



Cold tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird

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Sex biases in distributions of migratory birds during the non-breeding season are widespread; however, the proximate mechanisms contributing to broad-scale sex-ratio variation are not well understood. We analyzed a long-term winter-banding dataset in combination with spring migration data from individuals tracked by using geolocators to test three hypotheses for observed variation in sex-ratios in wintering flocks of snow buntings *Plectrophenax nivalis*. We quantified relevant weather conditions in winter (temperature, snowfall and snow depth) at each banding site each year and measured body size and condition (fat scores) of individual birds ($n > 5500$). We also directly measured spring migration distance for 17 individuals by using light-level geolocators. If the distribution pattern of birds in winter is related to interactions between individual body size and thermoregulation, then larger bodied birds (males) should be found in colder sites (body size hypothesis). Males may also winter closer to breeding grounds to reduce migration distance for early arrival at breeding sites (arrival timing hypothesis). Finally, males may be socially dominant over females, and thus exclude females from high-quality wintering sites (social dominance hypothesis). We found support for the body size hypothesis, in that colder and snowier weather predicted both larger body size and higher proportions of males banded. Direct tracking revealed that males did not winter significantly closer to their breeding site, despite being slightly further north on average than females from the same breeding population. We found some evidence for social dominance, in that females tended to carry more fat than males, potentially indicating lower habitat quality for females. Global climatic warming may reduce temperature constraints on females and smaller-bodied males, resulting in broad-scale changes in distributional patterns. Whether this has repercussions for individual fitness, and therefore population demography, is an important area of future research.

Variation in the distribution of the sexes during the non-breeding period over broad geographic ranges or locally by habitat is a widespread phenomenon among migratory taxa (Stewart 1997, Marra 2001, Phillips et al. 2004). These patterns are particularly evident in species also exhibiting sexual size dimorphism or differences in migration schedules (Myers 1981, Bai and Schmidt 2012). For birds wintering in temperate regions, the 'body size hypothesis' predicts that the larger sex (often males) will occupy colder non-breeding sites relative to the smaller sex, owing to a thermoregulatory advantage in cold-tolerance (Ketterson and Nolan Jr 1976, Cristol et al. 1999). Body mass is positively related to basal metabolic rate and improved fasting endurance, therefore larger birds may have a physiological advantage in colder and more snow-covered habitats (Scholander et al. 1950, Kendeigh 1969, Ketterson and King 1977).

An alternative and not mutually exclusive hypothesis for sex-bias in wintering populations is the 'arrival time hypothesis', which predicts that the sex that defends breeding territories (usually males) will overwinter closer to the breeding grounds in order to arrive on territory as early as possible (Ketterson and Nolan Jr 1976, Cristol et al. 1999).

However, birds can also arrive early to breeding sites via advancing spring departure dates or migrating at faster speeds (or stopping for fewer days) (Coppack and Pulido 2009). Nonetheless, the only mechanism that would necessarily result in sex-biased wintering populations is selection for shorter migration distances, which would promote a male bias in the wintering range at its closest point to the breeding range. This hypothesis has been difficult to test, as most birds are only measured at one point during the annual cycle (e.g. at winter site, migration stopover, or at breeding site), thus the true migration distance of individuals has been elusive.

Last, the 'social dominance hypothesis' predicts that dominant individuals (usually males) exclude subordinates from preferred habitats, forcing subordinate individuals to migrate further away from breeding sites or to suboptimal habitats (Gauthreaux Jr 1978). This prediction assumes that migration is inherently costly and that dominant individuals benefit from increased survival by migrating shorter distances (Cristol et al. 1999). Social dominance at the scale of a single flock is relatively easy to determine by behavioural observations of colour-marked individuals (Smith and

Metcalf 1997). Measuring such effects at a larger scale is more difficult, but assessing relative body condition of predicted dominant and subordinate individuals can provide indirect support for this hypothesis. For example, subordinate birds forced into lower-quality habitats may trade-off carrying heavier loads of body fat to compensate for lower food availability, at the expense of their ability to evade predators (Witter and Cuthill 1993). Thus at a broad geographic scale, we might predict females to migrate farther than males, and that they occupy lower-quality habitats, leading to increased fat levels during the winter.

Untangling the hypotheses for sex-ratio bias during the non-breeding season is surprisingly difficult, as predictions tend to overlap: larger birds are often better able to tolerate the coldest weather (body size hypothesis), while also being socially dominant (social dominance hypothesis). The coldest wintering sites are also usually closer to the breeding grounds, further confounding effects of body size with migration distance (arrival time hypothesis and social dominance hypothesis). As such, observed distributional patterns of the sexes in winter are likely the result of multiple interacting mechanisms (Ketterson and Nolan Jr 1979). An integrative approach that examines multiple hypotheses within the same population is useful, as the relative strength of each effect can be assessed for the same study sample.

