

Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird

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Received: 8 May 2015 / Accepted: 30 November 2015
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Abstract Patterns of connectivity between breeding and wintering grounds can have important implications for individual fitness and population dynamics. Using light-level geolocators and stable hydrogen isotopes ($\delta^2\text{H}$) in feathers, we evaluated differential migration of Savannah sparrows (*Passerculus sandwichensis*) breeding on Kent Island in the Bay of Fundy, New Brunswick, Canada in relation to sex, age, and body size. Based on geolocators recovered from 38 individuals between 2012 and 2014, the winter distribution was centered in North Carolina (median latitude 34°, range 26°–41°), with males overwintering, on average, approximately 275 km further north than females. Based on analyses of tail feather samples collected from 106 individuals from the same population between 2008 and 2012, males and adults had more negative $\delta^2\text{H}$ values

than females and juveniles, respectively, providing additional evidence that males wintered north of females and that adults wintered north of juveniles. Winter latitude and $\delta^2\text{H}$ values within each sex were not found to be related to body size. From geocator data, males returned to the breeding grounds, on average, 14 days earlier than females. For males, there was some evidence that arrival date on the breeding grounds was negatively correlated with winter latitude and that individuals which arrived earlier tended to breed earlier. Thus, benefits for males of early arrival on the breeding grounds may have contributed to their wintering farther north than females. Social dominance may also have contributed to age and sex differences in winter latitude, whereby dominant males and adults forced subordinate females and juveniles further south.

Communicated by Toni Laaksonen.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3527-8) contains supplementary material, which is available to authorized users.

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Keywords Carryover effects · Light-level geocator · Protandry · Savannah sparrow · Stable isotopes

Introduction

For migratory species, decisions about when and how far to migrate can have important implications for fitness and population dynamics (Kokko 1999; Webster et al. 2002; Marra et al. 2006; Taylor and Norris 2007; Boyle et al. 2011; Vel-mala et al. 2015). At an individual level, migration timing can influence the ecological conditions experienced on the way to winter and breeding areas and, in turn, the costs of migration (Wikelski et al. 2003; Klaassen et al. 2014; Lok et al. 2015). Where an individual spends the winter can influence its condition and survival in the short term, but also carry over to influence performance in subsequent seasons (Norris et al. 2004; Harrison et al. 2011). If populations are segregated by age or sex during the non-breeding season,

exposure to different ecological conditions at different winter areas could impact age- and/or sex-specific vital rates, such as survival or productivity in the subsequent breeding season (Webster et al. 2002; Calvert et al. 2009; Taylor and Norris 2010; Betini et al. 2015). Consequently, knowledge of how migration patterns vary within species and populations and of the factors underlying this variation is important for our understanding of the ecology of migratory species.

Differential migration of sex (and to a lesser extent age) classes during winter is common in migratory birds. For species breeding in the northern hemisphere, males typically overwinter north of females and adults north of juveniles or first-time migrants (Ketterson and Nolan 1976; Holberton and Able 2000; Catry et al. 2004; Mazerolle and Hobson 2007; Dale and Leonard 2011). Three non-mutually exclusive hypotheses have been proposed to explain differences in winter latitude among sex and age classes, each of which is based on the assumptions that migrating long distances and overwintering at more northern latitudes are associated with high energetic costs. The *early arrival* hypothesis proposes that the sex that experiences the most intense intraspecific competition for resources (including mates) on the breeding grounds will overwinter at more northern latitudes to expedite arrival to the breeding grounds (Ketterson and Nolan 1976; Myers 1981). In most songbirds, males are the territorial sex and, in turn, tend to arrive at breeding areas earlier in spring than females to compete for and establish breeding territories (Francis and Cooke 1986, 1990; Morbey and Ydenberg 2001; Mazerolle and Hobson 2007; Morbey et al. 2012). A key assumption of this hypothesis that has yet to be adequately validated is that winter latitude is directly related to arrival date in spring and timing of breeding (but see Mazerolle and Hobson 2007; Dale and Leonard 2011). The *body size* hypothesis proposes that larger individuals (typically males) winter further north than smaller individuals because they are more capable of withstanding the harsh winter conditions of more northern latitudes (Ketterson and Nolan 1976). The third hypothesis, the *social dominance* hypothesis, proposes that dominant individuals (typically males and adults) will out-compete subordinates for winter resources, thereby forcing subordinates to migrate further south in search of available habitat (Gauthreaux 1978).

To date, the difficulty of determining where individuals spend the winter and, in turn, linking events during the breeding and non-breeding (migration and winter) seasons has limited our ability to gain a full understanding of the patterns and causes of differential migration. We combined estimates of winter latitude and migration timing from light-level geolocators and the stable hydrogen isotope ($\delta^2\text{H}$) content of feathers to evaluate these three hypotheses for differential migration in Savannah sparrows (*Passerculus sandwichensis*) breeding on Kent Island in the Bay of

Fundy, New Brunswick, Canada. Geolocators are archival, battery-powered, animal-borne devices that measure light intensity over time. Downloaded light records are used to determine day length and times of solar noon and midnight, which are then used to estimate latitude and longitude for every 12-h period. For studies of bird migration, geolocators are typically deployed during the breeding season and retrieved the following year, thereby providing information on an individual's whereabouts and timing of movements for the full annual cycle. The $\delta^2\text{H}$ content of feathers grown on the winter grounds can be used to approximate winter latitude because $\delta^2\text{H}$ from the local environment is incorporated into inert feather tissue through an individual's diet (Hobson and Wassenaar 1997) and environmental $\delta^2\text{H}$ follows a predictable latitudinal gradient in eastern North America (Bowen et al. 2005).

