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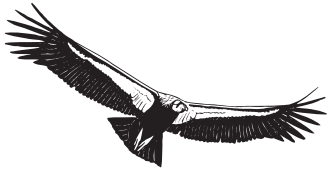
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SHORT COMMUNICATIONS

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MIGRATORY CONNECTIVITY AND RATE OF POPULATION DECLINE IN A VULNERABLE SONGBIRD

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Abstract. It has been hypothesized that populations that are strongly connected between two periods of the year (i.e., individuals that breed in similar locations and also spend the nonbreeding season in similar locations) will be most vulnerable to population perturbations. Using stable-hydrogen isotopes in feathers and data from the North American Breeding Bird Survey, we examined this hypothesis for a vulnerable songbird, the Cerulean Warbler (*Dendroica cerulea*). Cerulean Warblers exhibit a parallel migration system, whereby western breeding populations are generally connected to southwestern wintering sites and eastern breeding populations are generally connected to northeastern wintering sites. As predicted, breeding populations that exhibited the strongest degree of migratory connectivity with a specific wintering region were also those populations that experienced the most severe declines over the past 40 years. Our results suggest that the strength of migratory connectivity should be an important factor when making resource-allocation decisions for the management and conservation of migratory species.

Key words: *Cerulean Warbler, Dendroica cerulea, migratory connectivity, population dynamics, stable-hydrogen isotopes.*

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Resumen. Se ha propuesto la hipótesis de que las poblaciones que están fuertemente conectadas entre dos periodos del año (i.e., los individuos que se reproducen en localidades similares también pasan la época no reproductiva en localidades similares) serán las más vulnerables a las perturbaciones poblacionales. Mediante la evaluación de isótopos estables de hidrógeno presentes en las plumas y el uso de datos del censo de aves reproductivas de América

del Norte, examinamos esta hipótesis en *Dendroica cerulea*, un ave vulnerable. Esta especie exhibe un sistema de migración paralelo: las poblaciones que se reproducen en el oeste generalmente están conectadas con áreas de invernada en el suroeste, mientras que las poblaciones que se reproducen en el este generalmente están conectadas con áreas de invernada del noreste. Como se había predicho, las poblaciones reproductivas que presentaban el mayor grado de conectividad migratoria con una región específica de invernada fueron las que experimentaron las disminuciones más severas en los últimos 40 años. Nuestros resultados sugieren que el grado de conectividad migratoria debería ser un factor importante a considerar al tomar decisiones relacionadas con la asignación de recursos para el manejo y la conservación de las especies migratorias.

Knowledge of how migratory populations are geographically connected among different periods of the year (migratory connectivity) is critical for understanding the factors that influence population dynamics and for developing sound conservation plans (Webster et al. 2002, Marra et al. 2006, Martin et al. 2007). Migratory connectivity patterns can vary from strong, where most individuals from a given population migrate to a single location the following season, to weak, where individuals spread out over many areas in the following season. It has been hypothesized that strongly connected populations may be more vulnerable to perturbation because they have fewer individuals arriving from other regions that could buffer populations from severe declines, compared to weakly connected populations (Dolman and Sutherland 1994, Esler 2000, Marra et al. 2006). This hypothesis has not been tested because of the difficulty in tracking migratory animals over large distances. Studies have demonstrated that stable isotopic signatures in animal tissues can be an important tool for estimating the geographic origin of migrating individuals (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Stable-hydrogen isotope (δD) signatures vary geographically according to large-scale patterns of precipitation and evaporation (Bowen et al. 2005); this geographic variation is reflected in the δD signatures of tissues of

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higher-order consumers (Cormie et al. 1994). As feathers are metabolically inert after they are grown, their isotopic signatures can be used to estimate the geographic origin of individuals during the period in which the feather was formed and to examine population dynamics in relation to connectivity patterns.

We used stable-hydrogen isotopes and long-term trend data from the North American Breeding Bird Survey (BBS) to examine the hypothesis that more strongly connected populations are more susceptible to population declines. We tested the prediction that the rate of population decline would be related to the degree of connectivity in the Cerulean Warbler (*Dendroica cerulea*), a vulnerable Neotropical-Nearctic songbird (IUCN 2006) that breeds in deciduous forests of eastern North America and winters in the South American Andes (Hamel 2000). Analysis of 1996–2007 BBS data indicates an average population decline of 2.9% per year (Sauer et al. 2008), one of the fastest declines of any North American migratory songbird.

