

Strong Migratory Connectivity in a Declining Arctic Passerine

Abstract

Determining how animal populations are linked in space and time is important for identifying factors influencing population dynamics and for effective conservation and management. Arctic-breeding migratory passerines are declining and at risk due to forecasted climate change, but are a challenge to monitor due to their inaccessible breeding locations, long-distance migration routes and small body size. For the first time, we combine sub-gram geolocator technology and stable-isotope analysis with mark-recapture (banding) and citizen science data to determine patterns of migratory connectivity for multiple populations of a declining North American Arctic-breeding passerine, snow bunting (*Plectrophenax nivalis*). We show strong evidence for an east-west parallel migratory system, with Hudson Bay acting as a migratory divide. While band recoveries suggest strong migratory connectivity among eastern wintering populations (more than 95% of band recoveries reveal connections between western Greenland and eastern North America), novel application of geolocators and stable-hydrogen isotope analysis to a Canadian breeding population revealed a high degree of migratory connectivity within western North American wintering populations. Our results also show distinct differences in migratory distance between eastern and western populations, and illustrate how applying multiple techniques can effectively be used to track migration patterns of remote populations. Differences in annual distribution and migratory distance suggest that separate consideration of eastern and western wintering populations may improve future conservation and management efforts for this species.

Keywords

Snow bunting (*Plectrophenax nivalis*) • Geolocators • Stable isotopes • Band recoveries • Citizen science • Migratory divide • Migration ecology.

© Versita Sp. z o.o.

Macdonald C.A.^{1,2*},
Fraser K.C.³,
Gilchrist H.G.²,

Kyser T.K.⁴,
Fox J.W.⁵,
O.P. Love¹

¹Department of Biological Sciences,
University of Windsor, Windsor, Ontario,
Canada N9B 3P4

²Environment Canada, National Wildlife
Research Centre, Carleton University,
Ottawa, Ontario, Canada K1A 0H3

³Department of Biology, York University,
Toronto, Ontario, Canada M3J 1P3

⁴Department of Geological Sciences
and Geological Engineering, Queen's
University, Kingston, Ontario, Canada
K7L 3N6

⁵British Antarctic Survey, Cambridge,
United Kingdom CB3 0ET. Current:
Migrate Technology Ltd, Cambridge,
United Kingdom CB1 0QY

Received 01 August 2012
Accepted 21 October 2012

Introduction

Determining links between populations of migratory animals across the various stages of the annual cycle is necessary for understanding population dynamics and for effective wildlife conservation and management [1]. Long-distance migratory songbirds pose particular challenges as breeding and non-breeding areas may be thousands of kilometers apart, migratory connectivity [2] has been determined for few species, and small body size has limited direct tracking using devices such as satellite transmitters [3]. Arctic-breeding migratory passerines may be the most difficult migrants to study because their polar breeding distribution represents a challenging environment that is relatively inaccessible to researchers. Additionally, nomadic winter movements may be unpredictable and cover great distances [4,5] making it difficult to define population boundaries or monitor population trends. As a result, the migratory connectivity of most Arctic-breeding passerines has never been assessed. These challenges have led to a poor understanding of declining population trends [6], which is of particular concern

considering broad-scale habitat changes predicted for high latitudes [7].

The snow bunting (*Plectrophenax nivalis*) is a small (<50g) circumpolar Arctic-breeding passerine that, in North America, overwinters throughout southern Canada and the northern United States (Figure 1). While a common and globally abundant species (est. 40 million adults) [8], recent evidence from a long-term North American winter census (the Christmas Bird Count - CBC) suggests that this species has undergone a range-wide population decline of 64% over 40 years [9], particularly in the western wintering range (O. Love, unpublished data), which contains a high proportion (approx. 75%) of the North American wintering population (eBird 2012). Broad-scale citizen science driven surveys (e.g. CBC) and regional observations (e.g. databases such as eBird) can provide valuable information for detecting general changes in the distribution and abundance of many passerines [9]. However, we remain limited in our ability to effectively respond to those changes without first identifying the spatial linkages of populations across more than one life history or migratory stage (i.e. migratory connectivity). Only then can

* E-mail: cmacdonald414@gmail.com

we link regionally-specific population trends with limiting factors throughout the annual cycle [1].

Like many other passerines, banding effort in snow buntings has had a recovery rate of less than 0.5% (estimated <2% across all passerines) [10]. Nonetheless, with >70,000 snow buntings banded since 1930, these data are still useful for suggesting broad movement patterns since recoveries span the breeding and non-breeding (wintering) stages. Stable-hydrogen isotope analysis has yielded important insights into range-wide migratory connectivity patterns of small passerines [10-13] and can supplement mark-recapture data where band recoveries are sparse [10,13]. Additionally, the recent application of archival light-level loggers (geolocators) to track small passerines has provided novel insight into the specific migratory routes and timing for tagged individuals [14-18]. However, this direct-tracking technique requires the recapture of tagged individuals for data retrieval, and several recent studies have resulted in relatively low sample sizes of tracked individuals [14-17, although see 18]. Ideally, studies should take advantage of the opportunity to integrate multiple techniques to examine movement patterns and identify possible mechanisms driving regional population declines.