To evaluate the three hypotheses, we first tested for differences in winter latitude in relation to age and sex across all individuals in our study. Based on all three hypotheses, we predicted that males would winter further north than females since they are the larger, territorial, and socially dominant sex in our study population. Based on the *social dominance* hypothesis, we expected adults to winter further north than juveniles. To evaluate the *body size* hypothesis, we tested for relationships between winter latitude and body size (tarsus and wing length) within each sex. Based on the *body size* hypothesis, larger individuals were expected to winter further north than smaller individuals. Lastly, we evaluated links between winter latitude, timing of arrival to the breeding area, and breeding performance. Based on the *early arrival* hypothesis, we predicted that males that wintered further north would return to the breeding grounds earlier in spring and, in turn, that early arriving males would breed earlier than later arriving males. In relating winter latitude to arrival timing, we also evaluated a key, but undertested, assumption of the *early arrival* hypothesis that winter latitude influences timing of arrival to the breeding grounds.

Materials and methods

Study species and population

We studied Savannah sparrows breeding on Kent Island, New Brunswick, Canada (Fig. 1; 44.48°N, -66.79°W), an approximately 100-ha island that forms part of the Grand Manan Archipelago in the Bay of Fundy. Savannah sparrows are short-distance, migratory, grassland songbirds whose breeding range encompasses much of Canada and the northern United States and whose primary winter range includes the southern USA and Mexico (Wheelwright and Rising 2008).

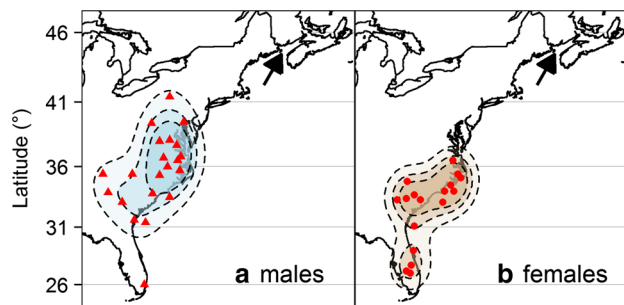


Fig. 1 Winter distribution of male (**a**; $n = 21$) and female (**b**; $n = 17$) Savannah sparrows (*Passerculus sandwichensis*) breeding on Kent Island in the Bay of Fundy, New Brunswick, Canada estimated from light-level geolocators recovered between 2012 and 2014. *Black arrow* Location of Kent Island, *triangles* centroid of the primary stationary winter distribution of each individual, *contours* delineate the 75, 50, and 30 % kernel densities for each sex

The breeding population on Kent Island has been monitored annually since 1987 (Wheelwright et al. 1992; Wheelwright and Mauck 1998; Mitchell et al. 2012; Williams et al. 2013). Each year from late May to the end of July, nests within an approximately 10-ha study plot are found during the egg-laying stage and monitored every second day until fledging or failure. Nestlings are banded on the seventh day after hatching with a USFWS/CWS aluminum leg-band and single-color leg-band. Nestlings that return to Kent Island to breed in subsequent years are recaptured with mist-nets and given a unique three-color leg-band combination. Un-banded immigrants that enter the breeding population are also captured and banded with a USFWS/CWS aluminum leg-band and a unique three-color leg-band combination, such that all breeding individuals in the study population are marked and uniquely identifiable. Wing chord (unflattened ± 1 mm), tarsus length (± 0.1 mm), and body mass (± 0.1 g) are also measured at the time of capture. The sex of nestlings that return to breed on Kent Island and of un-banded immigrants is determined at the time of capture by the presence of a cloacal protuberance (males) or brood patch (females) and confirmed by behavioral observation (e.g., singing by males and brooding by females). The age of nestlings that return to breed on Kent Island is known exactly, whereas immigrants are only known to be 1 year or older when first captured. Hereafter, we will describe individuals from which we collected geolocator and/or stable isotope data as either ‘juvenile’ or ‘adult’. We use ‘juvenile’ to describe individuals that were sampled during their first year of life, such that geolocator and stable isotope data provided information on their first migration. We use ‘adult’ to describe individuals that had bred in the study population and experienced migration at least once before being sampled.

Geolocator deployment

Between July and September from 2011 to 2013, we deployed 163 light-level geolocators on 148 individuals using a modified leg-loop harness (Stutchbury et al. 2009). Of the 163 geolocators, 68 % ($n = 111$) were affixed to adults and 32 % ($n = 52$) were affixed to juveniles. Thirteen individuals were affixed with a geolocator in 2 years, and one individual was affixed with a geolocator in 3 consecutive years. At the time of deployment, juveniles were given a complete three-color leg-band combination to facilitate identification and recapture the following year. All adults had previously been given a three-color leg-band combination.

