

Research



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Physiology

Local adaptation from afar: migratory bird populations diverge in the initiation of reproductive timing while wintering in sympatry

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The initiation of reproduction in many seasonally breeding animals is controlled by photoperiod and tends to be clinal: populations at higher latitudes breed later than those at lower latitudes, often reflecting a higher photoperiodic threshold. Migratory animals presumably time reproduction to match conditions at their breeding grounds, at least in part, by cues perceived on their wintering grounds. We asked how closely related dark-eyed junco (*Junco hyemalis*) populations that overwinter in sympatry but breed in allopatry respond to their shared winter environment by comparing early spring indices of readiness to migrate (fat and muscle condition) and breed (baseline and elevated testosterone). We measured stable hydrogen isotopes from feathers grown the preceding year and claws grown during winter to estimate breeding and wintering latitudes, respectively. We predicted that if reproductive initiation is adapted to the emergence of resources at their respective breeding destinations, then birds migrating to higher latitudes (slate-coloured junco; *J. h. hyemalis*) should delay breeding as compared with those migrating to lower latitudes (pink-sided junco; *J. h. mearnsi*) despite a common overwinter environment. We found higher testosterone in pink-sided juncos, consistent with earlier reproductive initiation, suggesting local adaptation in reproductive phenology is achieved through differential responses to predictive environmental cues.

1. Introduction

Vertebrate populations vary in seasonal reproductive timing in relation to when they activate the hypothalamic–pituitary–gonadal (HPG) axis [1–5]. Activation is associated with breeding latitude, as high-latitude populations breed later [6,7]. Within-population variation in reproductive timing is under selection and early breeding is often favoured [8–10]. Photoperiod is the primary proximate cue used by temperate zone birds to organize their annual cycle [1,2]. During winter, the reproductive system collapses and gonads are small. As daylength increases in spring, the HPG axis is activated: birds are photostimulated to release gonadotropin-releasing hormone (GnRH) from the hypothalamus (H), which stimulates the release of hormones from the pituitary (P), which initiates gonadal (G) recrudescence, ultimately producing sex steroids and gametes. Migratory animals face a challenge to optimize reproductive timing because suitable breeding conditions occur later in the year at their migratory destinations than at overwintering sites, raising the question: how do they synchronize their cyclic life-history stages with environmental conditions at distant breeding grounds? Captive studies have shown that migratory birds overwintering in the tropics and breeding in temperate zones rely on endogenous rhythms (unrelated or loosely related

to daylength changes) to time the onset of migration and reproduction [11]. In species that overwinter and breed in the temperate zone, reproductive initiation is driven by photoperiodic changes [12]. However, little is known regarding the role of photoperiod in regulating within-species geographic variation of reproductive development in wild temperate zone migrants.

Many migratory species have multiple populations (groups, subspecies) that breed in allopatry but overwinter in sympatry in a distribution pattern known as heteropatry [6]. Sympatric wintering populations experience the same environment, but we lack knowledge of how they incorporate these cues to regulate differences in phenology. The dark-eyed junco (*Junco hyemalis*) provides an excellent system to answer this question, as it is a species with remarkable diversity in reproductive timing, plumage coloration and migratory behaviour [13]. There are at least six major North American junco populations (grey-headed, Oregon, pink-sided, red-backed, slate-coloured and white-winged) with distinct breeding ranges but overwintering ranges that often overlap [13,14]. Migratory propensity within the junco complex ranges from completely sedentary to obligatory long-distance migrants [15]. These groups allow comparisons of distinct phenological divergences in migratory and reproductive timing.

In this study, we asked whether populations that winter together but differ in where they breed also differ in their physiological responses (migratory and breeding readiness) to locally experienced conditions on their wintering grounds prior to migrating in early spring. If yes, population-level differences in phenology may be regulated, at least in part, by differential responsiveness to conditions experienced in a common environment. We captured seasonally sympatric pink-sided (PSJU) and slate-coloured juncos (SCJU) prior to spring migration and injected them with GnRH to measure naturally occurring testosterone (T) variation. Exogenous GnRH is commonly used to measure maximum gonadal T production [16–19]. We used stable isotope analyses of hydrogen in feathers ($\delta^2\text{H}_f$) to estimate breeding latitude and claws ($\delta^2\text{H}_c$) to confirm that both groups overwintered at the capture site rather than being sampled at a stopover site during vernal migration. We also measured fat score, pectoral muscle condition and size-corrected body mass as metrics of migratory preparedness. We hypothesized that HPG activity and migratory physiology would reflect variation in migratory patterns. Specifically, we predicted that T elevation in response to GnRH would be greater in the shorter-distance migrant (PSJU) than the longer-distance migrant (SCJU). We also predicted that SCJU would have a higher migratory preparedness index (more fat, greater pectoral muscle development and higher size-corrected body mass) than PSJU because of their longer migratory distance.