Studies of birds during the non-breeding season have yielded evidence for the body size (Palacin et al. 2009, O'Neal et al. 2011, Arizaga et al. 2014) and social dominance hypotheses (Campos et al. 2011, Danner et al. 2013) in driving sex-bias in distributional patterns. Testing the arrival-timing hypothesis has been more challenging because tracking birds directly from winter to breeding arrival to determine sex-specific migration distance has been difficult, especially for small species, owing to limitations in the size and performance of tracking devices. Despite these challenges, studies of the partial-migrant European blackbird *Turdus merula*, found that obligate migrants were more likely to be female, and year-round residents more likely to be male, lending support for the arrival time hypothesis (Fudickar et al. 2013). In this same study no age differences were observed in migration patterns, as would be expected under the social dominance hypothesis (Fudickar et al. 2013). Additionally, a recent study of reed buntings *Emberiza schoeniclus* found that males wintered closer to obligate spring migration pathways (Arizaga et al. 2014), offering further support for the arrival time hypothesis. Finally, studies often assume that differences in wintering latitude correlate with differences in migration distance, when in fact exact migration routes and breeding sites are not known (Stouffer and Dwyer 2003, Arizaga et al. 2014). Recent miniaturization of light-level geolocation tags (geolocators) for tracking small migratory songbirds (Stutchbury et al. 2009) presents the opportunity to incorporate direct measures of migration behaviour to test for variation in distance traveled and arrival timing by sex (McKinnon et al. 2013).

In this study, we combined long-term winter banding data and migration data obtained by direct-tracking to test the mechanisms for observed spatial variation in wintering sex ratios of snow buntings *Plectrophenax nivalis*. The snow bunting is a circumpolar Arctic-breeding and temperate-wintering passerine, which exhibits geographic sex-segregation

during the winter (Rae and Marquiss 1989, Banks et al. 1991) (Fig. 1, range map Supplementary material Appendix 1, Fig. A1). Snow buntings provide a model system to study hypotheses for wintering sex-bias. Snow buntings form flocks of up to 1000 individuals during the winter, in which males and females are distinguishable by plumage (Montgomerie and Lyon 2011). They are also readily captured in large numbers by using baited ground-traps; thus, body condition and size measurements can be obtained for many individuals. Furthermore they occupy cold temperate regions in winter where extreme low temperatures and frequent snow cover (which limits access to food) are easy to measure and should provide strong selective forces on winter behaviour.

Snow buntings are sexually dimorphic in body size (males larger than females) (Montgomerie and Lyon 2011). The body-size hypothesis would therefore predict that temperature and snow cover would limit the area occupied by females during the winter, resulting in sex-segregation based on environmental conditions. Snow cover reduces food accessibility for ground-foraging species, and thus, the abundance of temperate wintering granivorous birds (Best et al. 1998). Snow buntings are well-adapted to cold temperatures year-round (Montgomerie and Lyon 2011); thus, wintering in locations that are too warm would also likely have negative physiological costs, especially for larger birds. Wintering in warmer sites would also require more time and energy spent on migration. As such, buntings may trade-off costs of increasing migration distance with physiological tolerance of environmental conditions, based on their size and related thermoregulatory capabilities. More specifically, we predicted that colder and more snow-covered sites would support larger-bodied individuals, and this relationship should be found both within and across sexes.

Snow buntings also exhibit differential spring migration, where males arrive at breeding sites before females, and earlier arrival dates are associated with obtaining high-quality breeding territories (Guindre-Parker et al. 2013a). As such, male-biased sex ratios in the northern part of the winter range (Fig. 1) could be a result of males reducing spring migration distance as a strategy to advance arrival dates. By tracking male and female birds directly from the same breeding sites by using geolocators, we tested the hypothesis that males were reducing spring migration distance by wintering further north.

Finally, previous studies have provided evidence for a sex- and age-related dominance hierarchy in wintering flocks of snow buntings. Smith and Metcalfe (1997) found that males would most often out-compete females, and juvenile birds tended to be dominant over adults within a given sex. Therefore, by the social dominance hypothesis we predict that birds with subordinate status (i.e. female snow buntings), which might be excluded from high quality sites by dominant individuals (i.e. males), would carry more fat as insurance against starvation (McNamara et al. 1994, Higginson et al. 2012).

