

Cerulean Warbler Reproduction, Survival, and Models of Population Decline

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ABSTRACT We present and compare demographic data for cerulean warblers (*Dendroica cerulea*) from 5 study sites across the range of the species from 1992 to 2006. We conducted field studies to collect data on daily nest survival, nest success, and young fledged per successful nest, and we used data to estimate fecundity. Daily nest survival, nest success, young fledged, and fecundity varied widely across the cerulean range and among years. Study sites in agriculture-dominated landscapes (Mississippi Alluvial Valley, IN, and MI, USA) had negative growth rates in all years monitored because measured values of nest success and young produced per successful nest were incapable of offsetting apparent mortality. Ontario (Canada) and Tennessee (USA) populations had greater nest success and fecundity but still appeared to be incapable of producing stable populations ($\lambda = 1$) under field-measured and assumed conditions. We had survival data only for one site (Ontario); thus, additional survival data are greatly needed to enable more reliable estimates of population growth. Conservation strategies for cerulean warblers in agriculture-dominated landscapes (e.g., Mississippi Alluvial Valley, IN, and MI) may require major landscape-level habitat reconfiguration to change agriculture-dominated landscapes to forest-dominated landscapes to increase fecundity. Conservation strategies in predominantly forested landscapes in the core of the range (e.g., TN) require a focus on minimizing habitat loss and developing management prescriptions capable of improving fecundity. In both cases, based on sensitivity and elasticity analyses, efforts to improve survival during the nonbreeding season would have the greatest positive effect on population growth. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):646-653; 2008)

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Nearctic–Neotropical migrant songbirds have evolved life-history strategies taking advantage of favorable conditions in temperate regions for reproduction while retreating to more favorable environs in the Tropics for the nonbreeding period. These strategies in part reflect the presumption that enhanced reproduction should be capable of offsetting the apparent survival cost of migrating long distances over unfamiliar pathways. Many migrant songbirds have undergone recent population declines documented by the North American Breeding Bird Survey (BBS; Sauer et al. 2006). Cerulean warbler (*Dendroica cerulea*) populations, for example, are declining at one of the greatest rates for Nearctic–Neotropical migrant songbirds and have been identified as a priority for conservation action (Robbins et al. 1992; Hamel 2000a, b; Hamel et al. 2004). Reliable estimates of population size and population trend for ceruleans are important to aid in development of appropriate conservation strategies. Because of declining populations, management attention has focused on identifying potential

limiting factors for ceruleans in terms of factors affecting reproduction or survival on the breeding grounds, during migration, and on the wintering grounds. A hierarchical analysis of BBS data estimated the rate of cerulean population decline at 2.89% per year from 1966 to 2006 (J. Sauer, United States Geological Survey, personal communication). The current population represents a >75% decline compared to the 1966 population. The BBS data may reflect changes in both habitat quantity (e.g., habitat loss from urbanization) and habitat quality (e.g., reduction in fecundity from fragmentation). However, BBS data analyses to date have not been able to discriminate between habitat quantity and habitat quality limitations for ceruleans.

The cerulean warbler life-history strategy includes limited fecundity for a songbird, raising one brood of typically 3–4 young per breeding season (Hamel 2000b). To balance this limited fecundity, survival may have to be greater than that reported for many other passerines that have larger clutch sizes or are capable of rearing multiple broods in one breeding season (Martin 1995). Cerulean migration may

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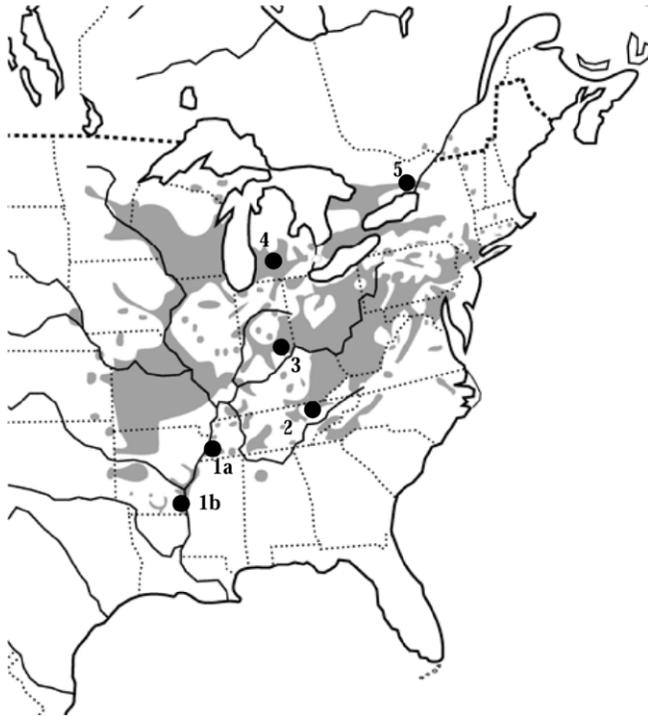