2. Materials and methods

Detailed methods are presented in the electronic supplementary material.

(a) Classification

Within the junco complex, PSJU is a short-distance migrant that breeds in the northern Rocky Mountains to eastern Idaho, whereas SCJU is a long-distance migrant that breeds across Canada and Alaska [13]. Following the fall migration, both groups overwinter

east of the Rocky Mountains along with other members of the junco complex.

(b) Capture

We captured overwintering PSJU ($n = 7$) and SCJU ($n = 11$) from 18 to 24 March 2019 in Littleton, CO and Peyton, CO. Birds were caught in baited Potter traps and standard morphometric measurements were taken [16–18], including mass, body fat and pectoral muscle condition as metrics of migratory physiology (see electronic supplementary material). We selected males for this study, later confirmed by sexing PCR. We classified the two forms using plumage coloration (electronic supplementary material, figure S1).

(c) Stable isotope analyses

We collected the most distal secondary feather from the right wing and approximately 2 mm of the right hallux claw for stable hydrogen isotope analyses at the Indiana University Stable Isotope Research Facility (SIRF). Based on the feather and claw $\delta^2\text{H}$ values, we performed geographic assignments of individual birds during the breeding and overwintering months, respectively, using the assignR package in R [20] (see the electronic supplementary material).

(d) Testosterone assays

We collected blood samples (approx. 150 μl) for baseline T (T_0) immediately after capture by puncturing the brachial wing vein. Birds then received an intrapeitoral GnRH injection [16–19], and a second blood sample (approx. 150 μl) was collected after 30 min to measure elevated T (T_{30}) levels. Plasma samples were stored at -20°C until analysis at Indiana University. Circulating T concentrations were determined from 20 μl plasma aliquots using high-sensitivity testosterone kits (Enzo Life Sciences, ADI-900-176, Farmingdale, NY). The GnRH-induced change in T levels (dT) was calculated by subtracting T_0 from T_{30} . All samples were measured in duplicate and randomized over plates. The intra- and inter-plate coefficients of variation were $2.7 \pm 0.54\%$ (0.9–4.0%) and 5.2%, respectively.

(e) Statistical analyses

Data were analysed using R (version 3.2.0) and SPSS (version 20). We calculated residual values from an ordinal least square regression of body mass and tarsus length and used the residual values as a measure of size-corrected body mass. We tested all variables for normal distribution and homogeneity of variances (detailed in electronic supplementary material, methods; electronic supplementary material, table S1a,b). We used the first axis (PC1) of a principal component analysis that included pectoral muscle condition, fat score and size-corrected body mass to calculate a migratory preparedness score. Two-sample t -tests were used to test differences in isotope values, dT and PC1 scores between PSJU and SCJU, followed by Benjamini–Hochberg multiple corrections (false discovery rate, $\text{FDR} < 0.05$). A Mann–Whitney U -test was used to test differences in T_0 between PSJU and SCJU. Population data were pooled, and a linear regression was used to assess covariation between $\delta^2\text{H}_f$, dT and PC1 values ($p < 0.05$).

3. Results

(a) Feather and claw hydrogen isotope values

The $\delta^2\text{H}_f$ values were significantly higher and predicted latitudes were significantly lower in PSJU than in SCJU (table 1; figure 1*a,b,e,f*; electronic supplementary material, figures S2 and S3). The groups exhibited non-intersecting ranges of

