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Research Paper

Quantifying rosy-finch migration with stable hydrogen isotope feather markers highlights the need for inter-state collaboration to reach conservation goals

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ABSTRACT. The Black Rosy-Finch *Leucosticte atrata* is a species of conservation concern because their alpine breeding habitat is threatened by climate change and their population size is relatively small. Rosy-finches are notoriously difficult to study and information gaps include migratory connectivity across their range. In Idaho, Montana, Nevada, Utah, and Wyoming, Black Rosy-Finches can be found throughout the year and it is unknown if these populations are short-distance altitudinal migrants or are traveling to and from other regions. Understanding a species' full annual cycle can improve conservation and management between states and management entities. To understand migration patterns, we measured stable hydrogen isotopes from feathers of Black Rosy-Finches that were using three mountain sites in Utah during the non-breeding season. Samples from Gray-crowned Rosy-Finches *Leucosticte tephrocotis* were also included to support validation of methods. From each sample, we produced odds of origin surfaces that allowed us to summarize the distance and direction traveled between the location where feathers were formed and their collection site during the non-breeding season. Stable hydrogen isotope values of feather samples from 38 Black Rosy-Finches ranged -113.71‰ to -37.03‰ and probable breeding-season origins of these birds included central Idaho, southwestern Montana, western Wyoming, and the Uinta Mountains of Utah. Black Rosy-Finches traveled on average (median) 428 km between breeding and non-breeding locations. These results suggest that northern Utah's wintering Black Rosy-Finches migrate regionally between breeding and non-breeding sites rather than making local-scale altitudinal migrations from nearby breeding sites within Utah. Managers and conservationists across state boundaries need to ensure they are providing habitat resources to sustain Black Rosy-Finches across the annual cycle.

La quantification de la migration du Roselin noir à l'aide de marqueurs d'isotopes stables de l'hydrogène met en évidence la nécessité d'une collaboration interétatique en vue de sa conservation

RÉSUMÉ. Le Roselin noir *Leucosticte atrata* est une espèce dont la conservation est préoccupante, car son habitat de nidification alpin est menacé par les changements climatiques et la taille de sa population est relativement petite. Ce roselin est notoirement difficile à étudier et les lacunes en matière de connaissance comprennent la connectivité migratoire dans l'ensemble de son aire de répartition. Les Roselins noirs fréquentent l'Idaho, le Montana, le Nevada, l'Utah et le Wyoming tout au long de l'année et on ne sait pas si ces populations sont composées de migrateurs altitudinaux sur de courtes distances ou d'oiseaux qui se déplacent vers et à partir d'autres régions. La compréhension du cycle annuel complet d'une espèce peut améliorer la conservation et la gestion entre les États et les entités de gestion. Pour comprendre les schémas de migration, nous avons mesuré les isotopes stables de l'hydrogène dans des plumes de Roselins noirs qui utilisaient trois sites montagneux de l'Utah en dehors de la saison de nidification. Des échantillons de Roselins à tête grise *Leucosticte tephrocotis* ont également été analysés pour valider la validation. À partir de chaque échantillon, nous avons produit des surfaces de cotes d'origine qui nous ont permis de résumer la distance et la direction parcourues entre l'endroit où les plumes ont poussé et leur site de collecte pendant la saison hors reproduction. Les valeurs des isotopes stables de l'hydrogène des échantillons de plumes de 38 Roselins noirs ont varié entre -113,71‰ et -37,03‰ et les origines probables de ces oiseaux pendant la saison de nidification comprennent le centre de l'Idaho, le sud-ouest du Montana, l'ouest du Wyoming et les monts Uinta de l'Utah. Les Roselins noirs ont parcouru en moyenne (médiane) 428 km entre les lieux de nidification et ceux hors nidification. Ces résultats laissent croire que les Roselins noirs hivernant dans le nord de l'Utah migrent de façon régionale entre les sites de nidification et hors reproduction plutôt que d'effectuer des migrations altitudinales à l'échelle locale depuis des sites de nidification proches dans l'Utah. Les gestionnaires et les responsables de la conservation au-delà des frontières de l'Utah devraient s'assurer qu'ils fournissent les ressources en habitat nécessaires à la survie des Roselins noirs tout au long du cycle annuel.