Due to developments in geolocator technology concurrent with our study, we used three different models of geolocator. In 2011, we used MK12 geolocators (weight 0.7 g, approx. battery life 1 year; British Antarctic Survey, Cambridge, UK). In 2012 and 2013, we used MK5 and MK6 geolocators (weight 0.64–0.73 g, approx. battery life 9 months; Biotrack, Wareham, UK). All three models recorded light measurements at 2-min intervals. The combined weight of geolocators and harness material ranged from approximately 0.75 to 0.90 g, which comprised < 5 % of the average body mass of the individuals on which they were attached [mean \pm standard deviation (SD) 19.5 ± 1.4 g; $n = 163$]. To reduce shading by plumage, light sensors for the MK5 and MK6 geolocators used in 2012 and 2013 were mounted on a 5- or 10-mm long stalk extending out from the body of the geolocator at a 30° angle. In 2011, light sensors were mounted on the body of the heavier MK12 model, not on a stalk, to minimize weight. To account for potential differences in light measurements due to the presence/absence of a light stalk, we estimated separate sun elevation angles for each recovered geolocator (see details below).

From 2012 to 2014, we recovered 43 geolocators from 39 individuals, corresponding to recovery rates of 42 % (21/50), 18 % (11/60), and 21 % (11/53), respectively, across the 3 years. Geolocators were recovered from two individuals in 2 consecutive years and from one individual in 3 consecutive years. Data were successfully downloaded from 42/43 geolocators of which 40/42 recorded light measurements for the full period (deployment to recovery). The two geolocators that did not record light data for the full period stopped recording in early- to mid-April, before individuals had returned to Kent Island.

Analysis of geolocator light data

Position estimates were derived from light-level recordings using the ‘threshold method’, which we implemented using the GeoLight package (Lisovski and Hahn 2012) in

R 3.1.1 (R Core Team 2014). We defined sunrise and sunset times using a light threshold value of 3. Erroneous sunrise and sunset times caused by shading events during the day or lighting events during the night were identified using a local polynomial regression (loessFilter function; $k = 3$) and either corrected (i.e., the point was shifted to the nearest realistic sunrise or sunset time) or excluded from subsequent calibration and position derivation when light data were too noisy to extract a realistic sunrise or sunset time. We estimated a sun elevation angle for each individual using on-board calibration of filtered sunset and sunrise times. For most individuals, sun elevation angles were estimated using sunrise and sunset times from the first 7–10 days post-deployment when they were known to be at the breeding site. However, in some cases we had to adjust our calibration approach. Four geolocators that were recovered in 2013 were deployed between early- and mid-July of 2012; for these individuals we calibrated between 15 August and 01 September when the majority of geolocators were deployed. For several individuals, we were unable to estimate a sun elevation angle from the breeding period that provided reasonable estimates of winter latitude (e.g., bulk of winter position estimates were over the ocean). In these cases, we derived sun elevation angles using the Hill–Ekstrom calibration for the primary stationary non-breeding period (Hill and Braun 2001; Ekstrom 2004). For this procedure, we used shifts in longitude to determine the beginning and end of the primary stationary winter period. Estimated sun elevation angles averaged $-3.87 \pm 0.1^\circ$ [standard error (SE)], with a range of -5.40° to -2.25° ($n = 42$). Following calibration, positions were derived for every 12-h period using individual-specific sun elevation angles. Based on 522 position estimates from the breeding season calibration period for 39 individuals, total location error averaged 185 ± 186 km (SD), latitudinal error averaged 171 ± 189 km (SD), and longitudinal error averaged 46 ± 40 km (SD).

Following position estimation, we then determined the center of the primary stationary winter period as well as the date of fall departure from the breeding grounds and spring arrival to the breeding grounds for every individual. We defined the primary stationary winter period as the longest period following fall migration and preceding spring migration during which latitude and longitude fluctuated over a narrow range of values with a constant mean, a similar pattern to that observed during the stationary breeding season. We then defined the center of the stationary winter period as the centroid of the 30 % kernel density polygon, which we estimated using the ‘kernelUD’ and ‘getverticeshr’ functions from the R package ‘adehabitatHR’ (Calenge 2006). When estimating the utilization distribution for the stationary winter period, we excluded at least 14 days of latitude estimates surrounding the autumnal and vernal equinoxes because of similar day lengths across the globe. For some

individuals the effect of the equinox on latitude estimates was apparent beyond 14 days, in which cases we excluded additional points based on visual assessments of latitudinal variability (Lisovski et al. 2012). Stationary winter periods (excluding days affected by the vernal equinox) averaged (\pm SE) 114 ± 3 days in length (range 74–167 days; $n = 42$). Lastly, we defined fall departure from the breeding grounds as the date in September/October at which latitude and longitude estimates stopped fluctuating narrowly around the known coordinates of Kent Island and started moving to the southwest. Conversely, we defined arrival at the breeding grounds as the date between April and June at which latitude and longitude stopped moving to the northeast and stabilized around the coordinates for Kent Island.