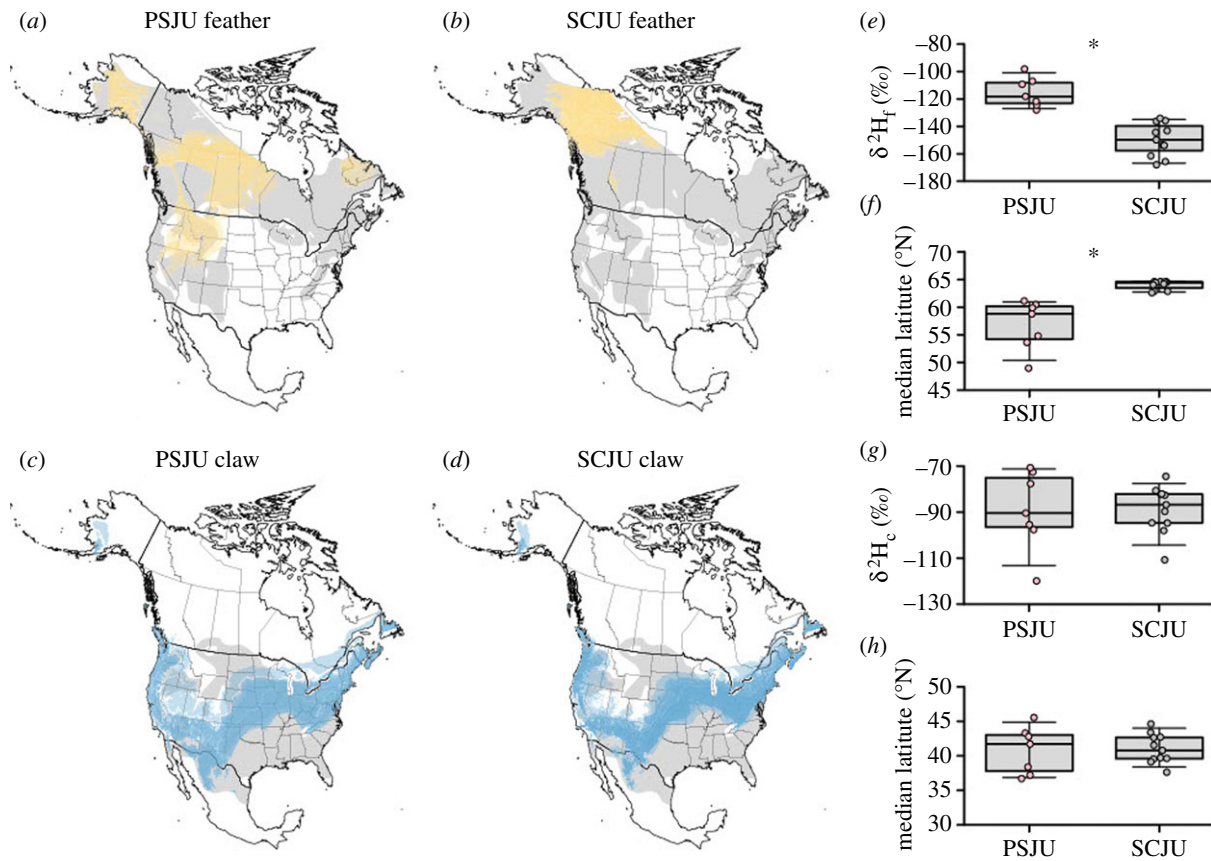


Figure 1. Overlapping geographic assignments of PSJU (a,c) and SCJU (b,d) individuals based on hydrogen isotopic composition of feathers (in yellow) and claws (in blue), representing estimated breeding and overwintering locations, respectively. Estimates reflect cells within the top 10% highest posterior probability based on Bayesian assignment [20–22]. Seasonal ranges for *Junco hyemalis* [23] are shown in light grey underneath estimates (the species' full range map was used to construct geographic assignment maps). The $\delta^2\text{H}$ (e,g) values were used to estimate median latitudes of formation for individual feathers (f) and claws (h), with asterisks indicating significant differences between PSJU and SCJU.

Table 1. Results of *t*-test ($\delta^2\text{H}$, dT, and PC1) and Mann–Whitney *U*-test (T_0) comparing PSJU and SCJU juncos. Results are given as mean \pm standard error mean. **p*-value < 0.05. d.f., degrees of freedom. T_0 , baseline testosterone; dT, GnRH-induced change in testosterone.