In this study we combine multiple tracking techniques to reveal patterns of migratory connectivity of North American snow bunting populations. Historically, banding and encounter records have been limited to the eastern part of the species range (96% of encounter records occur east of -86°W). No banding records currently provide information on the geographical linkages of Canadian breeding populations (Figure 2). Here, we use stable-hydrogen isotope analysis and light-level geolocators to identify the wintering range of a Canadian breeding population, and test whether this eastern band encounter bias is due to strong migratory connectivity within eastern and western migratory sub-populations (i.e.: parallel migration system). This research is the first to track multiple populations of an Arctic-breeding migratory passerine throughout its entire North American migratory cycle, and can provide a model for understanding movement and its influence on population dynamics for this, and other Arctic-breeding passerines.

Methods

Authorization for the use of experimental animals:

All animals were handled in accordance to guidelines and protocols approved by the Canadian Council for Animal Care as reviewed by Environment Canada, bird banding permit (10808) issued by the Environment Canada, scientific collection permit (0276) for tissue sampling issued by the Canadian Wildlife Service and under University of Windsor Animal Utilization Project Proposal (AUPP # 9-14).

Mark-recapture data

We obtained mark-recapture data from the Canadian Bird Banding Office (for data on snow buntings banded in North America) and the Copenhagen Bird Ringing Centre (for data on

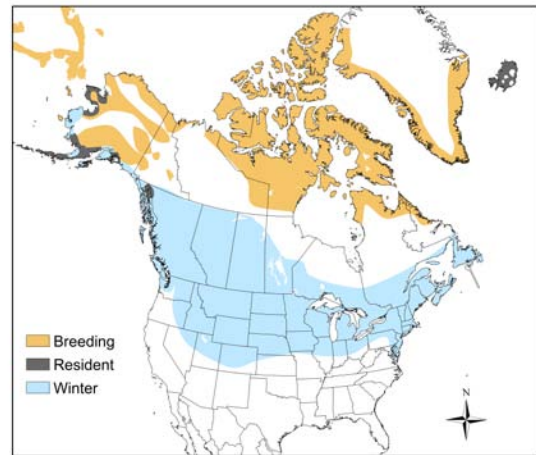


Figure 1. Annual distribution of snow buntings (*Plectrophenax nivalis*) in North America. Species distribution dataset for provided by BirdLife International and NatureServe (2011). Map generated using ArcMap v. 10.0 (ESRI 2010).

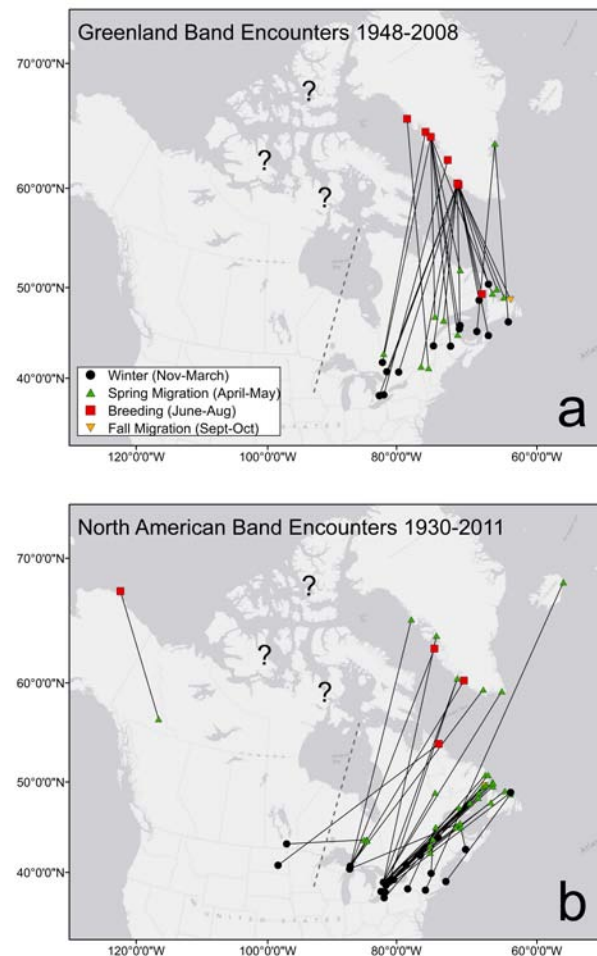


Figure 2. Inter-seasonal movement patterns of Nearctic snow buntings illustrated through band recoveries originating from (a) Greenland (Copenhagen Bird Ringing Centre, 2012) and (b) North America (Canadian Bird Banding Office, 2011). Dashed lines represent a proposed east-west migratory divide around Hudson Bay. Question marks represent breeding areas with no corresponding winter or migration band recoveries. Lines link banding and encounter sites, but do not represent the actual path travelled by individual birds.

birds banded in Greenland) from 1930 to present ($n = 347$). We filtered data to remove encounters that represented movements of less than 200km (following [19]). We grouped banding and encounter locations to represent the annual stages of breeding (June-August), fall migration (September-October), wintering (November-March) and spring migration (April-May) (following [20]). The resulting dataset included a total of 69 inter-seasonal band encounters used to estimate migratory connectivity (Figure 2), and 23 intra-seasonal band encounters used to identify migration routes (Figure 5). Maps of band encounter data were generated using ArcMap (version 10.0, ESRI).