Key Words: *Leucosticte atrata; isoscapes; migration; stable hydrogen isotopes*

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INTRODUCTION

Understanding the entire annual life cycle of migratory species, including breeding, migration, and non-breeding seasons, is essential for effective conservation and management (Marra et al. 2015). The mechanisms that threaten and limit populations can vary depending on the time of year and location, meriting different conservation approaches depending on where individual birds and populations are located throughout the year. Management actions and policy decisions are implemented at different scales by different entities, so understanding a species' full annual cycle can help identify key stakeholders and geographic regions that need to be included to achieve effective conservation outcomes. Specifically, understanding the connectivity between breeding and non-breeding populations is essential to monitoring responses to global environmental change as well as enacting effective conservation interventions (Webster et al. 2002, Martin et al. 2007, Small-Lorenz et al. 2013).

The Black Rosy-Finch (*Leucosticte atrata*) is a migratory songbird native to western North America and is a species of conservation concern throughout its range (Utah Wildlife Action Plan Joint Team 2015, Oregon Department of Fish and Wildlife 2016, Rosenberg et al. 2016, Idaho Department of Fish and Game 2017, Wyoming Game and Fish Department 2017, Nevada Department of Wildlife 2022). This medium-sized songbird is rated as highly vulnerable to becoming endangered because they have a restricted high-elevation breeding range and are estimated to have a relatively small population size compared to other landbirds (Rosenberg et al. 2016). The extent of the Black Rosy-Finch breeding distribution is relatively small and includes six western states (i.e., Idaho, Nevada, Montana, Oregon, Utah, and Wyoming; Johnson 2002, Marshall et al. 2003, Brown et al. 2018, Paprocki and Pope 2019, Fink et al. 2022). Because of the difficulty of accessing high elevation breeding sites, occupancy or abundance of Black Rosy-Finches is not well-documented. Rosenberg et al. (2016) also describe rosy-finches as highly vulnerable because their breeding habitat is threatened by climate change. Rosy-finch breeding habitat is limited to high-elevation talus slopes and cliffs in the alpine tundra (often above 2620 m, but varies between mountain ranges) that are subject to disproportionately higher temperature shifts with climate change (Johnson 2002, Mountain Research Initiative EDW Working Group 2015, Brown 2021). Suitable breeding habitat for rosy-finch species is correlated to the absence of shrub and tree vegetation (Stanek 2009, Brown 2021) and climate-induced tree line encroachment into the alpine may degrade rosy-finch breeding habitat (Formica et al. 2014, Scharnagl et al. 2019, Verrall and Pickering 2020). Other key information gaps hamper conservation and management actions, including uncertainty regarding breeding and winter distributions, migratory connectivity, and movements across geopolitical boundaries that might necessitate interagency collaboration.

One aspect of Black Rosy-Finch ecology that is particularly poorly understood is their migratory behavior. During the post-breeding season (August through September), Black Rosy-Finches are observed in flocks of adults and juveniles in the alpine tundra (French 1959a, Johnson 2002, Fink et al. 2022). During October and November they begin to be seen at lower elevations (as low as 1070 m), and in the winter months (December through April), their distribution broadens and they are observed in flocks of tens to hundreds, often interspersed with other rosy-finch species (i.e., Gray-crowned Rosy-Finch [*Leucosticte tephrocotis*] and Brown-capped Rosy-Finch [*Leucosticte australis*]). Despite over 5000 Black Rosy-Finches being banded between 1960 and 2022, only three of these birds have been recaptured away from their banding site. Two Black Rosy-Finches captured in Colorado and Wyoming were recaptured in different parts of the state in which they were banded. One Black Rosy-Finch banded in February 2019 in Gunnison, Colorado was re-sighted in the foothills of the Wind River Range, Wyoming in May 2022. In the absence of movement data, migration patterns have largely been inferred from seasonal changes in abundance, but this is an imperfect glimpse into their movement. For example, the species is not known to breed in Colorado, but it can be found across the state in the winter. Winter records of Black Rosy-Finches exist south of the known breeding range and into Arizona, the Sandia Mountains of New Mexico, and occasionally the southern Sierra Nevada Mountains of California (Townsend 1925, French 1959a, Fink et al. 2022). Based on observations of winter flocks, Black Rosy-Finches have been described as altitudinal migrants in some parts of their range, moving along shorter elevational gradients in response to weather conditions (Gullion 1957, Johnson 2002, Boyle 2017) while in other regions they are presumed to migrate longer distances (280 miles, Johnson 2002). It has also been hypothesized that migration strategies may differ between sexes, which is hinted at by skewed sex ratios. Black Rosy-finch populations have fewer females than males (Twining 1938, French 1959b, King and Wales 1964, Johnson 1965, Bailey 1974, and Shreeve 1980), which may reflect differential risk born by females that may disperse farther than males (as has been suggested for the Gray-crowned Rosy-finch by Shreeve 1980 and Bailey 1974).