Methods

Banding data

We obtained historical bird banding data from the Canadian Bird Banding Office for 1976–2012 to determine sex ratios

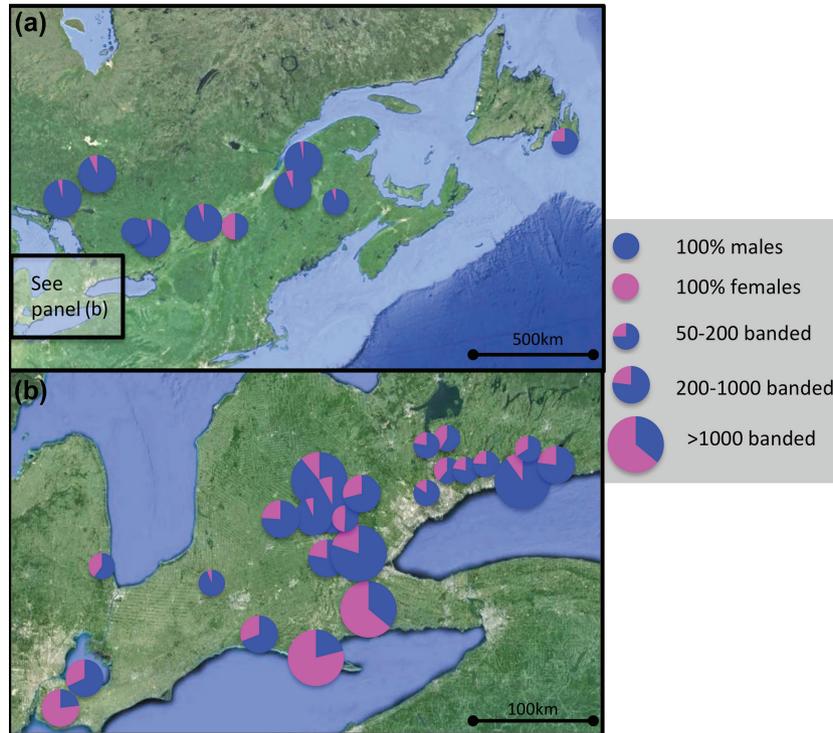


Figure 1. Sex-ratios of snow buntings banded across southern and eastern Canada varied extensively, although overall more males were captured than females. Pie charts indicate the sex ratio at a given banding site, and the size of the pie indicates the total number of birds banded at that site in a single winter. For sites where more than one year of data was available we show the year with the most individuals banded.

of wintering flocks. In addition to sex and age, unflattened wing chord to 1mm and subcutaneous fat scores (scale of 0–7, Kaiser 1993) were recorded during more recent banding efforts (2009–2012) by the Canadian Snow Bunting Network (CSBN). We used wing chord as a measure of size (independent of stored resources, i.e. fat) and we used measures of stored fat (fat scores) in separate analyses to assess relative access to food (higher fat scores should indicate lower predictability of resources).

For all banding, birds were captured by using seed-baited ground traps in open habitats. Sex was determined by examining plumage characteristics (Pyle 1997) and age was determined by colour patterns on the greater secondary covert feathers (D. Hussell pers. comm.) (Rae and Marquiss 1989). To simplify age classifications, we collapsed hatch-year (HY, before 31 Dec) and second-year (SY, after 31 Dec), and after-hatch-year (AHY, before 31 Dec) and after-second-year (ASY, after 31 Dec) age classes into ‘SY’ and ‘ASY’, respectively.

Assessing site-specific sex-ratios

Banding records were conservatively truncated by the wintering period, defined for our study population as 1 Nov to 15 Mar, based on pre-migration behavioural changes beginning in mid-March (Vincent and Bédard 1976). This resulted in a database of 39 126 known-sex individuals captured at 25 independent sites throughout the defined winter period over 36 yr of banding. Capturing snow buntings outside of this period is difficult due to sparse snow cover, which reduces bunting visitation to baited traps. We

tested for significant within-winter changes in sex-ratio by using a generalized mixed effects model with binomial error distribution on sex (subset of birds with known captured date, $n = 37\ 185$ individuals), including date of capture as a fixed factor and site-year interaction as a single random factor. Sex ratio did not change significantly with date (likelihood ratio-test, $\chi^2 = 0.76$, $DF = 1$, $p = 0.38$), therefore we used a single site- and year-specific sex-ratio calculated from the total number of birds banded at each site between 1 Nov and 15 Mar. Sites with low trapping effort ($n = 4$) were further excluded to avoid inherent bias in sex-ratios associated with small sample sizes.