Field methods

We captured snow buntings at Mitivik Island (East Bay Island) in the East Bay Migratory Bird Sanctuary, Nunavut, Canada ($64^{\circ}01'N$, $81^{\circ}47'W$) (Figures 3 and 4). For stable isotope analysis, we collected a 2mm sample from the left hind claw tip during the spring migration and breeding arrival period (May 25-June 15, 2010 and 2011) from migrant and breeding adults, and stored samples in paper envelopes until laboratory analysis. We deployed 90 light-level geolocators (British Antarctic Survey, BAS, MK12S in 2010 and MK20AS in 2011) on post-breeding adults and fledged juveniles. Geolocators were deployed during the post-breeding period (July 15-30th) using a leg-loop harness [21] and 2.5mm Teflon ribbon [14]. Total mass of the attachment (1.1g, geocator plus harness) represented $3.01\% \pm 0.25$ (SD, $n=310$) and $3.23\% \pm 0.32$ (SD, $n=213$) of male and female body weight, respectively, for birds captured at East Bay Island during the breeding season (May-July); this represents <5% recommended limit of body weight [22]. Geolocators were retrieved in June 2011 and 2012.

Light data analysis

Geolocators measured ambient light levels every 60s and recorded maximum light intensity for every 120s interval. Transitions were visually displayed and ranked for confidence using the software TransEdit (version 19.0, BAS). Transitions indicating sunset and sunrise events were defined using a light threshold of 5. We determined the average sun elevation that corresponded with this light threshold at the breeding site for each geocator model (-4.15 for MK12S and -4.02 for MK20AS) using the software LocatorAid (BAS) for a portion of the pre-migration period where clear sunrise and sunset periods were observed (July 15-30th). Because light-levels can be obscured by cloudy weather or shading events on the light sensor [23], and such errors can be converted to errors in estimates of longitude and latitude, we included only locations calculated from high-confidence transitions (i.e.: confidence ≥ 6 ; see [14]). We excluded latitude estimates for 15 days on either side of the fall and spring equinoxes (Sept. 7-Oct. 7 and March 5-April 5) because day length is equal at all latitudes during these periods, and relied on longitude estimates during this period to determine directional changes.

We present annual distribution estimates for the East Bay Island breeding population ($n=13$) during the fall migration, wintering and spring migration periods (Figure 3).

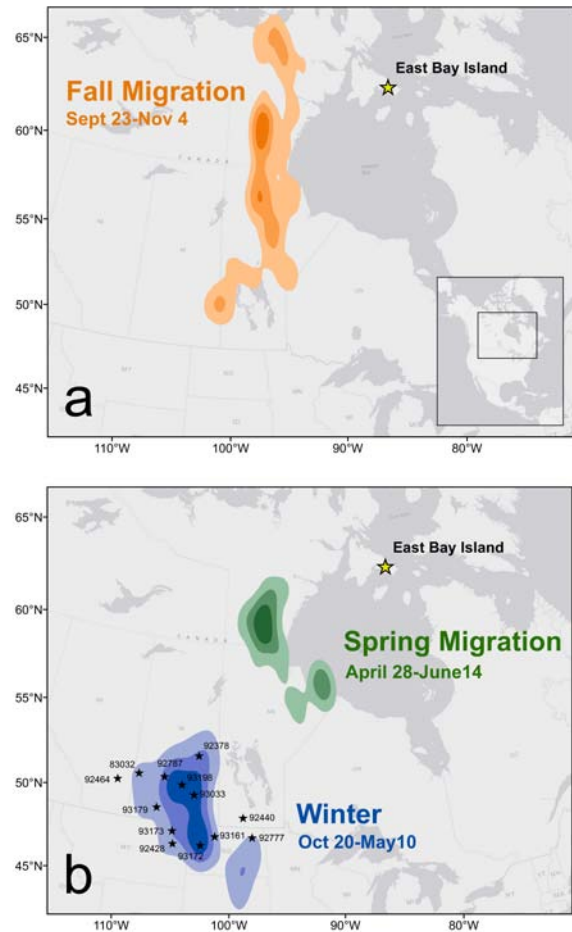


Figure 3. Annual distribution of a Canadian-breeding snow bunting population tracked with geolocators ($n=13$) from East Bay Island, Nunavut (2010-2011 and 2011-2012). Maps represent 90, 75 and 50% kernel density of daily location points combined for all 13 tracked individuals. Range of dates represents earliest initiation and latest completion date of each stage across all 13 individuals. ★ represents mean wintering

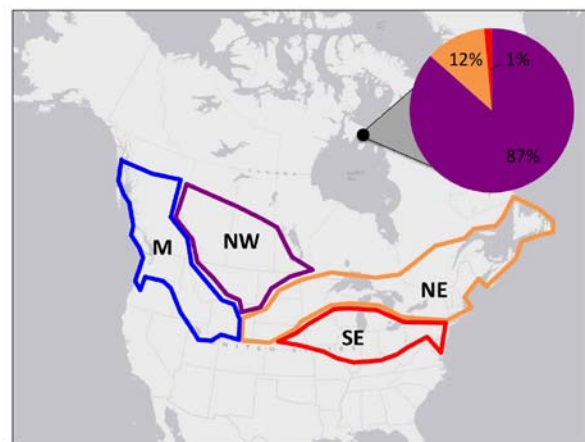


Figure 4. Estimated wintering origin of a Canadian-breeding snow bunting population at East Bay Island using stable-hydrogen isotope analysis of claws collected during the spring arrival period (May 25-June 15, 2010 and 2011).

