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Seasonal migration and natal dispersal represent the major large-scale movements in the lives of animals. Individuals that are relatively prone to movement and exploration might thus be more likely to disperse and also to migrate farther. Such movement might be either negatively associated with parasitic infection (if infection prevents hosts from successful long-distance migration) or positively associated (e.g., if longer-distance migrants encounter more abundant or more diverse parasites). We examined whether natal dispersal tendency predicts seasonal migration distance in song sparrows (*Melospiza melodia*), and whether migration distance predicts infection with bloodborne parasites upon arrival at the breeding grounds. Migration distance, inferred from stable-hydrogen isotope analysis (δ^2H) of winter-grown tissue, was repeatable (repeatability = 0.41) over years. Birds that were more likely to have immigrated from outside the breeding grounds, as inferred from genetic assignment tests, also overwintered farther south, as inferred from stable isotope analysis. The finding that individuals more prone to movement in the context of natal dispersal also tended to travel farther on average in the context of seasonal migration suggests consistent individual variation in large-scale movements across these two contexts. Although statistically significant, this effect was modest in scope and subtle relative to sex differences in inferred migration distance. Among after-second-year individuals, but not yearlings, longer-distance migrants were more likely on average to be infected with bloodborne parasites. Individual variation in propensity to long-distance movement may interact with age-related variation in exposure or susceptibility to parasites, to shape the role of animal migration in transporting infectious disease.

Significance statement: In many animal species, individuals vary consistently in activity and movement over small geographic scales. Large-scale movements such as seasonal migration are of particular interest because they can influence disease risk, but until recently such movements have been difficult to track. We used stable isotope analysis to estimate overwintering latitude of song sparrows returning to their breeding grounds. Individuals overwintering farther south were also more likely to have immigrated from outside the breeding site, indicating that movement is correlated across the contexts of migration and dispersal. Rates of infection with bloodborne parasites increased with migration distance in older birds, but not in yearlings. Our findings suggest that individual variation in movement may interact with age-related variation in infection risk, to shape the role of animal migration in transporting parasites.

Keywords: deuterium, dispersal, *Melospiza melodia*, migration, parasites, philopatry, song sparrows, stable isotopes.

In many animal species, individuals show consistent variation in activity and movement, which may extend over multiple contexts. In great tits (*Parus major*), for example, exploratory behavior in a novel environment is positively associated with post-fledging dispersal (Dingemanse et al. 2003). Similarly, individual killifish (*Rivulus hartii*) that are relatively quick to leave a refuge within an aquarium also move greater distances upon release into their native stream (Fraser et al. 2001). Due to the logistic difficulty of tracking and monitoring the movement of free-living animals over large geographic scales, most studies of behavioral correlations regarding animal movement have measured activity either in captivity or over a very fine geographic scale (< 1 km). Larger-scale movements such as seasonal migration and natal dispersal have historically been much less tractable to study, despite their clear relevance to the fitness of individuals and the viability and connectivity of populations. In particular, such movements are likely to influence encounter rates with parasites (Møller and Erritzøe 1998; Møller et al. 2004). Individual variation in movement may therefore have important consequences for the spread of infectious disease (Altizer et al. 2011; Hill et al. 2012; Hoye et al. 2012).

In this study, our first objective was to examine individual consistency in large-scale movements of migratory song sparrows (*Melospiza melodia*). We inferred relative migration distance along a north-south axis using stable-hydrogen isotope analysis (δ^2H) of claw tissue collected soon after arrival on the breeding grounds but grown the previous winter, taking advantage of a latitudinal gradient in deuterium content in precipitation across North America that is directly transferred to animal tissues (Wassenaar and Hobson 2000; Wassenaar 2008; Hobson et al. 2014). We investigated the repeatability of

migration distance over multiple years, and the degree to which this trait varied with natal dispersal as determined through genetic assignment testing. If individuals vary consistently in the degree to which they move across the landscape, relative migration distance should be (a) repeatable across years and (b) positively associated with natal dispersal.

Our second objective was to characterize the relationship between relative migration distance and haematozoan infection status upon return to the breeding grounds. Migration may have important consequences for the spread of disease, via exposure to parasites (Møller and Erritzøe 1998), and trade-offs between flight and immune defence (Nebel et al. 2013). Migration distance might be negatively associated with parasitism if infected animals cannot migrate long distances (i.e., migratory culling: Bradley and Altizer 2005). Alternatively, migration distance could be positively associated with parasitism, if trade-offs between migration and immune defence compromise immune investment during migration (Nebel et al. 2013), or if individuals traveling greater distances encounter more abundant or diverse parasite assemblages (Møller and Erritzøe 1998, 2001; Figuerola and Green 2000; Møller et al. 2004; Møller and Szép 2011).