Feather sampling and scoring

We collected 146 central tail feathers in whole from known-age individuals (76 juveniles and 70 adults) between May and July from 2008 to 2012. Adult Savannah sparrows typically replace their tail feathers in a complete pre-basic molt after the breeding season, and an estimated 42 % of individuals undergo a partial molt that includes one to two central tail feathers during winter (Pyle 1997). However, whether a given individual replaces its tail feathers in winter likely depends in part on the quality of habitat occupied and feather wear (Rohwer et al. 2005). To use the isotopic composition of feathers as a geographic marker of winter latitude, it is important that feathers grown on the wintering grounds can be distinguished from those grown at the end of the previous breeding season. Based on the assumption that feathers grown in winter would be in better condition than those grown during the previous breeding season, we assigned a wear score ranging from 0 to 3 to all feather samples (Willoughby 1986). Feathers were scored ‘0’ when little or no wear was evident; ‘1’ when few barb tips were missing from the distal one-eighth of the feather; ‘2’ when many barbs were missing tips from the distal one-eighth of the feather; ‘3’ when complete barbs were missing from more than the distal one-eighth portion of the feather and when more than one-half the vane area was missing. Of the 146 samples collected, 99 were scored ‘0’, 42 were scored ‘1’, four were scored ‘2’, and one was scored ‘3’.

Stable isotope analysis

Stable isotope analysis was performed at the Stable Isotope Hydrology and Ecology Laboratory of Environment Canada, Saskatoon, Canada. Stable hydrogen isotope analyses of feathers were conducted using the comparative equilibration method (Wassenaar and Hobson 2003), through the use of previously calibrated keratin hydrogen-isotope reference materials [Caribou Hoof Standard: $\delta^2\text{H} -197 \pm 1.8 \text{ ‰}$

Vienna standard mean ocean water (VSMOW) ($n = 10$); Kudu Horn Standard: $\delta^2\text{H} = -54.1 \pm 0.6 \text{ ‰ VSMOW}$ ($n = 10$); Spectrum Keratin Fine Powder Lot #SJ1400: $\delta^2\text{H} = -121.6 \pm 1.9 \text{ ‰ VSMOW}$]. Feathers were first rinsed in a 2:1 mixture of chloroform:methanol to remove surface oils, after which a distal portion (length 3–5 mm) of each feather was sampled, weighed to $350 \pm 10 \text{ ug}$, and placed into a $4 \times 6\text{-mm}$ silver capsule. Hydrogen isotopic measurements were performed on H_2 derived from $1350 \text{ }^\circ\text{C}$ flash pyrolysis of the feather subsamples and keratin standards using continuous-flow isotope-ratio mass spectrometry. All results reported for stable hydrogen isotope ratios ($^2\text{H}/^1\text{H} = R$) are expressed in the typical delta notation (δ), where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ and R_{standard} is the hydrogen isotope ratio ($\delta^2\text{H}$) of V-SMOW and Standard Light Antarctic Precipitation (VSMOW-SLAP). All stable hydrogen isotope ratios are in per mil units (‰).

Statistical analysis

To examine variation in winter latitude from the geolocator data and $\delta^2\text{H}$ values from feathers in relation to sex, age, and body size, we fitted generalized linear models with a Gaussian distribution and identity link function (hereafter referred to as GLMs). In cases where we had more than 1 year of data from the same individual, we only used values from the first year; this applied to both geolocator and $\delta^2\text{H}$ data. For analyses involving $\delta^2\text{H}$ values, we also excluded samples (1) from worn feathers (scores >1) because these may not have been grown during the winter, and (2) when we had geolocator data from the same individual in the same year to maintain independence between the two datasets. Final sample sizes for subsequent analyses using winter latitude and $\delta^2\text{H}$ values were 38 and 106, respectively (Table 1).

In the first step of our analysis, we examined variation in winter latitude and in $\delta^2\text{H}$ across all individuals in relation to sex (male or female) and age (juvenile or adult). To account for potential annual variation in winter latitude and $\delta^2\text{H}$, we also included year as a categorical explanatory variable. We excluded body size from these two models because both tarsus and wing length were confounded with sex. In the second step of our analysis, we examined variation in winter latitude and $\delta^2\text{H}$ within each sex in relation to body size (tarsus or wing length), while controlling for effects of age and year. Tarsus and wing length were modeled separately, resulting in four models for each response variable (winter latitude and $\delta^2\text{H}$)—one for each sex by body size combination. For tarsus and wing length, we used a single measurement taken at the time of feather sampling or geolocator recovery. Given that the geolocator and stable isotope datasets differed in both number of observations and units of measure for the response, we calculated

Table 1 Parameter estimates from two linear models examining variation in winter latitude and feather $\delta^2\text{H}$ content of Savannah sparrows breeding on Kent Island in the Bay of Fundy, New Brunswick, Canada in relation to sex, age, and year

