BIODIVERSITY RESEARCH

Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird

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ABSTRACT

Aim Measuring dispersal is crucial for estimating demographic rates that inform conservation plans for rare and threatened species. We evaluated natal dispersal patterns in Bicknell's thrush (*Catharus bicknelli*) across most of the breeding range using a 10-year data set of stable-hydrogen isotope ratios in feathers (δ^2H_F) grown on the natal area and sampled 1 year later at the first breeding site.

Location North-eastern United States and south-eastern Canada.

Methods We used δ^2H_F values of adult thrushes sampled at 25 breeding sites as prior information for assigning first-time breeders to their natal site. We calculated the minimum distance birds moved from their natal to first breeding site and fit these data to three statistical distributions for characterizing the importance of long-distance dispersal: the exponential, Weibull and half-Cauchy. Finally, we assessed differences in the probability of dispersal across the breeding range and through time to understand spatio-temporal variation in demographic connectivity.

Results The δ^2H_F values of first-time breeders were lower compared with those of adults, a difference that was greater at the southern compared with northern breeding range extreme. Assignment tests accounting for age differences in δ^2H_F suggested that most birds dispersed < 200 km from their natal area and within the centre of the breeding range, whereas comparatively few individuals dispersed up to 700 km. A Weibull distribution provided the best fit to these data. Two of three corrections for age differences in δ^2H_F indicated that natal dispersal probability declined by 30–38% from 1996 to 2005.

Main conclusions Our findings suggest that estimating natal dispersal with δ^2H_F measurements may contribute to understanding the resilience of geographically isolated Bicknell's thrush populations. Declining natal dispersal may be symptomatic of observed population declines and could compound this trend by limiting demographic exchange between habitat patches predicted to be increasingly isolated by natural and anthropogenic habitat changes.

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INTRODUCTION

Dispersal plays a fundamental role in many ecological and evolutionary processes. In recent years, theoretical models have focused on the importance of dispersal for metapopulation persistence (Ovaskainen & Hanski, 2004), metacommunity structure (Leibold *et al.*, 2004) and range expansion (Phillips *et al.*, 2010). Despite these contributions, dispersal remains one of the most poorly understood life history traits because the complete distribution of dispersal distances is so difficult to measure empirically. Common methods, such as mark–recapture techniques, are useful for documenting relatively short-distance dispersal, but are poorly suited to detecting long-distance dispersal beyond study area boundaries (Koenig *et al.*, 1996; Nathan *et al.*, 2003). Overcoming this limitation is an important challenge in applied ecology because long-distance dispersal estimates are key to understanding how organisms will respond to habitat loss and other environmental changes (Trakhtenbrot *et al.*, 2005). Quantifying dispersal estimates is especially important for rare or threatened species whose persistence may depend in part on movement dynamics among isolated habitat patches.

Although long-distance dispersal comprises a small fraction of the overall dispersal distribution, it can have a disproportionate effect on the genetic structure and dynamics of populations (Hanksi, 1999; Clobert *et al.*, 2001). Dispersal is probably the most important contributor to gene flow; thus, long-distance dispersal plays a central role in determining the scale of local adaptation and the extent of genetic variation among subpopulations (Lenormand, 2002). Long-distance dispersal facilitates colonization of new habitats during range expansion, particularly when the distribution of suitable habitat is patchy or ephemeral. Importantly, even when long-distance dispersal rates are sufficient to promote genetic mixing, they may be too low to prevent subpopulations from functioning as demographically discreet units with divergent growth trajectories (Lowe & Allendorf, 2010). Long-distance dispersal also can be a key determinant of whether species undergo range shifts as part of an adaptive response to land cover change or other environmental disturbances that alter the availability of suitable habitat on the landscape (Wiegand *et al.*, 1999; Trakhtenbrot *et al.*, 2005).

In many animal species, natal dispersal distances exceed those of adults (Gaines & McClenaghan, 1980; Paradis *et al.*, 1998; Semlitsch, 2008). For adults, fidelity to breeding sites may enhance future reproductive success through the acquisition of social information about local habitat suitability or conspecific competitors (Doligez *et al.*, 2002; Nocera *et al.*, 2006). Although juveniles might also benefit from breeding in familiar locations near the natal site, several life history constraints are thought to favour natal dispersal. For example, females of many bird species may disperse away from the natal site to reduce the risk of inbreeding depression (Greenwood & Harvey, 1982), whereas males of some mammals are thought to disperse to reduce the probability of kin competition for territories (Bowler & Benton, 2005). Such

pressures to disperse can vary temporally owing to changes in habitat quality associated with density dependence or habitat degradation (Pasinelli *et al.*, 2004). Recent evidence suggests that long-term changes in climate also can mediate these effects on dispersal propensity, potentially by altering food supply (Møller *et al.*, 2006).

New technologies such as daylight-level geolocators have revolutionized the study of seasonal movements in small, passerine birds (Stutchbury *et al.*, 2009; Conklin *et al.*, 2010). Despite the ability of these devices to track individuals across the annual cycle, they are of limited use for studying long-distance dispersal because individuals must be recaptured to acquire data. For migratory birds, the use of endogenous markers such as stable isotopes remains one of the most successful techniques for characterizing long-distance dispersal (Hobson, 2005; Studds *et al.*, 2008). In North America, stable-hydrogen isotope ratios in growing season precipitation (δ^2H_P) show a strong north-south gradient and correlate strongly with δ^2H of locally grown tissues, especially in the eastern region of the continent (Hobson & Wassenaar, 1997). In many species, juvenile birds grow their feathers in the nest and adults moult their flight feathers in late summer on or close to the nesting site (Pyle, 1997). Stable-hydrogen isotope values in feathers (δ^2H_F) sampled from birds arriving for their first breeding attempt can therefore provide information about dispersal distance from the natal site (Hobson *et al.*, 2004; Studds *et al.*, 2008). Unlike daylight-level geolocators, birds need to be captured only once to obtain information about dispersal.