METHODS

ISOTOPIC DETERMINATIONS

To provide an estimate of wintering location we collected crown feather samples from male Cerulean Warblers ($n = 103$) at five breeding locations in Ontario, Illinois, Pennsylvania, West Virginia, and Tennessee from 2001 to 2003. Cerulean Warblers molt and regrow their crown feathers during the stationary winter period prior to northward migration (G. Colorado, Universidad Nacional de Colombia, unpubl. data); hence, crown feather isotopic signatures reflect the chemical signature of where an individual spent the winter. We captured males in mist nets using song playback and painted model presentation. No individuals were sampled after mid-July to ensure that sampling occurred before the annual prebasic molt. We aged individuals as second-year (SY) or after-second-year (ASY) based on plumage coloration (Pyle 1997) and molt limits (Mulvihill 1993).

Stable-hydrogen isotopic ratios (δD) are expressed in delta notation in units of ‰, where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and R_{standard} is the hydrogen isotope ratio of the international standard, Vienna Standard Mean Ocean Water (VSMOW). We washed feathers in a 2:1 chloroform:methanol mixture to remove surface contaminants and left them to air dry under a fume hood for 72 hr. Because a fraction of the hydrogen in feathers rapidly exchanges with ambient moisture (Wassenaar and Hobson 2000), feathers were equilibrated with local atmosphere for 72 hr to ensure that all samples had an equal opportunity to exchange with the local atmosphere (Norris et al. 2006). Based on controlled experiments, we found only a small proportion of exchangeable hydrogen (3%–5%) in tail feathers (MKG, DRN, and TKK, unpubl. data). To control for potential seasonal differences in the atmospheric moisture of δD values in the laboratory, all analyses were performed within a span of two months. We cut 0.10–0.15 mg from each feather (taking care to select the same portion from each), loaded each sample separately into a silver capsule, and heated the capsules at 100°C for 24 hr to remove potential surface water. After the capsules were crushed with metal tweezers, they were loaded into a reduction furnace (Finnigan TC/EA, Thermo Electron Corporation, Waltham, Massachusetts) at 1450°C, and introduced on-line to an isotope ratio mass spectrometer (Finnigan MAT Delta Plus XL). Within each run of 20–22 samples we ran three different standards (brucite, Georgia kaolinite clay, and an in-house keratin standard of domestic chicken [*Gallus gallus*] feathers), ensuring that at least one standard was run after every five samples (Norris et al. 2006). Previous work

with these standards (Norris et al. 2006), as well as repeated measurements of the crown feathers used in this study, indicate that δD values were reproducible to $\pm 3\%$.

STATISTICAL ANALYSES

We used a likelihood-based assignment test to estimate the location of breeding birds during the previous winter season (Royle and Rubenstein 2004, Norris et al. 2006). During the winter, Cerulean Warblers occupy an elevational range of 500–1750 m above sea level, largely on the eastern slope of the Andes of South America (Hamel 2000). Although there are scattered winter records of Cerulean Warblers in Bolivia and the tepuis of Venezuela, the majority of records come from the Andes of Venezuela, Colombia, Ecuador, and Peru. Accordingly, we divided the wintering range into two regions (southern: Ecuador and Peru; northern: Venezuelan Andes and Colombia) and constrained these regions by the elevational range used by Cerulean Warblers. For both regions we derived expected mean \pm SD δD values from an equal area grid of long-term average growing season δD values of precipitation (δD_p ; data available at <<http://www.waterisotopes.org>>) adjusted according to the estimated isotopic discrimination between δD in feathers and δD_p (–13‰; Bowen et al. 2005, Norris et al. 2006). The southern region δD was $-48\% \pm 10\%$ and the northern region δD was $-43\% \pm 11\%$. Assuming a normal distribution of winter values and assuming that individuals are equally likely to come from all locations within a region, we calculated the likelihood of each individual sampled on the breeding grounds originating from one of the two regions as:

$$f(y^*|\mu_w, \sigma_w) = \frac{1}{\sqrt{2\pi}\sigma_w} \left[-\frac{1}{2\sigma_w^2} (y^* - \mu_w)^2 \right],$$

where μ_w and σ_w are the mean and SD δD from a given wintering region and y^* is the δD value for a given individual sampled on the breeding grounds (Royle and Rubenstein 2004). We considered the most likely region of origin as the one with the highest probability (Norris et al. 2006). Despite the wide range of elevation contained in each of our designated regions, and its likely influence on isotopic variation, stratification by elevation did not increase our assignment probabilities; hence, we do not report any elevation data.