Our third objective was to determine whether the relationship between migration and parasitism varies among age classes. Individuals during their first year of life may differ in important ways from older individuals. For example, if young-of-the-year are less likely than older individuals to survive parasitic infection during migration, migratory culling may be most pronounced in the first year of life, contributing to a more negative migration-parasitism relationship for this age class. Selective mortality could also result in age-related differences in average migration distance or (in the case of

93 stabilizing selection) reduced variance of migration distance among older individuals.
94 Age classes may also differ in immune plasticity, potentially making older individuals
95 more susceptible to unfamiliar parasites and contributing to a more positive migration
96 distance-parasitism relationship for this age class. In birds, for example, B-cell immune
97 repertoires become established during the first year of life, after which adaptive immune
98 defences remain relatively crystallized (Møller and Erritzøe 2001). Accordingly, we
99 examined migration distance and its interaction with age class as predictors of
100 haematozoan parasitism.
101

102 **Methods**

103 Study population and site

104 We investigated relative migration distance, natal dispersal, and haematozoan infection
105 status in song sparrows breeding on land owned by the Queen's University Biological
106 Station, near Newboro, Ontario, Canada (44.633°N, 76.330°W). The study area consists
107 of old fields, forest edge and wetlands, and is not physically isolated from other suitable
108 breeding habitat for this species. Song sparrows in this region are seasonally migratory,
109 and band-recovery data suggests considerable intraspecific variation in migration
110 distance (Davis and Arcese 1999). Birds banded at our study population during the spring
111 breeding season have never been re-sighted at this location during winter, but have been
112 recaptured during winter in Maryland (n = 1) and Tennessee (n = 1), USA.
113

114 Field methods

115 We captured after-hatch-year (AHY) song sparrows in seed-baited Potter traps during
116 April and May of 2012 (n = 39), 2013 (n = 55), and 2014 (n = 60), shortly after their
117 return from migration. Seventeen birds were captured in two years and four birds
118 captured in all three years, thus we had 154 capture records from 129 individuals. We
119 determined sex based on the presence (male) or absence (female) of a cloacal
120 protuberance and banded each bird with a numbered aluminum leg band and a unique
121 combination of three colored plastic leg bands. As outlined below, we collected samples
122 of claw tissue for stable-isotope analysis (δ^2H) of migration distance (n = 146 samples
123 from 124 individuals); blood samples for genetic analysis of natal philopatry (n = 100
124 individuals, corresponding to 121 claw samples as some individuals were captured in
125 multiple years); and blood samples for microscopic examination of haematozoan
126 infection status (n = 149 samples from 125 individuals). We then released the birds at the
127 site of capture. All study subjects were subsequently either re-captured or re-sighted later
128 in the season, confirming that all were resident (breeding) birds. Animal procedures were
129 approved by the Animal Use Subcommittee of the University of Western Ontario
130 (protocol 2008-054).

131 We determined age class (i.e., second-year, hereafter SY, or after-second-year,
132 hereafter ASY) based on previous years' band records. Age class was known with
133 certainty for birds that had been banded in previous years as hatch-year (HY, i.e.,
134 juveniles) or after-hatch-year. AHY individuals that had not been previously banded
135 (adult recruits) were assumed to be SY upon first capture. In support of this assumption,
136 such individuals had shorter wings than did birds known to be ASY (Supplementary

Material), suggesting that adult recruits had not yet undergone their first basic moult (Smith et al. 1986). Moreover, adult philopatry at the study site is high (~50% annual return rate, presumably most or all all of those surviving), with most individuals returning to the same breeding territory or moving less than 200 m between years (Potvin et al. 2015). Finally, each spring we intensively searched the study area to capture and band >95% of breeding individuals. Given this high capture effort, combined with low levels of territorial movement between years, we are confident that birds categorized as SY were indeed yearlings returning from their first overwinter migration.

Stable isotope analysis

The stable hydrogen isotope deuterium (^{2}H, depicted as δ^2H) shows a latitudinal gradient in amount-weighted, growing-season precipitation across North America, such that δ^2H values increases with decreasing latitude (Wassenaar and Hobson 2000). These isotopic patterns are transferred up the food web to the consumer, which permits estimating the approximate latitude at which metabolically inert tissues were grown (Wassenaar and Hobson 2000; Hobson et al. 2014). In the field, we clipped the distal 2.5 mm of each bird's hallux (back) claw. Pilot data from a closely related species (white-throated sparrow *Zonotrichia albicollis*) determined that this portion of claw corresponds to tissue grown at the wintering grounds (Supplementary Material). Claw samples were stored at room temperature in capped microcentifuge tubes, then cleaned of surface oils using 2:1 chloroform: methanol, air-dried, shaved to 350 mg and crushed in silver capsules. Samples were analyzed at Environment Canada's Stable Isotope Laboratory (Saskatoon, Canada) for nonexchangeable hydrogen, using online continuous-flow isotope ratio mass

spectrometry (CF-IRMS) on a Micromass Isoprime mass spectrometer (Micro-mass UK, Manchester, UK) interfaced with a Eurovector elemental analyzer (Milan, Italy). Isotopic measurements were performed on H_2 gas derived from high-temperature (1350 °C) flash pyrolysis of claw samples and keratin standards. Stable isotope analysis was done blind with respect to genotype and infection status.

Three Environment Canada keratin standards (caribou hoof standard, CBS: -197‰; spectrum keratin, SPK: -121.6‰; kudu horn standard, KHS: -54.1‰) were used to correct for the effects of H exchange with ambient water vapor using the comparative equilibrium method (Wassenaar and Hobson 2003). Based on within-run replicate analyses of five of each keratin standard, the analytical precision was estimated to be ± 2‰. We report non-exchangeable δ^2H values expressed in delta notation of units per mil (‰) and normalized on the Vienna Standard Mean Ocean Water- Standard Light Antarctic Precipitation (VSMOW-SLAP) scale.