Bicknell's thrush is a long-distance, Neotropical–Nearctic migratory bird and is one of the rarest breeding passerines in North America, classified as globally 'vulnerable' by the International Union for the Conservation of Nature (IUCN; BirdLife International 2004) and 'threatened' in Canada (COSEWIC, 2009). Bicknell's thrush occupies a restricted, naturally fragmented range throughout its annual cycle and faces multiple threats, including habitat loss on the non-breeding grounds in Hispaniola (Rimmer *et al.*, 2005a), mountaintop development (Strong *et al.*, 2002), mercury contamination (Rimmer *et al.*, 2005b), commercial forestry (Chisholm & Leonard, 2008), acid ion deposition (Graveland & vanderWal, 1996; Hames *et al.*, 2002) and climate change (Rodenhouse *et al.*, 2008). From 1993 to 2003, a core breeding population of Bicknell's thrush in White Mountain National Forest declined by 7% per year along 40 survey routes and was estimated to contain as few as 4900 individuals (Hale, 2006; King *et al.*, 2008; Lambert *et al.*, 2008). Monitoring in Atlantic Canada from 2002 to 2010 indicated annual declines of 11–16%, and annual surveys at Mont Gosford, Quebec from 2001 to 2007 revealed a pronounced reduction in the number of sites occupied (COSEWIC, 2009; Campbell, 2011). Quantifying the complete distribution of dispersal distances is likely to be important for refining conservation plans for this species of concern.

We analysed δ^2H_F values of Bicknell's thrush captured during their first breeding season from 1996 to 2005 to evaluate

patterns of natal dispersal across the majority of the breeding range. We used δ^2H_F values of adult thrushes (i.e. those with at least one previous breeding season) sampled at 25 montane breeding sites in the north-eastern United States and southern Canada as prior information for assigning first-time breeders to their natal site. We calculated the minimum distance that birds could have moved from their natal to first breeding site and fit these data to three common statistical distributions for characterizing the importance of long-distance dispersal: the exponential, Weibull and half-Cauchy. Finally, we assessed differences in the probability of dispersal across the breeding range and through time to understand spatio-temporal variation in how isolated populations of this species are demographically connected.

METHODS

Bicknell's thrush feather samples were collected from 1996 to 2005 at 25 montane forest breeding sites in the north-eastern United States and south-eastern Canada. These sites were dominated by dense stands of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), white birch (*Betula papyrifera*) and mountain ash (*Sorbus americana*) and ranged in elevation from 340 to 1400 m. Birds were captured in mist nets, aged and sexed using criteria from Pyle (1997) and Collier & Wallace (1989), banded with a unique combination of plastic colour and United States Geological Survey (USGS) or Canadian Wildlife Service (CWS) aluminium leg bands, and released. One tail feather was removed from each bird before release and stored in a glassine envelope for return to the laboratory.

Isotope analyses were performed at the Isotope Hydrology and Ecology Laboratory of Environment Canada in Saskatoon, Canada. Feathers were washed in a 2:1 chloroform/ methanol solution to remove surface oils and air-dried for 48 h. Because feather analysis spanned a substantial time period, two different methods were used to account for the fraction of H in feathers that exchanges with ambient water vapour. From 1996 to 1999, feather samples were individually equilibrated with steam under controlled conditions prior to isotope analysis as fully described in Wassenaar & Hobson (2000). From 2000 to 2005, non-exchangeable H was determined by linear regression with previously calibrated in-house keratin standards (Wassenaar & Hobson, 2003). Feather samples were packed in silver capsules, transferred to an autosampler and pyrolized at 1450°C to a single pulse of H_2 gas in an elemental analyser (EA3000; EuroVector, Milan, Italy). The H_2 sample pulse was then introduced to an isotope ratio mass spectrometer (Micromass Isoprime; Micromass, Manchester, England) via an open-split capillary. We report δ^2H_F of non-exchangeable H in per mil units (‰) relative to the Vienna Standard Mean Ocean Water Standard-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale. Because the same keratin laboratory standards were used in both analytical procedures, the results are directly comparable; however, analytical error was higher before 2000 (± 4‰) compared with after (± 2‰).

We used a model developed by Royle & Rubenstein (2004) to assign 192 first-time breeders to their natal origin where the likelihood that each δ^2H_F value, $y*$, originates from a given natal location is

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

and μ_b and σ_b are the mean and standard deviation of expected δ^2H_F values in each location. The model thus explicitly incorporates prior information about isotopic variation across the landscape to predict a posterior probability of origin for each δ^2H_F measurement. We used δ^2H_F values of 500 adults to develop prior information about the predicted isotopic composition of breeding sites from which dispersing thrushes could have fledged. Mark–recapture analyses comprising 19 years of data from across the breeding range indicate fairly high annual survival ($\phi = 0.68 \pm 0.06$ SE, 95% CI: 0.56–0.78) and recapture probabilities (males: $P = 0.75 \pm 0.03$ SE, 95% CI: 0.69–0.80; females: $P = 0.62 \pm 0.05$ SE, 95% CI: 0.52–0.71), suggesting that adult site fidelity is considerable. Adult δ^2H_F values therefore provided a reasonable approximation of δ^2H_P values at each breeding site. To directly evaluate whether adult δ^2H_F values predicted local isotopic conditions, we acquired independently modelled data on amount-weighted growing season δ^2H_P (Bowen et al., 2005; http://www.waterisotopes.org) and compared them using least-squares regression.