Figure 1. Range of the cerulean warbler (gray shading; adapted from Hamel 2000b) and study sites (1a = Mississippi Alluvial Valley–Meeman Shelby State Forest and Chickasaw National Wildlife Refuge, TN, USA; 1b = Desha Delta Hunt Club, AR, USA; 2 = Cumberland Mountains, TN, USA; 3 = Big Oaks National Wildlife Refuge, IN, USA; 4 = Southwestern MI, USA; and 5 = Queen’s University Biological Station, ON, Canada) used to monitor reproduction and survival and to model population change for various years (1992–2006).

contribute to population decline because migration pathways between breeding grounds in North America and wintering grounds in the Andes Mountains of South America may span up to 4,000 km one-way, longer than most other migrant passerines (Hamel 2000b). Increased migration distances may increase probability of mortality during this part of the life cycle.

Demographic modeling has been used recently to identify source–sink populations for a variety of Nearctic–Neotropical migrant songbirds (Donovan et al. 1995, Powell et al. 2000, Giocomo 2005, Knutson et al. 2006), including ceruleans in Ontario, Canada (Jones et al. 2004). We used a similar demographic modeling approach to ask 3 fundamental questions for cerulean warbler populations: 1) how do reproductive rates for cerulean warblers vary over space and time, 2) how do population growth rates (λ) vary over space and time, and 3) what are the implications of these results in terms of developing a cerulean warbler conservation strategy?

STUDY AREA

Our study area encompassed 5 sites across the range of cerulean warblers (Fig. 1). We chose each site opportunistically based on presence of cerulean populations that were sufficiently large to support the study and based on interests of individual investigators and support of project coopera-

tors. The Mississippi Alluvial Valley (MAV) site included Meeman Shelby Forest State Park, Shelby County, and Chickasaw National Wildlife Refuge, Lauderdale County in southwestern Tennessee (USA), and Desha Delta Hunt Club in southeastern Arkansas (USA). The site in the Cumberland Mountains of eastern Tennessee included Frozen Head State Park, Royal Blue Wildlife Management Area, and Sundquist Forest Wildlife Management Area. The Indiana (USA) site was Big Oaks National Wildlife Refuge (formerly the Jefferson Proving Grounds, United States Army). The Michigan site included Barry State Game Area, Barry County, and the Fort Custer United States Army National Guard Reservation in Kalamazoo County, both in southern Michigan, USA. The Ontario site was the Queen’s University Biological Station (QUBS), north of Kingston, in eastern Ontario, Canada. Forest types for the study sites encompassed the breadth of conditions that cerulean warblers occupy across the breeding range including bottomland hardwood forests along the Mississippi River, montane mixed mesophytic forests in the Cumberland Mountains of eastern Tennessee, mixed deciduous forests in Indiana and Michigan (oak [*Quercus* spp.], hickory [*Carya* spp.], black locust [*Robinia pseudoacacia*], black walnut [*Juglans nigra*], and black cherry [*Prunus serotina*]), and northern hardwood forests in Ontario. Landscape context varied as well, including isolated forest tracts in an agricultural or human-developed landscape in the MAV, Indiana, and Michigan, a mixed landscape with large forested tracts interspersed with openings (abandoned farms, beaver meadows, and dry ridges) in Ontario, and an extensively forested landscape (85% forest cover) in the Cumberland Mountains of Tennessee. Elevation and slopes varied greatly across sites. The MAV sites were slightly above sea level with little elevational relief, whereas other sites contained more rolling terrain, and the Cumberland Mountains sites had elevations up to 900 m and steep slopes. Predominant land uses included coal mining and forest management (Cumberland Mountains, TN) and agriculture (MAV, IN, and MI). The Ontario site was largely undisturbed, occupying late-stage successional habitat following abandonment of small-scale farming and selective logging >80 years ago. Human development was highly variable across sites; some sites were located adjacent to urban areas (e.g., Meeman Shelby is located outside Memphis, TN, and Fort Custer is adjacent to Battle Creek, MI), whereas other sites had much lower human populations (e.g., QUBS, Ontario). All sites were publicly owned except for the Desha Delta Hunt Club in Arkansas and QUBS.