Environmental conditions in winter

Historical weather data for the wintering period was obtained from the Environment Canada Weather Office (<<http://climate.weather.gc.ca/>>) for 42 site-year combinations (21 sites), using the weather station closest to each banding site (12.75 ± 0.78 km, mean \pm SE, range = 3.17–30.25 km). Sites ranged in the number of sampled years from 1–10, and years ranged between 1976–2012 (total 42 site-year combinations). For each year, we extracted two snowfall variables and one temperature variable per site. We calculated total snowfall (cm) by summing daily snowfall over the entire wintering period (Nov–Mar). Snow depth was calculated as the average monthly snow depth for each site-year. As a measure of temperature, we calculated total heating degree-days (HDD), defined as $[18^\circ\text{C} - (\text{mean daily temperature})]$, summed over the wintering period. High values for HDD represent periods with

colder temperatures, whereas low values for HDD represent warmer temperatures. We used HDD as it was positively correlated with snowfall and snow depth (i.e. high values of all three indicate sites with the harshest weather). The three measures of weather were significantly positively correlated (i.e. colder sites also had more total snowfall and deeper snow); therefore, we combined all three into one measure of winter weather by using principal components analysis. Principal component 1 was positively loaded by all three weather variables (HDD: 0.87, total snowfall: 0.90, average snow depth: 0.87) and explained 77.53% of the variance in the dataset (eigenvalue = 2.33). We extracted PC1 as a measure of weather severity, hereafter PC1weather. To facilitate interpretation of estimates, we scaled PC1weather by setting the lowest score (−3.23, corresponding to warmest site-year combination) to zero. Higher values of PC1weather are indicative of colder, snowier sites.

Spring migration distance

We used light-level geolocators to compare spring migration distances of males and females breeding at a long-term study site at East Bay Island, in the East Bay Migratory Bird Sanctuary, Nunavut, Canada (64°02'N, 81°47'W). Geolocators were deployed over three breeding seasons (2010–2012), following animal care guidelines of the Canadian Council for Animal Care (Environment Canada) and the Univ. of Windsor Animal Utilization Project Proposal (AUPP #9–14), and under master bird banding permit #10808 (see methods in Macdonald et al. 2012). Snow buntings were captured beginning in late May by using seed-baited ground traps. All captured birds were colour-banded for field identification and assigned a numbered metal band provided by the Canadian Banding Office. In 2010 and 2011, we also collected a small blood sample from the brachial vein and trimmed 2 mm from the left hind claw for concurrent studies (Macdonald et al. 2012, Guindre-Parker et al. 2013b).

Geolocators have had negative fitness effects on some migratory birds (Arlt et al. 2013, Scandolaro et al. 2014), presumably because of the increased energetic costs of flight with a heavier or less aerodynamic body shape. Because snow buntings exhibit sexual size-dimorphism, we tested for a sex-bias in return rates of geolocator-outfitted birds, to assess the potential for differential effects on migration or survival that could have influenced our results (Supplementary material Appendix 1). We found equal return rates by sex for geolocator-outfitted snow buntings suggesting no detectable cost of wearing a geolocator associated with differences in tag to body size ratio by sex (Supplementary material Appendix 1). Geolocators were collected from returning birds ($n = 21$; see Supplementary material Appendix 1 for return rates by age, sex, and year) and light data were downloaded, decompressed, and edited to remove light transitions affected by shading by using BASTrak software (British Antarctic Survey, ver. 19.0). Light data were generally free of shading events, owing to the open-country habitat preferences of this species. Batteries failed in three of 21 geolocators collected from returning birds (2 males from 2010 deployments, 1 female from 2012 deployment); therefore migration distance was determined for 18 individuals (8 females, 10

males). One male was tracked in two consecutive years; we only used the first track from this individual in analyses (total males = 9).

We used two approaches to determine spring migration distance. The first method conservatively estimated spring migration distance as a straight-line measure between winter site and breeding site for each bird. Since snow buntings are nomadic in winter and can travel several hundred kilometres within the wintering period (Macdonald, McKinnon and Love unpubl.), we used a weighted mean winter site, taking each winter location for a bird and weighting it by the proportion of days spent at that site. Our second approach estimated the actual migration route of each snow bunting by mapping spring migration stopover sites and connecting each stopover by straight lines, beginning at the final winter location and ending at the breeding site (East Bay). Snow buntings nest and roost in rock cavities at their breeding sites, therefore the arrival date of individuals at East Bay was evidenced by an abrupt change in light level patterns indicative of cavity use. Departure on spring migration was defined as the first date the bird was located north of the mean wintering range of all birds ($> 53.5^\circ\text{N}$), and or continued movements north and eastwards towards the known breeding site. Two consecutive noon or midnight locations $< 2^\circ$ different in longitude were considered one stopover. Longitudinal shifts $> 2^\circ$ between consecutive noon or midnight locations were considered migration nights.

