

# MINIMUM ESTIMATES OF SURVIVAL AND POPULATION GROWTH FOR CERULEAN WARBLERS (*DENDROICA CERULEA*) BREEDING IN ONTARIO, CANADA

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**ABSTRACT.**—The Cerulean Warbler (*Dendroica cerulea*) tops many lists of species of conservation concern because of severe population declines and habitat loss. Here we present the first robust estimates of annual survival and population growth rates for this species. We used capture–mark–recapture models to estimate survival of adult male Cerulean Warblers in an eastern Ontario population that has been studied since 1994. Adult male survival probability ( $\phi$ ) was constant over time in our best-supported model. Our second-best-supported model indicated a negative effect of a 1998 ice storm on survival. The third-best-supported model indicated a significant year effect on survival. On the basis of those results and previously published estimates of annual fecundity, we calculated a population growth rate using a two-stage Leslie matrix. Population growth rate ( $\lambda$ ) was 0.73, using the estimate for constant survival. Model elasticities imply that adult mortality had a stronger effect on  $\lambda$  than did seasonal fecundity. Oversummer survival estimates suggest that events during migration or on wintering grounds are responsible for most adult male mortality. It appears that our study population, thought to be one of the healthiest known for this species, may not be currently reproducing at a high enough rate to accommodate adult mortality. However, caution must be used when interpreting those results, given the possibility of underestimating survival and fecundity of this species. Received 8 June 2002, accepted 28 August 2003.

**RESUMEN.**—*Dendroica cerulea* encabeza muchas listas de especies cuyo estado de conservación es preocupante debido a sus disminuciones poblacionales severas y a la pérdida de hábitat. Aquí presentamos la primera estimación robusta de la supervivencia anual y de las tasas de crecimiento poblacional para esta especie. Empleamos modelos de captura, marcado y recaptura para estimar la supervivencia de machos adultos de *D. cerulea* en una población del este de Ontario que ha sido estudiada desde 1994. La probabilidad de supervivencia de los machos adultos ( $\phi$ ) fue constante a lo largo del tiempo ( $0.49 \pm 0.05$ ) en el modelo con mayor respaldo. El modelo en segundo orden de respaldo indicó un efecto negativo en la supervivencia de una tormenta de hielo ocurrida en 1998: sin tormenta de hielo  $\phi = 0.54 \pm 0.06$ ; tormenta de hielo  $\phi = 0.40 \pm 0.08$ . El modelo en tercer orden de respaldo indicó un efecto significativo de año en la supervivencia. Basados en estos resultados y en estimaciones anuales de fecundidad previamente publicadas, calculamos una tasa de crecimiento poblacional usando una matriz de Leslie de dos etapas. La tasa de crecimiento poblacional ( $\lambda$ ) fue de 0.73, usando el parámetro estimado para supervivencia constante. La elasticidad de los modelos implica que la mortalidad de los adultos tuvo un efecto mayor sobre  $\lambda$  que la fecundidad estacional. La supervivencia a fines del verano fue estimada en  $0.98 \pm 0.05$ , sugiriendo que eventos durante la migración o en las áreas de invernada son responsables de la mayor parte de la mortalidad de los adultos. Aparentemente, nuestra población de estudio, que se supone es una de las más saludables que se conoce para esta especie, podría no estar reproduciéndose actualmente a una tasa suficientemente alta para balancear la mortalidad de los adultos. Sin embargo, debe actuarse con cautela al interpretar estos resultados, dada la posibilidad de subestimar la supervivencia y fecundidad de esta especie.

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DECLINE OF SPECIES that migrate between Nearctic breeding grounds and Neotropical wintering grounds is one of the most pressing North American bird conservation issues of the past two decades (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990). Although concern for Neotropical migrants as a group may have waned in recent years (Faaborg 2002), certain species remain in the spotlight. The Cerulean Warbler (*Dendroica cerulea*) is of particular concern, with documented declines of up to 3% per year since 1966 (Robbins et al. 1992, Link and Sauer 2002), probably resulting from habitat loss in both North and South America. The Cerulean Warbler has been variously designated as threatened, rare, or of special concern in the United States and as a species of special concern in Canada (Robbins et al. 1992, Committee of the Status of Endangered Species in Canada 2000, Hamel 2000). Most of what is known about this species involves general habitat associations and reproductive ecology (Oliarnyk and Robertson 1996, Hamel 2000, Jones and Robertson 2001, Jones et al. 2001), and there is no published information on adult survivorship.

