Research Papers

Long-distance Dispersal Patterns of Male Cerulean Warblers (*Dendroica cerulea*) Measured by Stable-hydrogen Isotopes

Patrons de dispersion sur de longues distances de Parulines azurées mâles (*Dendroica cerulea*) mesurés à l'aide d'isotopes stables d'hydrogène

M. Katherine Girvan [1], *Jason Jones* [2], *D. Ryan Norris* [3], *Jennifer J. Barg* [4], *T. Kurt Kyser* [5], *and Raleigh J. Robertson* [6]

ABSTRACT. Despite the fundamental role played by long-distance dispersal in population dynamics, the mechanisms promoting or inhibiting dispersal by migratory songbirds are poorly understood. We used stable-hydrogen isotopes (δD) to evaluate several hypotheses related to long-distance dispersal in the Cerulean Warbler (*Dendroica cerulea*), a migratory songbird at the center of considerable conservation attention. Feather samples were collected from 103 males throughout the breeding range. We assumed feathers were molted in late summer on the breeding grounds and thus δD values provided an estimate of breeding or hatching location for the previous year. We used a likelihood-based assignment test to estimate the origin of birds the previous year and derived expected δD values for the entire Cerulean Warbler breeding range from precipitation-based maps. Using Bayes' Rule, we also incorporated a prior probability of breeding origin based on estimated rates of site fidelity and survival between breeding seasons. We found that long-distance breeding dispersal by adult male Cerulean Warblers was a fairly common occurrence with 20 of 71 (28.2%) individuals originating from a region other than the one they were sampled in. Surprisingly, long-distance natal dispersal was uncommon; only three of 32 (9.4%) second-year birds were estimated to have hatched in a region outside their capture region. Young males may be using a form of post-fledging prospecting or conspecific attraction when selecting their first breeding habitats. Populations on the breeding range periphery, such as Ontario and Tennessee, tended to receive fewer long-distance dispersers than did other regions but produced more dispersing individuals than did core regions, suggesting that these areas could act as important sources for other regions. The tendency of a region to produce dispersing individuals was not significantly related to its relative abundance, implying that population abundance is not a good indicator of population health for this species. Range-wide variation in long-distance dispersal patterns may contribute to variation in sensitivity to habitat loss and fragmentation, further complicating conservation and management efforts for the Cerulean Warbler.

RÉSUMÉ. En dépit du fait que la dispersion sur de longues distances joue un rôle fondamental dans la dynamique des populations, les mécanismes qui la favorisent ou la freinent sont peu connus chez les passereaux migrateurs. Nous avons utilisé des isotopes stables d'hydrogène (δD) pour tester plusieurs hypothèses en rapport avec la dispersion sur de longues distances de la Paruline azurée, un passereau dont la conservation fait l'objet d'une grande attention. Des échantillons de plumes ont été récoltés sur 103 mâles dans l'ensemble de l'aire de reproduction de l'espèce. Nous présumons que la mue de ces plumes s'est produite à la fin de l'été sur les sites de reproduction et que les valeurs δD fournissent, par conséquent, une estimation du lieu de reproduction ou d'éclosion de l'année précédente. Nous avons utilisé un test d'attribution axé sur la vraisemblance pour estimer le lieu d'origine de l'année précédente des oiseaux et avons calculé les valeurs δD probables pour l'ensemble de l'aire de reproduction de la Paruline azurée à

[1]Sedbergh School, [2]Vassar College, [3]University of Guelph, [4]Upper Valley Humane Society, [5]Dept of Geological Sciences and Geological Engineering, Queen's University, [6]Department of Biology, Queen's University

partir de cartes fondées sur les précipitations. À l'aide du théorème de Bayes, nous avons aussi inclus une probabilité a priori quant au lieu de reproduction de l'année précédente en se basant sur les taux estimés de fidélité au site et de survie entre les saisons de reproduction. Nous avons trouvé que la dispersion sur de longues distances des mâles adultes était assez fréquente : 20 des 71 individus (28,2 %) provenaient ainsi d'une région différente de celle dans laquelle ils avaient été échantillonnés. Étonnamment, la dispersion natale sur de longues distances n'était pas fréquente : nous avons estimé que seulement 3 des 32 oiseaux de deuxième année avaient éclos dans une région différente de celle de leur capture. Les jeunes mâles pourraient utiliser une forme de prospection post-envol ou d'attraction conspécifique au moment de choisir leur premier habitat de reproduction. Les régions à la périphérie de l'aire de reproduction, comme l'Ontario et le Tennessee, ont eu tendance à accueillir moins d'oiseaux qui se sont dispersés sur de longues distances que les autres régions, mais ont produit plus d'individus qui se sont dispersés que l'ont fait les régions situées au cœur de l'aire, ce qui semble indiquer qu'elles pourraient agir comme sources importantes pour les autres régions. La tendance d'une région à produire des individus qui se dispersent n'était pas significativement liée à l'abondance relative de sa population, ce qui suggère que la taille de la population ne représente pas un bon indicateur de l'état de santé de la population pour cette espèce. La variation des patrons de dispersion sur de longues distances dans l'ensemble de l'aire de reproduction peut contribuer à la variation de la sensibilité à la perte et à la fragmentation de l'habitat, ce qui rend, par ailleurs, les efforts de conservation et de gestion pour la Paruline azurée encore plus complexes.