Statistical analyses

To test whether birds wintering in colder or snowier areas were larger on average (body size hypothesis), we used a linear mixed-effects model of wing length including PC1weather, sex, and age as fixed effects, and site-year interaction as a random effect. For this analysis we used 5616 individual wing measurements from 9 site-year combinations (each with unique weather values). We used likelihood ratio test of the full model (including sex, age, PC1weather and site-year) compared to a model without the variable of interest, PC1weather, to determine if weather was a significant factor. We also tested for fixed effects of weather (PC1weather) on the proportion of males captured at 42 site-year combinations, including a site-year random effect in a binomial generalized mixed-effects model. This model was based on captures of 39 126 individual birds across 42 site-years. If body size is the primary driver of distribution, higher proportions of males (the larger sex) should be found in colder and snowier sites. We tested for the effects of PC1weather on the proportion of males captured by using a likelihood-ratio test to compare the model with PC1weather to the null model (site-year only) (Faraway 2006).

To test whether sex-biases in winter are consistent with males minimizing spring migration distance, we compared straight-line spring migration distance and spring route length between male and female geolocator-tracked birds by using ANOVA, with sex nested by year as an independent factor ($\alpha = 0.05$). We included year as a nesting term to account for any overall changes in distribution between winters. In a similar analysis, we compared the latitude and longitude of wintering sites between males and females by using ANOVA, with sex nested by year.

If males are excluding females from areas with high food abundance (i.e. high quality habitat) through social dominance (Smith and Metcalfe 1997), females may carry relatively more fat as a response to this unpredictable food access (Witter and Cuthill 1993). Therefore, we modeled fat scores as a dependent variable with sex, weather (PC1weather), and age as fixed effects, and site-year as a random effect, by using a generalized linear model with Poisson error distribution to account for the categorical response. All analyses were conducted by using R ver. 3.1.1 (R Development Core Team), and means are reported with standard error unless otherwise noted. Mixed effects models were run by using the function 'glmer' (generalized models) and 'lmer' (linear models) in the package lme4 (Bates et al. 2014).

Data available from FigShare: <<http://dx.doi.org/10.6084/m9.figshare.1447275>> (Macdonald et al. 2015).

Results

Body size hypothesis

Weather (PC1weather) was a significant positive predictor of the size of snow buntings captured ($n = 5616$; $\chi^2 = 9479$, $DF = 1$, $p < 0.001$), in that larger individuals of both sexes tended to be captured in colder and snowier sites (Fig. 2) (estimate 0.32 ± 0.24 increase in wing length with increasing PC1weather), after controlling for significant and expected differences in wing size by age and sex (Table 1). However, the relationship between weather and wing size was very weak, and the confidence intervals overlapped zero (95% CI: -0.15 to 0.79), indicating that the effect was negligible.

Weather was a significant predictor of variation in sex ratios of snow buntings (logit estimate 0.48 ± 0.17 , $z = 2.85$, $p = 0.004$) (Fig. 3) ($n = 42$, $\chi^2 = 430.83$, $DF = 1$,

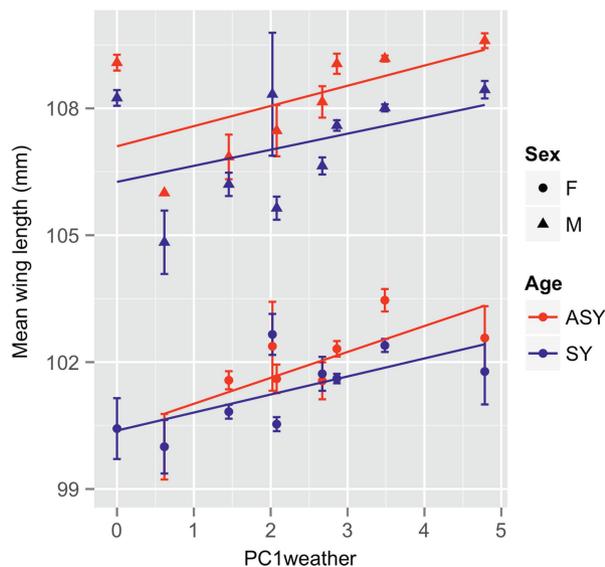


Figure 2. PC1weather (higher values are colder and snowier sites) was a significant predictor of wing length for wintering snow buntings, after accounting for variation across sexes and age classes. Males and females tended to be larger at colder and snowier wintering sites. Lines are from linear regressions, vertical bars indicate standard error of the mean wing length by sex and by age.