Particularly in Idaho, Montana, Nevada, Utah, and Wyoming, Black Rosy-Finches can be found during the breeding and non-breeding season. It is unknown if these populations are remaining within a small area for their entire lifecycle or are traveling to and from other regions. This knowledge gap is concerning considering the relatively small geographic range and total population size for the species, and their potential to be negatively impacted by climate change (Rosenberg et al. 2016). Predicted future climate conditions differ by region and latitude, so it is important to understand whether wintering and breeding populations are spending part of their lives elsewhere. For example, monitoring the trend of a population that migrates altitudinally between nearby non-breeding and breeding habitat would be more straightforward than monitoring one or more populations that move longer distances latitudinally. An understanding of how the population utilizes the range through the full annual cycle will allow state and federal agencies to better coordinate management of the species and its habitats.

We used stable hydrogen isotopes from feathers (δ^2H_f) to understand the migration patterns of Black Rosy-Finches that are found in Utah during the non-breeding season. Stable hydrogen isotope analysis of animal tissue is a minimally invasive and cost-effective method of inferring the geographic origins of animal tissue (Chamberlain et al. 1996, Hobson and Wassenaar 1996, Vander Zanden et al. 2018). The technique relies on predictable geographic variation in the stable hydrogen isotope ratios of precipitation, which in North America broadly decrease with increasing latitude and elevation. As organisms assimilate hydrogen from their local environment through food and water, their tissues reflect the stable hydrogen isotope values of the local environment. Thus, given some knowledge of the timing and process of tissue formation, measurement of stable hydrogen isotope ratios in animal tissues can be used to infer the location where they were formed. The definitive pre-basic molt in North American rosy-finches, during which all body and flight feathers are replaced, occurs between late July and late August while adult birds are still utilizing high alpine breeding habitats (French 1959b, Pyle 1997, Johnson 2002). Stable hydrogen isotopes can therefore be used to link two scales of information: precise location and timing reflecting the capture and sample of an individual, and more general estimates of the timing and area of tissue formation (Campbell 2023).

Because this study is the first to apply stable hydrogen isotope analysis to Black Rosy-Finch feathers, a secondary objective was to validate key assumptions about the relationship between the stable hydrogen isotope values of the environment (i.e., that of local precipitation) and of Rosy-Finch feathers. This relationship, often called a transfer or rescaling function (Bowen et al. 2005, Wunder 2010, Hobson et al. 2012, Bowen et al. 2014), is key to making statistically sound models of likely origin. To validate this approach, we analyzed feather samples of a closely-related species with a more disjunct breeding and non-breeding range, the Gray-Crowned Rosy-Finch, alongside those of the Black Rosy-Finches. Because Gray-Crowned Rosy-Finches have both broader and more northerly breeding grounds than Black Rosy-Finches, we expected that the modeled origins of their feathers would be both more geographically diverse and fall within a separate geographic area that overlapped with their breeding range.

This project comprised two primary objectives: (1) use stable hydrogen isotopes within the keratin of Black Rosy-Finch feathers (δ^2H_f) collected in Utah during the non-breeding season to describe their breeding season origins; and (2) validate the application of stable hydrogen isotope analysis to examine rosy-finch movement generally by comparing the inferred origins of Gray-crowned Rosy-Finches that breed at more northern latitudes.