INTRODUCTION

Dispersal is one of the least understood life-history characteristics (Clobert et al. 2001) despite the fact that it is a fundamental component of population dynamics and individual fitness. Determining the frequency and direction of dispersal is critical for the conservation and management of species at risk, especially those with patchy or fragmented distributions (Macdonald and Johnson 2001). In birds, there are several hypotheses that attempt to explain long-distance dispersal patterns related to age, population, and range dynamics.

First, juvenile birds tend to disperse more frequently and further than adults (Greenwood and Harvey 1982, Hansson et al. 2002, Blums et al. 2003; but see Dale et al. 2005). Reasons for this are still not clear but could be because they are not as competitive as more site-faithful adults (Greenwood and Harvey 1982) or because they are avoiding inbreeding (Johnson and Gaines 1990). For migratory birds, juveniles returning to the breeding grounds for their first breeding season might use the presence of conspecifics as an index of habitat quality (Ray and Gilpin 1991, Muller et al. 1997, Stamps 1988, 2001), sort of a "go with what they know" strategy. Alternatively, relatively short natal dispersal distances could be construed as evidence of post-fledging prospecting (Danchin et al. 2001), sort of a "go with what you know" strategy. The distance traveled by natal dispersers may also be related to habitat availability; in regions where habitats are limited, it is reasonable to expect longer natal dispersal distances (Hansson et al. 2002).

Second, spatial and temporal fluctuations in environmental conditions as well as demographic stochasticity can promote dispersal (Hastings 1983, Holt 1985, McPeek and Holt 1992, Holt and McPeek 1996, Johst and Brandl 1999, Holt and Barfield 2001). In species whose geographic ranges are restricted by either resource availability and/or climatic conditions, geographically peripheral populations tend to experience higher spatial and temporal variability in environmental conditions relative to more centrally located populations (Holt and Keitt 2000, Gaston 2003) and, therefore, should be expected to produce more dispersing individuals.

Third, source–sink dynamics theory (Levins 1969, Pulliam 1988, Hanski and Gilpin 1991, Pulliam and Danielson 1991) predicts a net movement of individuals down a productivity gradient; simply put, a population that produces or consists of more individuals produces more potential dispersers.

Population abundance alone might not be sufficient to identify source and sink populations, given that immigration can "artificially" maintain sink populations at high levels of abundance (Pulliam 1988); however, quantifying dispersal within the context of population abundance may provide important information in the identification of productive populations.

Previous studies have demonstrated that stable-hydrogen isotope ratios (δD) in feathers can be used to estimate geographic origins of birds at the time of molt (Chamberlain et al. 1997, Hobson and Wassenaar 1997), and thus could provide insight into dispersal patterns in migratory birds (Meehan et al. 2001, Graves et al. 2002, Hobson et al. 2004, Hobson 2005). Feathers provide an ideal tissue for stable isotope analysis because they retain an isotopic signature after growth. Given that most feathers are only molted once a year, individuals can be sampled in one season to estimate their geographic location in the previous year (Mizutani et al. 1991, Hobson and Clark 1992). The distributions of stable isotopes vary naturally over large scales as a result of physiochemical processes, and these signatures are incorporated into animals through local food webs. In North America, δD values tend to be more negative (deuterium depleted) in the Northwest, and more positive (deuterium enriched) in the Southeast (e.g., Rozanski et al. 1993, Bowen et al. 2005). δD gradients occur as a result of hydrogen isotopic fractionation influenced by factors such as elevation, distance from the coast, and temperature (e.g., Rozanski et al. 1993).

In this paper, we use stable-hydrogen isotopes (δD) in feathers to examine long-distance dispersal patterns in Cerulean Warblers (*Dendroica cerulea*). The Cerulean Warbler is a small (8–10 g), Neotropical migratory songbird that breeds in deciduous forests of eastern North America and winters along the eastern slope of the South American Andes (Hamel 2000). Cerulean Warblers are experiencing one of the fastest rates of decline of any migratory songbird; hierarchical analysis of Breeding Bird Survey (BBS) data from 1966–2006 indicates an average decline of 2.89%/year (J. Sauer, *personal communication*). Factors implicated in their decline include the loss and alteration of suitable mature forest on breeding and wintering grounds, and alteration of migratory stopover habitats (Robbins et al. 1992, Hamel 2000, Committee on the Status of Endangered Wildlife in

Canada (COSEWIC) 2003). For Cerulean Warblers, there are only limited data on life-history characteristics such as dispersal behavior and philopatry (Hamel 2000, Hamel et al. 2004, Jones et al. 2004, Veit et al. 2005). The breeding range of Cerulean Warblers encompasses variation in δD values found in precipitation (International Atomic Energy Agency/World Meteorological Organization (IAEA/WMO) 2001), and thus stable isotope analysis provides a potential method for examining movement patterns in this species. Cerulean Warblers engage molt twice a year, with one complete molt on their breeding grounds beginning in mid-July just before migration and one partial molt on their wintering grounds (replacing crown and body feathers; Pyle 1997). Tail feathers collected from Cerulean Warblers early in the breeding season provide isotopic signatures from the previous year's natal or breeding grounds (but see Norris et al. 2004).