METHODS

Monitoring Reproduction

We located cerulean nests by observing parental behavior, including following females with nest-building material, locating females that chipped from the nest during incubation, and observing adults carrying food to nestlings. We monitored nests every 2–3 days to determine nest fate

(failure or fledging) on the 5 study sites across a range of years from 1992 to 2006, depending on the site. We checked nests daily in the latter stages of the nestling cycle as fledging became imminent. We used the Mayfield (1975) method to calculate daily nest survival rates based on nest exposure days. We used Program Contrast (Hines and Sauer 2004) to compare cerulean daily nest survival rates (DSR) among study sites, for all years pooled within individual sites. We calculated Mayfield estimates of nest success by raising DSR to the 25th power, based on number of exposure days in the typical nesting cycle (4 days laying, 11 days incubation, and 10 days nestling stage). We determined number of young fledged from successful nests by using binoculars and spotting scopes to count young in the nest on the day prior to fledging. In Ontario, we also counted young postfledging to confirm nestling counts. For each study site, except the MAV, we calculated annual values and an overall mean and standard error (Johnson 1979) for Mayfield (1975) nest success and young fledged per successful nest. For the MAV site, we collected data from 3 areas (Meeman Shelby Forest, Chickasaw National Wildlife Refuge, and Desha Delta Hunt Club) from 1992 to 2005, but data for individual years were generally too limited to calculate annual parameter estimates. As a result, we simply calculated a total estimate of nest success for each MAV site alone with all data pooled. We limited number of nesting attempts in the analysis to 3 attempts to produce one brood. We followed the recommendation of Gryzbowski and Pease (2005) by basing this parameter estimate on observed nesting behavior, observed length of the breeding season (approx. 60 days), and time needed for renesting (5 days), constrained by nesting success (Ricklefs 1973).

We calculated fecundity as female young produced per breeding female with the following assumptions: 1) 100% pairing success and renesting rate for females, 2) constant average annual rates of Mayfield (1975) nest success and number of young per successful nest, 3) all females bred in their first breeding season after hatch year, 4) cerulean warblers are single-brooded, and 5) no age-related differences in parameters. To calculate fecundity (F), we used the following equation:

$$F = \text{mean number of young fledged} \\ \times \text{sex ratio} \times (3p - 3p^2 + p^3),$$

where mean number of young fledged came from our nest-monitoring data, sex ratio was assumed to be 0.5, and p was apparent nest success rate (DSR^{25} where 25 is no. of days in the nesting cycle). The $3p - 3p^2 + p^3$ term accounts for 2 renesting attempts after a failed nest (Giocomo 2005). Based on our field observations, pairing and renesting rates probably approach 100%; assumed rates biased estimates of F slightly high. Nest success and young per successful nest may vary across the nesting season; because we monitored nests throughout the season, we believe our data account for this source of variability. Based on our observations, we know that ceruleans breed in their first breeding season after hatching and are generally single-brooded. We assumed

cerulean sex ratios were 50:50. Sex ratios are generally thought to be 50:50 in passerines, and recent work on golden-winged warblers (*Vermivora chrysoptera*), for example, reported 50:50 ratios in that species (R. Vallender, Cornell Lab of Ornithology, unpublished data).

Survival Estimates

Although we banded and color-marked male ceruleans on each study site, only the Ontario site had consistent enough effort at resighting marked individuals to estimate adult survival rates. We used the estimate of Jones et al. (2004) of minimum after-hatch-year male survival rate (AHY ϕ) of 0.54 ($\pm 6\% = 1$ SE), excluding the year in their study that had very poor return rates after a catastrophic ice storm damaged nesting habitat. Annual adult survival may vary over time and space; however, Jones et al. (2004) found that a constant survival over time model had the most support for ceruleans in Ontario at QUBS. We lacked data on adult female survival rates, so we assumed that adult female survival was no greater than adult male survival rates, similar to Donovan et al. (1995) and Michaud et al. (2004). We also lacked data on juvenile survival in ceruleans, so we assumed that juvenile survival was 50% of adult survival. Estimates of juvenile survival were 45% of adult survival for Swainson's thrush (*Catharus ustulatus*; Gardali et al. 2003), 49% of adult survival for red-eyed vireo (*Vireo olivaceus*; Noon and Sauer 1992), and 77% of adult survival for wood thrush (*Hylocichla mustelina*; Noon and Sauer 1992).

Population Projection Model Development

To estimate the rate of population change (λ) for each study site, we constructed a 2-stage deterministic Leslie matrix population projection based on methods described by Caswell (2001), using Poptools in a Microsoft Excel (Redmond, WA) spreadsheet (Hood 2006). Model input parameters included fecundity (F ; defined above) and adult (after-hatch-year [AHY]) and juvenile (hatch-year [HY]) survival. We assumed immigration and emigration rates for this species were approximately equal because we lacked data suggesting otherwise.