Values of δ^2H_P change across altitude in a similar manner to latitude (Bowen et al., 2005), and the spruce-fir habitat used by thrushes occurs across an elevational gradient throughout the breeding range. To directly examine how potential variation in the altitude of moult could have affected adult δ^2H_F priors, we first calculated the difference in elevation between each montane study site and the lower limit of spruce-fir habitat. We used these data to estimate the expected difference in adult δ^2H_F at each site based on a world-wide trend of a 2.2‰ change in δ^2H_P for every 100 m of altitude (Poage & Chamberlain, 2001). We then averaged these estimates weighted by the sample size of δ^2H_F at each site. The resulting value thus reflected the maximum expected effect on δ^2H_F priors if adults moulted feathers at the altitudinal extremes of suitable breeding habitat.

Previous research has shown that δ^2H_F values can vary by age in birds, with recently fledged hatch-year individuals and nestlings showing lower values than adults (Cooper's hawk: Meehan et al., 2003; American redstart: Langin et al., 2007; Ovenbird: Haché et al., 2012). Potential explanations for this pattern include isotopic enrichment of the adult water body pool owing to higher metabolic rate and subsequent evaporative cooling (McKechnie et al., 2004), differences in dietary routing of macronutrients by nestlings (Langin et al., 2007) or seasonal variation in the timing of feather growth (Hobson, 2008). This trend could have biased our assessment of natal dispersal because first-time breeders could appear to originate from further north than

their true site of origin. Prior to making assignments, we therefore evaluated age-related patterns in $\delta^2 H_F$ by comparing values of adults, first-time breeders and recently fledged hatch-year birds. If necessary, we then adjusted the $\delta^2 H_F$ value of each first-time breeder to account for any systematic depletion relative to adults.

We evaluated age-related differences in $\delta^2 H_F$ values using a general linear model with age of each thrush as a fixed effect and made post hoc comparisons among the three age-classes with Tukey's HSD. We assessed variation in the direction of natal dispersal and differences between males and females by using Pearson's chi-square test. To assess whether the probability of natal dispersal varied spatially across the breeding range and whether it changed across the 10-year study period, we fit a generalized linear model that included latitude of the assigned natal origin and year as fixed effects. Because long-term study sites in Vermont were the only locations monitored for the full 10-year duration of the study, our analysis of temporal change in dispersal probability across the breeding range could be heavily influenced by patterns at these areas. Therefore, we used the approach described above to conduct a separate analysis of annual variation in dispersal probability on the subset of sites in Vermont. Our estimates of temporal change in dispersal probability would be flawed if adult $\delta^2 H_F$ values used as priors also varied over time. We therefore examined temporal change in adult $\delta^2 H_F$ by fitting a linear mixed model with year as a fixed effect. We specified random intercepts for breeding region and random slopes for year because feather sample sizes in each region varied over the study. To test the year effect, we fit a second model without this variable and compared the two models with a likelihood ratio test with 1 d.f.

We used ARCGIS software (ESRI, Redlands, CA, USA) to calculate the minimum linear distance that thrushes could have dispersed between the natal area and site of capture during their first breeding attempt. We then fit these data to three statistical distributions commonly used to characterize the relative importance of long-distance dispersal movements: the exponential, Weibull and half-Cauchy (Paradis *et al.*, 2002). The exponential distribution was expected to provide the best fit to the data if natal dispersal showed a geometric decline with increasing distance from the natal area. The half-Cauchy distribution was expected to provide the best fit if the data exhibited a heavy tail of infrequent long-distance natal dispersal movements. Finally, the Weibull distribution was expected to provide the best fit if long-distance dispersal occurred with greater frequency at the right tail than under the half-Cauchy. We fit the data on dispersal distance to each distribution with maximum likelihood and selected the one that provided the best fit by using Akaike's Information Criteria weights (AICw). All analyses were performed with the stats package in program R 2.14 (R Development Core Team, 2011) except for the assessment of temporal variation in adult $\delta^2 H_F$, which was performed with package lme4 (Bates *et al.*, 2011), and distribution fitting,

which was performed with the bbmle package (Bolker & R Development Core Team, 2011).

RESULTS

The 500 $\delta^2 H_F$ values of adult Bicknell's thrush captured at 25 montane breeding sites from 1996 to 2005 were strongly correlated with amount-weighted growing season $\delta^2 H_P$ values ($r^2 = 0.563$, $P < 0.001$, $n = 500$; Bowen *et al.*, 2005). To improve accuracy of assignment tests, we combined breeding sites with similar adult $\delta^2 H_F$ values, resulting in six breeding regions from which dispersing thrushes could have originated: the Catskill Mountains of New York ($-57 \pm 13\%$; mean $\pm$ SD), southern Vermont ($-64 \pm 12\%$), the Adirondacks and northern New England ($-74 \pm 9\%$), southern Quebec ($-83 \pm 7\%$), New Brunswick ($-89 \pm 18\%$) and the Gaspé Peninsula of Quebec ($-100 \pm 10\%$; Fig. 1). Because $\delta^2 H_F$ values vary in relation to latitude but not longitude, some montane sites that were grouped into a single breeding region showed considerable longitudinal spread, particularly in northern New England and the Gaspe Peninsula. See Table S1 in Supporting Information for the distribution of adult $\delta^2 H_F$ sample sizes among the six breeding regions.