Using δD in feathers, we estimated long-distance dispersal patterns of adult and juvenile male Cerulean Warblers and used this information to evaluate the following hypotheses and predictions. First, if habitat is a limited resource for Cerulean Warblers and adult (after-second-year (ASY)) males are dominant over second-year (SY) males, we predicted higher rates of natal dispersal relative to breeding dispersal. Alternatively, if habitat is not limited or if SY males utilize conspecific attraction and/or post-fledging prospecting to select their first breeding habitat, we predicted little or no difference in natal and breeding dispersal rates. Second, geographically peripheral Cerulean Warbler populations experience stronger fluctuations in climatic variables (e.g., actual evapotranspiration) than do core populations (Jones et al. 2005). Accordingly, we predicted that peripheral Cerulean Warbler populations would generate more dispersing individuals, a prediction that is supported by genetic evidence that suggests gene flow is primarily directed from the northern periphery to more centrally located regions (Veit et al. 2005). Finally, we hypothesized that Cerulean Warbler population size is a reliable indicator of population health and predicted that regions with the highest relative abundance (estimated from BBS data) would be the largest sources of dispersing individuals.

MATERIALS AND METHODS

Sampling Locations

We collected feather samples (outer right retrix; n = 103) from male Cerulean Warblers (CERW) during May–July of 2001, 2002, and 2003 from five regions (four states and one province) across the breeding range (Fig. 1) located within four North American Bird Conservation Initiative Bird Conservation Regions (BCRs): Lower Great Lakes/ Saint Lawrence Plane (BCR 13), Eastern Tallgrass Prairie (BCR 22), Mississippi Alluvial Valley (BCR 26), and Appalachian Mountains (BCR 28). The BCRs are ecologically defined regions in North America that share habitats, bird communities, and resource management issues. We chose to use these BCRs as our analytical units as they are becoming the standard organizational unit for avian conservation in North America.

We captured males in mist nets, luring them with a combination of song playback and model presentation. Females were not included in this study as they rarely respond to playback. We sampled individuals from populations sequentially from south to north to avoid catching migrating birds. No individuals were sampled after mid-July to ensure sampling occurred before the annual pre-basic molt; none of the captured individuals showed evidence of molt. In addition, we are confident that molt-migration of flight feathers is minimal. This assertion is supported by observations at banding stations and by field observations of adults molting flight feathers while feeding non-independent fledglings on the breeding grounds in late July and early August (Jones, *personal observation*; Robert Mulvihill, *personal communication*). Although there are one or two records of Cerulean Warblers molting body feathers in Panama during fall migration (Gabriel Colorado, *personal communication*), there are no records of flight feather molt. We aged individuals as either SY or ASY birds based on plumage coloration (Pyle 1997), tail shape, and molt limits (Mulvihill 1993). Feather samples were stored in glycine or paper envelopes until isotopic analysis.

Isotope Analysis

Stable-hydrogen isotopic ratios are expressed in delta notation in units of ‰ where $\delta = [(R_{sample}/R_{standard})-] \times 1000$, 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 fumehood for 72 h. 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 h 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 (Girvan et al., unpublished 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 2 months. We cut 0.10–0.15 mg from each feather, loaded each sample separately into silver capsules and heated them at 100°C for 24 h to remove potential surface water. After the capsules were crushed with metal tweezers, they were loaded into a reduction furnace (Finnigan TC/EA) 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 kaolinte 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, as well as repeated measurements of feathers, indicates that δD values were reproducible to ±3‰ (Norris et al. 2006).

Statistical Analysis

We used a likelihood-based assignment test to estimate the origin of birds during the previous breeding season (Royle and Rubenstein 2004, Norris et al. 2006). To do this, we first derived expected mean and standard deviation (SD) δD values from an equal-area grid (North American Lambert Equal-Area projection) of long-term average growing season δD_p (growing season = mean temperature >0°C; Bowen et al. 2005) for each BCR region within the Cerulean Warbler breeding range (BCRs: 13, 22, 23, 24, 26, 27, 28, 29). We then adjusted according to isotopic discrimination between δD in feathers (δD_f) and δD_p (-13‰; see Norris et al. 2006 for details). Because some of the mean δD values for each region (denoted as $\delta D_{BCR(i)}$) were similar, we chose to amalgamate some that