Model	Variable	$\beta \pm \text{SE}$	t	P
Latitude	Intercept	33.7 ± 1.5	22.9	<0.01
	Sex (male)	2.5 ± 1.1	2.3	0.03
	Age (adult)	0.2 ± 1.3	0.2	0.87
	Year (2012)	-2.2 ± 1.3	-1.7	0.09
	Year (2013)	-2.6 ± 1.3	-2.0	0.05
$\delta^2\text{H}$	Intercept	-49.7 ± 3.8	-13.2	<0.01
	Sex (male)	-5.6 ± 2.2	-2.5	0.01
	Age (adult)	-6.2 ± 2.5	-2.4	0.02
	Year (2008)	8.0 ± 4.6	1.7	0.08
	Year (2009)	6.2 ± 4.3	1.4	0.15
	Year (2010)	4.5 ± 4.3	1.1	0.29
	Year (2012)	3.0 ± 4.3	0.7	0.48

Winter latitude was estimated from geolocators ($n = 38$) and $\delta^2\text{H}$ values were measured from feathers grown on the winter grounds ($n = 106$). For both models, reference levels for categorical variables were ‘female’ for sex, ‘juvenile’ for age, and ‘2011’ for year

SE standard error

standardized effect sizes for age, sex, and body size to allow for direct comparison of effects between models. We calculated Cohen’s d for age and sex, and r for wing and tarsus length (Eqs. 10 and 11, respectively, in Nakagawa and Cuthill 2007).

To test for relationships between winter latitude, spring arrival date, and breeding performance, we first fitted a GLM for each sex with the Julian date that individuals returned to the breeding grounds in spring as the response and winter latitude as the explanatory variable. Age was excluded from these models because arrival times of adult and juvenile males were similar and our sample size for juvenile females was too small ($n = 2$) to compare their arrival times with adult females (Fig. 2b). We then tested for relationships between arrival date and time of breeding (Julian date) and between time of breeding and winter latitude for both sexes using GLMs. We used hatch date of an individual’s first clutch as a measure of timing of breeding because clutch initiation dates are rarely known in this population since most nests are found when they have a complete or nearly complete clutch, not during the nest-building stage. Nests were found for 18/21 males and 14/17 females from which we recovered geolocators. Hatch dates of replacement nests were excluded from analyses when an individual’s first nest failed (males: $n = 6$; females: $n = 4$), resulting in sample sizes of twelve for males and ten for females.

All statistical analyses were conducted in R 3.1.1 (R Core Team 2014).

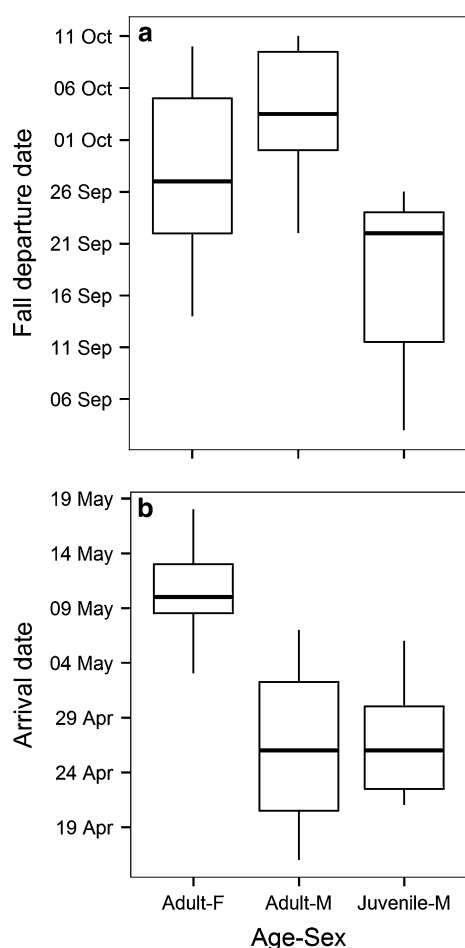


Fig. 2 Timing of fall migration (a) and spring arrival to the breeding grounds (b) in relation to age (adult and juvenile) and sex (*M* male, *F* female). Box-and-whisker plots show the median (horizontal line in box) and 25 % (lower edge of box) and 75 % (upper edge of box) quantiles. The lower whisker shows the smallest observation that was greater than or equal to the lower edge $- [1.5 \times \text{interquartile range (IQR)}]$, whereas the upper whisker shows the largest observation that was less than or equal to the upper edge $+ [1.5 \times \text{IQR}]$. Two juvenile females from which we recovered a geolocator initiated their fall migration on 28 September and 04 October and returned to the breeding grounds on 22 May and 18 May, respectively

Results

Based on 42 geolocators recovered from 38 individuals (14 adult males, 15 adult females, 7 juvenile males, 2 juvenile females) between 2012 and 2014, we identified the winter range of Savannah sparrows from Kent Island to be centered in North Carolina (median latitude 34°), with a range from southern Florida (minimum latitude 26°) to Pennsylvania (maximum latitude 41° ; Fig. 1). For 16 individuals from which we had geolocator and stable hydrogen isotope data from the same year, winter latitude and $\delta^2\text{H}$ were found to be weakly negatively correlated (i.e., higher latitudes corresponded to more negative $\delta^2\text{H}$ values;

Spearman's $\rho = -0.22$, 95 % confidence interval -0.59 to 0.38). Adult males (median departure date 03 October, $n = 14$; Fig. 2a) departed the breeding grounds in the fall approximately 6 days later than adult females (median departure date 27 September, $n = 15$; Fig. 2a), and adults of both sexes departed later than juvenile males (median departure date 22 September, $n = 7$; Fig. 2a).