Genetic analysis of philopatry

In the field, we collected small blood samples (approximately 20 μL) via brachial venipuncture and blotted a portion of blood onto high wet-strength filter paper. Blots were treated with 0.5 M Na-EDTA (pH 8.0), air-dried, and stored at room temperature awaiting DNA extraction via an ammonium acetate salting-out protocol. We genotyped birds at 12 microsatellite loci developed for use in song sparrows and other Emberizid species: Mme 1 and 12 (Jeffrey et al. 2001); Pdoμ 5 (Griffith et al. 1999); and Sosp 1, 2, 3, 4, 5, 7, 9, 13 and 14 (Sardell et al. 2010). PCR conditions and genotyping methods are

182 detailed in Supplementary Material. Genotyping was performed blind with respect to
183 claw δ^2H.

184 We entered each individual's microsatellite genotype into GeneClass2 (Piry et al.
185 2004), together with the genotypes of an additional 308 song sparrows that were captured
186 at the main study site plus ten other sites within 50 km and genotyped at the same loci as
187 part of another study (Supplementary Material). We inferred natal philopatry using the
188 L_home option implemented in GeneClass2 based on 10,000 simulated multilocus
189 genotypes. L_home is a continuous measure ranging between 0 and 1, and represents the
190 probability of a specific genotype occurring in the population in which it was sampled
191 such that higher values of L_home indicate relatively philopatric individuals, and lower
192 values indicate individuals more likely to have been born outside the capture site. Unlike
193 other potential assignment indices, L_home does not require that all potential source
194 populations have been sampled (Piry et al. 2004). As a complementary analysis to
195 confirm that we had adequately sampled peripheral source populations, we re-calculated
196 L_home three times, using same computation parameters but with a randomly selected
197 subset of five peripheral populations. We then compared each individual's value of
198 L_home calculated using all ten peripheral source populations to that calculated using the
199 reduced number of source populations. The absolute value of the difference between
200 these two metrics was very low (average values ranging from 0.0043 - 0.0051 across the
201 three re-calculations), suggesting diminishing returns from additional sampling beyond
202 five peripheral populations. Thus, ten peripheral source populations likely provides
203 adequate coverage of surrounding allele frequencies in this system.

We interpreted L_home as a continuous variable rather than arbitrarily classifying individuals as immigrants or philopatric, for two reasons. First, suitable breeding habitat is continuously rather than discretely distributed around the main study site. Second, observed values of L_home were distributed fairly continuously (range = 0.056 to 1.000, mean ± SE = 0.767 ± 0.018, n = 100).

Haematozoan infection status

Immediately after collecting each blood sample, we prepared a thin-film blood smear by placing a small drop of blood onto a clean glass microscope slide and gently pulling the blood across the slide using a second slide. Smears were air-dried, immersed for 60 s in 100% methanol, air-dried again, and stored at room temperature. After the field season, we treated smears with Wright-Giemsa stain (Sigma-Aldrich) and examined them under 1000× magnification with an oil-immersion light microscope. We took digital photographs at regular intervals from the tail end of the smear to visualize 10,000 erythrocytes per bird. We examined these images for haematozoan parasites, and classified each bird as either infected (one or more haematozoa detected in an examination of 10,000 erythrocytes) or uninfected. For the subset of birds that were infected, we also noted the total number of haematozoa detected in an examination of 10,000 erythrocytes (hereafter 'parasite load'). Parasites were identified to genus with reference to Valkiūnas (2005), except that we did not distinguish between *Haemoproteus* spp. and *Plasmodium* spp. To minimize observer bias, we assessed infection status and parasite load while blind to claw δ^2H.

Diagnosing infection by microscopy rather than by PCR-based methods (e.g. Hellgren et al. 2004) can underestimate the actual prevalence of infection, but this issue varies across parasite genera (Garamszegi 2010). Indeed, for the major bloodborne parasites found in this study (genera *Plasmodium*, *Haemoproteus*, *Leucocytozoon*) sensitivity of microscopy and molecular methods is very similar (Valkiūnas et al. 2008). We focused on infections detectable through microscopy rather than molecular methods for two reasons. First, infections detectable by PCR but not by microscopy are likely to be very low-intensity (< 0.01% erythrocytes parasitized), making them only minimally transmissible in the wild. Second, low-intensity infections detectable through PCR but not microscopy may have been acquired much earlier in the bird's lifetime, and we were primarily interested in recent infections, i.e. those acquired over the preceding winter or on migration.

Data analysis

We calculated the repeatability of claw δ^2H values based on among- and within-individual components of variance (Lessells and Boag 1987), derived from a one-way ANOVA on the 21 birds from which claw tissue had been sampled in multiple years.