Here we present annual and seasonal survival estimates and estimates of population growth rates for Cerulean Warblers breeding in eastern Ontario. That population is thought to have historically enjoyed high reproductive success (Oliarnyk and Robertson 1996). However, a major ice storm that swept through the region in January 1998, causing widespread damage to forest structure (Kerry et al. 1999), negatively influenced short-term fecundity (Jones et al. 2001). To estimate annual and seasonal survival probabilities and to assess the ice storm's effect on survival, we used capture-mark-recapture models.

In modeling ice-storm effects, we initially considered two scenarios. The first involved birds returning in the spring of 1998, assessing the damage, and deciding to move elsewhere. Under that scenario, we would have predicted a decrease in the 1997–1998 survival estimate. However, given the tendency for songbirds to exhibit a lag response to habitat disturbance (e.g. Brooks et al. 1999), we considered that scenario unlikely. Using a second scenario, we predicted that any effect of the ice storm on survival and recapture probabilities would be apparent in the year following the storm (i.e.

1998–1999 survival). That scenario was based both on the likelihood of the aforementioned lag effect and on the significant decrease in reproductive output experienced by our study population in the spring of 1998. Finally, we constructed a single-sex two-stage Leslie matrix model (Caswell 2001) to calculate population growth rate ( $\lambda$ ) and to examine the relative contributions of survival and fecundity to  $\lambda$ .

## METHODS

*Study area.*—Our investigation was conducted at the Queen's University Biological Station (QUBS), Ontario, Canada (44°34'N, 76°20'W), within the Great Lakes–St. Lawrence mixed-forest region. Our study area was restricted to within 2,600 ha of QUBS-managed research tracts (Jones et al. 2000a), characterized as mature, second-growth, upland mixed deciduous forest with a canopy layer dominated by sugar maple (*Acer saccharum*), and to a lesser extent oak (*Quercus* spp.) and elm (*Ulmus* spp.).

Cerulean Warblers were banded over the entire 2,600 ha of QUBS property, although the primary banding efforts took place at a core 30-ha study site (see Jones and Robertson 2001). Between May and July of each year (1995–2001), Cerulean Warblers were captured using a combination of blanket mist-netting, song playbacks, and targeted netting at nests. Each adult bird was fitted with a unique combination of two colored-plastic leg bands and one aluminum Canadian Wildlife Service band. Birds were aged using plumage characteristics (Pyle 1997). Out of a total of 132 marked individuals (males, females, and nestlings), recapture data for this study were based on resightings of 74 adult (i.e. after-second-year [ASY]) males banded at the core site. Our focus was on ASY males because of small sample sizes for females (they are extremely difficult to catch) and yearling (SY) males (very few breed on our study site). Resighting efforts for the 74 ASY males were undertaken over most of the 2,600-ha QUBS property, although with somewhat less intensity outside our core study area.

*Modeling.*—Survival ( $\phi$ ) and recapture probabilities ( $p$ ) of the 74 males were analyzed with Cormack-Jolly-Seber (CJS) models (Pollock et al. 1990, Lebreton et al. 1992) using program MARK (White and Burnham 1999). The set of candidate models (Table 1) was selected prior to data analysis based on our knowledge of Cerulean Warbler biology and on limitations inherent in our small data set. In ice-storm models,  $\phi$  and  $p$  for May 1998–May 1999 were compared to those estimates for all other years. Model selection methods based on Akaike's information criterion (AIC; Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 1998) were used to (1) provide the best estimates of  $\phi$  and  $p$ , and (2) assess the statistical evidence for