Latitudinal distribution during winter

We found significant differences in winter latitude and $\delta^2\text{H}$ values between males and females and in $\delta^2\text{H}$ values between adults and juveniles. Although there was a substantial amount of overlap in winter latitude and $\delta^2\text{H}$ values between sexes, both datasets suggested that males wintered further north than females. Based on estimates of winter latitude from geolocators for 38 individuals, we estimated that males overwintered ($\beta \pm \text{SE}$) $2.5 \pm 1.1^\circ$ north of females ($t_{33} = 2.3$, $d = 0.81$, $P = 0.03$), which corresponds to a difference of approximately 275 km (Fig. 1). We found no evidence for a relationship between age and winter latitude ($\beta \pm \text{SE}$: 0.22 ± 1.3 , $t_{33} = 0.2$, $d = 0.07$, $P = 0.87$). Based on feather samples from 106 individuals, males were found to have $\delta^2\text{H}$ values that were ($\beta \pm \text{SE}$) 5.6 ± 2.2 ‰ more negative than those of females ($t_{99} = -2.5$, $d = -0.50$, $P = 0.01$). In addition, adults had $\delta^2\text{H}$ values that on average were ($\beta \pm \text{SE}$) 6.2 ± 2.5 ‰ more negative than those of juveniles ($t_{99} = -2.4$, $d = -0.51$, $P = 0.02$), suggesting that adults wintered further north than juveniles. Both winter latitude and $\delta^2\text{H}$ varied among years, but not significantly so (see Table 1 for full model results).

Within each sex and controlling for age and year effects, we found no evidence for relationships between tarsus length and winter latitude [males: 1.76 ± 1.01 ($\beta \pm \text{SE}$), $t_{16} = 1.7$, $r = 0.40$, $P = 0.10$; females: -1.21 ± 1.15 ($\beta \pm \text{SE}$), $t_{12} = -1.1$, $r = -0.29$, $P = 0.31$] or $\delta^2\text{H}$ values [males: -0.70 ± 3.03 ($\beta \pm \text{SE}$), $t_{44} = -0.23$, $r = 0.03$, $P = 0.82$; females: 3.34 ± 3.70 ($\beta \pm \text{SE}$), $t_{42} = 0.9$, $r = 0.14$, $P = 0.37$] nor between wing length and winter latitude [males: 0.79 ± 0.53 ($\beta \pm \text{SE}$), $t_{16} = 1.5$, $r = 0.35$, $P = 0.15$; females: -0.17 ± 0.52 ($\beta \pm \text{SE}$), $t_{12} = -0.32$, $r = -0.09$, $P = 0.76$] or $\delta^2\text{H}$ values [males: -1.73 ± 0.99 ($\beta \pm \text{SE}$), $t_{46} = -1.7$, $r = -0.25$, $P = 0.09$; females: 0.00 ± 0.98 ($\beta \pm \text{SE}$), $t_{43} = 0.0$, $r = 0.00$, $P = 0.99$]. Full model results are presented in Electronic Supplementary Material Table S1.

Timing of migration and breeding

Arrival time at the breeding grounds differed by sex (Fig. 2b), and we found some evidence for a negative correlation with winter latitude in males (Fig. 3a). Adult males ($n = 12$) and juvenile males ($n = 7$) returned to Kent Island at approximately the same time (median arrival date

for both 26 April) and 14 days earlier than adult females ($n = 15$; median arrival date 10 May; one-way analysis of variance: $F_{1,34} = 61.7$, $P < 0.001$). Across all individuals within each sex, the correlation between arrival date and winter latitude was non-significant for both males ($\beta \pm \text{SE}: -0.77 \pm 0.42$, $t_{17} = -1.8$, $P = 0.08$) and females ($\beta \pm \text{SE}: -0.28 \pm 0.45$, $t_{15} = -0.6$, $P = 0.54$). However, when we excluded one male that wintered in southern Florida (2.34 SD south of the mean winter latitude of males), the correlation between arrival date and latitude was significant and negative ($\beta \pm \text{SE}: -1.48 \pm 0.53$, $t_{16} = -2.8$, $P = 0.01$; Fig. 3a). In 12 males that successfully hatched their first nest after returning to the breeding grounds and for which arrival date was known, we found a significant positive correlation between arrival date and hatch date, such that those that returned earliest hatched their first nest earliest ($\beta \pm \text{SE}: 0.40 \pm 0.17$, $t_9 = 2.4$, $P = 0.04$; Fig. 3b). For females ($n = 10$), hatch date and arrival date

were weakly correlated ($\beta \pm \text{SE}: 0.60 \pm 0.34$, $t_8 = 1.8$, $P = 0.11$; Fig. 3b). When we related hatch date directly to winter latitude the correlation was marginally significant for males ($\beta \pm \text{SE}: -0.70 \pm 0.34$, $t_{10} = -2.1$, $P = 0.07$) and non-significant for females ($\beta \pm \text{SE}: 0.04 \pm 0.67$, $t_8 = 0.1$, $P = 0.96$).