We used linear mixed models to identify predictors of claw δ^2H (i.e., relative latitudinal migration distance). Models were constructed with lmer in the R package lme4 (Bates et al. 2015). We first constructed a fully-fitted model, with claw δ^2H as the dependent variable and fixed effects of age (i.e., SY or ASY), sex, L_home (i.e., inferred philopatry), plus all interactions (age × sex; age × L_home; sex × L_home; age × sex × L_home); and random effects of bird ID and year. Model simplification was done with

likelihood ratio testing (LRT; West et al. 2015). We used restricted maximum likelihood (REML) estimates to compare the fit of the initial model to that of a model omitting the random effect of year. We then used maximum likelihood (ML) estimation and LRT to determine which fixed effects could be removed without significantly worsening model fit. We tested interactions first, followed by main effects, to arrive at a minimal adequate model which we report using REML estimation (West et al. 2015). To ensure that all models compared were based on the same dataset, we deleted records with missing data for claw δ^2H or L_home (final n = 119 records from 100 individuals). We tested for differences in the variance of claw δ^2H or L_home between sexes and between age classes, and found no evidence of heteroscedasticity (Levene's test; δ^2H and sex, $F_{1,117}$ = 0.17, p = 0.68; δ^2H and age, $F_{1,117}$ = 0.63, p = 0.43; L_home and sex, $F_{1,117}$ = 2.01, p = 0.16; L_home and age, $F_{1,117}$ = 0.002, p = 0.97). We checked the final model for disproportionately influential datapoints using the R package influence.ME (Nieuwenhuis et al. 2012), and found no evidence for this (all Cook's distances < 0.50).

To investigate the relationship between claw δ^2H values and infection status (i.e., parasitized or unparasitized), we constructed generalized linear mixed models with binomial error distribution using glmer in the R package lme4 (Bates et al. 2015). The dependent variable was infection status, and the fully-fitted initial model included random effects of bird ID and year, plus fixed effects of claw δ^2H, age, capture date, sex, and second-order interactions with age (i.e., claw δ^2H × age, date × age, sex × age). We did not include L_home as a predictor of infection status, because L_home was collinear with migration distance and also because L_home data were unavailable for 28 records. We used LRT as outlined above for model simplification, and report results from a

minimal adequate model using ML estimation. The final model included one disproportionately influential datapoint (Cook's distance >1), but re-running the model excluding this point (exclude.influence in the R package influence.ME; Nieuwenhuis et al. 2012) yielded qualitatively identical findings regarding the statistical significance of predictor terms.

Within the subset of individuals classified as parasitized (i.e., one or more parasites detected in a scan of 10,000 erythrocytes) we investigated the relationship between claw δ^2H values and parasite load (i.e., number of parasites per 10,000 erythrocytes). We used the R function glmer.nb (Bates et al. 2015) to construct generalized linear mixed models with negative binomial error distribution. The dependent variable was parasite load, and the fully-fitted initial model included random effects of bird ID and year, plus fixed effects of claw δ^2H, age, capture date, sex, and second-order interactions with age (i.e., claw δ^2H × age, capture date × age, sex × age). Model simplification was done as outlined above.

Results

Claw δ^2H values ranged from -4.4‰ to -116.8‰ (mean ± SE = -65.10 ± 1.34 ‰, n = 146). Among individuals that were sampled over multiple years, claw δ^2H values were significantly repeatable (repeatability = 0.41; $F_{20,25} = 2.53$, $p = 0.015$).

Table 1 summarizes predictors of claw δ^2H values that were retained in the minimal adequate model. Claw δ^2H was negatively associated with L_home, indicating that individuals that overwintered farther north (i.e. migrated shorter distances) were also relatively philopatric (Fig. 1). Values of claw δ^2H were also lower for males than for

295 females, indicating that males overwintered farther north and migrated shorter distances
296 than did females (Table 1). As a post hoc analysis, we used a median split to classify each
297 individual as either "more philopatric" (top 50% of L_home) or "less philopatric"
298 (bottom 50% of L_home). On average, birds categorized as more philopatric had more
299 negative values of claw δ^2H than did less philopatric individuals (mean ± SE = -66.4 ±
300 1.8 ‰, -62.5 ± 2.2 ‰ respectively). However, this difference was less pronounced than
301 that associated with sex (mean ± SE = -68.6 ± 1.9 ‰, -58.8 ± 1.8 ‰ for males and
302 females respectively).

303 Overall, 34% of birds were infected with one or more haematozoa at the time of
304 capture (21% with *Leucocytozoon* spp., 20% with *Plasmodium* spp. and/or *Haemoproteus*
305 spp., and 2.1% with *Trypanosoma* spp.; these prevalences include individuals with
306 multiple infections). Table 2 summarizes predictors of infection status retained in the
307 minimal adequate model. Infection risk was higher for individuals with more positive
308 values of claw δ^2H (interpreted as having overwintered farther south and migrated longer
309 distances), and was higher for ASY than SY birds. We also found a significant δ^2H × age
310 interaction, reflecting an age-specific relationship between claw δ^2H and infection status
311 (Fig. 2). Among SY birds, claw δ^2H did not differ significantly between infected (mean ±
312 SE = -63.6 ± 2.5 ‰) vs. uninfected individuals (-64.5 ± 2.0 ‰), but among ASY birds,
313 claw δ^2H was more positive for infected (-57.7 ± 3.1 ‰) than for uninfected individuals
314 (-77.4 ± 3.0 ‰). Post hoc median split analysis showed that within the ASY age class,
315 infection risk was approximately three times greater for longer-distance than shorter-
316 distance migrants (19/23 and 6/23, respectively, for birds above and below the median
317 value of claw δ^2H). Infection risk increased somewhat with later capture dates (Table 2).

