D. 1996. *Southern Illinois birds*. Southern Illinois Univ. Press, Carbondale and Edwardsville.
- Salvin, O., and F. D. Godman. 1879-1904. *Biol. Cent.-Am. Aves*. Vol. 1.
- Sample, B. E., R. J. Cooper, and R. C. Whitmore. 1993. Dietary shifts among songbirds from a diflubenzuron-treated forest. *Condor* 95: 616-624.
- Sauer, J. R. 1993. Monitoring goals and programs of the U.S. Fish and Wildlife Service. Pp. 245-251 in *Status and management of neotropical migratory birds*; 21-25 Sep 1992; Estes Park, CO (D. M. Finch and P. W. Stangel, eds.). U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. RM-229, Fort Collins, CO.
- Smith, W. P., P. B. Hamel, and R. P. Ford. 1996. Mississippi Alluvial Valley forest conversion: implications for eastern North American avifauna. Proc. 1993 Annu. Conf. Southeast Assoc. Fish Wildl. Agencies 47: 460-469.
- Smithe, F. B. 1975. *Naturalist's color guide*. Am. Mus. of Nat. Hist., New York.
- Spector, D. A. 1992. Chapter 6. Wood-warbler song systems: a review of Paruline singing behaviors. Pp. 199-238 in *Current ornithology*. Vol. 9 (D. M. Power, ed.). Plenum Press, New York.
- Stevenson, H. M., and B. Anderson. 1994. *The birdlife of Florida*. Univ. Press of Florida, Gainesville.
- Stiles F. G., and A. F. Skutch. 1989. *A guide to the birds of Costa Rica*. Cornell Univ. Press, Ithaca, NY.
- Taylor, W. K., and B. H. Anderson. 1973. Nocturnal migrants killed at a central Florida TV tower; autumns 1969-1971. *Wilson Bull.* 85: 42-51.
- Terborgh, J. 1989. *Where have all the birds gone?* Princeton Univ. Press, Princeton, NJ.
- Thompson, M. C., and C. Ely. 1992. *Birds in Kansas*. Vol. 2. Univ. Kans. Mus. Nat. Hist. Public Ed. Ser. no. 12.
- Turcotte, W. H., and D. L. Watts. 1999. *Birds of Mississippi*. Univ. Press of Mississippi, Jackson.
- Vanderah, G. C. 1993. Habitat preferences of the declining Cerulean Warbler. *Ill. Nat. Hist. Surv. Rep.* 320: 3-4.
- Vanderah, G. C., and S. K. Robinson. 1995. Habitat selection of Cerulean Warblers in Illinois. Abstract. Presented at 113th stated meeting, Am. Ornithol. Union, Cincinnati, Ohio, 15-19 Aug 1995.
- Veit, M., R. Robertson, and V. Friesen. 1998. Estimation of gene flow among populations of Cerulean Warbler *Dendroica cerulea* using molecular methods. Abstract of poster, 22nd Int. Ornithol. Congr., Durban, South Africa, 16-22 Aug 1998. *Ostrich* 69: 357.
- Verner, J., and M. F. Willson. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Am. Ornithol. Union Monogr.* 9.
- Villard, M.-A., and B. A. Maurer. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. *Ecology* 77: 59-68.
- Widmann, O. 1895a. Swainson's Warbler an inhabitant of the swampy woods of southeastern Missouri. *Auk* 12: 112-117.
- Widmann, O. 1895b. The Brown Creeper nesting in the cypress swamp of southeastern Missouri. *Auk* 12: 350-355.
- Widmann, O. 1897. The summer home of Bachman's Warbler no longer unknown. *Auk* 14: 305-309.
- Widmann, O. 1907. A preliminary catalog of the birds of Missouri. *Trans. Acad. Sci. St. Louis* 17: 1-296.
- Wiedenfeld, D. A., and M. G. Wiedenfeld. 1995. Large kill of Neotropical migrants by tornado and storm in Louisiana, April, 1993. *J. Field Ornithol.* 66: 70-80.
- Wilson, A. 1811. *American ornithology*. Vol. 3. Bradford and Inskeep, Philadelphia, PA.
- Wood, N. A. 1951. *The birds of Michigan*. Univ. Mich. Mus. Zool. Misc. Publ. no. 75.
- Woodward, R. L. 1997. Characterization and significance of song variation in the Cerulean Warbler (*Dendroica cerulea*). Master's thesis, Queen's Univ., Kingston, ON.

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