Discussion

Our study using geolocators and feather $\delta^2\text{H}$ values from Savannah sparrows breeding on Kent Island in the Bay of Fundy, New Brunswick, Canada revealed significant sex differences in winter latitude and migration timing. The stationary winter distribution of this population was centered in North Carolina, with a range from southern Florida to Pennsylvania, with males overwintering, on average, approximately 275 km further north than females and returning to breed, on average, 14 days earlier than females. Sex differences in winter latitude were also supported by males having more negative feather $\delta^2\text{H}$ values than females and are consistent with several other studies documenting sexual segregation of migratory passerines on the wintering grounds (Ketterson and Nolan 1976; Dolbeer 1982; Rising 1988; Holberton and Able 2000; Catry et al. 2004; Mazerolle and Hobson 2007; Dale and Leonard 2011; Gow and Wiebe 2014), including the closely related Ipswich sparrow (*P. s. princeps*) which breeds on Sable Island, approximately 530 km east of Kent Island in the northwest Atlantic (Dale and Leonard 2011).

Given that male Savannah sparrows are larger, more socially dominant, and experience a greater level of intraspecific competition for breeding resources than females, the pattern of males wintering farther north than females is consistent with that predicted by the three hypotheses that have been proposed to explain differential migration, namely, the *early arrival*, *body size*, and *social dominance* hypotheses. In further support of the *early arrival* hypothesis, which predicts that the sex that experiences greater competition for breeding resources will winter farther north to facilitate early arrival at the breeding grounds (Ketterson and Nolan 1976; Myers 1981), we found some evidence that arrival date on the breeding grounds was negatively correlated with winter latitude in males (dependent on the exclusion of one male that wintered over 2 SD south of the average winter latitude of males) and individuals that arrived earlier hatched their first nests earlier. The benefits of early arrival for male reproductive success have been found in several bird species (Lack 1954; Myers 1981; Aebischer et al. 1996; Norris et al. 2004). Although we do not know the exact mechanism by which early arrival leads to earlier hatch dates in this population, there are several possible explanations,

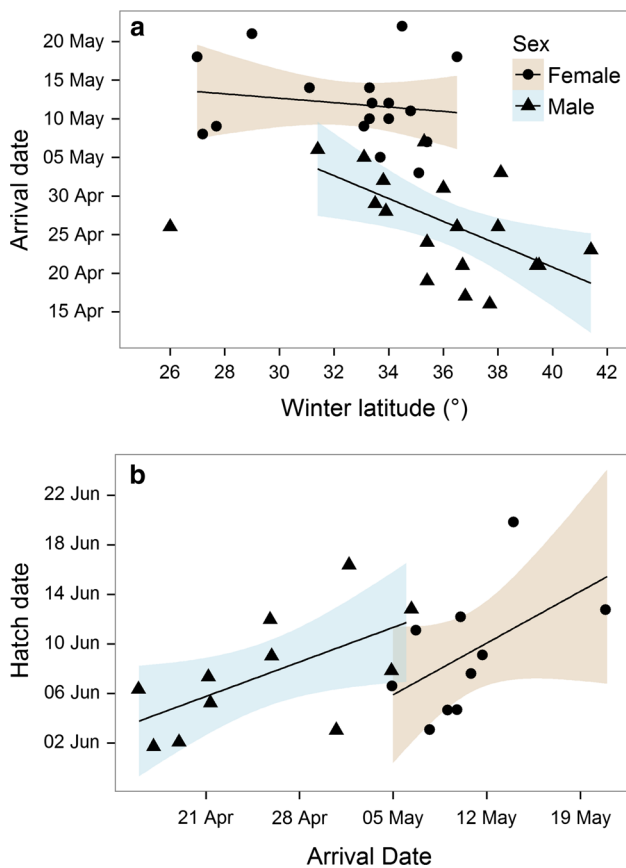


Fig. 3 **a** Arrival dates of males and females at the breeding grounds on Kent Island in relation to winter latitude, **b** first nest hatch dates of males ($n = 12$) and females ($n = 10$) in relation to arrival date. Shading 95 % confidence interval estimated from a linear model for each sex (see color figure online). For males, we excluded an individual whose primary stationary winter range was centered at approximately 26° (2.34 standard deviations south of the mean male winter latitude) from the linear model

with possibly the simplest being that early-arriving males are able to start breeding earlier because they pair up with the earliest arriving females. However, in our study, there was very little overlap in spring arrival of males and females (i.e., only 2/17 female arrival dates were earlier than the latest male arrival date), suggesting that the vast majority of males arrived before the first-arriving females. A likely alternative explanation is that males which arrive earlier are able to acquire higher quality breeding territories than those which arrive later (Bensch and Hasselquist 1991; Lozano et al. 1996; Aebischer et al. 1996; Smith and Moore 2004). Early-arriving males may also be preferred by females because they are in better condition—having migrated shorter distances and/or having had more time to recover from migration prior to female arrival—than males which arrive relatively later (Holberton and Able 2000; Dale and Leonard 2011).