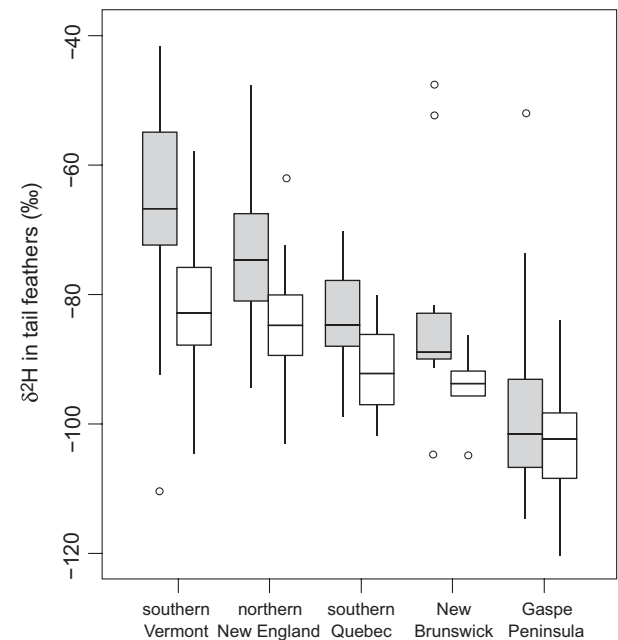**Figure 1** Median, quartiles, range and outliers of $\delta^2 H_F$ for Bicknell's thrush captured at 25 montane breeding sites across the breeding range in the north-eastern United States and Canada from 1996 to 2005. Sites with similar adult $\delta^2 H_F$ values were grouped to define six breeding regions (grey bars) that yielded prior information for assigning $\delta^2 H_F$ values of first-time breeders (white bars) to natal areas. Differences between $\delta^2 H_F$ of adults and first-time breeders were lowest at northern latitude sites and highest at southern ones, with a minimum difference of 6‰ in the north, a mean difference of 12‰ and maximum difference of 18‰ in the south.

The mean elevational difference between montane breeding sites and the lower spruce-fir ecotone boundary on each peak was 252 m. Because $\delta^2 H_P$ values vary world-wide by a mean of 2.2‰ for every 100-m change in altitude (Poage & Chamberlain, 2001), 5.5‰ of the variance in adult $\delta^2 H_F$ priors potentially could be accounted for by elevational differences in feather growth.

Comparison of $\delta^2 H_F$ values among age-classes revealed substantial variation ($F_{3,725} = 47.93$, $P < 0.001$; Fig. 1). The $\delta^2 H_F$ values of adult thrushes were more positive compared with those of both first-time breeders (Tukey's HSD: $P < 0.001$) and hatch-year birds (Tukey's HSD: $P < 0.001$). In contrast, first-time breeders and hatch-year birds had similar $\delta^2 H_F$ values (Tukey's HSD: $P = 0.945$). On average, $\delta^2 H_F$ values of first-time breeders were 12‰ more negative than those of adults; however, isotopic variation between age groups was more pronounced at the southern compared with the northern part of the breeding range (Fig. 1). The $\delta^2 H_F$ values of first-time breeders in southern Vermont were lower by 18‰ compared with adults, whereas those at the northern end of the breeding range were lower by only 6‰. To account for this variation across latitude, we adjusted $\delta^2 H_F$ values of first-time breeders by the mean (12‰), northern minimum (6‰) and southern maximum (18‰) and assigned birds to their potential natal origin under all three

scenarios. Although this approach introduced substantial uncertainty to our analyses, it was preferable to performing a single correction that would yield one estimate of each dispersal parameter and thus fail to reflect the extent of variation in the data. Performing assignments under the 6‰ northern minimum and 18‰ southern maximum enabled us to depict the complete range of uncertainty in dispersal around the 12‰ mean. We report the results of these assignments as the 12‰ mean (6–18‰ range).