	PSJU	SCJU	<i>t</i> -value	<i>U</i> -value	d.f.	<i>p</i> -value	adjusted <i>p</i> -value ^a
feather $\delta^2\text{H}$ (‰)	-115.28 ± 4.08	-9.59 ± 3.62	6.14	—	16	<0.0001*	<0.0001*
claw $\delta^2\text{H}$ (‰)	-89.21 ± 6.55	-88.81 ± 3.07	-0.62	—	16	0.95	0.95
T_0 (ng ml ⁻¹)	5.43 ± 0.79	9.08 ± 3.89	—	31	16	0.49	0.49
dT (ng ml ⁻¹)	41.95 ± 4.46	18.96 ± 3.91	3.79	—	16	0.001*	0.003*
migratory preparedness ^b	0.32 ± 0.49	-0.21 ± 0.23	1.25	—	16	0.25	0.33

^aAdjusted *p*-value using Benjamini–Hochberg multiple corrections.

^bMigratory preparedness: PC1 from a principal component analyses incorporating size-corrected body mass, fat score and pectoral muscle condition.

$\delta^2\text{H}_f$ values, suggesting non-overlapping breeding latitudes (PSJU = -128.06 to -98.13‰ ; SCJU = -134.15 to -167.97‰ ; electronic supplementary material, figures S2 and S3). The $\delta^2\text{H}_c$ values and predicted latitudes did not significantly differ between PSJU and SCJU (table 1; figure 1c,d,g,h).

(b) Testosterone and migratory preparedness score

T_0 did not significantly differ between PSJU and SCJU (table 1), but PSJU had significantly higher dT than SCJU (table 1). PC1 explained 64% of the variation in migratory preparedness, with more positive values indicating fatter birds with larger pectoral muscles and heavier for their body size (electronic supplementary material, figure S4). The populations did not differ in their

migratory preparedness scores (table 1, electronic supplementary material, figure S4).

(c) Seasonal phenology and stable isotope values

There was a significant positive relation between dT and $\delta^2\text{H}_f$ values ($r^2 = 0.26$, $p = 0.03$; figure 2; table 2), but not between migratory preparedness score PC1 and $\delta^2\text{H}_f$ values ($r^2 = 0.06$, $p = 0.35$; table 2).

4. Discussion

This paper addresses the physiological differences between closely related heteropatric populations, with implications

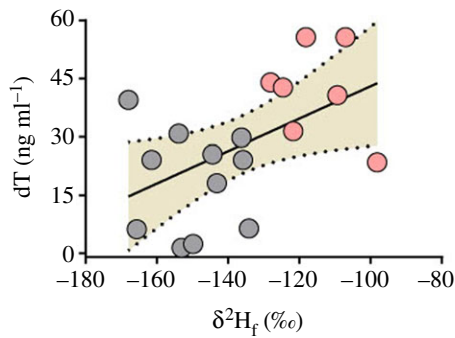


Figure 2. Linear regression with 95% confidence interval (tan shading) between GnRH-induced change in testosterone (dT) and feather isotope (δ^2H_f) values in PSJU (pink circles) and SCJU (grey circles). Statistical significance is defined by $p < 0.05$.

Table 2. Linear regression between GnRH-induced change in testosterone (ng ml^{-1}) (dT), PC1 and stable isotope values (‰) of hydrogen in feathers (δ^2H_f). Variables are significantly related at p -value < 0.05 (*).

variables	coefficient of determination (r^2)	p -value
δ^2H_f versus dT	0.26	0.03*
δ^2H_f versus migratory preparedness ^a	0.06	0.35
dT versus migratory preparedness ^b	0.16	0.10

^a δ^2H_f : stable isotope values (‰) of hydrogen in feathers.

^bMigratory preparedness: PC1 from a principal component analysis incorporating size-corrected body mass, fat score and pectoral muscle condition.

for local adaptation and the role of timing mechanisms in population divergence. We compared early spring indices of reproductive initiation between two migratory populations of the junco complex and found population-level differences in reproductive timing despite exposure to the same environmental cues at their overwintering location. The δ^2H_f values reflect non-overlapping geographic origins of PSJU and SCJU as expected based on plumage differences [19,24]. Significantly higher δ^2H_f values in PSJU indicate a lower breeding latitude, and thus a shorter migratory distance than SCJU [13]. By contrast, both populations co-occur during winter as indicated by the capture location and geographic predictions based on the isotopic composition of claws grown on the wintering ground [25]. There were no significant differences in indices of migratory preparedness, suggesting similar physiological states for migration.