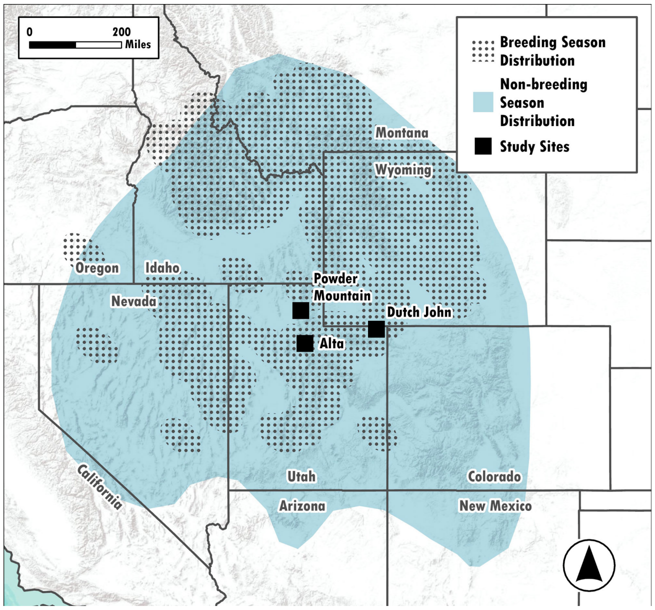
METHODS

Sample collection

We captured non-breeding Black Rosy-Finches and Gray-crowned Rosy-Finches at three study sites in northern UT, USA: Alta (2620 m ASL; 40° 35' 25.8468", -111° 38' 14.7516"), Dutch John (1950 m ASL; 40° 55' 45.7788", -109° 23' 25.62"), and Powder Mountain (2620 m ASL, 41° 22' 15.528", -111° 46' 5.4114"; Fig. 1). The study sites are located within the core winter range of Black and Gray-crowned Rosy-Finches, in close proximity to previously established bird feeders known to attract rosy-finches and other bird species.

To collect stable isotope samples for this investigation, we captured Black and Gray-crowned Rosy-Finches between December and May of 2020 and 2021 using mist nets or baited walk-in traps around established bird feeders. Upon capture each bird was fitted with a metal U.S. Geological Survey band and was aged and sexed using criteria from Pyle (1997). For each bird, we recorded standard morphological measurements including mass and fat and noted any pertinent molt information (e.g., adventitious replacements). We then collected a tail feather (R3) from the right side from each individual and placed each in an individually labeled envelope. All samples were then stored at room temperature until isotopic analysis. A selection of samples from adult birds (second year or after second year) that was distributed across the collection sites, sex of bird, and capture months were analyzed for stable isotopes.

Fig. 1. The breeding and non-breeding season distribution (adapted from Fink et al. 2022) of the Black Rosy-Finch (*Leucosticte atrata*) and sites where feather samples were collected for stable hydrogen isotope analysis.



Stable isotope analysis

Black and Gray-crowned Rosy-Finch feather subsamples were prepared for analysis by cleaning and drying according to Coplen and Qi (2012). Each subsample consisted of a 2 cm length of feather cut midway along the vane with an attempt to avoid cutting near the rachis (Gordo 2020). We measured the non-exchangeable stable hydrogen isotope values (δ^2H) of each sample using a comparative equilibration approach (Wassenaar and Hobson 2003). Approximately 0.2 mg of each cleaned sample was allowed to equilibrate with ambient air for 72 hours prior to analysis alongside matrix-matched international standards with known values of non-exchangeable hydrogen (USGS42, -72.9‰; USGS43, -44.4‰; CBS [Caribou Hoof Standard] -157.0‰; and KHS [Kudu Horn Standard], -35.3‰; Coplen and Qi 2012) and an internal standard (porcine keratin product #K3030; Spectrum Chemicals, New Brunswick, NJ, USA).