To examine the degree of connectivity for a given breeding population, we used a goodness-of-fit test to compare the observed distribution of individuals wintering in the two regions to an expected distribution based on the total area of each region; the northern region represents 64% of the available winter range, the southern region 36%. We used the Chi-square statistic from these tests as an index of connectivity strength; the larger a Chi-square value is, the greater the departure from the expected distribution. Population trend estimates were taken from hierarchical analyses of 1966–2006 BBS data (Link and Sauer 2002) compiled for all Bird Conservation Regions in which Cerulean Warblers breed (available at <<http://www.nabci-us.org>>). As reliable trend estimates were not available for the Bird Conservation Region in which the Tennessee breeding population is located, we used the trend estimate from a neighboring Bird Conservation Region, which has its boundary less than 50 km from the sampled population.

RESULTS

We found no significant differences in the assignment distributions of SY versus ASY individuals for three of the breeding populations: Ontario (Fisher's exact test, regional $P = 0.2$), Pennsylvania

TABLE 1. Cerulean Warblers ($n = 103$) were captured on the breeding grounds in five locations. Crown feathers were collected from second-year (SY) and after-second-year (ASY) males and the stable-hydrogen isotopic ratios (δD) were measured for each. These ratios were compared to South American precipitation δD values from two geographic regions: northern = Venezuelan Andes and Colombia, southern = Ecuador and Peru. The assignment probabilities reflect the likelihood that a given male grew his crown feathers in a given region.

Sampling location	Age	δD (‰) of crown feather	Assignment probability	Assigned region
Illinois	SY	-40.00	0.64	Northern
Illinois	ASY	-57.39	0.70	Southern
Illinois	ASY	-55.55	0.68	Southern
Illinois	ASY	-54.46	0.67	Southern
Illinois	ASY	-53.46	0.65	Southern
Illinois	ASY	-53.23	0.65	Southern
Illinois	ASY	-53.00	0.65	Southern
Illinois	ASY	-51.00	0.61	Southern
Illinois	ASY	-49.00	0.58	Southern
Illinois	ASY	-49.00	0.58	Southern
Illinois	ASY	-48.29	0.56	Southern
Illinois	ASY	-48.00	0.56	Southern
Illinois	ASY	-48.00	0.56	Southern
Illinois	ASY	-47.18	0.54	Southern
Illinois	ASY	-45.84	0.51	Southern
Illinois	ASY	-43.00	0.56	Northern
Illinois	ASY	-42.07	0.59	Northern
Illinois	ASY	-41.00	0.62	Northern
Illinois	ASY	-38.00	0.70	Northern
Ontario	SY	-54.64	0.67	Southern
Ontario	SY	-53.74	0.66	Southern
Ontario	SY	-52.40	0.64	Southern
Ontario	SY	-51.00	0.61	Southern
Ontario	SY	-49.60	0.59	Southern
Ontario	SY	-48.00	0.56	Southern
Ontario	SY	-40.00	0.64	Northern
Ontario	SY	-45.00	0.51	Northern
Ontario	ASY	-65.00	0.75	Southern
Ontario	ASY	-49.26	0.58	Southern
Ontario	ASY	-48.52	0.57	Southern
Ontario	ASY	-47.48	0.55	Southern
Ontario	ASY	-47.01	0.54	Southern
Ontario	ASY	-45.73	0.51	Southern
Ontario	ASY	-44.17	0.53	Northern
Ontario	ASY	-42.00	0.59	Northern
Ontario	ASY	-41.00	0.62	Northern
Ontario	ASY	-40.93	0.62	Northern
Ontario	ASY	-37.87	0.70	Northern
Ontario	ASY	-37.08	0.72	Northern
Ontario	ASY	-36.87	0.73	Northern
Ontario	ASY	-35.09	0.77	Northern
Ontario	ASY	-51.27	0.62	Southern
Pennsylvania	SY	-52.00	0.63	Southern
Pennsylvania	SY	-48.83	0.57	Southern
Pennsylvania	SY	-43.00	0.56	Northern
Pennsylvania	SY	-43.00	0.56	Northern
Pennsylvania	SY	-42.00	0.59	Northern
Pennsylvania	SY	-38.00	0.70	Northern
Pennsylvania	SY	-31.95	0.84	Northern
Pennsylvania	ASY	-52.13	0.63	Southern