TABLE 1. Models of annual survival ( $\phi$ ) and recapture ( $p$ ) probabilities for adult male Cerulean Warblers at Queen's University Biological Station, Ontario, Canada, 1995–2001. Columns give model notation, number of estimable parameters ( $K$ ), second-order Akaike's information criterion values ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta_i$ ), and  $AIC_c$  weights ( $w_i$ ). Statistics for the best-fit model are in bold. Subscripts describe parameterizations of  $\phi$  and  $p$ : "storm" = 1998–1999 compared to all other years; "year" = annual variation; no subscript = constant. Based on program RELEASE (Burnham et al. 1987), the global model ( $\phi_{year} p_{year}$ ) provided a good fit to the data ( $\chi^2 = 4.10$ ,  $df = 9$ ,  $P = 0.90$ ).

| Model                   | $K$      | $AIC_c$       | $\Delta_i$ | $w_i$       |
|-------------------------|----------|---------------|------------|-------------|
| $\phi, p$               | <b>2</b> | <b>200.44</b> | <b>0</b>   | <b>0.31</b> |
| $\phi_{storm} p$        | 3        | 201.06        | 0.62       | 0.23        |
| $\phi_{year} p$         | 7        | 202.08        | 1.63       | 0.14        |
| $\phi_{year} p_{year}$  | 11       | 205.57        | 5.12       | 0.02        |
| $\phi, p_{year}$        | 7        | 205.74        | 5.30       | 0.02        |
| $\phi_{storm} p_{year}$ | 8        | 206.71        | 6.27       | 0.01        |

year- and storm-related differences in those parameters. Following Burnham and Anderson (1998), models in each candidate set were ranked by second-order AIC differences ( $AIC_c$ ) and the relative likelihood of each model was estimated with AIC weights ( $w_i$ ).

A subset of our study population ( $n = 52$  males) was monitored throughout the breeding season. Those males were systematically surveyed every one to seven days from mid-May through 31 July, the last day to reliably resight breeding individuals. Seasonal  $\phi$  was modeled separately for the May–August breeding period, and for the August–May period encompassing migration and overwintering periods. Notation for this model structure is ( $\phi_{season} p$ ). To test whether survival during the summer stationary period differed from monthly survival during the remainder of the year, model ( $\phi_{season} p$ ) was compared to a model of constant survival between seasons, ( $\phi_{no\_season} p$ ). Small sample sizes did not permit an analysis of the seasonal influences of the 1998 ice storm. The value  $p$  was fixed at 1.0 in those CJS models because no banded individuals that disappeared before 31 July were ever resighted, and none of the 52 focal males that returned to our study area were missed during May surveys. Thus, model ( $\phi_{season} p$ ) estimated two parameters, whereas model ( $\phi_{no\_season} p$ ) estimated only one parameter.

To estimate  $\lambda$  and to examine the relative contributions of survival and fecundity to  $\lambda$ , a single-sex, two-stage Leslie matrix model (Caswell 2001) was constructed. Model was parameterized with estimates of survivorship (see below) and fecundity (Jones et al. 2001, J. Jones unpubl. data) from the Cerulean Warbler population at QUBS. However, data on survival of Cerulean Warblers from fledging until their

first breeding season are lacking. We used 0.3 as our estimate of fledgling  $\phi$ ; survival of small passerines from fledging until their first breeding seasons ranges from 0.1 to 0.3 (Anders et al. 1997). Although we have no data on SY fecundity for Cerulean Warblers, younger individuals of other warbler species tend to have lower reproductive output; on the basis of literature values, SY fecundity was modeled as 80% that of ASY males (Nolan 1978, Sæther 1990, Forslund and Part 1995, Holmes et al. 1996). Matrix elements were SY per SY, SY per ASY, SY survival, and ASY survival; elasticities of the four matrix elements were computed (de Kroon et al. 1986, Caswell 2001). All model calculations were performed in Microsoft EXCEL using the POPTOOLS add-in module (Hood 2002).