Although the observed pattern of males wintering farther north than females provided support for the *body size* hypothesis, we did not find evidence for a direct relationship between body size and winter latitude or $\delta^2\text{H}$ values within either sex. Similarly, Dale and Leonard (2011) found no association between body size and winter latitude in the closely related Ipswich sparrow. Dolbeer (1982) found that the degree of sexual segregation in Red-winged blackbirds (*Agelaius phoeniceus*), Brown-headed cowbirds (*Molothrus ater*), Common grackles (*Quiscalus quiscula*), and European starlings (*Sturnus vulgaris*) was highest for populations exhibiting the greatest sexual dimorphism, with maximum segregation occurring in Red-winged blackbirds in which females were 65 % the size of males. Given that males and females in our study differed by <10 % in both tarsus and wing length, combined with the lack of a correlation between winter latitude or $\delta^2\text{H}$ and body size, it seems unlikely that body size contributes greatly to patterns of differential migration in this population.

We found mixed support for age-related differences in winter latitude. From the geolocator data, there was no evidence for a difference in winter latitude between age groups. However, $\delta^2\text{H}$ values were found to be significantly more negative in adults compared to juveniles, suggesting that adults wintered further north than juveniles. In many passerines, older birds and males are dominant over younger birds and females, respectively (Gauthreaux 1978). Thus, age-related differences in $\delta^2\text{H}$ values, as well as sex-related differences in winter latitude and $\delta^2\text{H}$ values (discussed above), could support the *social dominance* hypothesis, which predicts that the dominant age and/or sex will outcompete subordinates for suitable habitat close to the breeding grounds, thereby forcing subordinates to migrate further south (Gauthreaux 1978). Indeed, age- and sex-related segregation among habitats during the

non-breeding season has been demonstrated in some bird species (Marra 2000; Catry et al. 2004), but it is unlikely that habitat quality declines directly with decreasing latitude for most species. As such, the extent to which dominance-mediated habitat segregation might contribute to latitudinal segregation of age- and sex-classes is unclear. Alternatively, age-related differences in winter latitude could be due to juveniles experiencing less pressure to return to the breeding grounds early, given that they are unlikely to outcompete adults for the best breeding territories (Francis and Cooke 1990). However, we found no difference in spring arrival dates between adult and juvenile males. Lastly, we cannot rule out the possibility that the observed difference in feather $\delta^2\text{H}$ values between age groups reflected differences in physiology or diet between adults and juveniles (Langin et al. 2007; Studds et al. 2012; van Dijk et al. 2014) and not differences in winter latitude.

In summary, combining estimates from geolocators and stable hydrogen isotopes in feathers, we have provided strong evidence for sexual segregation during the winter and mixed evidence for age-related differences in winter latitude. The observed pattern of males wintering farther north than females is consistent with that predicted by the *early arrival*, *body size*, and *social dominance* hypotheses. Males that wintered further north arrived on the breeding grounds earlier in spring, and, in turn, hatched young earlier, providing some additional support for the *early arrival* hypothesis. Tests of the relationship of winter latitude and $\delta^2\text{H}$ to body size failed to provide additional support for the *body size* hypothesis. Lastly, elucidating the mechanism(s) by which dominance may shape the non-breeding distribution of species will require more focused studies of their behavioral ecology at winter sites. Describing patterns of connectivity between breeding and non-breeding sites, as we have done here, is also critical for understanding the dynamics of migratory populations. Several recent studies have linked non-breeding conditions with trends in population growth and vital rates based on limited knowledge of species- or population-specific winter grounds (e.g., Sillett et al. 2000; Wilson et al. 2011; Pasinelli et al. 2011). Future work coupling information on population- and species-specific winter distributions, taking into account differences among age and sex classes, with long-term demographic data has the potential to greatly improve our understanding of the dynamics of migratory populations.

Acknowledgments We thank Jesse Pakkala, Katherine Smith, Graham Sorenson, and Elizabeth Christiansen for assistance with fieldwork, as well as Damon and Janet Gannon, Mark Murray, and Russell Ingalls for logistical support at the Bowdoin Scientific Station on Kent Island. This represents Bowdoin Scientific Station contribution no. 255.

Author contribution statement BKW, AEMN, SPT, BCD, NTW, and DRN conceived and designed the study. BKW, AEMN, SPT, BCD, GWM, NTW, and DRN conducted fieldwork. SPT and BCD prepared feathers for stable isotope analysis. KAH and LIW conducted stable isotope analyses. BKW conducted statistical analyses and wrote the manuscript; all authors provided editorial advice.

Funding This study was funded by the Natural Sciences and Engineering Research Council (DRN), Canada Foundation for Innovation (DRN), University of Guelph (DRN, BKW), a Bowdoin Scientific Station Summer Fellowship (BCD, SPT), the Bowdoin College Roberts Fund (BCD), and a Bowdoin College Grua/O'Connell Research Award (SPT).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and national guidelines for the care and use of animals were followed.

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