318 Added-variable plots showing infection risk as a function of claw δ^2H while controlling
319 for the effects of date are provided in the Supplementary Material.
320 Within the subset of individuals classified as infected, parasite loads ranged from
321 1-522 haematozoa per 10,000 cells screened (mean ± SE = 32.3 ± 12.5). The minimal
322 adequate model predicting parasite load of infected birds retained a random effect of
323 year, but did not retain any fixed effects. That is, parasite loads of infected individuals
324 were not predicted by claw δ^2H, age, capture date, sex, or any two-way interactions with
325 age (all $p > 0.20$).
326
327 **Discussion**
328 Latitudinal migration distance, as inferred from winter-grown claw δ^2H values, was
329 repeatable across years, and increased with dispersal tendency as inferred from genetic
330 assignment tests. These findings imply that migration distance is a stable trait that
331 covaries somewhat with the propensity to long-distance movements in the context of
332 natal dispersal. However, this relationship was modest in effect, with sex differences
333 explaining more variation in migration distance than individual variation in dispersal
334 tendency did. Interestingly, the relationship between movement and parasitism varied
335 between age classes. Longer migration distances were associated with somewhat greater
336 likelihood of arriving parasitized at the breeding grounds among ASY birds, on average,
337 but not among SY birds returning from their first winter migration. Our findings suggest
338 that models of optimal migration may benefit from considering biotic interactions such as
339 those between hosts and parasites (Møller and Szép 2011). Moreover, the role of animal

migration in transporting infectious disease may be mediated by stable individual variation in movement combined with age-related variation in susceptibility to parasites.

Individual consistency in claw δ^2H (migration distance)

Compared to relying on band recovery data, using δ^2H values to infer latitudinal migration distance radically expands our ability to study this key life-history trait. This is particularly true in eastern North America where avian tissue isotopic contours follow a fairly uniform north-south gradient (Hobson et al. 2014). Improved ability to track the seasonal movements of individual animals now permits quantifying the repeatability of wintering latitude and latitudinal migration distance. Our finding that song sparrows show consistent individual differences in δ^2H values of claw grown at the wintering grounds suggests that migration distance in this population represents a stable trait.

A recent meta-analysis (Bell et al. 2009) compared repeatability of many classes of behavior among multiple animal taxa (invertebrates, vertebrate ectotherms, vertebrate endotherms) and calculated a global average repeatability of 0.37, similar to the value of 0.41 reported here. However, of the thirteen classes of behavior examined, migration-related behaviors had the lowest repeatability (~ 0.20), perhaps due to the long time interval between measurements (generally one year) associated with field studies of seasonal migration. As well, the avian migration studies reviewed by Bell et al. (2009) were restricted to measures of migratory timing (i.e., arrival or departure date). Our finding that song sparrows show consistent individual differences in δ^2H values of claw grown at the wintering grounds is more directly comparable to δ^2H data of winter-grown feathers from collared flycatchers (*Ficedula albicollis*) breeding in Europe and wintering

363 in Africa (Hjernquist et al. 2009). In that study, repeatability of δ^2H was not significant,
364 perhaps due to lower quality and resolution of the latitudinal δ^2H isoscape in Europe and
365 Africa relative to eastern North America, and/or due to differences in sample size
366 between studies. However, repeatabilities of feather stable-carbon ($\delta^{13}C$) and nitrogen
367 ($\delta^{15}N$) isotope ratios were high (0.76 and 0.80, respectively; Hjernquist et al. 2009),
368 consistent with individual philopatry to the wintering grounds. In song sparrows,
369 repeatability of overwinter latitude suggests that individuals may show some degree of
370 wintering-ground philopatry, but without data on overwinter longitude, this possibility
371 remains entirely speculative.

372 Isotopic discrimination associated with claw δ^2H, the change in δ^2H between
373 amount-weighted precipitation and diet and drinking water and ultimately between
374 precipitation and claw tissue, was not examined in our study. Isotopic discrimination
375 varies with the species, isotope, and tissue being examined (Wassenaar 2008), and
376 without a known transfer function linking environmental water with song sparrow claw
377 for δ^2H, we were unable to use spatially explicit assignment algorithms to depict probable
378 wintering origins (e.g. Hobson et al. 2014). Thus, our analyses focus on relative
379 latitudinal migration distance and do not assign specific overwinter locations or absolute
380 migration distances. As a rough estimate, however, based on comparison to δ^2H values of
381 feathers (Hobson et al. 2014) the range of winter-grown claw δ^2H values measured in this
382 study corresponds to wintering latitudes between Pennsylvania and Florida, USA,
383 suggesting considerable individual variation in overwinter latitude. Net isotopic
384 discrimination is expected to be similar across samples collected from the same tissue in
385 the same species (Wassenaar 2008). Thus we think it unlikely that individual differences