Additionally, we present the mean wintering locations of all 13 individuals successfully tracked (Figure 3b) to show the variation in wintering sites of all individuals. We defined a stop in movement as the date at which the directional change in longitude consistent with migration is followed by a stationary period (10-day mean longitude has a standard deviation <1). We defined start of movement as directional change in >5 degrees longitude over a 24-hour period resulting in a new location that is >2 degrees different from the previous 10-day mean. Distributional maps were generated using the spatial analyst tool in program ArcMap (v.10.0, ESRI) by estimating the 50, 75 and 90% maximum kernel densities of point locations (following [15,24]). Kernel density estimates represent periods of movement, stationary periods (i.e.: stopovers), as well as some amount of error in daily position estimates [23]. However, we reduced the relative contribution of error to these distribution estimates by weighting the contribution of each point by its confidence ranking, such that low quality location estimates contribute proportionally less to the kernel density estimates.

Stable-hydrogen isotope analysis

Claws were prepared and analyzed according to standard stable-hydrogen isotope protocols for keratin [25,26]. Samples were placed in a drying oven at 100°C for 24h to remove surface moisture, which can contribute greater than 7% of the measured signal in keratin [27]. To account for the effects of exchangeable organic hydrogen we used a comparative equilibration technique [28] using calibrated keratin standards; THS (-38‰), EC2 (-54‰), Spectrum KP (-122‰) and EC1 (-197‰). Standards were weighed to the same target weight, allowed to equilibrate with local atmosphere alongside samples for at least 72 hours before analysis, and analyzed concurrently. After analysis we adjusted our raw sample values based upon known values of keratin standards [28]. All values are reported in permil (‰), relative to the standard Vienna standard mean ocean water (VSMOW) according to the formula: $\delta^2\text{H} = \left[\frac{^2\text{H}/^1\text{H}_{\text{sample}}}{^2\text{H}/^1\text{H}_{\text{standard}}} - 1 \right] \times 1000$. Replicate samples were repeatable to 6‰ ±4 (SD; n=9).

Because claw tissues reflect a period of continuous growth along their length (2-5 months within 1-2mm, or 3-7weeks within 0.08 to 0.22mg of the claw tip) [25,26] claws sampled at arrival are expected to represent winter growth. We used likelihood-based assignment tests to assign the $\delta^2\text{H}$ values of arrival claws to one of four wintering regions (Figure 4; mountains - M, northwest - NW, northeast - NE and southeast - SE) selected following known patterns of isotopic variation in precipitation [12] and encompassing the known wintering range of snow buntings [29] (Figure 4). We obtained mean annual precipitation $\delta^2\text{H}$ values for 30-50 randomly selected locations within each of the 4 regions using the Online Isotopes in Precipitation Calculator (OIPC) [30] and extracted mean±SD for each region and applied a discrimination factor of -25% [12] to account for the fractionation of $\delta^2\text{H}$ between keratin and precipitation. We also calculated the relative abundance

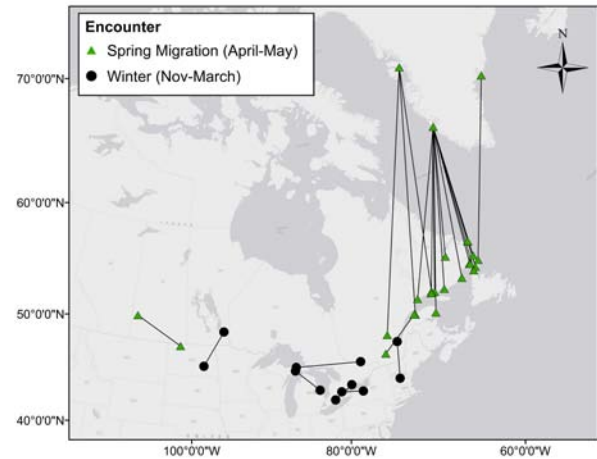


Figure 5. Intra-seasonal movements of Nearctic snow buntings illustrated through band recovery data within wintering and spring migratory periods (banding data from the Copenhagen Bird Ringing Centre and Canadian Bird Banding Office). Lines link banding and encounter sites, but do not represent the actual path travelled by individual birds.

of snow buntings in each of the four wintering regions using observational data from the eBird reference dataset [31]. Arrival claws were assigned a probability of origin based on a standard likelihood function incorporating mean and standard deviation of $\delta^2\text{H}$ values, and relative abundance for each region [32,33]. We only considered individuals with resulting assignment probabilities of 50% or higher [32].

Results

Band Recovery Data

Of the 71,277 snow buntings banded in North America and Greenland between 1930 and 2010, 92 were encountered at a distance of >200km from their original banding site (Canadian Bird Banding Office, unpublished data) (Figure 2 and 5). In total 96% (66 of 69) of inter-seasonal and 91% (21 of 23) of intra-seasonal band recoveries show linkages between wintering sites within eastern North America, migration routes throughout the Gulf of St. Lawrence, Newfoundland and Labrador, and breeding sites in western Greenland (Figure 2).