(Continued)

TABLE 1. (Continued)

Sampling location	Age	δD (‰) of crown feather	Assignment probability	Assigned region
Pennsylvania	ASY	-52.00	0.63	Southern
Pennsylvania	ASY	-47.63	0.55	Southern
Pennsylvania	ASY	-45.00	0.51	Northern
Pennsylvania	ASY	-44.00	0.54	Northern
Pennsylvania	ASY	-43.00	0.56	Northern
Pennsylvania	ASY	-41.20	0.61	Northern
Pennsylvania	ASY	-41.18	0.61	Northern
Pennsylvania	ASY	-41.00	0.62	Northern
Pennsylvania	ASY	-38.76	0.68	Northern
Pennsylvania	ASY	-37.37	0.71	Northern
Pennsylvania	ASY	-34.10	0.79	Northern
Tennessee	SY	-70.00	0.75	Southern
Tennessee	SY	-66.00	0.75	Southern
Tennessee	SY	-63.72	0.74	Southern
Tennessee	SY	-62.37	0.74	Southern
Tennessee	SY	-59.00	0.71	Southern
Tennessee	SY	-57.11	0.70	Southern
Tennessee	SY	-54.00	0.66	Southern
Tennessee	SY	-52.00	0.63	Southern
Tennessee	ASY	-64.00	0.74	Southern
Tennessee	ASY	-62.70	0.74	Southern
Tennessee	ASY	-62.55	0.74	Southern
Tennessee	ASY	-62.53	0.74	Southern
Tennessee	ASY	-60.00	0.72	Southern
Tennessee	ASY	-59.43	0.72	Southern
Tennessee	ASY	-58.72	0.71	Southern
Tennessee	ASY	-56.67	0.69	Southern
Tennessee	ASY	-56.00	0.68	Southern
Tennessee	ASY	-55.10	0.67	Southern
Tennessee	ASY	-53.00	0.65	Southern
Tennessee	ASY	-52.00	0.63	Southern
Tennessee	ASY	-49.00	0.58	Southern
West Virginia	SY	-53.06	0.65	Southern
West Virginia	SY	-46.75	0.53	Southern
West Virginia	SY	-46.00	0.51	Southern
West Virginia	SY	-46.00	0.51	Southern
West Virginia	SY	-45.30	0.50	Northern
West Virginia	SY	-45.00	0.51	Northern
West Virginia	SY	-42.00	0.59	Northern
West Virginia	SY	-38.00	0.70	Northern
West Virginia	ASY	-53.90	0.66	Southern
West Virginia	ASY	-53.34	0.65	Southern
West Virginia	ASY	-52.81	0.64	Southern
West Virginia	ASY	-51.07	0.62	Southern
West Virginia	ASY	-50.13	0.60	Southern
West Virginia	ASY	-49.00	0.58	Southern
West Virginia	ASY	-48.35	0.56	Southern
West Virginia	ASY	-45.00	0.51	Northern
West Virginia	ASY	-44.82	0.52	Northern
West Virginia	ASY	-44.48	0.52	Northern
West Virginia	ASY	-43.00	0.56	Northern
West Virginia	ASY	-41.00	0.62	Northern
West Virginia	ASY	-39.00	0.67	Northern

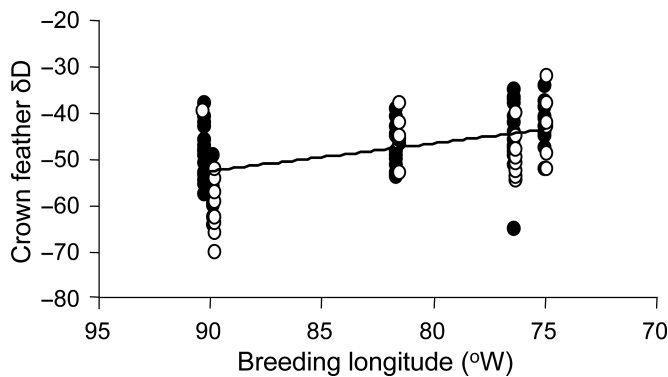


FIGURE 1. Stable-hydrogen isotopic composition (δD) in male Cerulean Warbler crown feathers was significantly correlated with the breeding longitude at which they were sampled; isotopic values increased in a west to east direction ($F_{1,101} = 38.6$, $r^2 = 0.3$, $P < 0.001$). Second-year (SY) symbols (unfilled) are offset from after-second-year (ASY; filled) for visual clarity. Tennessee and Illinois have been combined due to proximity of longitudinal values.