Table 1. Model estimates for generalized and general linear mixed effects models on wing length, fat scores, and sex ratio of wintering snow buntings. Likelihood ratio tests are shown for full models versus models without the variable of interest: PC1weather for wing and sex-ratio models, and sex for the fat score model. Base categories for fixed effects are indicated in brackets (e.g. for sex, M = males). Higher values of PC1weather indicate snowier and colder sites, and Year:Site indicates a single random intercept for each site by year combination.

Dependent variable (n)	Predictor estimates (\pm SE)	Random effects variance (\pm SD)	Likelihood ratio test	
			χ^2	p
Wing (5589)	Intercept	Year:Site	11147	<0.001
	102.80 \pm 0.40	0.91 \pm 0.95		
	Sex (M)	Residual		
	5.82 \pm 0.09	6.46 \pm 2.54		
	Age (SY)			
Sex ratio (42)	PC1weather	Year:Site	430.83	<0.001
	-0.72 \pm 0.50	1.68 \pm 1.30		
	PC1weather			
	0.66 \pm 0.14			
Fat score (5448)	Intercept	Year:Site	6651.7	<0.001
	0.99 \pm 0.22	0.12 \pm 0.33		
	PC1weather			
	0.08 \pm 0.08			
	Sex (M)			
	-0.02 \pm 0.02			
	Age (SY)			
-0.03 \pm 0.02				

$p < 0.001$). The probability of a bird at the warmest site (PC1weather = 0) being male decreased by 0.72, and each unit of increasing cold and snow increased the probability of captured birds being male by 0.66 (Table 1). Despite the significant effect of weather in both models (wing length and sex ratio), there remained extensive random variation by site-year (indicated by relatively large variance estimates for random effects, Table 1).

Arrival time hypothesis

Mean wintering location for males was on average $1.54^\circ N$ of female wintering location (mean $48.88^\circ N$ for females, $50.42^\circ N$ for males), and slightly further west (mean

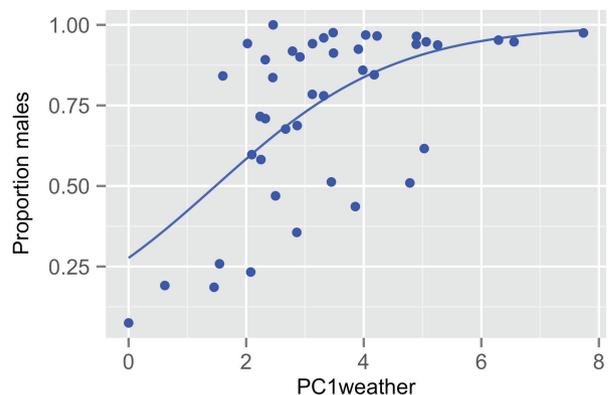


Figure 3. The proportion of males captured ($n = 42$ sites) increased with increasingly harsh weather (higher PC1weather indicating more snow fall, higher snow depth, and colder).

−105.09°W for females, −105.73°W for males). Latitude was significantly different by sex ($F = 7.67$, $DF = 1$, 13 , $p = 0.02$) but not sex nested by year (latitude, $F = 0.36$, $DF = 2$, 13 , $p = 0.71$). Longitude did not differ significantly by sex ($F = 0.08$, $DF = 1$, 13 , $p = 0.77$) or sex nested by year ($F = 1.43$, $DF = 2, 13$, $p = 0.27$). Straight-line migration distance for males was 2085.7 ± 82.7 km and for females was 2207.9 ± 34.8 km. Straight-line migration distance did not differ significantly by sex ($F = 1.83$, $DF = 1$, 13 , $p = 0.20$) or by sex nested within year ($F = 1.12$, $DF = 2$, 13 , $p = 0.36$). Straight-line migration distance was not correlated significantly with spring migration route distance ($r = 0.25$, $F = 1.84$, $DF = 1$, 15 , $p = 0.19$). Spring migration route distance for males was 2174.44 ± 125 km and for females was 2110.9 ± 63.64 km. Spring migration route length did not differ significantly by sex ($F = 0.18$, $DF = 1$, 13 , $p = 0.68$) or sex nested within year ($F = 0.57$, $DF = 2$, 13 , $p = 0.58$).

Social dominance hypothesis

Fat scores varied from 0–5 (out of a possible 7) across winter sites. We found sex was a significant predictor of fat scores, with females having slightly higher scores than males ($n = 5448$; $\chi^2 = 6.27$, $DF = 1$, $p < 0.01$), although the effect was small with confidence intervals overlapping zero (estimate for males = -0.02 ± 0.02) (Table 1). Age had a slightly larger effect on fat scores in that adults tended to carry more fat than juveniles (estimate for juveniles -0.03 ± 0.02).