Geolocators

Migration Timing

Individuals departed from the breeding grounds at East Bay between Sept. 23-Oct. 6 in 2010 and from Oct. 8-10 in 2011. Fall migration spanned 25±5 (SD, n=6) days in 2010; and 18±5 (SD, n=7) days in 2011. Arrival to the wintering grounds was between Oct. 20-28 in 2010; and Oct. 22-Nov. 4 in 2011. The wintering period was similar between years and spanned an average of 192±7 days (SD, n=11), representing 50-54% of the annual cycle. Spring migration was initiated between Apr. 28-May 8 in 2011 and Apr. 28-May 10 in 2012, representing a period of 40±4 (mean±SD, n=4) days in 2011 and 31±5 (mean±SD, n=7) days in 2012.

Annual Distribution

All thirteen birds migrated to the western part of the species' North American wintering range. Mean wintering locations for individuals spanned 5.5° latitude and 11.3° longitude, including one U.S. state (North Dakota) and three Canadian provinces (Manitoba, Saskatchewan and Alberta) (Figure 3b). Batteries in four of the thirteen geolocators failed at various dates (December 4, 2010, and January 25, May 19 and May 29, 2011) prior to retrieval at the breeding site (June 2011). Thus, for two individuals tracked between 2010-2011, mean wintering locations were calculated using daily point locations for only a partial wintering period and did not contribute point locations for spring migration. Estimated population distribution of 90% kernel densities for fall migration period represented a span of almost 20° latitude (Figure 3a) over a period of 22±6 days, with individuals initiating fall migration as early as Sept. 23 (2010) and completing no later than Nov. 4 (2011). Distribution of 90% kernel density for spring migration represented a narrower latitudinal span of ~7° (Figure 3b) over an average of 34±6 days.

Stable-hydrogen Isotope Analysis

Our results indicate that snow buntings breeding and migrating through East Bay Island preferentially overwinter in the Great Plains and prairies of southern Canada and the northern United States (Figure 4). Snow buntings were most abundant in the NW region, followed by NE, M and SE (Table 1). After incorporating relative abundance into the assignment tests, a total of 67 individuals were assigned to wintering regions (Table 1). There

was no sex-bias in the assignment probabilities, with each sex representing 50% of assignments to each region, except where only one individual (male) was assigned to SE. For the stopover migrants, 100% were assigned to the NW region, whereas, 80%, 18%, 2% and 0% of breeders were assigned to NW, NE, SE and M regions, respectively.

Discussion

Using a novel combination of tracking methods and citizen science data, our results reveal that snow buntings breeding in the Canadian Low Arctic have a high degree of migratory connectivity with the western North American wintering range. Furthermore, 96% of band recovery data linked the eastern wintering populations with migration routes and breeding sites in eastern North America and Greenland (east of -86°W). This range-wide pattern of connectivity suggests a parallel migration system, with Hudson's Bay acting as a migratory divide between eastern and western migratory sub-populations. This result is surprising, considering that another broadly-distributed Arctic-breeding passerine showed relatively weak connectivity, with tracked individuals sharing a broad wintering region in equatorial Africa [17]. This result is, however, relevant for applied conservation of the snow bunting, as regional declines vary between populations occurring on either side of this proposed migratory divide (O. Love, unpublished data). We also found that the wintering period makes up more than half the annual migratory cycle and individuals may spend more time at spring

Table 1. Results of probability-based assignment tests of $\delta^2\text{H}$ values for claws collected from snow buntings at East Bay Island during the spring arrival period (May 25-June 15, 2010 and 2011). Mean $\delta^2\text{H}$ values for precipitation were calculated using the Online Isotopes in Precipitation Calculator [30], and adjusted using a 25‰ discrimination factor for keratin [27]. Estimates of relative abundance for each wintering region were calculated using observational data from the eBird online database [31].

| Wintering Region | M | NW | NE | SE |
|--|---------|--------|---------|-------|
| Calculated mean±SD $\delta^2\text{H}$ for precipitation (‰) | -108±19 | -75±9 | -101±18 | -58±7 |
| Adjusted mean±SD $\delta^2\text{H}$ for precipitation (‰) | -133±19 | -100±9 | -126±17 | -83±7 |
| Proportion of samples assigned, not incorporating abundance (%) | 53.4 | 16.4 | 21.9 | 8.2 |
| Relative abundance (%) | 12.6 | 61.6 | 16.1 | 9.7 |
| Proportion of samples assigned, incorporating relative abundance (%) | 0 | 86.6 | 11.9 | 1.5 |

Table 2. Contributions of each method used to track North American snow bunting populations in this study.

| | Annual Distribution | Relative Abundance | Timing of Migration | Migratory Connectivity | Migratory Divide | Forest "Barriers" |
|----------------------------------|---------------------|--------------------|---------------------|------------------------|------------------|-------------------|
| Band Encounter Records | ✓ | | ✓ | ✓ | ✓ | ✓ |
| Citizen Science Observations | ✓ | ✓ | ✓ | | | ✓ |
| Geolocators | ✓ | | ✓ | ✓ | ✓ | ✓ |
| Stable-hydrogen Isotope Analysis | ✓ | | | ✓ | ✓ | |

migratory stopover sites than is necessary to refuel energy reserves for migration [34], suggesting some additional function of these sites.