Fig. 1. Location of sampling locations (red circles) relative to Bird Conservation Region boundaries. (Source: www.nabci-us-org.)
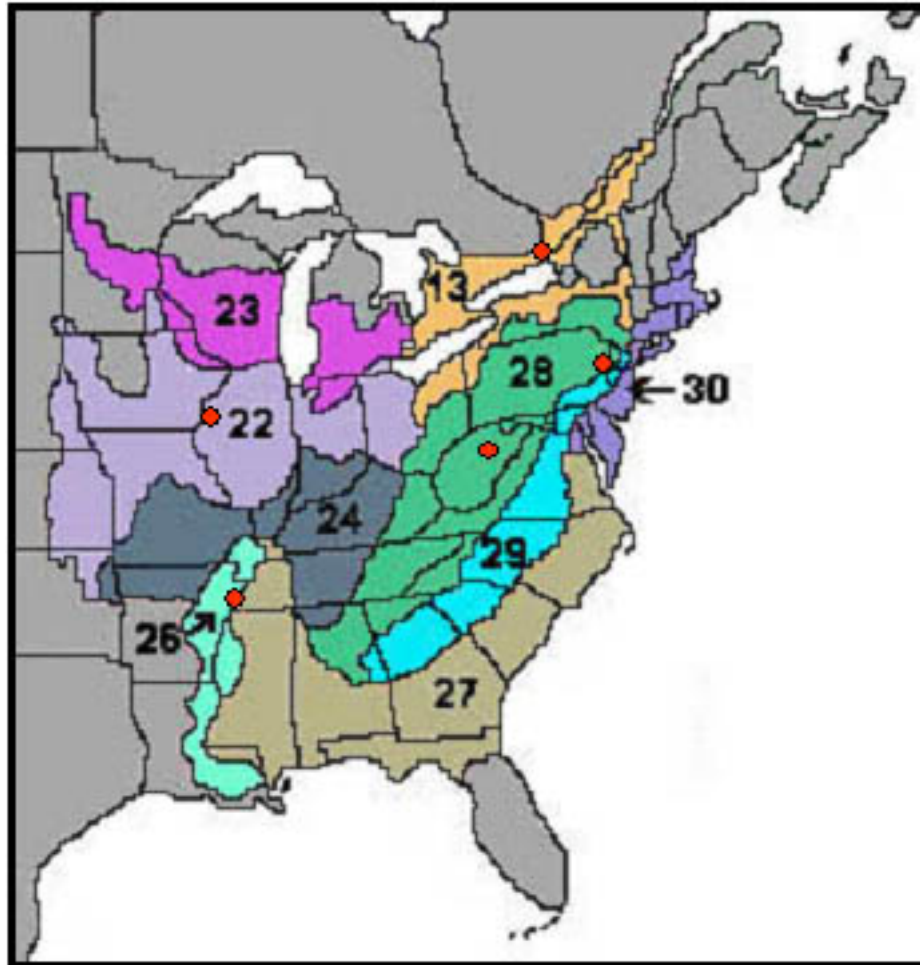
were in close geographic proximity (combined 13 and 23, 22 and 24, 26 and 27, 28 and 29, 30), leaving us with five total regions. For each of these regions, we also obtained regional abundance values from the BBS website (http://www.pwrc.usgs.gov/BBS/); these relative abundance values represent a standardized index of the average number of birds detected per route across all routes detecting a given species in a given time frame (Table 1).

Given mean and SD values for each BCR (considered here as occurring in year t-1), we then calculated the likelihood-based assignments for each individual sampled on the breeding grounds in

year t (δD_{CERW}). The estimated probability distribution of y (where y = $\delta D_{BCR(i)}$ and $BCR_{(i)}$ corresponds to the amalgamated BCR regions: BCR_{13-23}, BCR_{22-24}, BCR_{26-27}, BCR_{28-29}, BCR_{30}) for each region can be expressed by f (y | $BCR_{(i)}$). An individual CERW sampled on the breeding grounds in year t yields a value of y* (where y* = δD_{CERW}) and the likelihood of it originating from a given conservation region can be evaluated by f (y* | $BCR_{(i)}$). Assuming that δD_{CERW} is normally distributed, the likelihood corresponding to y* can, therefore, be written as:

Table 1. Stable-hydrogen isotope values (δD) and BCRmax of Cerulean Warbler breeding origins based on δD values from precipitation and the prior probability of site fidelity (see Methods). Values to left of slash are number of adult (ASY) males, values to right of slash are number of young (SY) males.

Capture Region (year t)	Feather δD values (mean ‰)	Most likely assignments to BCR regions (BCR^max)					Totals	Relative abund-ance
		BCR 13/23	BCR 22/24	BCR 26/27	BCR 28/29	BCR 30		
BCR 13 (ON)	-89/-88	14/8	0/0	0/0	0/0	1/0	15/8	0.08
BCR 22 (IL)	-78/-78	5/0	11/1	0/0	2/0	0/0	18/1	0.12
BCR 28 (PA)	-76/-77	2/0	1/0	0/0	9/7	0/0	12/7	0.01
BCR 28 (WV)	-68/-71	0/0	2/0	4/2	7/6	0/0	13/8	0.48
BCR 26 (TN)	-59/-61	0/0	1/0	10/7	0/1	2/0	13/8	0.12
Totals		21/8	15/1	14/9	18/14	3/0	71/32	

$$f(y^* | BCR_{(i)}) = \frac{1}{\sqrt{2\pi}\sigma_{BCR_{(i)}}} \exp\left[-\frac{1}{2\sigma^2_{BCR_{(i)}}}(y^* - \mu_{BCR_{(i)}})^2\right] \quad (1)$$