We created population replacement threshold plots by rearranging the 2-stage population model and solving for brood size per successful nest in terms of nest success using the following formula:

$$\lambda = \text{AHY}\phi + (\beta) \times (\text{HY}\phi),$$

where λ = population growth rate, AHY ϕ = annual adult survival, HY ϕ = annual juvenile survival, and $\beta = F \times [1 - (1 - p) \wedge n]$, where F = fecundity, p = probability one nest is successful, and n = number of nesting attempts (Ricklefs 1973). When $\lambda = 1$, the population is considered stable. We developed a graphical approach for the analysis to illustrate relationships between nest success, number of young fledged per successful nest, and survival rates capable of producing a stable population ($\lambda = 1$; Fig. 2).

We conducted sensitivity and elasticity analyses to explore how model inputs affected population growth for the individual study site population models using Poptools,

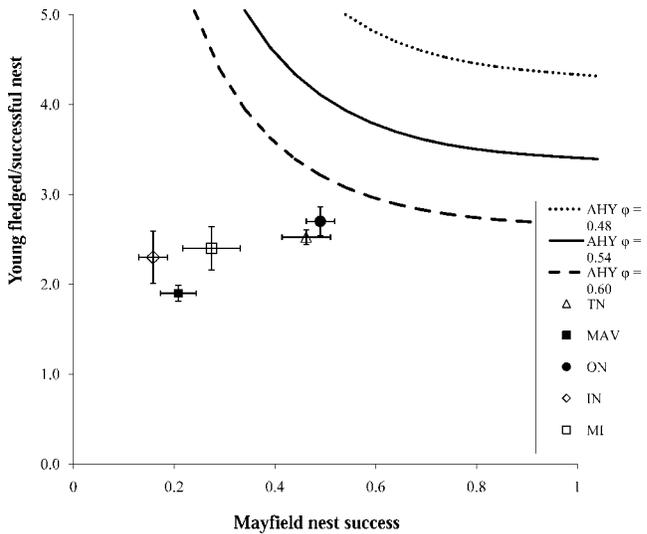


Figure 2. Point estimates of cerulean warbler Mayfield (1975) nest success (\pm SE) and young fledged per successful nest (\pm SE) for study sites in Ontario, Canada; and Tennessee Cumberland Mountains, Indiana, Michigan, and the Mississippi Alluvial Valley (USA) for various years (1992–2006). The threshold curves represent combinations of nest success and young per successful nest needed to produce a stable population ($\lambda = 1$) for adult female survival (AHY ϕ) = 0.54 ± 1 SE. Juvenile survival rates are assumed to equal 50% of adult survival rates. Points to the left of a threshold curve for given survival rates represent decreasing or sink populations and points to the right of the curve represent increasing or source populations. We display 3 lambda threshold curves based on assumed survival rates equal to the estimated rate from Ontario (54% ad M survival; Jones et al. 2004) and ± 1 SE of that estimate (48% and 60%, respectively).

Version 2.7.5 (Hood 2006). Sensitivity measures the net effect on λ of changing one input parameter while holding the other inputs constant. Elasticity is similar to sensitivity, except that the analysis is scaled so that all input parameters are changed proportionately, such that their respective elasticities sum to 1 (Caswell 2001).

RESULTS

Average annual daily nest survival rates varied ($P < 0.05$) among study sites: Cumberland Mountains, Tennessee, and Ontario sites had mean values ≥ 0.965 , whereas MAV and Indiana sites had mean values < 0.94 , with Michigan values (0.95) intermediate (Table 1). Mayfield (1975) nest success varied much more widely among study sites and years than daily survival rates (Table 1). For example, in the Cumberland Mountains, Tennessee nest success was estimated at 65.1% in 2005 but only 25.5% in 2006, a 61% decrease. Nest success in Ontario was similarly highly variable, with a range from approximately 70% in the first years of the study (1995–1997) to only 10% after an ice storm disturbance greatly altered canopy conditions in 1998, an 86% decrease (Table 1). All 3 MAV sites had consistently low values for nest success (approx. 20%). Mean nest success also was low for the Indiana site ($\bar{x} = 15.8\%$) and for the Michigan sites ($\bar{x} = 27.4\%$). Nest success at Barry Game Lands ($< 10\%$) appeared to be lower than at Fort Custer ($> 30\%$) in Michigan although we did not test these values statistically.