The δ^2H values of each sample were measured using a ThermoFisher high temperature conversion/elemental analyzer (TC/EA) pyrolysis unit interfaced with a ThermoFisher Delta V+ isotope ratio mass spectrometer. Values of δ^2H are reported in parts per mil (‰) on the Vienna Standard Mean Ocean Water-

Standard Light Antarctic Precipitation (VSMOW-SLAP) scale, which was calculated using a 2-point normalization curve using CBS and KHS. All preparation and analyses were conducted at the Central Appalachians Stable Isotope Facility at the University of Maryland Center for Environmental Science Appalachian Laboratory (Frostburg, MD). To test for differences in δ^2H values between Black Rosy-Finch sexes (sites pooled), a Welch Two Sample t-test was performed using the R software, version 4.0.2 (R Core Team 2023).

Relating feather δ^2H to spatial variation of δ^2H

To model the relationship between the stable hydrogen isotope values of precipitation (δ^2H_p) and bird feather keratin (δ^2H_f), we reproduced the linear modeling approach using data and methodology described in Hobson et al. (2012). The dataset comprised measurements of δ^2H_f from 1089 feather samples of known provenance from 39 species (Hobson et al. 2012). We first adjusted the measurements of δ^2H_f from the original calibration (Wassenaar and Hobson 2003) to the calibration protocol used to measure rosy-finch samples (VSMOW-SLAP) using the refTrans function of the assignR R package (v. 2.2.0; Ma et al. 2020, Magozzi et al. 2021). We then fit mixed linear models predicting the VSMOW-SLAP value of δ^2H_f given the growing season δ^2H_p at the site of feather formation (Bowen et al. 2005), foraging guild, and migration distance in multiple species of birds.

To model the expected values of rosy-finch δ^2H_f in geographic space, we selected the estimated model parameters and residuals for ground-feeding, short-distance birds (i.e., neither resident nor long-distance Neotropical migrants; Hobson et al. 2012). We then generated spatial models of precipitation stable isotope values (isoscapes; Bowen et al. 2005, Vander Zanden et al. 2018; Appendix 1) reflecting the mean average δ^2H_p for the period that should reflect the bulk of the precipitation input to local ecosystems and, by extension, rosy-finch tissues. We selected the interval over which rosy-finches are known to molt (August–September; French 1959b), which also reflects an interval where we were confident even high-elevation alpine habitats would remain entirely within the growing season. Isoscapes were projected to an Albers Equal Area Conic and masked to a broad potential range for each species. We used eBird Status and Trends abundance maps (5.2 km resolution) accessed from the *ebirdst* R package (Fink et al. 2022, Strimas-Mackey et al. 2022) to generate species ranges for Black and Gray-crowned Rosy-Finches, which we generated as a 200 km buffered convex hull drawn around all points with nonzero relative abundance in breeding and non-breeding seasons. Finally, we transformed isoscapes from δ^2H_p to reflect the expected δ^2H_f of rosy-finch tissue using the estimated model parameters for each species.

Modeling probable origins of feather samples

We created probability-of-origin maps for each tissue sample using the isotopeAssignmentModel function of the R package *isocat* (v. 0.2.6; Campbell 2020, Campbell et al. 2020). This approach applies a Bayesian estimation of the mean probability of origin at a particular site given the measured stable hydrogen isotope value of a tissue sample, the modeled stable hydrogen isotope of precipitation at a site (isoscape), and the parameters of the first-order linear relationship representing the assimilation of stable hydrogen isotopes from precipitation into tissue. Additionally, the framework incorporates error associated both with the spatial modeling of the isoscape (site-specific standard error of the krigged model) and of the linear relationship (standard deviation of residuals), as described in Royle and Rubenstein (2004) and Bowen et al. (2014).

We incorporated an informative prior to this analysis in the form of temporally explicit abundance maps generated using seasonal and weekly eBird abundance maps (Fink et al. 2022). We considered the breeding-season abundance estimates for Black and Gray-crowned Rosy-Finches to be reasonable proxies of abundance during the period of feather formation. Because we expected that the likelihood of an individual sample originating in a cell to be similar among cells with moderate and high relative abundances of each species, we transformed the relative abundance surfaces to more general likelihood-of-origin surfaces: moderately downweighting regions with no or very low expected abundances, and minimally downweighting regions with moderate or greater than expected abundance. To do so, we smoothed the relative abundance surfaces with a logistic equation of abundance quantiles-essentially, slightly downweighting relative abundance values below the bottom quartile threshold toward 0 and relativizing values of higher quartile abundances to be more similar to one another (similar to Rushing et al. 2017). Empirically, we observed that this slightly down weighted some low-elevation breeding habitat, but did not eliminate any potential mountain peaks from subsequent analyses. We combined smoothed abundance surfaces with the isotope-based probability-of-origin maps as in Fournier et al. (2017) to produce 5.2 km resolution odds of origin surfaces for each individual.