Using this approach, a probability of origin for each individual in each BCR can be calculated. For each individual, we considered the most likely breeding origin in year t-1 as the one that had the largest f $(y^* | BCR_{(i)})$. However, we can also consider that each individual sampled in year t had a prior probability of originating from the region where it was originally sampled in year t-1. This is because we have information on the return rates of Cerulean Warblers, at least from one site in Ontario (54% of birds return to breed at the same site they bred the year before; Jones et al. 2004). In this case, f (BCR$_{(i)}$) may be considered a prior probability. That is, in the absence of any information about $\delta D_{BCR(i),}$ the probability that a random individual originates from the same BCR region it was sampled can be estimated as 0.54. Making a conservative estimate that half the birds that do not return have died, we assumed a prior probability of 0.23 (0.446/2) that a given bird will disperse to another BCR region in year t. The probability of dispersing to another BCR region is likely also related to geographic distance from the sampling site, but as BCR regions are irregularly shaped, we chose to leave the remaining regions as "flat" priors. Using the conditional probability f (BCR(i) | y*), f (BCR$_{(i)}$) can be incorporated into the assignment test as a prior probability using Bayes' Rule:

$$f(BCR_{(i)} | y) = \frac{f(y | BCR_{(i)}) f(BCR_{(i)})}{f(y)} \quad (2)$$

Where f (y) is a normalizing constant:

$$f(y) = \sum_{BCR=i}^{BCR} f(y | BCR_{(i)}) f(BCR_{(i)}) \quad (3)$$

Here, f (y | BCR$_{(i)}$) is the likelihood assignment outlined above and f (BCR$_{(i)}$) is the probability of returning to that region (which is a function of where it was originally sampled). For each individual, the assignment test generates probabilities of origin for each region, where the most likely origin (denoted hereafter as BCR^max) is the breeding region with the largest f (BCR$_{(i)}$ | y*). For the 103 males included

in our analyses, the mean assignment test probability was 0.75 ± 0.21 SD.

RESULTS

The δD values of tail feathers varied by ~30‰ across the Cerulean Warbler breeding range (Table 1). The assignment tests revealed several interesting patterns. First, long-distance dispersal by breeding adult male Cerulean Warblers was a fairly common occurrence (Table 1): 20 of 71 (28.2%) breeding adult males lived in a location geographically different than their capture site the year before their capture. Second, long-distance natal dispersal was quite uncommon; only three of 32 SY birds originated (i.e., hatched) in a region outside their capture region (Table 1). Third, populations varied in the number of individuals they receive as immigrants (Fig. 2), ranging from 4% in Ontario to 38% in West Virginia. Fourth, the number of individuals contributed to other populations also varied among BCR regions (Fig. 2), ranging from 13% of dispersers in BCRs 28–29 and 30, to 30% of dispersers in BCRs 13–23. The tendency for a BCR region to act as a source of dispersers was not significantly correlated to the relative abundance of Cerulean Warblers in the region, as estimated from BBS data ($r = -0.46$, $P = 0.43$).

DISCUSSION

Due to the inherent difficulties in following migratory birds between seasons, most dispersal studies have relied predominantly on mark-recapture data (Drilling and Thompson 1988, Lebreton et al. 1993, Powell et al. 2000, Cilimburg et al. 2002). This approach cannot differentiate mortality from dispersal, and may result in an underestimation of survival rates, an important component in monitoring demographic changes (Cilimburg et al. 2002, Jones et al. 2004). Additionally, the ability to detect long-distance dispersal events is often limited by the size of study area, particularly in mobile organisms such as birds (Baker et al. 1995, Cilimburg et al. 2002). Our isotope-based estimates suggest that as many as 28% of ASY males disperse between breeding seasons. These results imply that relying on return rates to estimate male Cerulean Warbler survival (Jones et al. 2004) likely results in substantial underestimates.

Previous studies have used stable isotopes to estimate rates of dispersal (e.g., Hobson et al. 2001, 2004, Graves et al. 2002, Møller et al. 2006), but, to our knowledge, our study is the first to use isotopes to assign individuals to source regions across their breeding range. We also incorporate a prior probability of breeding origin into the likelihood-based assignment tests to estimate dispersal. Admittedly, our estimate of prior probability is somewhat crude (i.e., it is based on a single population's return rate estimate and assumes that half of non-returning birds have dispersed elsewhere) but our results suggest that the incorporation of a prior probability can have an important effect on the posterior distribution. Assignment tests based on likelihood alone identified 51 (49%) potential long-distance dispersal events (unpublished data), as opposed to the 23 (22%) identified incorporating the prior probability. From an analytical perspective, the difference between the outcomes of these two approaches is potentially due to the fact that δD values between some regions were relatively similar. Therefore, birds with δD values that fell within the mean and SD of more than one region could have been assigned to the wrong region. This is the disadvantage of using an intrinsic marker that does not have perfect resolution. The incorporation of site fidelity as a prior probability essentially had the effect of assigning birds that were on the isotopic boundary between two regions to the region in which it was originally sampled. Incorporation of a prior probability, therefore, provides a more conservative estimate of dispersal frequency when used in conjunction with stable isotopes. Another advantage of this approach is that probabilities can be readily improved and updated as life-history data are collected from other breeding populations. We felt that this conservative approach to the assignment tests was also appropriate given our relatively low site-specific sample sizes.