Mean number of young fledged from Ontario ($\bar{x} = 2.7$),

Cumberland Mountains, Tennessee ($\bar{x} = 2.5$), and Michigan ($\bar{x} = 2.4$) sites were greater than for MAV sites ($\bar{x} = 1.9$, $P < 0.05$; Table 1). Fecundity followed similar trends, with Ontario and Cumberland Mountains, Tennessee sites having the highest average fecundities (> 1), MAV and Indiana sites having the lowest fecundities (< 0.5), and Michigan having intermediate fecundities (0.73; Table 1).

Based on comparison of confidence intervals ($1.96 \times$ SE), calculated values of λ (Table 2; Fig. 2) were less than that required for stable populations ($\lambda = 1$) for all sites. Ontario and Cumberland Mountains, Tennessee sites were similar with λ approximately 0.83, Michigan was intermediate with $\lambda = 0.74$, and MAV and Indiana sites generally had $\lambda < 0.67$. Assumed female survival rates would need to increase by 11% for Ontario and Cumberland Mountains, Tennessee sites to achieve population stability, whereas MAV and Indiana sites would require increasing adult survival by 27% to achieve population stability (Table 2; Fig. 2). Ontario and Cumberland Mountains, Tennessee populations would need to produce > 0.5 more female young per successful nest, whereas the other sites would have to produce ≥ 1 additional female young per successful nest to achieve population stability (Table 2; Fig. 2).

For all 5 sites, the sensitivity analysis showed that adult survival was the parameter most strongly related to population growth rates, accounting for 39–66% of population variability in the elasticity analysis, depending on site (Table 3). The relative importance of fecundity differed among sites, with approximately 33% of variability in population growth attributable to fecundity (second yr and after second yr) in Ontario and Tennessee Cumberland Mountains sites, but $< 20\%$ of the population change for MAV and Indiana sites was attributed to fecundity. Similar to the reproduction data, Michigan was intermediate in the relative contribution of fecundity versus survival, with 27% of population change attributed to fecundity (Table 3).

DISCUSSION

Measured values of cerulean warbler daily nest survival rates, nest success, young produced per successful nest, and fecundity varied across the range of study sites. Much of the variability in fecundity within sites and among sites came from wide swings in nest success, where > 2 -fold changes were possible in successive years. Cerulean nests failed because of predation, nest destruction during inclement weather, and abandonment for largely unknown reasons (D. A. Buehler, University of Tennessee, C. P. Nicholson, Tennessee Valley Authority, and T. A. Beachy, University of Tennessee, unpublished data). Most nests failed from predation, which suggests there are likely wide swings in predation pressure, as suggested by Schmidt (2003), and occasionally in direct or indirect effects of weather (Jones et al. 2001, Nicholson 2004). Likely nest predators on our sites include American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), gray squirrels (*Sciurus carolinensis*), red squirrels (*Sciurus vulgaris*), and occasionally snakes. Mammalian predator populations and,

Table 1. Cerulean warbler summary reproduction statistics (nests, exposure days, nest losses, daily survival rates, nest success, young fledged, and fecundity) for study sites in Ontario, Canada; and Tennessee Cumberland Mountains, Indiana, Michigan, and the Mississippi Alluvial Valley (TN, AR), USA, for various years (1992–2006) by year and overall.