Of the 192 Bicknell's thrush sampled for $\delta^2 H_F$ during their first breeding season, 59% (56–62%) were classified as dispersing away from their natal region and 41% (38–44%) were classified as faithful to their natal region (Fig. 2). See Table S1 in Supporting Information for the distribution of first-time breeder $\delta^2 H_F$ sample sizes among the six breeding regions. Males and females dispersed with similar frequency (58% [53–58%] of males and 56% [56–61%] of females; $\chi^2 = 0.04$, $P = 0.998$). The geographical direction of natal dispersal varied depending on the offset used to account for the lower $\delta^2 H_F$ values of first-time breeders. Based on the 12‰ mean offset, there was no discernable pattern in the direction of natal dispersal (47% northerly and 53% southerly; $\chi^2 = 0.04$, $P = 0.842$). Under the 6‰ minimum offset, southern natal dispersal movements were more common than northern movements (17% southern and 80% northern;
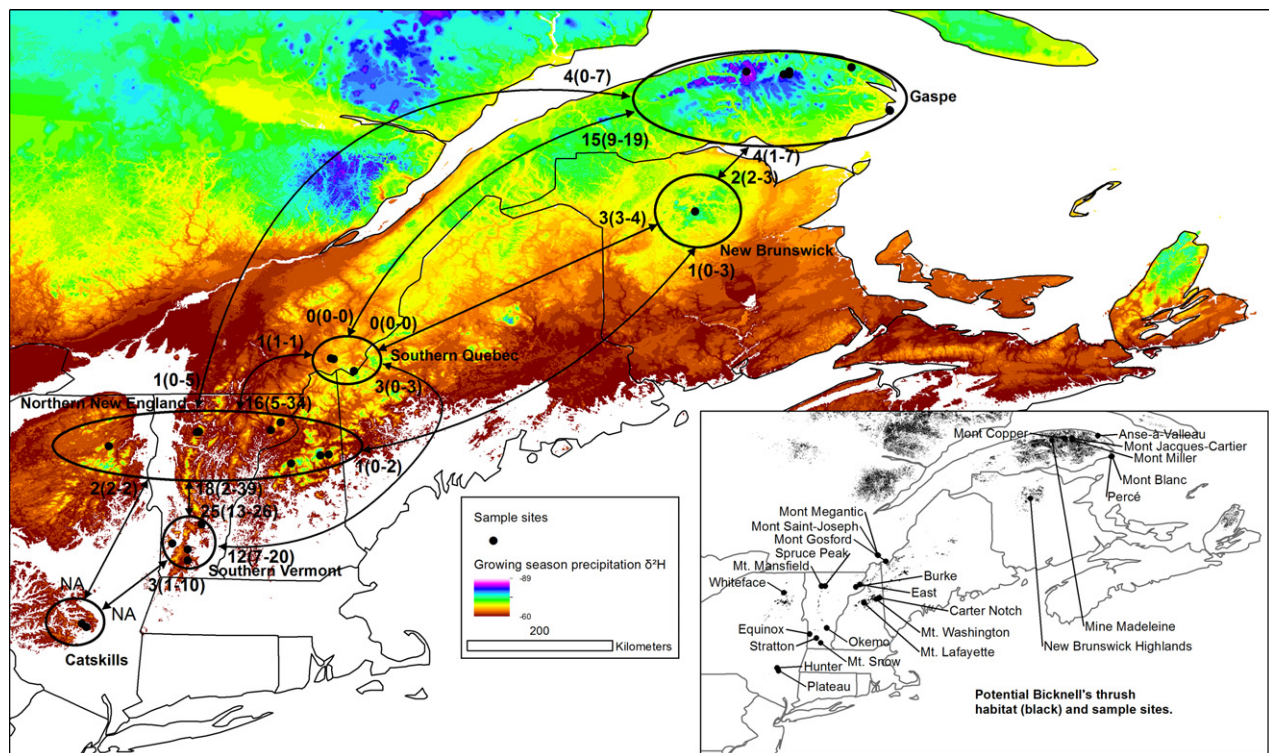

Figure 2 Patterns of natal dispersal among six breeding regions estimated with $\delta^2 H_F$ for 192 Bicknell's thrushes sampled during their first breeding attempt from 1996 to 2005. Values show the number of natal dispersers originating from regions linked by arrows. Estimates using each of the three offsets to account for age-related variation in $\delta^2 H_F$ values across latitude are shown as 12‰ mean (6–18‰ range). The inset shows potential breeding habitat (black) and locations where birds were sampled; see Table S1 for the distribution of sample sizes among the six breeding regions.

$\chi^2 = 43.56$, $P < 0.001$). Conversely, using the 18‰ maximum offset, the majority of natal dispersal occurred in a northern direction (79% northern and 21% southern $\chi^2 = 33.64$, $P < 0.001$).

Approximately 66% (63–67%) of natal dispersal events occurred between geographically adjacent regions (Fig. 2). Exchange of individuals was greatest between sites in southern Vermont and those in northern New England and New York, comprising 40% (26–44%) of all dispersal events. In contrast, we detected no natal dispersal among the most northern and southern sites sampled. Thrushes categorized as originating in the Catskills Mountains of southern New York dispersed no further north than northern New England. Similarly, individuals interpreted to have fledged on the Gaspé Peninsula in Quebec and in New Brunswick dispersed only as far south as northern New England. These patterns yielded a curvilinear relationship between natal dispersal probability and the assigned latitude of natal origin, with a strong peak at approximately 46°N and steep declines to the north and south under both the 6‰ ($z = -5.50$, $P < 0.001$; Fig. 3a) and 12‰ offsets ($z = -4.30$, $P < 0.001$; Fig. 3b). This latitudinal trend in dispersal probability shifted slightly to the south under the 18‰ offset, but the pattern was not statistically significant ($z = -1.53$, $P = 0.126$; Fig. 3c).

The change in natal dispersal probability from 1996 to 2005 depended on the correction factor used to adjust for the lower $\delta^2 H_F$ values of first-time breeders. Both the 6‰ and 12‰ offsets resulted in a marked reduction in natal dispersal probability across the 10-year study period, whereas the 18‰ offset resulted in a weak increase in dispersal probability. Dispersal probability declined by 38% using the 6‰ offset ($z = -2.95$, $P = 0.003$; Fig. 4a) and by 30% with the 12‰ offset ($z = -2.31$, $P = 0.021$; Fig. 4b). Conversely, natal dispersal probability increased by 13% under the 18‰ offset; however, this trend was not statistically significant ($z = -1.00$, $P = 0.315$; Fig. 4c). We found qualitatively similar temporal trends in dispersal probability when we analysed only a network of long-term study sites in Vermont, although these patterns were not statistically significant. Dispersal probability declined by 13% using the 6‰ offset ($z = -0.63$, $P = 0.532$) by 22% with the 12‰ offset ($z = -0.14$, $P = 0.154$), and increased by 17% under the 18‰ offset ($z = -1.15$, $P = 0.249$). Adult $\delta^2 H_F$ varied little over the 10-year study period ($\chi^2 = 0.211$, d.f. = 1, $P = 0.646$), suggesting that temporal changes in natal dispersal probability were not biased by temporal trends in prior information.