Band Recoveries

The route that eastern wintering populations take along the Gulf of St. Lawrence to breeding sites in western Greenland represents a much greater annual migration distance when compared to a more direct line path (potentially adding up to 2000 km per year when travelling between southern Ontario and Greenland). These data suggest that either large areas of Boreal forest in Ontario and Quebec act as a barrier to migration or that this species relies on southern coastal habitats during spring migration, or both. Snow buntings follow the advancing snowmelt during spring migration, migrating along the margin of snow-free areas where they forage on emerging berries, seeds and insects [35]. Coastal areas, with a more moderate annual climate regime, may provide relatively less harsh (e.g., largely snow-free) northern routes to Greenland when compared to a more direct continental route (through interior Quebec), or an alternative coastal route (migrating north along the eastern shores of Hudson Bay and the Ungava Peninsula). These coastal routes may allow snow buntings, especially early-arriving males [35], to migrate northwards earlier than expected based on snow cover in interior regions.

Geolocators

Geolocators provided novel insight into the temporal patterns of migration, as well as identified an important migration stopover area used by this population during spring and fall migration periods (Figure 3). Timing of migration estimated by geolocators closely matched seasonal arrival and departure observations from citizen-science reports compiled online using eBird [31]. Additionally, geocator data suggests that spring migration in snow buntings takes on average 12 days longer to complete than fall migration. This result is unique amongst songbirds, as spring migration is generally shorter [14,18,34]. However, the spatiotemporal distribution of individuals during the spring migration period (Figure 3b) suggests that long stopovers (represented by high density areas) account for much of this period, with relatively short flights (low density areas) across the Boreal forest and on route to and from the breeding site. Future priorities for this species should include determination of the value or function of these stopover sites, which may provide important nutritional resources to refuel migration. Alternatively, because snow buntings are one of the earliest spring migrants to arrive at Arctic latitudes, they constitute an important part of the diet for early arriving predators such as peregrine falcons (*Falco peregrinus*), before many terrestrial mammals or other avian prey species are available (Alastair Franke, unpublished data). Thus, these spring migration stopovers may serve as “muster” points where snow buntings form large flocks to forage sufficiently while remaining vigilant against potential predators during migration [37]. Future geocator analysis or deployment from other breeding populations could reveal additional important migratory stopover

sites, patterns of sex-specific migration strategies, or individual plasticity in timing and route selection for migration [18].

Kernel density estimates of the wintering range for this population show a high degree of migratory connectivity. Mean wintering locations are provided only to illustrate the variation among individual wintering locations (Figure 3b). However, these location estimates (or movement centers) do not represent individual stationary wintering sites, because snow buntings are nomadic during the winter, travelling several hundred kilometers across a single winter (Figure 5). Because observations of wintering snow buntings occur south of the Boreal forest [31], and migration stopovers were found north of the Boreal forest boundary (Figure 3), these forest habitats may be unsuitable for migration or wintering and act as a type of barrier, such that migration occurs primarily along coastal or de-forested inland corridors. Additionally, while anticipated effects of increasing temperature with climate change predict that many species will experience northward range expansions [7], snow buntings may be limited in their ability to expand into Boreal forest regions. Finally, due to the challenges of studying multiple breeding populations in the Arctic, and because more than 50% of the annual cycle is spent on the wintering grounds, wintering habitats may represent the best areas for future monitoring and management of Arctic passerines.

While the recapture rates in 2011 and 2012 were comparable to previous years of study (2008–2010), because geolocators were attached to all post-breeding adults during deployment years (i.e. no control group), we were not able to estimate the effect of geolocators on inter-annual survival rates for this population. However, a recent study using similar attachment methods on an aerial foraging passerine (purple martin, *Progne subis*) found no effect of geolocators on survival [36]. Thus, for snow buntings, which forage on the ground and have shorter annual migration distances, we estimate that the additional weight and drag caused by geolocators had little to no effect on inter-annual survival rates.

Stable Isotope Analysis

Results from stable-hydrogen isotope analysis of claws added further support for strong migratory connectivity and the hypothesis of an east-west parallel migration system in Nearctic snow buntings. Although a greater degree of uncertainty is associated with this indirect tracking method compared to geolocators [3] to estimate *individual* origin, stable isotope analysis allowed us to incorporate origin estimates for a greater number of individuals compared to direct tracking methods alone. Thus, estimating *population* origin using stable isotopes can easily occur following only a single season of sampling. Given the length of the wintering and spring migration periods estimated by geolocators (approx. 6 months and 1 month, respectively), and assuming the widest range of claw growth rates reported in claw turnover studies [25,26], we estimate that the standardized claw samples collected at breeding arrival and analyzed in our study reflect integration of $\delta^2\text{H}$ within a period of 1–7 months and, thus, represent $\delta^2\text{H}$ values of the wintering area. Additionally, results from individuals tracked using both

geolocators *and* stable-hydrogen isotope analysis provided similar estimates of wintering origin; however, the low sample size of 'dually-tracked' individuals in this study (n=4) prevented us from conducting a robust comparison of these two techniques.