Discussion

We found that spatial variation in sex-ratios in flocks of overwintering snow buntings (Fig. 1) was correlated with variation in weather (temperature, snowfall, and snow depth): colder and snowier sites hosted larger individuals (Fig. 2) lending support to the body size hypothesis. This effect was independent of sex and age effects on body size. Furthermore, there were higher proportions of males (the larger sex) at sites with more severe winter weather (colder temperatures, more snowfall, greater snow depth) (Fig. 3). There was a small effect of sex on fat levels, in that females tended to have slightly higher levels of fat than males; which could be indicative of social dominance effects. By directly tracking males and females from the same breeding site to their winter site, we were able to compare spring migration distances to determine whether males were selecting winter sites to minimize migration distance, resulting in sex-ratio biases in wintering flocks. Differences in migration distance could also be produced by social dominance, if males force females to migrate further through dominance interactions. However, we found no significant difference in either straight-line distance or spring migration route between males and females. Overall our results support the body size hypothesis as the primary driver of sex-ratio biases in wintering flocks of snow buntings, with some evidence for the social dominance hypothesis and no support for the arrival time hypothesis.

Higher proportions of the larger-bodied sex (i.e. males) at sites with harsher weather supports the hypothesis that metabolic temperature regulation is a proximate mechanism

for variation in sex-ratios among wintering snow bunting populations. If sex-ratios of wintering populations are driven by temperature tolerance, we would expect that inter-annual variation in climate conditions would lead to inter-annual variation in distributions by size and thus, sex-ratios across wintering populations. Such flexibility in migratory decisions has been found in partial migrants, particularly in males (Fudickar et al. 2013). There are records of snow buntings in Siberia where males do not migrate south at all but remain at their breeding sites year-round, possibly indicative of highly flexible migratory strategies in this species as well (Rae and Marquiss 1989). We analyzed measurements of body size collected from more recently established banding sites (2009–2012). While our sample size was large (> 5500 individuals), additional morphometric data from wintering snow bunting populations across the range would allow further exploration of how inter-annual variation in winter climate affects the distribution of this species and allow predictions for responses to changing climate.

Climate change models predict less snow and warmer temperatures for the current snow bunting wintering range (Krasting et al. 2013, Williams et al. 2014), and winter bird communities are already shifting to favour more warm-adapted species (Princé and Zuckerberg 2014). As winter temperatures increase, snow buntings may move further north within their winter range; however, they could be limited in the extent of northwards movement by the boreal forest, which stretches coast-to-coast across North America. Migration tracking work indicates that buntings avoid this heavily forested region by making stopovers either along the Hudson Bay coast, above the tree-line to the north, or below the tree-line in the prairies, agricultural lands, and prairie-parkland to the south (Macdonald et al. 2012). Detailed bioclimatic models of the expected distribution of snow buntings under various climate change scenarios would help elucidate where and when their optimal distribution will be in future (Thomas 2010).

Novel behavioural data from geolocators provided insight into migration distance of male and female buntings from the same breeding sites. While males wintered on average slightly further north than females (Fig. 4), surprisingly, this did not translate into a significantly shorter migration distance. Differences in winter distribution by sex observed during surveys or banding efforts are often assumed to correlate with differences in migration distance, which in turn are assumed to correlate with arrival timing. By using direct tracking, we showed that male and female migration distance was not significantly different despite latitudinal differences in winter sites, because males tended to winter slightly further west (-106.03°W for males versus -105.17°W for females). This resulted in approximately equal migration distance, although females wintered slightly further south, but also slightly eastward and thus closer longitudinally to their breeding sites. Straight-line migration distance for males was 126 km longer on average than for females, and migration route was 85 km shorter, relative to the female average. Distances within this range (80–130 km) could easily be covered in a single night's flight for an individual bird, given an average estimated flight speed of 446 km/night for this species (based on total migration duration in days, minus nights spent stopped), and thus would not result in a large