Calculation of the minimum linear distance that thrushes could have moved between the assigned natal region and the site of capture 1 year later suggested that the majority of dispersal events were < 200 km (Fig. 5). The frequency of natal dispersal fell sharply beyond this distance, but it rose again at 500–700 km from the assigned natal region. The distribution of observed natal dispersal distances was better approximated by a Weibull distribution than by an exponential or half-Cauchy under all three offsets used to account for
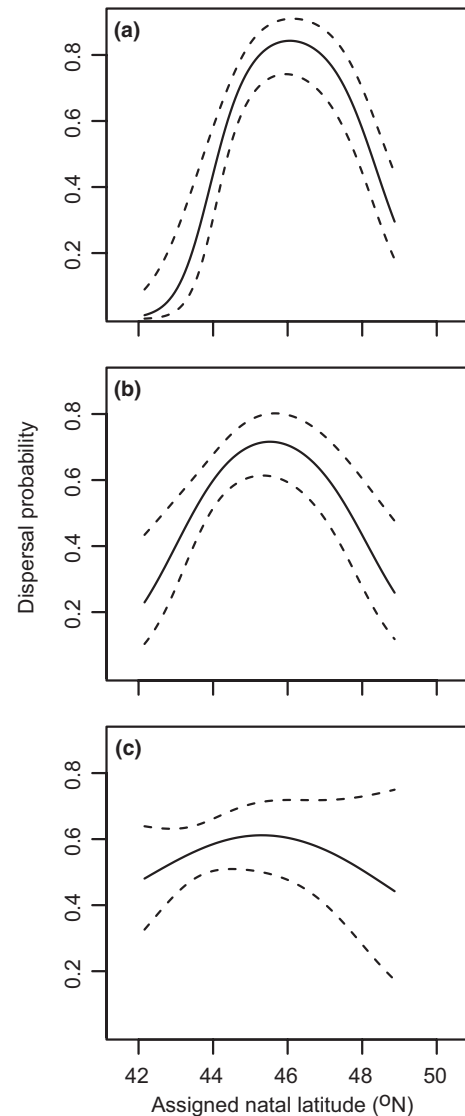

Figure 3 Patterns of natal dispersal probability in relation to latitude of the assigned natal origin for 192 Bicknell's thrush captured at 25 montane breeding sites across the breeding range in the north-eastern United States and Canada from 1996 to 2005 under three different offsets used to account for age-related variation in $\delta^2 H_F$. Under the (a) 6‰ and (b) 12‰ offsets, dispersal probability peaked at 45°N and declined sharply to the north and south. Under the (c) 18‰ offset, dispersal probability peaked further south, but the trend was weaker in comparison. Dashed lines depict 95% confidence intervals.

age-related variation in $\delta^2 H_F$ (Table 1). When analysed with the 12‰ mean offset, this distribution had a shape parameter of 0.72 and a scale parameter of 134.67. The Weibull distribution conforms precisely to an exponential distribution when the shape parameter = 1; therefore, a shape parameter = 0.72 indicated a heavier tail of long-distance dispersal events than expected under the exponential distribution and a lighter one than predicted by the half-Cauchy.
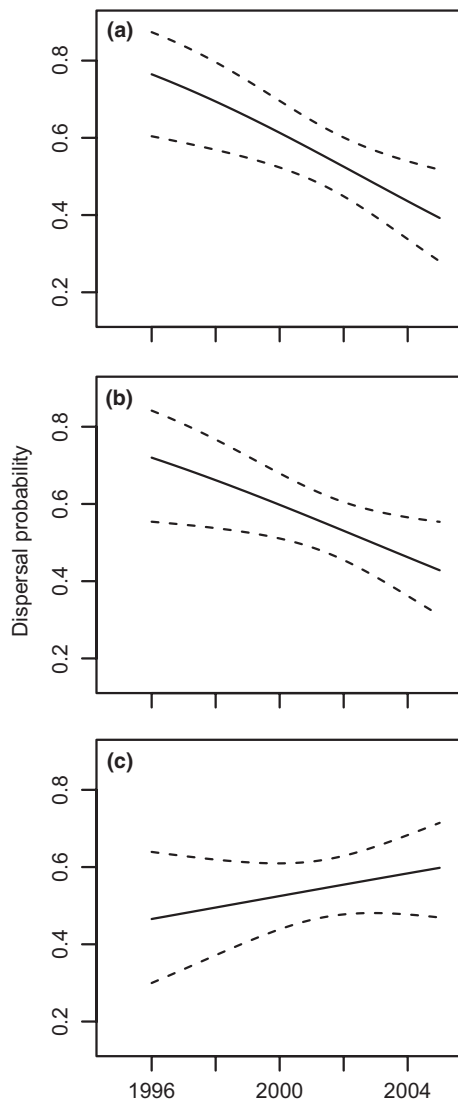
Figure 4 Change in natal dispersal probability from 1996 to 2005 for 192 Bicknell's thrush captured at 25 montane sites across the breeding range in the north-eastern United States and Canada under three different offsets used to account for age-related variation in δ^2H_F. Dispersal probability (a) decreased by 38% under the 6‰ offset (b) by 30% under the 12‰ offset and (c) increased by 13% under the 18‰ offset. Dashed lines depict 95 percent confidence intervals.
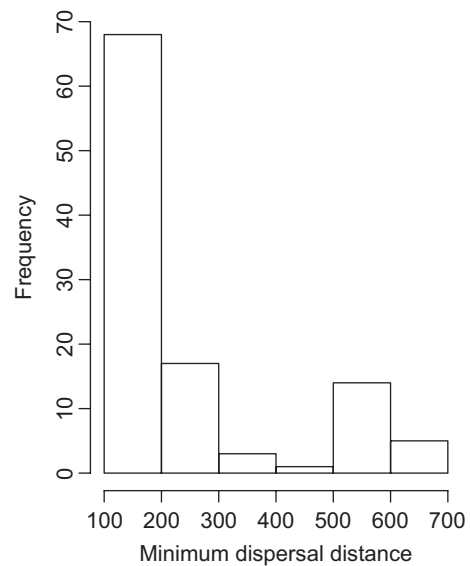