386 in discrimination should introduce substantive noise, much less systematic bias, into the
387 analyses. Our study population was assumed to migrate across the largely north-south
388 gradient in expected tissue δ^2H, providing a good proxy for wintering latitude (Hobson et
389 al. 2014). Band-recapture data from breeding and wintering grounds supports the
390 assumption that migration in this species occurs mainly along a north-south axis (Davis
391 and Arcese 1999).
392
393 Migration distance and natal dispersal
394 Seasonal migration distance, as inferred from δ^2H values of winter-grown claw tissue,
395 was negatively associated with inferred natal philopatry. This relationship was modest in
396 effect and relatively noisy, consistent with multiple other extrinsic and intrinsic factors
397 influencing each of migration distance and natal dispersal, but on average birds inferred
398 to have immigrated to the breeding population from outside the study area also tended to
399 overwinter farther south.
400 Migration distance and natal dispersal tendency might become correlated during
401 the first year of life because both are influenced by some aspect of phenotype, such as
402 hatch date (Morton 1992), early-life condition (Møller and Erritzøe 2001; Saino et al.
403 2014) or social dominance (Gauthreaux 1978). Alternatively, both traits might be subject
404 to similar selection pressures. For instance, individuals without robust immune defenses
405 might be less able to successfully migrate long distances or to successfully disperse, in
406 that both migration and dispersal increase the diversity of parasites encountered. In great
407 tits, for example, humoral immunity is greater in immigrants than in local recruits, a
408 pattern consistent with either phenotype-dependent dispersal or dispersal-by-phenotype-

409 dependent survival (Snoejis et al. 2004). A third possibility is that migration distance of
410 returning yearlings may influence their ability to obtain breeding territories near their
411 natal site, particularly if birds traveling longer distances arrive later or in poorer condition
412 to the breeding grounds. Finally, if dispersing juveniles prospect for breeding sites before
413 the first fall migration, anticipated natal dispersal could potentially influence migration
414 distance. Distinguishing between these last two alternatives requires further information
415 about whether young birds identify potential breeding sites before their first fall
416 migration or upon returning to the breeding grounds the following spring. In migratory
417 mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*), some individuals
418 appear to prospect for breeding sites during juvenile dispersal and before fall migration,
419 whereas other individuals do not select breeding sites until the following spring (Morton
420 1992). In non-migratory populations of song sparrows, natal dispersal occurs during the
421 hatch year (Arcese 1989) but whether this timing also applies to seasonally migratory
422 populations remains unclear.

423 In addition to being associated with natal dispersal tendency, seasonal migration
424 distance also varied between the sexes: on average, males overwintered farther north than
425 did females. This finding is consistent with patterns seen in other ecologically similar,
426 moderate-distance migrants (e.g. dark-eyed juncos *Junco hyemalis*, Ketterson and Nolan
427 1976; white-throated sparrows, Jenkins and Cristol 2002; savannah sparrows *Passerculus*
428 *sandwichensis*, Woodworth et al. 2016). Male song sparrows are slightly larger than
429 females and may thus be better able to withstand low temperatures and food shortages
430 associated with overwintering at high latitudes. Furthermore, migrating shorter distances
431 may allow an earlier return to the breeding grounds, which may be particularly

advantageous to males competing to obtain a breeding territory (Newton 2008). The observed relationship between migration and natal dispersal was, however, robust to including sex as a factor in predictive models of migration distance. Thus both sex differences and individual variation in behavior within each sex contribute to variation in migration distance.

Age, migration distance and parasitism

Age classes differed in the likelihood of returning from spring migration harbouring haematozoan infection: infection prevalence was greater for older birds (ASY) than for those returning from their first migration (SY). This pattern is frequently, although not universally, found in birds (Valkiūnas 2005) and may reflect older birds' greater cumulative exposure to parasites and/or reduced ability of younger birds to survive infection (i.e., tolerance). Moreover, age classes differed in the relationship between migration distance (inferred from winter-grown claw δ^2H) and infection status. Among ASY birds, longer migration distances (more southerly overwinter latitude) were associated with an increased likelihood of arriving at the breeding grounds infected by one or more haematozoa, whereas in SY birds migration distance did not predict infection status.

Although the relationship between claw δ^2H and infection in ASY birds was statistically significant, the overall pattern was noisy, suggesting that many other factors beyond overwinter latitude and migration distance likely influence the risk of parasitic infection. To the extent that migration distance covaries with infection status in this age class, several factors may contribute to this pattern. First, latitudinal gradients in parasite

455 abundance and diversity (Salkeld et al. 2008), and in the seasonal activity of vectors, may
456 increase encounter rates with haematozoan parasites for birds overwintering at low
457 latitudes. It remains to be determined whether parasite and/or vector abundance varies
458 over the geographic scale examined here, but the seasonal activity of insect vectors
459 almost certainly varies over the observed range of wintering latitudes. Birds
460 overwintering farther south may have more encounters with biting insects on the
461 wintering grounds and thus more opportunity to become infected with haematozoa.
462 Moreover, the energetic demands of long-distance flight may compromise immune
463 function (Buehler et al. 2010; Nebel et al. 2013), such that migrating longer distances
464 may increase susceptibility to parasitic infection. As well, particularly if density of
465 migratory birds at stopover sites is high, long-distance migrations requiring multiple
466 stops may increase the risk of acquiring infections. Finally, to the extent that parasite
467 assemblages vary geographically (Pagenkopp et al. 2008), overwintering farther from the
468 breeding grounds may increase encounters with unfamiliar parasites, to which individuals
469 may be relatively susceptible due to lack of previous exposure (Price et al. 1988; Gregory
470 1990; Møller and Erritzøe 1998).