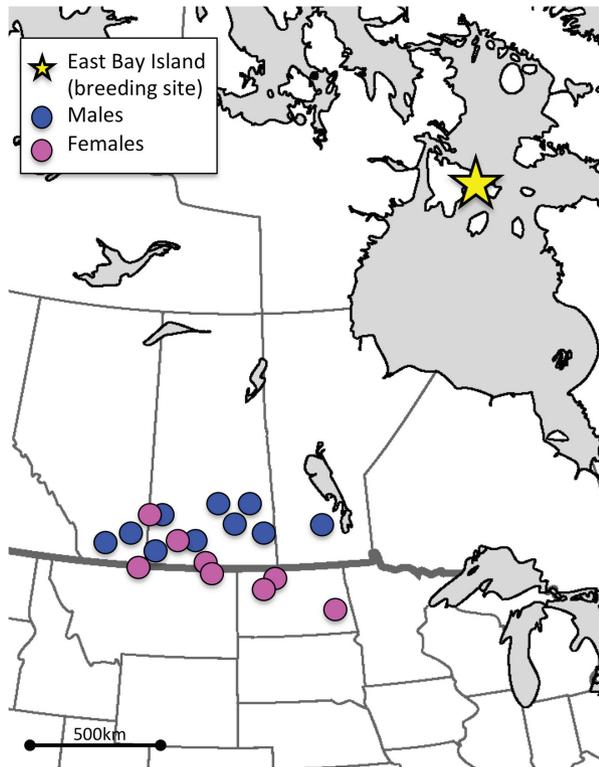


Figure 4. Weighted mean winter location for male and female snow buntings ($n = 10$ and 8 , respectively) tracked by using geolocators from a breeding site at East Bay Island, Nunavut. Despite slight differences in mean winter latitude, spring migration distance was not significantly different by sex.

difference in arrival dates. It may be that sexual selection on males to arrive early acts on body size to improve cold-tolerance in early spring at breeding sites, with the result that males can also tolerate wintering in colder sites. Thus, selection for improved cold tolerance early in the breeding season may be more important than reducing migration distance for males attempting to arrive early at breeding sites.

Despite significant effects on the overall variance explained in the model, weather was a relatively poor predictor of both wing length and fat scores, compared to the effects of sex, age and extensive random variation by site and year (Table 1). We assumed food availability was correlated with snow depth and total snowfall; however, we could not directly measure food abundance. Larger males may be able to persist in areas with lower food abundance (independent of availability), especially if they are dominant within flocks; therefore food abundance might be an additional important environmental factor that could influence sex-ratios. The abundance of predators, such as peregrine falcons *Falco peregrinus* or gyrfalcons *Falco rusticolus*, could also influence the distribution patterns of snow buntings, and could affect sex-ratios if one sex is subjected to higher predation risk. In western sandpipers *Calidris mauri*, predation risk was higher for female birds (due to higher wing loading), resulting in segregation by sex in the non-breeding range in relation to predator abundance (Nebel and Ydenberg 2005). This hypothesis for explaining the sex-biases in distribution of snow buntings deserves further attention in future studies.

Our results provided little support for social dominance interactions leading to the observed geographic sex-segregation (Table 1), although predictions for this hypothesis are difficult to disentangle from effects of body size and arrival time. We predicted that relatively high fat scores in females could indicate less access to food. Our results did suggest a small but significant effect of sex on fat scores (Table 1). Interestingly, in snow buntings second-year birds (juveniles) are known to be social dominant over adults within a sex (Smith and Metcalfe 1997) and our fat score analysis supported this finding in that adults carried slightly more fat than juveniles. It may be that social dominance plays more of a role in structuring small-scale distributional patterns (Smith and Metcalfe 1997), and contributes less to the range-wide distribution of the sexes in winter. A critical assumption of Gauthreaux's (1978) social dominance hypothesis is that there are survival costs to subordinates for wintering in lower-quality habitats (Cristol et al. 1999). However, it is also possible that subordinate individuals may simply adopt a differential foraging strategy or exploit a slightly different ecological niche relative to dominant individuals, with no associated fitness costs (Cristol et al. 1999). One avenue for further exploring the social dominance hypothesis would be to assess survival rates of snow buntings by age and sex, across wintering sites at different distances from their breeding sites. This would be challenging as the specific breeding sites of wintering birds are usually not known, there is low natal philopatry in this species, and winter survival is difficult to assess for a relatively nomadic species, although remote tracking systems are continually improving and may provide insight into these questions.

Overall, our results provide evidence for male cold tolerance and social dominance, but not selection for minimizing migration distance, as the mechanisms contributing to the geographic variation in sex ratios of snow buntings. Although it is often difficult to distinguish between these non-mutually exclusive hypotheses, our results provide new insights into the factors limiting the distribution of wintering snow buntings populations in North America and enable greater predictive capacity when estimating population responses to future climate change. Additionally, combined applications of traditional and modern tracking techniques provided a new ability to test longstanding hypotheses to further our understanding of the evolution of these distributional patterns and migratory strategies of small migratory songbirds.

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Supplementary material (Appendix JAV-00689 at <www.avianbiology.org/readers/appendix>). Appendix 1.