Data collected by citizen scientists is proving increasingly important for assessing the population status of migratory bird populations [9,38]; these observational data were useful for incorporating a measure of abundance in our assignment tests that was not available by any other means (i.e. Breeding Bird Survey). Incorporating relative abundance changed 68% of assignments when compared to tests based on equal abundance. This effect is high compared to other studies (i.e.: 5.9%) [33], which illustrates the importance of incorporating abundance into assignment tests for species such as snow buntings with high inter-region variation in abundance.

Conclusions

Our combination of multiple tracking techniques provided novel insights into the migratory patterns of Nearctic snow bunting populations throughout their breeding and wintering range and represents the first time a migratory passerine has been tracked throughout the full North American annual cycle. Our results provide strong evidence of east-west patterns of migratory connectivity and migration distance, which may be particularly relevant for conservation because long-term population trends vary across this migratory divide. Evidence that some populations may exist entirely within the boundaries of one or two countries suggests that North American nations, especially Canada, hold a significant global responsibility for the successful conservation and management of this species. By integrating spatial information from multiple concurrent sources, researchers can improve the strength of future population models aimed at predicting the response of populations to limiting factors occurring over the annual cycle, leading to more effective conservation and management of

migratory species [1]. Polar and high altitude environments are currently experiencing the strongest impacts of climate change [39], affecting the quality of breeding habitat available for snow buntings. Our ability to monitor regional variation in population trends may be limited to more accessible wintering ranges further south, thus, identifying patterns of migratory connectivity remain fundamentally important for our ability to monitor and implement effective conservation for Arctic-breeding species.

Acknowledgements

This research was supported by the Natural Science and Engineering Research Council (NSERC) of Canada (Discovery and Research Tools and Instruments grants to OPL, Canada Graduate Scholarship to CAM), Aboriginal Affairs and Northern Development Canada's Northern Scientific Training Program (NSTP), the Polar Continental Shelf Program (PSCP), Environment Canada and the University of Windsor. TKK Graciously acknowledges support of this research through the NSERC Discovery, NSERC Industry CRD, Canadian Foundation for Innovation, Ontario Innovation Fund and Queen's University.

We also thank the staff at the Canadian Bird Banding Office and the Copenhagen Bird Ringing Centre for providing banding data; Amie Black and the East Bay Island crew for support and assistance in the field; April Vuletich, Kerry Klassen and the staff at QFIR for assistance in the lab; Bridget Stutchbury, Kent McFarland and Greg Mitchell for geolocator attachment advice; Emily McKinnon for assistance with the analysis of geolocator data; Greg Campbell for advice interpreting citizen science-based observational data; and the members of the Canadian Snow Bunting Network for providing continuous support and enthusiasm for understanding migration patterns of arctic passerines. Nils Warnock and two anonymous reviewers provided valuable comments that significantly improved the quality of this manuscript.

References

- [1] Martin T.G., Chadès I., Arcese P., Marra P.P., Possingham H.P. and Norris D.R., Optimal conservation of migratory species. *PLoS ONE*, 2007, 2: 751.
- [2] Webster M.S., Marra P.P., Haig S.M., Bensch S., Holmes R.T., Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.*, 2002, 17: 76–83.
- [3] Faaborg J., Holmes R.T., Anders A.D., Bildstein K.L., Dugger K.M., et al., Recent advances in understanding migration systems of New World land birds. *Ecol. Monogr.*, 2010, 80(1): 3–48.
- [4] Grubb T.C. and Greenwald L., Sparrows and a bushpile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.*, 1982, 30: 637–640.
- [5] Brown D.R. and Long J.A., What is a winter floater? Causes, consequences, and implications for habitat selection. *Condor*, 2007, 109: 548–565.
- [6] North American Bird Conservation Initiative Canada. 2012. *The State of Canada's Birds, 2012*. Environment Canada, Ottawa, Canada. 36 pages.
- [7] Cox G., *Bird migration and global change*. Washington DC: Island Press, Washington DC, 2010.
- [8] Birdlife International, IUCN Red List for Birds, 2012, <http://www.birdlife.org> on 20/04/2012.
- [9] Butcher G.S. and Niven D.K., Combining data from the Christmas Bird Count and the Breeding Bird Survey to determine the continental status and trends of North American birds, 2007, <http://stateofthebirds.audubon.org/cbid/report.php>
- [10] Chabot A.A., Hobson K.A. Van Wilgenburg S.L., McQuat G.J. & Loughheed S.C., Advances in linking wintering migrant birds to their breeding-ground origins using combined