Study site	Yr	Nests	Exposure days	Nest losses	Daily survival rate (DSR) ^a	DSR SE	Nest success (NS; %) ^b	NS SE	Young fledged/successful nest (YFSN) ^c		Fecundity ^d
									YFSN SE	Fecundity ^d	
MI											
Barry State Game Lands	2003	6	41.5	4	0.904	0.046	7.9	3.7	3.0	1.0	0.33
Barry State Game Lands	2006	7	68	6	0.912	0.034	9.9	4.3	2.0	0.0	0.27
Fort Custer	2004	9	127	5	0.961	0.017	36.6	11.0	2.0	0.0	0.75
Fort Custer	2005	16	239	9	0.962	0.012	38.3	9.1	2.5	0.2	0.96
Overall		38	475.5	24	0.950A	0.010	27.4A	5.7	2.4A	0.2	0.73
TN											
Cumberland Mountains	1996	10	195	5	0.974	0.011	52.2	11.6	2.4	0.3	1.07
Cumberland Mountains	1997	17	385	11	0.971	0.008	48.4	8.6	2.8	0.3	1.21
Cumberland Mountains	1998	19	360	11	0.969	0.009	46.0	8.7	2.4	0.3	1.01
Cumberland Mountains	2005	19	293.5	5	0.983	0.008	65.1	10.4	2.5	0.3	1.18
Cumberland Mountains	2006	23	244.5	13	0.947	0.014	25.5	6.8	2.6	0.2	0.76
Overall		88	1478	45	0.970B	0.004	46.2A	4.8	2.5A	0.1	1.07
MS Alluvial Valley											
Chickasaw NWR ^e	1993–2001	26	271	16	0.941	0.014	21.8	5.9	2.1	0.3	0.55
Desha Delta Hunt Club	1992–1999	21	249	16	0.936	0.016	19.0	5.4	1.8	0.2	0.42
Meeman Shelby Forest	1993–2004	35	416	25	0.940	0.012	21.2	5.0	1.9	0.2	0.49
Overall		82	936	57	0.939C	0.008	20.8B	3.6	1.9B	0.1	0.49
Queen's University	1995	14	235	3	0.987	0.007	72.5	11.3	2.0	0.2	0.98
Queen's University	1996	5	95	1	0.989	0.010	76.8	15.9	2.2	0.8	1.09
Queen's University	1997	8	138	2	0.986	0.010	69.4	14.1	3.0	0.3	1.46
Queen's University	1998	36	363.5	32	0.912	0.015	10.0	2.8	3.2	0.2	0.43
Queen's University	1999	22	299.5	14	0.953	0.012	30.2	7.2	3.8	0.4	1.25
Queen's University	2000	24	370	13	0.965	0.010	40.9	8.1	3.0	0.3	1.19
Queen's University	2001	34	576.5	15	0.974	0.007	51.7	7.5	3.2	0.1	1.42
Queen's University	2002	26	428.5	12	0.972	0.008	49.2	8.3	2.8	0.3	1.22
Overall		179	2678	95	0.965B	0.004	40.5A	3.4	2.8A	0.1	1.11
IN											
Big Oaks NWR	2002	14	170	10	0.941	0.018	22.0	6.9	1.5	0.3	0.39
Big Oaks NWR	2003	26	258	23	0.911	0.018	9.7	3.0	2.7	0.3	0.35
Big Oaks NWR	2004	28	350	17	0.951	0.011	28.8	6.6	2.3	0.1	0.73
Big Oaks NWR	2005	25	221	21	0.905	0.020	8.2	2.8	2.8	0.1	0.31
Overall		93	999	71	0.929C	0.008	15.8B	2.8	2.3AB	0.3	0.46

^a Daily survival rates with different letters differed ($P < 0.05$) based on Program Contrast analysis (Hines and Sauer 2004).

^b Nest success (DSR 25) with different letters differed ($P < 0.05$) based on comparison of CI.

^c Average young fledged/successful nest with different letters differed ($P < 0.05$) based on comparison of CI.

^d Fecundity defined as the mean no. of F offspring produced/yr/ad F.

^e NWR = National Wildlife Refuge.

hence, predation pressure are likely related to acorn mast availability (Schmidt and Ostfeld 2003). Young produced per successful nest was a more consistent input to fecundity, suggesting that factors responsible for nest failure were not identical to factors responsible for egg or brood reduction.

Several contributing factors may be responsible for the

poor reproductive rates we observed in MAV, Indiana, and Michigan. First, unlike Ontario and Tennessee Cumberland Mountains populations, MAV, Indiana, and Michigan sites reported moderate levels of brown-headed cowbird (*Molothrus ater*) nest parasitism (e.g., 4 of 26 [15%] nests in Indiana that reached the nestling stage where observation of

Table 2. Cerulean warbler adult survival (AHY ϕ),^a fecundity (F),^b and population growth rates (λ) for study sites in Ontario, Canada; and Tennessee Cumberland Mountains, Indiana, Michigan, and the Mississippi Alluvial Valley (TN, AR), USA, for various years (1992–2006), with changes in survival (Δ AHY ϕ) and fecundity (ΔF) required for stable populations ($\lambda = 1$).

Study site	AHY ϕ	F	λ	SE	Δ AHY ϕ ($\lambda = 1$)	ΔF ($\lambda = 1$)
MI	0.54	0.73	0.740	0.045	+0.19	+0.97
TN	0.54	1.07	0.825	0.022	+0.11	+0.63
MS Alluvial Valley	0.54	0.49	0.669	0.011	+0.27	+1.19
ON	0.54	1.11	0.838	0.027	+0.11	+0.59
IN	0.54	0.46	0.665	0.026	+0.27	+1.24

^a Survival estimates from Jones et al. (2004) for ON.

^b Fecundity defined as the mean no. of F offspring produced/yr/ad F.

Table 3. Sensitivities and elasticities of cerulean warbler population growth models to changes in individual parameters for second-year (SY) and after second-year (ASY) fecundity (F) and hatch-year (HY) and after hatch-year (AHY) survival (ϕ) for study sites in Ontario, Canada; and Tennessee Cumberland Mountains, Indiana, Michigan, and the Mississippi Alluvial Valley (TN, AR), USA, for various years (1992–2006).