(regional $P = 0.6$), and West Virginia (regional $P = 0.6$). We could not test age differences for Illinois (only one SY individual sampled) or Tennessee (all birds assigned to the southern region). With ages combined, we found a significant relationship between δD values in crown feathers and breeding longitude (Fig. 1), suggesting a parallel migration system, whereby western breeding populations are generally connected to southwestern wintering sites and eastern breeding populations are generally connected to northeastern wintering sites (Fig. 2).

All breeding populations exhibited wintering distributions significantly different from expected (Ontario: $\chi^2 = 17.4$, $P < 0.001$; Illinois: $\chi^2 = 62.7$, $P < 0.001$; Pennsylvania: $\chi^2 = 4.3$, $P = 0.04$; West Virginia: $\chi^2 = 11.1$, $P = 0.001$; Tennessee: $\chi^2 = 177.8$, $P < 0.001$). Assignment probabilities were moderate: 19 of 103 were 70% or higher and 62 of 103 were 60% or higher (Table 1); assignment probabilities differed by $25\% \pm 13\%$ (mean \pm SD). We found a significant negative correlation between migratory connectivity strength and population trend for the Bird Conservation Region in which a breeding population was located ($r = -0.9$, $P = 0.02$; Fig. 3).

DISCUSSION

Parallel migration, a system in which western and eastern populations segregate on a west–east gradient during the nonbreeding season, has been documented using stable isotopes in other North American wood-warblers, including the Northern Yellow Warbler (*Dendroica petechia*, *aestiva* group; Boulet et al. 2006), American Redstart (*Setophaga ruticilla*; Norris et al. 2006), and Wilson's Warbler (*Wilsonia pusilla*; Clegg et al. 2003). Unlike these species, whose breeding ranges span the continent, the Cerulean Warbler occupies a relatively narrow longitudinal band in eastern North America, making it less probable that these breeding populations would segregate on the wintering grounds. Most Cerulean Warblers utilize a two-stage pathway involving a trans-Gulf of Mexico flight followed by movement along continental Central America to South America in the fall, with the reverse pattern in spring (D. Mehlman et al., The Nature Conservancy, unpubl. data). If most breeding individuals are following similar migratory pathways, population segregation may be occurring at the very end of the journey.