Figure 5 Distribution of natal dispersal distances for 114 Bicknell's thrush captured at 25 montane sites across the breeding range in the north-eastern United States and Canada from 1996 to 2005 under the 12‰ mean offset used to account for age-related variation in δ^2H_F. Minimum dispersal distance was estimated by measuring the minimum linear distance that thrushes could have moved between the closest possible site in the assigned natal region and the site of capture during the first breeding attempt. A Weibull distribution with a shape parameter of 0.72 and a scale parameter of 134.67 provided the best fit to these data.

DISCUSSION

The trend that we identified for age-related differences in Bicknell's thrush δ^2H_F values to increase at lower latitudes illustrates the complexity involved in using stable-hydrogen isotopes to assign birds to their natal origin. Despite this potentially confounding pattern, assignment tests correcting for the 12‰ mean, 6‰ northern and 18‰ southern variations in δ^2H_F all suggested that most birds dispersed < 200 km and near the centre of the breeding range, while comparatively fewer individuals dispersed up to 700 km. Under all three scenarios, a Weibull distribution provided

the best fit to the data, implying that long-distance dispersal, although infrequent, remains important for characterizing natal dispersal in this species. We also identified discrepancies in natal dispersal patterns under the three different δ^2H_F corrections. Assignments performed using the 6‰ offset indicated that over 80% of thrushes dispersed in a southern direction, whereas the 18‰ offset produced the opposite result. When assignments were performed using the 6‰ and 12‰ offsets, we detected a strong decline in the probability of dispersal across the breeding range over the 10-year duration of the study. In contrast, the 18‰ offset supported a weak increase in dispersal probability over time. Collectively, our findings suggest that estimating natal dispersal with δ^2H_F measurements may contribute to understanding the resilience of geographically isolated Bicknell's thrush populations.

Although much of the variation in δ^2H_F between adults and first-time breeders likely arose from age-related physiological or dietary differences (McKechnie et al., 2004; Langin et al., 2007), other sources of error common to both age-classes can also affect assignments made using δ^2H_F. Patterns of δ^2H_P at a given location can vary among years owing to differences in both the amount and source of growing season precipitation (Clark & Fritz, 1997). In addition, δ^2H_P values change in a similar manner with increasing altitude as with increasing latitude (Bowen et al., 2005), and montane

Table 1 Model fit indices for statistical distributions used to assess the importance of long-distance dispersal to the overall distribution of natal dispersal distances for 114 Bicknell's thrush among six breeding regions in the north-eastern United States and Canada from 1996 to 2005. Distributions were fit for each of the three offsets used to adjust for age-related variation in $\delta^2 H_F$ across latitude

Distribution	d.f.	AICc	ΔAICc	AICw
6‰ offset				
Weibull	2	2335.3	0.0	1.0
Exponential	1	2363.3	28.0	< 0.001
Half-Cauchy	2	5231.8	2986.5	< 0.001
12‰ offset				
Weibull	2	2311.0	0.0	1.0
Exponential	1	2357.6	33.3	< 0.001
Half-Cauchy	2	5729.7	2972.3	< 0.001
18‰ offset				
Weibull	2	2381.7	0.0	1.0
Exponential	1	2404.1	22.5	< 0.001
Half-Cauchy	2	5420.4	3038.8	< 0.001

breeding sites where thrushes were captured typically ranged across at least one hundred meters in elevation. Using adult $\delta^2 H_F$ values as prior information to assign dispersing thrushes to their putative natal areas enabled our analyses to incorporate both sources of variation, and explicit analyses of these errors suggested that they had little effect on our conclusions. Means and standard deviations of adult $\delta^2 H_F$ priors thus sufficiently encompassed any annual or altitudinal anomalies in $\delta^2 H_P$ that might have occurred across the 10-year sampling period, potentially leading to more realistic assignments than would have been possible using $\delta^2 H_P$ measurements to develop prior information.

Research on natal dispersal using conventional mark–recapture approaches indicates that most birds disperse < 3–50 km from the natal area, whereas movements of several hundred kilometres are comparatively rare (Paradis *et al.*, 1998; Pasinelli *et al.*, 2004; Winkler *et al.*, 2005). Studies that analysed the distribution of dispersal distances found that a half-Cauchy distribution consistently provided the best fit to the data (Paradis *et al.*, 2002; Winkler *et al.*, 2005). In contrast, we found that natal dispersal patterns of Bicknell's thrush were best approximated by a Weibull distribution. One explanation for this discrepancy is that $\delta^2 H_F$ values provide poor resolution of locations in close proximity to one another and are therefore cannot describe short-distance dispersal (Bowen *et al.*, 2005). The group of thrushes interpreted to have dispersed up to 200 km probably included a large number of individuals that moved markedly shorter distances, and homogeneity in their $\delta^2 H_F$ values may have masked considerable variation in short-distance dispersal. In particular, substantial short-distance dispersal could have occurred longitudinally among montane sites within breeding regions. Our analyses were incapable of detecting such

movements because $\delta^2 H_F$ values only provide information about latitudinal movements. Conversely, the longer distance dispersal events that we recorded, particularly those in excess of 500 km, were ideally estimated with $\delta^2 H_F$ values and would not have been detected using other available methods such as mark–recapture of banded birds or geolocator tracking. Thus, our limited ability to estimate short-distance dispersal and our enhanced capacity to detect long-distance dispersal were probably equally responsible for the finding that the Weibull distribution provided a better fit than the half-Cauchy.