Long-distance natal dispersal was less common than breeding dispersal in male Cerulean Warblers; this result needs to be viewed with some caution given the relatively low numbers of SY individuals captured. Low levels of natal dispersal imply that several mechanisms may be at play, including post-fledging prospecting, which may allow young birds to assess habitat availability before southward migration in the fall (Danchin et al. 2001), and conspecific attraction following northward migration in the spring (Stamps 1988, 2001). More research is needed to differentiate between these two options;

Fig. 2. Percentage of immigrants originating from outside a BCR region (white bars) and the percentage of dispersers contributed by a BCR region (black bars) from BCRmax values (see Methods). The BCRs are arranged in an approximately North–South direction from left to right.
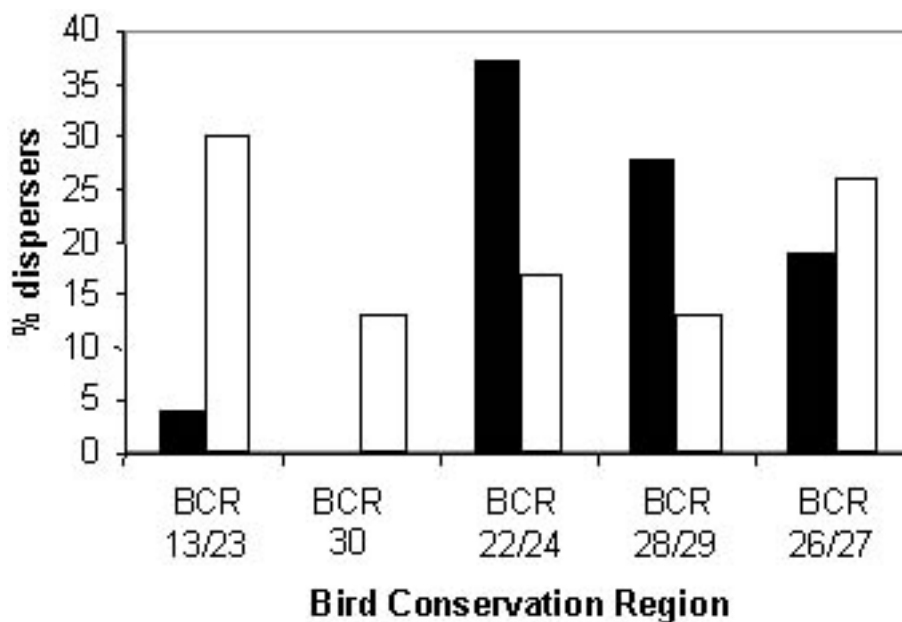
however, for either to be responsible for the observed low rates of long-distance natal dispersal, Cerulean Warbler breeding habitat cannot be limiting at a local scale. Additional evidence of natal site philopatry is available from banding data from an Ontario Cerulean Warbler population. Although sample sizes are small, return rates suggest natal site philopatry may be relatively high in this species; a total of 20 Cerulean Warbler nestlings have been banded on the Ontario study plot at the Queen's University Biological Station, of which three have returned to the study site in subsequent years (Barg et al., unpublished data). Data for other *Dendroica* warblers imply far lower rates of natal philopatry (e.g., Black-throated Blue Warblers, Holmes (1994)).

In general, mechanisms promoting long-distance adult breeding dispersal are not well understood. Variables thought to promote high rates of breeding dispersal include poor reproductive success (Doligez et al. 1999, Daniels and Walters 2000, Sedgwick 2004), high predation risk (Weisser 2001), individual quality (Ims and Hjermann 2001),

and low territory quality (Montalvo and Potti 1992, Stanback and Rockwell 2003). In many songbirds, reproductive success increases with age, thus Cerulean Warblers may show relatively high natal site fidelity but, if unsuccessful in their first breeding attempt, may disperse to other regions as ASY adults. Our samples from Ontario came from a population of Cerulean Warblers that have been intensively studied for the last 12 years at the Queen's University Biological Station (QUBS) in southeastern Ontario. Each season, researchers have attempted to band all males holding territories on a 23-ha study plot and surrounding forest patches. Despite these yearly intensive banding efforts, between 40%–70% of ASY males found on the study plot each spring were not banded (Jones et al. 2004). Results from this study suggest that most of these unbanded birds may represent relatively local recruitment at a spatial scale too narrow to be detected from δD analysis, and that only a few (one in this study) are long-distance immigrants. Given the tendency of adult Cerulean Warblers to cluster their breeding territories (Robbins et al. 1992, Roth and Islam 2007), it is likely that conspecific

attraction is also used by adults when selecting new breeding habitats.