471 In contrast to the pattern observed in ASY birds, migration distance did not
472 predict infection status among birds returning from their first migration (SY age class).
473 Age-related differences in immune function, particularly immune plasticity, may help to
474 explain this discrepancy. In birds, B-lymphocyte development (and thus the development
475 of antibody diversity and immunological memory) occurs in the bursa of Fabricius, a
476 structure that regresses before individuals reach sexual maturity (Møller and Erritzøe
477 2001; Scott 2004). Adaptive immune memory may thus be more phenotypically plastic

478 and responsive to specific antigens during early life than during adulthood. If so, the
479 relatively plastic immune systems of juvenile birds may buffer them from novel parasites
480 encountered during migration or the first winter of life. That is, geographic variation in
481 parasite assemblages between breeding and wintering grounds may be more salient to
482 older individuals with relatively crystallized immune defenses than to younger
483 individuals whose immune defenses remain somewhat plastic.

484 Age-specific effects of parasites on mortality (Martin et al. 2001) may also help to
485 explain why migration distance varied positively with infection likelihood in ASY but not
486 in SY birds. If these age classes differ in their ability to tolerate infection and to migrate
487 while infected, the degree to which migratory culling occurs (Bradley and Altizer 2005)
488 should also vary with age. Thus, the age-specific relationship between migration distance
489 and infection status could reflect migratory culling during the first year of life, such that
490 individuals unable to balance long-distance flight while surviving parasitic infection are
491 unlikely to survive their first winter. If so, ASY individuals may contribute more than
492 yearlings do to the long-distance transport of infectious disease. This possibility
493 emphasizes the importance of considering host-parasite interactions in an age-specific
494 context (Martin et al. 2001).

495 The combined use of genetic assignment tests and stable isotope analyses to
496 identify the natal and overwintering origins of individual animals advances our
497 understanding of population connectivity. The positive association between natal
498 dispersal and seasonal migration distance, two key life history traits, suggests that a
499 common mechanism may underpin long-distance movement across multiple contexts in
500 song sparrows. One promising avenue for future study would be determining whether

501 variation in large-scale movement covaries with movement at finer spatial and temporal
502 scales, for example exploratory tendency in a captive setting or latency to approach novel
503 objects. Overall, our findings implicate individual variation in movement as one of
504 several factors that may influence exposure to parasites, but also suggest that age-related
505 variation in susceptibility or tolerance may further mediate host-parasite interactions and
506 the role of migration in transporting infectious disease.

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510 **Compliance with Ethical Standards**

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

514 Ethical approval: All applicable international, national and institutional guidelines for the
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Table 1 Minimal adequate model (linear mixed model with bird ID as a random effect) predicting claw δ^2H values of song sparrows sampled after spring migration. Claw δ^2H was more negative (interpreted as overwintering farther north and migrating shorter distances) in males than females, and became more negative with increasing L_home (probability of a genotype occurring in the population in which it was sampled; interpreted as natal philopatry). *p* values for eliminated variables are derived from likelihood ratio tests comparing models with and without the variable

Predictor	β ± SE (‰)	95% CI (‰)	*t*	*p*
Intercept	-43.38 ± 6.19	-55.44 – 31.32	-7.01	<0.0001
Sex (male)	-10.05 ± 2.75	-15.41 – -4.69	-3.66	0.0003
L_home	-19.89 ± 7.50	-34.50 – -5.28	-2.65	0.008
Eliminated variables: 1 | year ($p > 0.999$); age × sex × L_home ($p = 0.779$); sex × L_home ($p = 0.054$); age × L_home ($p = 0.085$); age × sex ($p = 0.276$); age ($p = 0.738$)				