Study site	Sensitivity				Elasticity			
	SY F	ASY F	HY ϕ	AHY ϕ	SY F	ASY F	HY ϕ	AHY ϕ
MI	0.2703	0.3649	0.5406	0.7297	0.0731	0.1972	0.1972	0.5325
TN	0.3454	0.3273	0.6908	0.6546	0.1193	0.2261	0.2261	0.4285
MS Alluvial Valley	0.2191	0.3905	0.4381	0.7809	0.0372	0.1557	0.1711	0.6099
ON	0.3794	0.3103	0.7589	0.6206	0.1440	0.2355	0.2355	0.3851
IN	0.1882	0.4059	0.3763	0.8118	0.0354	0.1527	0.1527	0.6591

cowbirds was possible). Of 12 documented nest failures in Michigan, 3 (25%) failed because of cowbird parasitism (Rogers 2006). Actual parasitism rates may be greater because we did not routinely check nest contents during incubation and >50% of nests failed before it was possible to observe the presence of cowbird nestlings. Thus, brown-headed cowbird parasitism was likely responsible in part for increased nest abandonment and predation, as well as brood reduction for successful nests (Hamel and Woodson 2000). In addition to cowbird effects, nest predation rates were likely greater in MAV, Indiana, and Michigan populations than elsewhere because these study sites were embedded in landscapes with <50% forest cover within a 10-km radius, in spite of the fact that forest patch size is relatively large for the individual study sites (i.e., >250 ha). Similar landscapes in the Midwest (i.e., <50% forest cover) have been shown to have greater parasitism and predation rates for other forest passerines (Robinson et al. 1995).

Population Change

None of the study sites appeared to be capable, on average, of producing stable populations, based on measured inputs to the population model and assumed conditions. Ontario and Tennessee Cumberland Mountains populations appeared to be demographically capable of producing stable populations in years when fecundity was good and if assumed survival rates were slightly too conservative (approx. 5% low). Midwestern populations in agriculture-dominated landscapes (MAV, IN, and to a lesser extent MI), in contrast, appeared to be incapable, even when considering the variance surrounding reproduction and survival inputs (Fig. 2), of producing sufficient young to offset mortality, leading to declining populations in all years monitored. Given the relative estimates of population change for these sites (26–35% declines/yr), cerulean populations would undoubtedly be extirpated quickly without sufficient immigration to offset poor reproduction and annual mortality.

For the Ontario and Cumberland Mountains, Tennessee populations, number of young produced per successful nest appeared to be a key factor limiting productivity and the ability to achieve stable populations, because even high levels of nest success (e.g., 70%) did not produce stable populations in most years. There are 2 possible explanations for the inability to achieve stable populations. First, cerulean warblers may have experienced high rates of partial egg or

nestling predation or brood reduction from various potential sources. Typical clutch size for ceruleans in Ontario and Tennessee was slightly <4 eggs per clutch (ON: 3.8 eggs/clutch, TN: 3.7 eggs/clutch; Oliarnyk and Robertson 1996, Nicholson 2004). Thus >1 egg or nestling per nest was lost prior to fledging, on average, to produce the number of fledglings we observed (ON: 2.7 young/successful nest, TN: 2.5 young/successful nest). This partial loss of eggs and nestlings may be occurring at greater rates than that reported for other tree-nesting species that co-occur with ceruleans. For example, red-eyed vireo, wood thrush, and American redstart (*Setophaga ruticilla*) nests in largely unparasitized, eastern United States populations fledged, on average, >78% of the clutch in successful nests (Southern 1958, Roth et al. 1996, Sherry and Holmes 1997). However, accounting for potential error associated with partial loss of eggs or nestlings in the models (i.e., using the average of 78% obs for other species) was insufficient to produce stable populations. In fact, about 3.5 young would need to be produced per successful nest, along with nest success of 70%, to achieve stable populations assuming that adult survival was 54%.

Another possible explanation for the reported number of fledglings is observation bias (i.e., we consistently underestimated no. of young fledged). In Ontario and Michigan, Jones et al. (2004) and Rogers (2006) noted the possibility of observation bias but did not believe it was sufficient to explain the low rates of fecundity. Because ceruleans often nest higher than most other canopy nesters on our study sites (mean nest ht = 15.9 m; Nicholson 2004), observation error was possible. Bias likely resulted in underestimation because the steep observation angle to the nest may have obscured nestlings on the opposite side of the nest from the observer.