As predicted, populations on the periphery of the breeding range, such as Ontario and Tennessee, are acting as sources of dispersing individuals for populations in the core of the range. This finding has two main implications. First, it supports observations that peripheral environmental conditions are somewhat distinct from and may be more variable than those in the core of the range (Jones et al. 2001, 2005). Second, it counters earlier findings suggesting that the Ontario population was not reproducing at replacement levels and was likely not a source population (Jones et al. 2004); the results of our current study indicate that Jones et al. (2004) significantly underestimated adult male survival due to breeding dispersal. Taken in combination, these observations underscore the potential importance of conserving peripheral populations (Hunter and Hutchison 1994, Lesica and Allendorf 1995) and of adopting regional population models for Cerulean Warblers (Rogers 2006).

Finally, the tendency of a population to act as a source was not positively related to relative abundance, contrary to our predictions. Even with our limited sample of breeding populations, this suggests that Cerulean Warbler population abundance is not a good indicator of population health or habitat quality, thereby limiting the utility of population abundance as a metric of success for management and conservation strategies. If individuals are using the presence of conspecifics as habitat-selection cues, a possibility raised by our estimate of low natal dispersal, regions of high population abundance have the potential to act as ecological traps for dispersing Cerulean Warblers, particularly in the core of the breeding range.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss2/art3/responses/

LITERATURE CITED

Baker, M., N. Nur, and G. R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wrentits. *Condor* **97**:663–674.

Blums, P., J. D. Nichols, J. E. Hines, M. S. Lindberg, and A. Mednis. 2003. Estimating natal dispersal movement rates of female European ducks with multistate modelling. *Journal of Animal Ecology* **72**:1027–1042.

Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* **143**:337–348.

Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Fend, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* **109**:132–141.

Cilimburg, A. B., M. S. Lindberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probability of adult yellow warblers (*Dendroica petechia*). *Auk* **119**:778–789.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. 2001. *Dispersal.* Oxford University Press, Oxford, UK.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2003. COSEWIC Assessment and update status report on the Cerulean Warbler *Dendroica cerulea* in Canada. COSEWIC, Ottawa, Ontario, Canada.

Dale, S., A. Lunde, and O. Steifetten. 2005. Longer breeding dispersal than natal dispersal in the ortolan bunting. *Behavioral Ecology* **16**:20–24.

Danchin, E., D. Heg, and B. Doligez. 2001. Public information and breeding habitat selection. Pages 243–258 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.

Daniels, S. J., and J. R. Walters. 2000. Dispersal and inbreeding in Red-cockaded Woodpeckers. *Condor* **102**:482–491.

Doligez, B., E. Danchin, J. Clobert, and L. Gustafsson. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* **68**:1193–1206.

Drilling, N.E., and C. F. Thompson. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *Auk* **105**:480–491.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges.* Oxford University Press, Oxford, UK.

Graves, G. R., C. S. Romanek, and A. R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proceedings of the National Academy of Sciences USA* **99**:8096–8100.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**:1–21.

Hamel, P. B. 2000. Cerulean Warbler (*Dendroica cerulea*). Number 511 *in* A. Poole and F. Gill, editors. *Birds of North America.* Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists' Union, Washington, D.C., USA. [online] URL: http://bna.birds.cornell.edu/BNA/.

Hamel, P. B., D. K. Dawson, and P. D. Keyser. 2004. How we can learn more about the Cerulean Warbler (*Dendroica cerulea*). *Auk* **121**:7–14.

Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.

Hansson, B., S. Bensch, D. Hasselquist, and B. Nielsen. 2002. Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia* **130**:536–542.

Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? *Theoretical Population Biology* **24**:244–251.

Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions* **11**:157–164.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. *Condor* **94**:181–188.

Hobson, K. A., K. P. McFarland, L. I. Wassenaar, C. C. Rimmer, and J. E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. *Auk* **118**:17–23.

Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* **109**:142–148.

Hobson, K. A., L. I. Wassenaar, and E. Bayne. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with Ovenbirds and American Redstarts. *Condor* **106**:732–743.

Holmes, R. T. 1994. Black-throated Blue Warbler (*Dendroica caerulescens*). Number 87 *in* A. Poole and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists' Union, Washington, D.C., USA. [online] URL: http://bna.birds.cornell.edu/BNA/.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an

optimal habitat distribution. *Theoretical Population Biology* **28**:181–208.

Holt, R. D., and M. Barfield. 2001. On the relationship between the ideal free distribution and the evolution of dispersal. Pages 83–95 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.

Holt, R. D., and T. Keitt. 2000. Alternative causes for range limits: a metapopulation perspective. *Ecology Letters* **3**:41–47.

Holt, R. D., and M. A. McPeek. 1996. Chaotic population dynamics favors the evolution of dispersal. *American Naturalist* **148**:709–718.

Hunter, M. L. Jr., ad A. Hutchinson. 1994. The virtue and shortcomings of parochialism: conserving species that are locally rare, but globally common. *Conservation Biology* **8**:1163–1165.