RESULTS

Three CJS models for annual  $\phi$  and  $p$  (Table 1) had strong statistical support (i.e.  $\Delta AIC_c \leq 2$ ). Warbler survival probability was constant over time in the best-supported model ( $[\phi, p]$ :  $\phi = 0.49 \pm 0.05$ ; 1 SE). In the second model ( $\phi_{storm} p$ ),  $\phi$  was higher in normal years ( $0.54 \pm 0.06$ ) compared to 1998, the ice storm year ( $0.40 \pm 0.08$ ). Survival probabilities in the third model ( $\phi_{year} p$ ) varied by year and were markedly higher in 1995 and 1999 (Fig. 1). Recapture probabilities in

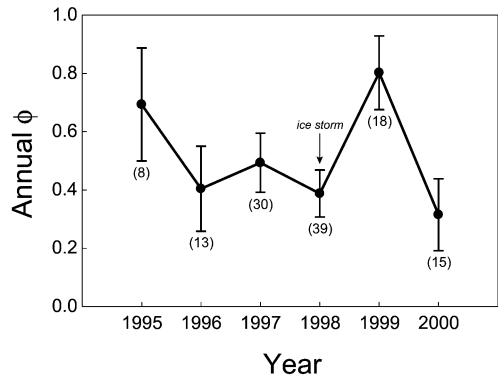


FIG. 1. Annual survival probabilities ( $\phi$ ) for adult male Cerulean Warblers breeding at Queens University Biological Station in Ontario, Canada varied considerably from 1995 to 2001. The x axis indicates capture year. The y axis gives estimated  $\phi$  to the following year from model ( $\phi_{year} p$ ) in Table 1. Survival probabilities are from capture year to capture year + 1. Error bars represent 1 SE. The downward arrow labeled "ice storm" indicates the year in which the massive ice storm of January 1998 (see text) would have affected warbler survival. Annual sample sizes of captured birds are given in parentheses.

those three models were constant over time ( $p = 0.83 \pm 0.07$ ). All poorly supported models in the candidate set were parameterized with  $p$  varying annually (Table 1). On the basis of  $\Sigma w_i$  from all candidate models (see Burnham and Anderson 1998), constant survival (Table 1: models 1, 5) was 1.4× more likely to best fit our data than storm-specific survival (Table 1: models 2, 6) and 2.1× more likely than year-specific survival (Table 1: models 3, 4). Constant  $p$  was 11.4× more likely than year-specific  $p$ , given our data.

Monthly survival of adult male Cerulean Warblers at QUBS differed during the May–August breeding season compared to the interval of August–May, which encompasses migration and overwintering ( $[\phi_{\text{season}}, p]$ :  $\text{AIC}_c = 155.35$ ,  $w = 0.99$ ;  $[\phi_{\text{no\_season}}, p]$ :  $\text{AIC}_c = 163.83$ ,  $w = 0.01$ ). Nearly all warblers survived the May–August stationary period (monthly  $\phi_{\text{May-August}} = 0.98 \pm 0.01$ ). In contrast, the majority of apparent mortality occurred either during migration or on wintering grounds in South America (monthly  $\phi_{\text{August-May}} = 0.93 \pm 0.01$ ). Monthly mortality rates during the migration and overwinter periods were ~3.5× higher than mortality rates between May and August.

The two-stage Leslie matrix model resulted in  $\lambda < 1.0$  (Table 2). Model elasticities indicated that adult survival had a greater effect on  $\lambda$  from 1995 to 2001 than did fecundity (Table 2).

TABLE 2. Parameter values for the two matrix models and associated elasticities for male Cerulean Warblers at Queen's University Biological Station, Ontario, Canada, 1995–2001. Starting population size for matrix projections was 100 individuals (85 ASY males and 15 SY males). One model included the effect of the ice storm on survival and fecundity (i.e. mean demographic rates, 1995–2001), and the other did not (i.e. 1998 data not included).

|                            | No ice storm | Ice storm |
|----------------------------|--------------|-----------|
| Survival ( $\phi$ )        | 0.54         | 0.49      |
| ASY fecundity (males/male) | 0.94         | 0.85      |
| SY fecundity (males/male)  | 0.75         | 0.68      |
| <b>Elasticities</b>        |              |           |
| SY per SY                  | 0.09         | 0.09      |
| SY per ASY                 | 0.22         | 0.22      |
| SY $\phi$                  | 0.23         | 0.23      |
| ASY $\phi$                 | 0.46         | 0.46      |
| Years to extinction        | 48           | 31        |