Balancing Reproduction With Mortality in a Single-Brooded Species

Because cerulean warblers are generally observed to be single-brooded and have a small clutch size (typically 3–4), population stability for this species places a large premium on survival. Sensitivity and elasticity results demonstrated that most of the variation in population change was related to survival parameters. For a Nearctic–Neotropical migrant that winters relatively far south (Andes of South America; Hamel 2000b) compared to other migrant passerines, annual adult (F) survival needs to be >0.60 to produce stable

populations. Compared to many other Nearctic–Neotropical warblers, 0.60 is a high survival rate (Martin 1995, Sillett and Holmes 2002, Michel et al. 2005). In fact, given the measured levels of nest success and young fledged in this study, annual adult female survival of 0.65 is required to achieve population stability for Ontario and Tennessee Cumberland Mountains populations. Given the land use pressures on wintering grounds and during migration as a trans-Gulf migrant (Hamel 2000b), adult female survival equal to 0.65 may be difficult to achieve in most populations in most years. Declining populations are a likely consequence.

Comparing Demographic Model Results With BBS Trends

Our modeled rates of population change were consistently much less than survey-wide or state-specific values calculated from BBS data for 1995–2005 ($\lambda = 0.94$ survey-wide; Sauer et al. 2006). It is difficult to separate factors related to demographic processes (e.g., reproduction, survival, immigration and emigration) from effects of habitat change (loss or gain). An understanding of which of these factors (demographic vs. habitat change) is contributing to population decline is important for effective management. Because our study sites had intact, suitable breeding habitat for the duration of the study, our measured reproduction rates reflected limitations in habitat quality, as opposed to habitat loss (unless there was a time-lag effect; see Tilman et al. 1994). The BBS population declines, in contrast, reflected loss of ceruleans along roadside routes because of direct habitat loss (e.g., clearing of land for human development) and also reflected consequences of demographic processes (i.e., reproduction and survival, immigration and emigration). Our models and BBS both have problems accounting for effects of immigration and emigration; our models ignored these effects, whereas BBS included these effects but could not separate them. Because our survival estimates were based on return rates corrected for detection probabilities, they did not account for birds that survived but did not return to the study site (e.g., emigration; Jones et al. 2004). Emigration may in part be responsible for the gap between our population trend estimates and BBS (Girvan et al. 2007). In fact, in >10 years of monitoring sites in Ontario and the Cumberland Mountains of Tennessee, breeding densities have remained relatively stable (D. A. Buehler and T. A. Beachy, unpublished data; C. P. Nicholson, unpublished data; J. Jones, J. Barg, and R. J. Robertson, Queen's University, unpublished data), in spite of declining regional population trends based on BBS data and in spite of our estimates of population change. Immigration, in contrast, may be responsible for minimizing the BBS rate of decline in the Midwest compared to our demographic-based results. Our results suggest, however, that cerulean populations are declining at rates at least as great as BBS trends suggest and provide evidence to suggest that rates of decline in intact habitat may even be greater.

Model Limitations

Our modeling exercise demonstrated limitations of the field data collected to date for making a meaningful determination of population status for ceruleans, consistent with limitations in wildlife population modeling identified by Etterson and Bennett (2006). Several key types of data are needed to produce more reliable results. First, we need to address the degree of observation error in the number of young fledged per successful nest. Secondly, we were forced to use minimum adult male survival rates from Ontario as an estimate of adult female survival for our other study sites. Because the population models were sensitive to estimates of adult female survival, additional survival estimates from color-marked populations are critically needed across the range of ceruleans to allow for reliable population growth modeling. These parameters are difficult to determine unless there are color-marked females in the population; unfortunately, we have yet to develop reliable methods to capture females on the breeding grounds.

MANAGEMENT IMPLICATIONS

Breeding habitat quality appears to be limiting fecundity and may in part be responsible for the population declines. For the sites located in nonforested landscapes (MAV, IN, MI), these cerulean populations appear to be destined to remain as sinks without major landscape reconfiguration. We suspect these cerulean populations are being maintained in part from immigration from other regions, although data are lacking to confirm this hypothesis. Although there are major afforestation projects ongoing in the Mississippi Alluvial Valley (P. Hamel, United States Forest Service, personal communication), a large amount of afforestation is needed to reconfigure landscapes from agriculture-dominated to forest-dominated. This level of effort may be required to increase fecundity and reverse MAV, Indiana, and Michigan cerulean population declines. Cerulean populations in Ontario and Tennessee appear to be capable of stable populations in good years, especially if survival estimates were too conservative. Conservation strategies for ceruleans in these areas should minimize habitat loss from various potential sources (e.g., coal mining or human development [Buehler et al. 2006]), and identify the management prescriptions capable of improving fecundity (Hamel and Rosenberg 2007).

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