Some of the best evidence for the existence of long-distance dispersal comes from studies examining geographical variation in neutral genetic markers (Bensch *et al.*, 2002; Trakhtenbrot *et al.*, 2005; Colbeck *et al.*, 2008; Pearce *et al.*, 2009). Most Neotropical–Nearctic migratory birds show little phylogeographical structure across latitude, suggesting that long-distance dispersal events are common enough to prevent genetic differentiation of neutral markers (Lovette *et al.*, 2004; Boulet *et al.*, 2007). In the present study, dispersal events in excess of 200 km occurred approximately once every generation. Dispersal movements of this distance were concentrated near the central portion of the range in northern New England and the Estrie region of southern Quebec. In contrast, we did not detect dispersal between the northernmost sites in the Gaspé Peninsula and sites at the opposite edge of the breeding range in southern Vermont and the Catskills. These natal dispersal patterns are consistent with measures of genetic relatedness of Bicknell's thrush across the breeding range. Breeding sites in the Catskills and Gaspé Peninsula contain at least two unique haplotypes not found elsewhere, suggesting that gene flow between northern and southern range extremes is rare (Ellison, 2001; Wilson *et al.*, 2004). The general corroboration between our estimates of dispersal distance and the extent of genetic differentiation at range extremes suggests that $\delta^2 H_F$ values provided a reasonably accurate profile of natal dispersal in this species.

Our estimates of natal dispersal also imply limited demographic connectivity between naturally isolated montane breeding populations of Bicknell's thrush. Long-distance demographic exchange of a few individuals per generation may be sufficient to promote genetic mixing throughout much of the breeding range, but is likely inadequate to sustain strong demographic connectivity (Lowe & Allendorf, 2010). Although the majority of first-time breeders dispersed within 200 km of their natal region, these movements peaked near the geographical centre of the breeding range where populations appear to reach their highest abundance. These patterns are consistent with frequency-dependent dispersal and suggest that the majority of natal dispersal events act to connect presently abundant populations where suitable habitat reaches its highest availability.

Low demographic connectivity at broad spatial scales can render isolated populations vulnerable to both temporary and sustained environmental disturbance. Populations weakly connected by dispersal may fluctuate asynchronously because

of demographic and environmental stochasticity, potentially increasing the risk of local extinction (Peltonen *et al.*, 2002; Jones *et al.*, 2007). Bicknell's thrush is a mid-successional specialist whose habitat is naturally ephemeral owing to disturbances such as fir waves or severe weather events (*sensu* Sprugel, 1976). Although these disturbances ultimately generate new habitat, they temporarily reduce habitat availability (Lamontagne & Boutin, 2007) and force birds to disperse in search of breeding sites. Our results suggest that natal dispersal is likely to synchronize and buffer populations against natural disturbances in regions with a substantial network of breeding sites within 200 km. Conversely, breeding sites separated by greater distances, with a low frequency of demographic exchange, may fluctuate out of phase with one another and be at higher risk of local extinction. Long-distance demographic rescue of population sinks by individuals from distant population sources therefore is currently unlikely in this species.

Habitat degradation and loss through anthropogenic disturbance has the potential to indirectly limit natal dispersal. On the breeding grounds in the north-eastern United States and Canada, Bicknell's thrush habitat is directly threatened by commercial timber harvesting, mountaintop recreational development, and energy and communication infrastructure (Strong *et al.*, 2002; Chisholm & Leonard, 2008; IBTCG *et al.*, 2010). Wet atmospheric deposition of acid ions occurs at a high rate in the northern Appalachians, which may reduce the quantity and quality of calcium-rich prey important to both adults and nestlings (Hames *et al.*, 2002). In addition, climatic warming represents a potential long-term risk to Bicknell's thrush habitat. Modelling efforts suggest that regional warming of 1°C could reduce Bicknell's thrush habitat by more than half, and an increase of 2°C may be sufficient to eliminate all breeding sites from the Catskill Mountains of New York and most of Vermont (Rodenhouse *et al.*, 2008). Shrinking and further isolation of habitat patches owing to these processes, coupled with ongoing population declines, perhaps partially driven by events in the tropical non-breeding period (Rimmer *et al.*, 2001, 2005a), may reduce natal dispersal rates and lead to a negative feedback loop of further population declines and range contraction.

Our finding that natal dispersal probability declined by 30–38% over 10 years throughout the north-eastern United States and Canada under two of the three δ^2H_F offsets is consistent with independently observed local population declines and extinctions (Atwood *et al.*, 1996; King *et al.*, 2008; Lambert *et al.*, 2008) and may signal that a range-wide population decline is underway. However, we also found that one δ^2H_F offset resulted in a statistically insignificant increase in dispersal probability over the same time frame, a result that limits inference about the link between natal dispersal and observed population declines. Understanding which of these trends is most robust will be important for predicting how Bicknell's thrush populations will cope with natural and anthropogenic disturbances that will undoubtedly limit future habitat availability and suitability. This uncertainty

highlights the need for research into the mechanisms underlying age-related variation in δ^2H_F. Until this phenomenon is better understood, population viability analyses that explicitly incorporate different scenarios of dispersal are needed to refine conservation plans for Bicknell's thrush.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Sample sizes of stable-hydrogen isotope values in Bicknell's thrush tail feathers (δ^2H_F) used to assess natal dispersal patterns among six breeding regions in the northeastern United States and southern Canada from 1996–2005.

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