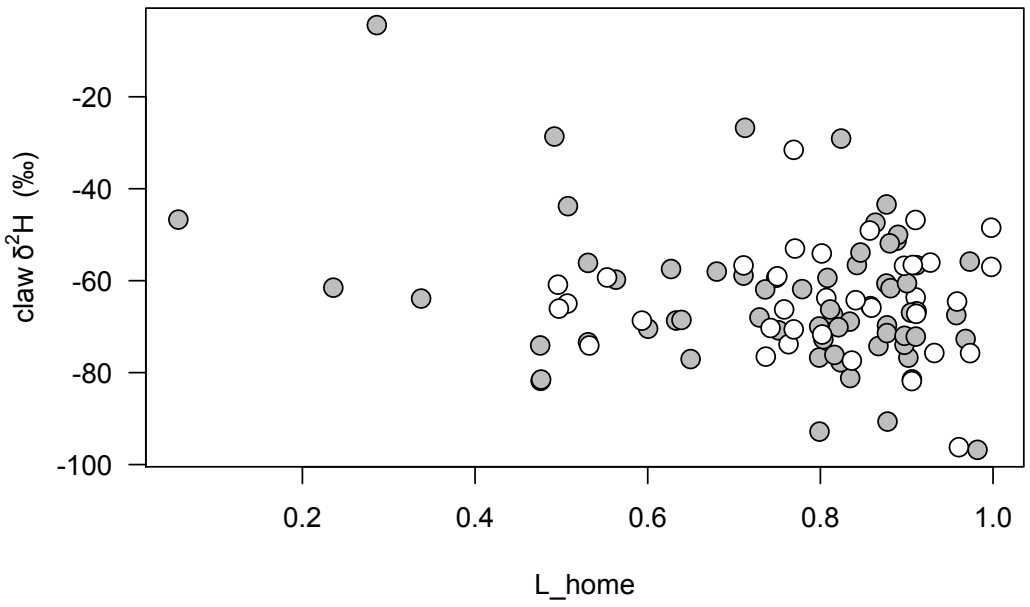
649 **Table 2** Minimal adequate model (binomial GLMM with bird ID as a random effect)
650 predicting haematozoan infection status of song sparrows captured after spring
651 migration. Infection risk increased with more positive claw δ^2H (interpreted as
652 having overwintered farther south and migrating longer distances), was lower
653 for second-year (SY) than after-second-year (ASY) birds, and increased
654 somewhat with later capture dates. There was also an interaction between claw
655 δ^2H and age. *p* values for eliminated variables are derived from likelihood ratio
656 tests comparing models with and without the variable
657

Predictor	β ± SE (‰)	95% CI	*Z*	*p*
Intercept	0.67 ± 0.47	-0.25 – 1.60	1.42	0.16
Claw δ^2H	2.36 ± 0.82	0.75 – 3.97	2.87	0.0041
Age (SY)	-1.73 ± 0.66	-3.02 – -0.44	-2.63	0.0086
Capture date	0.47 ± 0.25	-0.02 – 0.95	1.90	0.058
Claw δ^2H × age (SY)	-2.35 ± 0.86	-4.04 – -0.67	-2.74	0.0062

Eliminated variables: 1 | year ($p > 0.999$); date × age ($p = 0.12$); sex × age ($p = 0.69$); sex ($p = 0.059$)

658

659 **Fig. 1** δ^2H values of winter-grown claw tissue (interpreted as latitudinal migration
660 distance) decreased with increasing L_home (probability of a genotype
661 occurring in the population in which it was sampled; interpreted as natal
662 philopatry) in male (filled symbols) and female (open symbols) song sparrows



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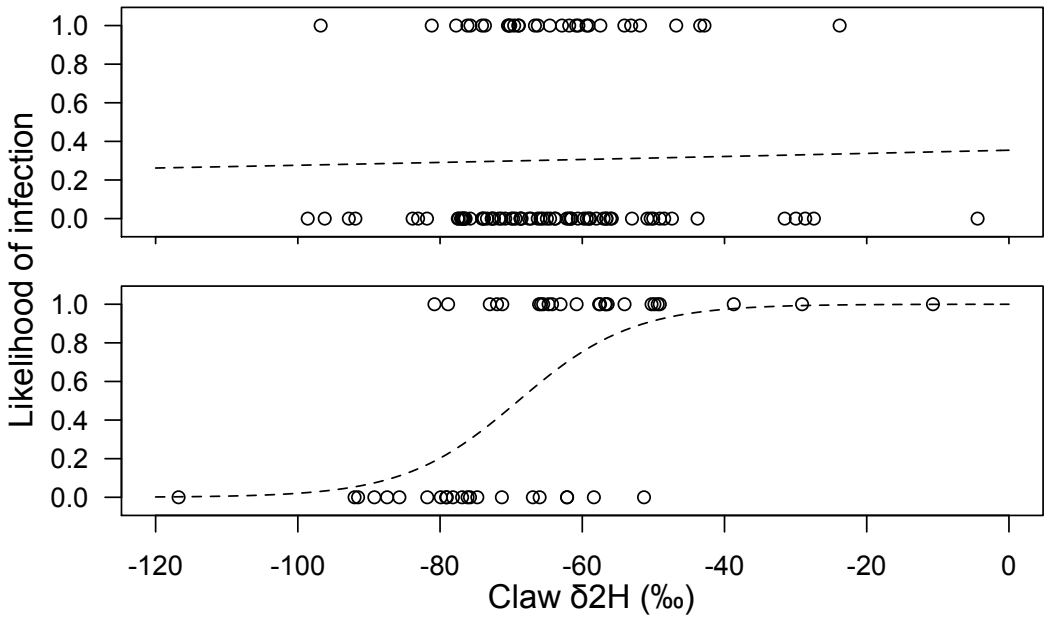
664

665 **Fig. 2** Age-specific relationship between winter-grown claw δ^2H and haematozoan
666 infection status. Within the SY age class (yearlings; upper panel), claw δ^2H did
667 not predict likelihood of infection. Within the ASY age class (older birds; lower
668 panel), likelihood of infection increased with more positive δ^2H values
669 (indicating more southerly wintering latitude and longer latitudinal migration).
670 Curves show predicted infection risk as a function of claw δ^2H



671