- analyses of genetic and stable isotope markers. *PLoS ONE*, 2012, 7:e43627. (doi:10.1371/journal.pone.0043627)
- [11] Hobson K.A., Wassenaar L.I. (Eds.), *Tracking animal migration with stable isotopes*, Academic Press, 2008.
- [12] Bowen G.J., Wassenaar L.I., Hobson K.A., Application of stable hydrogen and oxygen isotopes to wildlife forensic investigations at global scales, *Oecologia*, 2005, 143: 337–348.
- [13] Hobson K.A., Wassenaar L.I., Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers, *Oecologia*, 1997, 109: 142–148.
- [14] Stutchbury B.J.M., Tarof S.A., Done T., Gow E., Kramer P.M., Tautin J., et al., Tracking long-distance songbird migration by using geolocators, *Science*, 2009, 323: 896.
- [15] Ryder TB, Fox JW, Marra PP (2011) Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geocator and mark-recapture data. *Auk* 128: 448–453.
- [16] Tøttrup A., Klaassen R., Strandberg R., Thorup K., Kristensen M., Jørgensen P.S., et al., The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration, *Proc. R. Soc. Biol. Sci. Ser. B*, 2011, 279: 1008-1016.
- [17] Bairlein F., Norris D.R., Nagel R., Bulte M., Voigt C., Fox J.W., et al., Cross-hemisphere migration of a 25 g songbird, *Biol. Lett.*, 2012 doi:10.1098/rsbl.2011.1223 1744-957X
- [18] Stanley C.Q., MacPherson M., Fraser K.C., McKinnon E.A., Stutchbury B.J.M., Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route, *PLoS ONE*, 2012, 7(7): e40688. doi:10.1371/journal.pone.0040688
- [19] Reichlin T.S., Schaub M., Menz M.H.M., Mermod M., Portner P., Arletta R., et al. Migration patterns of Hoopoe Upupa epops and Wryneck Jynx torquilla: an analysis of European ring recoveries, *J. Ornithol.*, 2009 150: 393–400.
- [20] Lyngs P., Migration and wintering ranges of birds in Greenland: An analysis of ringing recoveries, *Dansk Ornithologisk Forenings Tidsskrift*, 2003, 97(1): 1-167.
- [21] Rappole J.H., Tipton A.R., New harness design for attachment of radio transmitters to small passerines, *J. Field Ornithol.*, 1991, 62: 335–337.
- [22] Caccamise D.F. and Hedin R.S., An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin*, 1985, 97: 306-318.
- [23] Lisovski S., Hewson C.M., Klassen R.H.G., Korner-Nievergelt F., Kristensen M.W. and Hahn S. Geolocation by light: accuracy and precision affected by environmental factors. *Methods Ecol. and Evol.*, 2012, 3(3): 603-612.
- [24] Bächler E., Hahn S., Schaub M., Arletta R., Jenni L., Fox J.W., et al., Year-round tracking of small trans-Saharan migrants using light-level geolocators, *PLoS ONE*, 2010, 5: e9566.
- [25] Bearhop S., Furness R.W., Hilton G.M., Votier S.C. and Waldron S., A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material, *Funct. Ecol.*, 2003, 17(2): 270-275.
- [26] Fraser K.C., Kyser T.K., Robertson R.J. and Ratcliffe L.M., Seasonal patterns in hydrogen isotopes of claws from breeding wood-warblers (Parulidae): utility for estimating migratory origins. *Avian Cons. Ecol.*, 2008, 3(1):2 <http://www.ace-eco.org/vol3/iss1/art2/>
- [27] Bowen G.J., Chesson L., Nielson K., Cerling T.E. and Ehleringer J.R., Treatment methods for the determination of delta H-2 and delta O-18 of hair keratin by continuous-flow isotope-ratio mass spectrometry. *Rapid Commun. Mass Spectrom.*, 2005, 19:2371–2378.
- [28] Wassenaar L.I. and Hobson K.A., Comparative equilibrium and online technique for determination of non-exchangeable hydrogen for keratins for use in animal migration studies, *Isotopes Environ. Health. Stud.*, 2003, 39(3): 211–217.
- [29] BirdLife International and NatureServe (2011) Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.
- [30] Bowen G.J., The Online Isotopes in Precipitation Calculator, version 2.2, 2012: <http://www.waterisotopes.org>
- [31] eBird: an online database of bird distribution and abundance [web application], Version 2, eBird, Ithaca, New York, 2012. Available <http://www.ebird.org>.
- [32] Royle J.A., Rubenstein D.R., The role of species abundance in determining the breeding origins of migratory birds using stable isotopes, *Ecological Applications*, 2004, 14: 1780–1788.
- [33] Norris D.R., Marra P.P., Kyser T.K., Sherry T.W. and Ratcliffe L.M., Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird, *Proc. R. Soc. Lond. B Biol. Sci.*, 2004, 271:59– 64.
- [34] Newton I. *The Migration Ecology of Birds*, Academic Press, Elsevier, London, 2008.
- [35] Lyon B. and Montgomerie R., Snow bunting (*Plectrophenax nivalis*), *The Birds of North America Online* (A. Poole, Ed.), Ithaca: Cornell Lab of Ornithology; Retrieved from the *Birds of North America Online*, 2011: <http://bna.birds.cornell.edu/bna/species/198>
- [36] Fraser K.C., Stutchbury B.J.M., Silverio C., Kramer P.M., Barrow J., Newstead D., et al. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore, *Proc. R. Soc. B.*, 2012, 279(1749): 4901-4906 doi: 10.1098/rspb.2012.2207.
- [37] Beauchamp G., What is the magnitude of the group-size effect on vigilance? *Behav. Ecol.*, 2008, 19(6):1361-1368.
- [38] Hurlbert A.H. and Liang Z., Spatiotemporal variation in avian migration phenology: citizen science reveals effect of climate change, *PLoS ONE*, 2012, 7(2): e31662. doi:10.1371/journal.pone.0031662
- [39] Intergovernmental Panel on Climate Change, Fourth assessment report (AR4) of the IPCC on climate change part I - the physical science basis. IPCC, Geneva, Switzerland, 2007.