Ims, R. A., and D. Ø. Hjermann. 2001. Condition-dependent dispersal. Pages 203–216 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.

International Atomic Energy Agency/World Meteorological Organization (IAEA/WMO). 2001. Global network for isotopes in precipitation, the GNIP database.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* **21**:449–480.

Johst, K., and R. Brandl. 1999. Natal versus breeding dispersal: evolution in a model system. *Evolutionary Ecology Research* **1**:911–921.

Jones, J., J. J. Barg, T. S. Sillett, M. L. Veit, and R. J. Robertson. 2004. Minimum estimates of survival and population growth for Cerulean Warblers breeding in Ontario, Canada. *Auk* **121**:15–22.

Jones, J., R. D. DeBruyn, J. J. Berg, and R. J. Robertson 2001. Assessing the effects of a natural disturbance on a Neotropical migrant songbird. *Ecology* **82**:2628–2635.

Jones, J., C. E. Gibb, S. C. Millard, J. J. Barg, M. K. Girvan, M. L. Veit, V. L. Friesen, and R. J.

Robertson. 2005. Multiple selection pressures general adherence to Bergmann's rule in a Neotropical migratory songbird. *Journal of Biogeography* **32**:1827–1833

Lebreton, J. D., R. Pradel, and J. Clobert. 1993. The statistical analysis of survival in animal populations. *Trends in Ecology and Evolution* **8**:91–95.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? *Conservation Biology* **9**:753–760.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.

Macdonald, D. W., and D. D. P. Johnson. 2001. Dispersal in theory and practice: consequences for conservation biology. Pages 358–372 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* **140**:1010–1027.

Meehan, T. D., C. A. Lott, Z. D. Sharp, R. B. Smith, R. N. Rosenfield, A. C. Stewart, and R. K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. *Condor* **103:**11–20.

Mizutani, H., Y. Kabaya, and E. Wada. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. *Isotopenpraxis* **27**:166–168.

Møller, A. P., K. A. Hobson, T. A. Mousseau, and A. M. Peklo. 2006. Chernobyl as a population sink for barn swallows: tracking dispersal using stable-isotope profiles. *Ecological Applications* **16**:1696–1705.

Montalvo, S., and J. Potti. 1992. Breeding dispersal in Spanish pied flycatchers *Ficedula hypoleuca*. *Ornis Scandinavica* **23**:491–498.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willis. 1997. The effects of conspecific

attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* **150**:650–661.

Mulvihill, R. S. 1993. Using wing molt to age passerines. *North American Bird Bander* **18**:1–7.

Norris, D. R., P. P. Marra, T. K. Kyser, R. Montgomerie, and L. M. Ratcliffe. 2004. Reproductive effort, molting latitude and feather color in a migratory songbird. *Science* **306**:2249–2250.

Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). *Ornithological Monographs* **61**:29–70.

Powell, L. A., M. J. Conroy, J. E. Hines, J. D. Nichols, and D. G. Krementz. 2000. Simultaneous use of mark-recapture and radio-telemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* **64**:302–313.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* **137**: S50–S66.

Pyle, P. 1997. *Identification guide to North American birds. Part1.* Slate Creek Press, Bolinas, California.

Ray, C., and M. Gilpin. 1991. The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society* **42**:123–142.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea.* Pages 549–562 *in* J.M. Hagan, III, and D.W. Johnston, editors. *Ecology and conservation of Neotropical migrant landbirds.* Smithsonian Institution Press, Washington, D.C.

Rogers, C. M. 2006. Nesting success and breeding biology of Cerulean Warblers in Michigan. *Wilson Journal of Ornithology* **118**:145–151.

Roth, K. L., and K. Islam. 2007. Do Cerulean Warblers (*Dendroica cerulea*) exhibit clustered territoriality? *American Midland Naturalist* **157**:345–355.

Royle, J. A., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* **14**:1780–1788.

Rozanski, K., L. Araguas-Araguas, and R. Gonfiantini. 1993. Isotopic patterns in modern global precipitation. *Geophysical Monographs* **78**:1–36.

Sedgwick, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *Auk* **121**:1103–1121.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* **131**:329–347.

Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate versus ultimate approaches. Pages 230–242 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.

Stanback, M. T., and E. K. Rockwell. 2003. Nest-site fidelity in Eastern Bluebirds (*Sialia sialis*) depends on the quality of alternative cavities. *Auk* **120**:1029–1032.

Veit, M. L., R. J. Robertson, P. B. Hamel, and V. L. Friesen. 2005. Population genetic structure and dispersal across a fragmented landscape in cerulean warblers (*Dendroica cerulea*). *Conservation Genetics* **6**:159–174.

Wassenaar, L. I., and K. A. Hobson. 2000. Stable carbon and hydrogen isotope ratios reveal breeding origins of Red-winged Blackbirds. *Ecological Applications* **10**:911–916.

Weisser, W. W. 2001. The effects of predation on dispersal. Pages 180–188 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal.* Oxford University Press, Oxford, UK.