## DISCUSSION

Obtaining reliable estimates of survival for highly mobile organisms is difficult, primarily because of the uncertain fates of individuals that disappear from study populations (Clobert and Lebreton 1991, Lebreton et al. 1992). However, three lines of evidence lead us to believe that our estimate for adult male survival probability may be relatively close to the “true” survival rate. The first is the apparently high site-fidelity of males at QUBS. For example, only once in seven years did we record a between-season move by an adult male of >500 m from the point of capture over the 2,600-ha QUBS property (J. J. Barg, pers. obs.). That does not, however, preclude birds from moving larger distances (see below). The second line of evidence is our high recapture probability ( $0.83 \pm 0.07$ ), indicating that we rarely failed to detect a marked individual present on the study site. The third is that, although comparative CJS data for other canopy-nesting *Dendroica* are rare, our estimate of  $\phi$  for Cerulean Warblers ( $0.49 \pm 0.05$ ) falls within the range of published values. Our estimate is low compared to estimates for Yellow-rumped Warblers (*D. coronata*;  $0.70 \pm 0.09$ ), but high compared to Townsend's Warblers (*D. townsendi*;  $0.37 \pm 0.09$ ; DeSante et al. 1998). Annual survival estimates in another closely related canopy-nester, American Redstart (*Setophaga ruticilla*), range from 0.44 to 0.67 (Nichols et al. 1981, DeSante et al. 1998, Marra and Holmes 2001). On the other hand, as we discuss below, there are also reasons to believe that we might have underestimated ASY male survival to a certain extent. As a consequence, our survival estimates should be viewed as minimum estimates.

Our high estimate of oversummer survival compared to survival during the nonbreeding period suggests that events on the wintering grounds or during migration are responsible for most adult male mortality. Other studies (Conway et al. 1995, Marra and Holmes 2001, Sillett and Holmes 2002) have documented high overwinter survival of parulids in relatively undisturbed habitats. Cerulean Warblers winter on the eastern slopes of the Andes Mountains of South America in mature, humid evergreen forests. That landscape is also ideal for human settlement and agriculture, notably the production of coffee, cacao, tea, hill rice, and coca



(Robbins et al. 1992, Stotz et al. 1996). Excepting the Atlantic forests of Brazil, humid montane forests in the Andes have been altered more drastically than any other South American forest type (Robbins et al. 1992, Stotz et al. 1996). As a result, habitat degradation on winter quarters could negatively affect adult survival. Cerulean Warblers do use modified forests (e.g. shade coffee plantations) on their wintering grounds (Jones et al. 2000b, 2002), although their survival rates in disturbed habitats are unknown.

Survival of Cerulean Warblers during migration is probably low compared to the summer and winter stationary periods. Mortality of a congener, the Black-throated Blue Warbler (*D. caerulescens*), appears to be concentrated during the migratory period, and at least 15× higher than mortality during either summer or winter (Silleit and Holmes 2002). Cerulean Warblers have an unusually protracted spring (two months) and fall (four months) migration compared to other *Dendroica* (Hamel 2000). That long traveling period probably exposes individuals to high physiological stress as well as habitat disturbances along the length of their migration routes. Further data are needed to determine whether Cerulean Warbler populations are suffering high migration-related mortality.

Results of our matrix model indicate that the QUBS population may not be self-sustaining and that adult mortality has the dominant effect on  $\lambda$ . Those features add a layer of complexity to the conservation outlook for the species because our survivorship analyses implicate the migratory and overwinter periods as major sources of adult mortality. That not only necessitates the involvement of multiple cultures and government agencies in the development of conservation or management schemes, but also dramatically increases the amount of land area that needs to be considered. Given the almost complete lack of information on Cerulean Warbler winter and stopover ecology, we propose that the two most pressing research needs for the Cerulean Warbler are (1) the delineation of overwinter range and collection of habitat-specific demography data during that period, and (2) a detailed examination of migratory pathways and habitat needs (see also Hamel 2000).