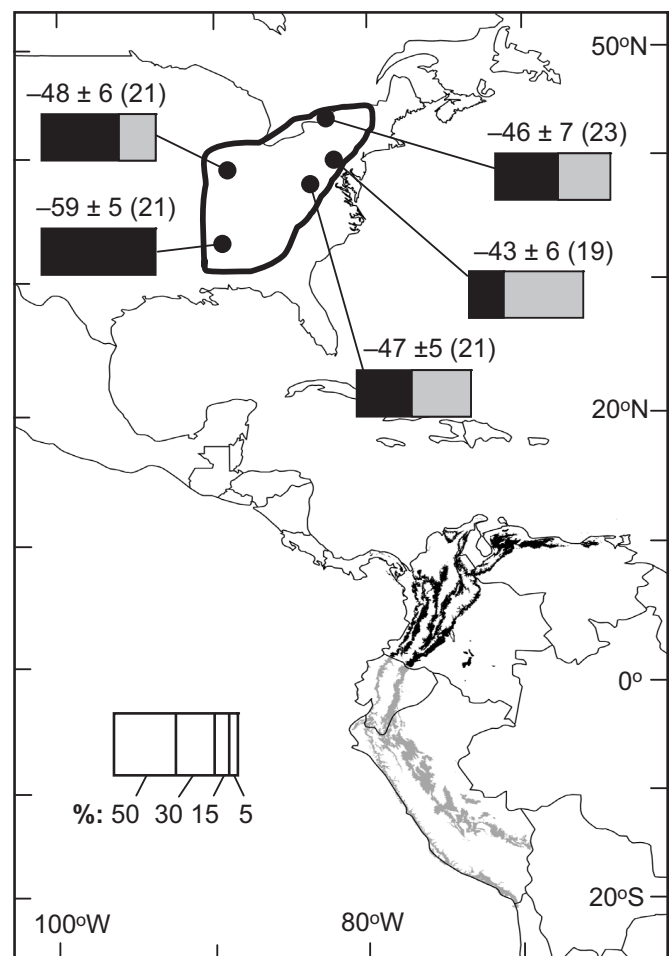


FIGURE 2. Distribution of the most likely wintering location from assignment tests for individual male Cerulean Warblers (ages combined) at each breeding location suggested a parallel migration system in which western breeding populations were connected to southwestern wintering sites and eastern breeding populations were connected to northeastern wintering sites. The proportion of individuals assigned to each wintering region (only areas at 500–1750 m elevation are shown) is indicated by the width of each bar: black = northern range, gray = southern range. The box in the lower left of the panel provides the scale to which the proportions can be compared. Values above bars represent stable-hydrogen isotopic composition (δD) values: mean \pm SD (n). The solid line in North America approximates the breeding range boundary.

As predicted, our results support the hypothesis that the most strongly connected migratory populations are likely to be the most susceptible to population declines (Dolman and Sutherland 1994, Esler 2000). Further work is required to identify the causes of population decline in Cerulean Warblers, but the loss of suitable forested habitats on both the breeding and wintering grounds has been implicated (Hamel 2000). The degree of migratory connectivity may exacerbate the consequences of these habitat losses by limiting the potential for local populations to ‘rescue’ one another at times of low abundance; strongly connected breeding populations tend to receive few immigrants from other breeding

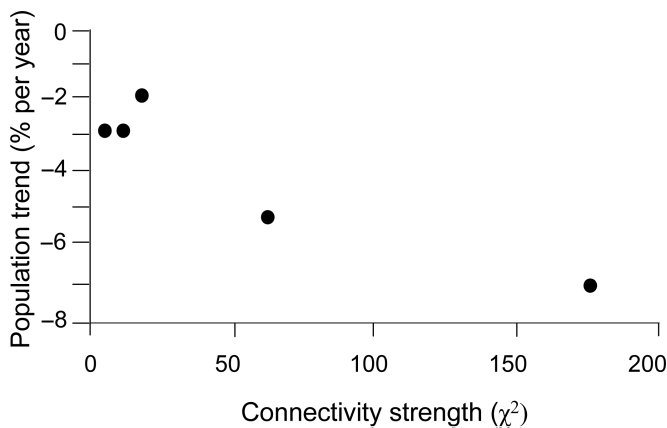


FIGURE 3. Stronger migratory connectivity between the breeding and wintering grounds (as indexed by χ^2 value magnitude) was correlated with greater declines in Cerulean Warbler populations.

populations (Johst et al. 1999). Notably, analysis of both neutral genetic markers and stable-hydrogen isotopes suggests that some Cerulean Warbler populations experience high levels of inter-population dispersal between breeding seasons (Veit et al. 2005, Girvan et al. 2007). Of the two study populations that received few dispersers from other breeding regions, one (Tennessee) exhibited strong connectivity while the other (Ontario) exhibited weak connectivity; the apparent contradiction of low immigration and weak connectivity for Ontario is likely due to the population's position at the northern extreme of the breeding range. It is not yet clear how connectivity between summer and winter seasons and dispersal between breeding seasons are linked. A breeding population in which individuals originate from a number of wintering areas does not necessarily mean that those individuals dispersed from other breeding regions in the previous year. Clearly, further work is needed to understand the link between dispersal and long-distance migration patterns, two of the most difficult life-history traits to study in migratory animals.

While intriguing, these results should be treated as preliminary. First, the South American isotopic base map has only recently been developed; catching birds on the wintering grounds and assigning them to breeding regions would certainly improve the completeness of knowledge of Cerulean Warbler migration patterns, as the North America isotopic base map is more precise. Secondly, we only sampled males. Documenting the migration patterns of females should add valuable information, although available evidence suggests that there are broad similarities in adult male and female wood-warbler migratory patterns (Rubenstein et al. 2002, Norris et al. 2006). Despite these caveats, our results suggest that migratory connectivity is playing an important role in structuring Cerulean Warbler population dynamics. As a consequence, it may be most effective to focus conservation efforts on strongly connected populations, if the management goal is to maximize the number of individuals across this species' range.

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