Reproductive initiation was estimated using T_0 and dT. We observed that PSJU elevated T more than SCJU, indicating larger gonads [16] that were more receptive to a hormone challenge. Higher dT also corresponds to a higher density of gonadal luteinizing hormone receptors in other closely related junco populations [26]. PSJU breed at lower latitudes, where conditions favourable to successful reproduction occur earlier in the year. The most likely explanation for the observed increase in dT is that the populations differ in the minimum stimulatory day length (critical photoperiod) that elicits an HPG response [18]. We interpret this as a mechanism that

serves to match reproductive development to the timing of resource emergence for reproduction, which occurs earlier in the year at lower latitudes. However, we cannot exclude potential roles of endogenous rhythms or differential sensitivity to supplementary cues.

Other studies examining reproductive timing corroborate our findings. Singh *et al.* [18] found covariation between the latitude of origin and critical photoperiod in captive migrant and resident juncos that overwinter in the eastern United States. Resident juncos (*J. h. carolinensis*) had elevated T earlier than migrant SCJUs; among migratory SCJUs, the T response was negatively correlated with breeding latitude [18]. Studies on collared flycatchers (*Ficedula albicollis*) and bar-tailed godwits (*Limosa lapponica*) provide convincing evidence that breeding latitude influences the timing and duration of life-history stages in the subsequent year [27–29].

In temperate zone birds, reproductive initiation is regulated by photoperiod, but the progression of gonadal development is fine-tuned by supplementary cues [30–33]. It remains to be determined how local supplementary cues affect the advancement of seasonal breeding in populations that differ in photoperiodic response. In sum, our results indicate that the timing of annual life-history stages is influenced by breeding latitude as experienced at the overwintering latitude. We interpret this as matching the time of appearance of resources sufficient to support reproduction, which occurs earlier in the year at lower latitudes.

In addition, because migration and breeding are physiologically demanding processes, and their timing is important for individual fitness, the delay in breeding in the long-distance migrants may reflect a tradeoff to maintain a balance between the energetic demands of migration and reproduction. The early elevation of T may provide fitness benefits for males that arrive on the breeding grounds in a more advanced reproductive state with an increased ability to establish a high-quality territory [34]—but only if this tradeoff is not too costly [35]. For example, male and female song sparrows (*Melospiza melodia*) that migrated shorter distances had higher androgen levels upon spring arrival even after controlling for sex and date [25]. Another possibility is that elevated T contributes to migratory preparation. Tonra *et al.* [36] found that androgens simultaneously affect the timing of migratory and breeding preparation; captive male dark-eyed juncos treated with exogenous T began migratory preparation 10 days before T-inhibited and control birds [37]. However, we did not observe differences in migratory preparedness and therefore our results do not support this explanation.

To our knowledge, this study is the first to measure variation in the timing of reproductive initiation in relation to the migratory distance among wild sympatric wintering populations. This variation appears to result in timing that matches resource availability at the respective destinations [38]. Our results may also have evolutionary implications. If local adaptation leads to differences in timing, selection might act against hybrids, leading to population divergence. Future studies should incorporate more populations, use geolocator data to establish departure and arrival dates, and determine which components of the HPG axis regulate variation in critical photoperiods. Understanding the mechanisms of changes in phenology is important not only for understanding species divergence by reproductive isolation, but also for predicting how populations breeding at different latitudes will respond to environmental changes.

Ethics. All research was done in compliance with Indiana University's Institutional Animal Care and Use Committee (no. 18-030), US Fish and Wildlife Service (no. MB093279-0), United States Department of Interior (no. 20261), State of Colorado Department of Natural Resources (no. 19TRb2448), Colorado Parks and Wildlife, and Denver Parks and Recreation.

Data accessibility. Data are available on the Dryad Digital repository: <http://dx.doi.org/10.5061/dryad.k3j9kd559> [39].

Authors' contributions. E.D.K., S.M.W. and D.S. conceived the idea. S.M.W., A.J.B. and E.D.K. collected data. D.S. performed hormone assays. T.M.S. performed the hydrogen stable isotope analyses and geographic assignments. S.M.W., E.D.K. and D.S. wrote the manuscript with the

help of all authors. All authors approved the final manuscript version and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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