It is important to remember, however, that our CJS estimate of adult survival falls within the range of estimates for other parulids that are not exhibiting widespread population declines.

As a consequence, low fecundity must also be considered as a major contributor to our negative population projection. Average fecundity over the duration of the study was less than one male per male (mean = 0.94; range 0.4–2.2). Unfortunately, the factors that directly affect Cerulean Warbler fecundity across the breeding range or across years are poorly understood, indicating a third critical research need. The Cerulean Warbler is a classic example of a Nearctic–Neotropical migrant songbird that may need to be managed during all stages of the annual cycle to ensure long-term species viability (Robbins et al. 1992, Rappole 1995).

Interestingly, the Cerulean Warbler population at QUBS has persisted at approximately the same size over the past eight years (J. Jones et al. unpubl. data), despite our negative  $\lambda$  estimate. At least three reasons could account for that inconsistency, acting independently or in concert. First, we were unable to effectively incorporate variance or stochasticity into the models (Caswell 2001), which may have led to an underestimate of  $\lambda$ . However, given our lack of empirical data for certain parameters included in the models (e.g. juvenile survival, SY fecundity), we were uncomfortable with arbitrarily assigning variance for modeling purposes. Second, because we were unable to directly examine the nest contents of all found nests, we could have underestimated fecundity. However, fledgling Cerulean Warblers are conspicuous after leaving the nest, and we were able to estimate the reproductive success of the monitored pairs with relative accuracy. With our calculated survival estimates, average fecundity would have to be 1.7 male nestlings per breeding male (assuming an equal fledgling sex ratio) to account for the observed population stability. Although we may have underestimated fecundity to a small degree, we consider it highly unlikely that we have done so by 50%, given our confidence that we found all successful nests on our study area.

Finally, we could have underestimated adult survival because CJS models cannot separate mortality and permanent emigration. However, for such an underestimate to be solely responsible for the differences between models and reality, adult survival would have to equal 0.76 to maintain a stable population size ( $\lambda = 1.0$ ) with known fecundity. Although we acknowledge the likelihood of some underestimation, we

consider it unlikely that we have underestimated survival by 36% in our study area. However, our study population was receiving immigrants from other populations; in any given spring, 40–70% of the study population was composed of unbanded males. Furthermore, microsatellite data have revealed enough gene flow between QUBS and four other Cerulean Warbler populations to prevent genetic differentiation through drift (Veit 1999, M. L. Viet et al. unpubl. manuscript). We do not know where those unbanded males are coming from. There is a large population of Cerulean Warblers at QUBS, so many of those new individuals could be dispersing from nearby. There is also genetic evidence of individuals dispersing to QUBS from as far away as Illinois and Arkansas (M. L. Viet et al. unpubl. manuscript). Thus, dispersal probably plays an important role in the population dynamics of the Cerulean Warbler throughout its breeding range. More data are needed to estimate both natal and adult dispersal, to assess the potential role of metapopulation dynamics in maintaining healthy population networks, and to more accurately document adult survival.

The additive effects of low fecundity and low adult survival during the nonbreeding season relative to the breeding season combine to create a potentially grim outlook for the Cerulean Warbler, despite the apparent resilience of the species to certain habitat disturbances (Jones et al. 2001). Admittedly, our assessment of population health was further limited by not having a direct estimate of female survivorship or of juvenile survival. However, not having those data has probably led us to overestimate the health of the study population because female passerines typically have lower survival rates than males (see Marra 2000 and references therein). Furthermore, we used the highest published value of juvenile passerine survival; actual survival for juvenile Cerulean Warblers could be lower. It appears that our study population, thought to be one of the largest known of this species (Rosenberg et al. 2000), may potentially be a sink population (i.e. both receiving immigrants and not replacing itself). Any data collected along the research paths we have identified (see also Hamel 2000) will add considerable power to our ability to halt the decline of the species that has become, for many, a symbol of the health of mature deciduous forests in eastern North America.

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