Analysis and summary of probability-of-origin surfaces

For each individual sample, we summarized the likely distances traveled by measuring the shortest possible distances on an ellipsoid between the sampling site and each likely potential origin. We considered any location a “likely” origin if the probability-of-origin values exceeded a 2:1 odds ratio threshold (e.g., Hobson et al. 2009). We calculated the 5th, 25th, 50th, 75th, and 95th percentiles of potential distances traveled for each sample, effectively summarizing the probability distribution of likely distances traveled for each individual. We also estimated the general direction of movement between those sites as follows: we first calculated the minimum distance traveled as the shortest distance on an ellipsoid between the sampling location and the nearest origin over the 2:1 threshold. We report the bearing between the sample site and that location as the generalized direction of travel. We also summarized the overlap of likely origins with respect to breeding bird region (Bird Studies Canada and North American Bird Conservation Initiative 2014) and state for each individual sample. We then estimated expected abundance of breeding Black Rosy-Finch by summing the abundance estimates from Fink et al. (2022) within each geographic unit.

Migratory connectivity

We further used the probability-of-origin surfaces from feather samples to quantify the strength of migratory connectivity of each species. Migratory connectivity measures the degree to which individuals that co-occur during one period of the annual cycle remain close during subsequent periods (Cohen et al. 2018) and the strength of migratory connectivity (denoted MC) can vary from -1 to 1. MC values are typically > 0, with values close to 0 indicating weak connectivity (individuals that co-occur during one season tend to spread out and mix during subsequent periods) and values closer to 1 indicating strong connectivity (individuals that co-occur during one season remain close during subsequent periods). The MigConnectivity R package (version 0.4.2; Hostetler and Hallworth 2023) estimates MC from a variety of data types, including stable isotopes. Importantly, the package uses bootstrapping to account for uncertainty in the origin of each individual when calculating MC. Estimating MC requires dividing both the winter and breeding ranges into discrete regions. For both species, we treated each banding location as a separate region and used state/province boundaries to delineate breeding regions. Using political boundaries was used because we were interested in providing migratory connectivity information to state agencies interested in improving management decisions. Breeding regions were limited to states and provinces with known breeding populations (Black Rosy-Finches: Utah, Nevada, Idaho, Wyoming, and Montana; Gray-crowned Rosy-Finches: California, Washington, British Columbia, Alberta, Yukon, Northwest Territories, and Alaska). We also used the diffMC function from the MigConnectivity package to compare the strength of migratory connectivity between species.

All analyses were conducted in R (version 4.1.2 except when specified otherwise). The stable isotope measurements, R code, and package version details are available at https://github.com/cjcampbell/RosyFinchesdD and at https://doi.org/10.5281/zenodo.14035945. Beyond the packages referenced above, we relied particularly on the R packages tidyverse (Wickham et al. 2019), raster (Hijmans 2020), and terra (Hijmans 2022).

RESULTS

From 15 April through 1 May in 2020 and 20 January through 30 April in 2021, we collected and analyzed feather samples from 38 Black Rosy-Finches (18 female, 19 male, and 1 unknown sex) and 37 Gray-crowned Rosy-Finches (14 female, 22 male, and one unknown sex; Table 1). Stable hydrogen isotope values of feather samples from Black Rosy-Finches ranged -113.71‰ to -37.03‰. Feather samples from Gray-crowned Rosy-Finches were on average lower, ranging from -152.15‰ to -95.24‰. Stable hydrogen isotope values did not differ between male and female Black Rosy-Finches (*t*(33.79) = 0.59, p = 0.56, n = 37, 95% CI = [-15, 8.5]).

Table 1. Number of feather samples collected for stable hydrogen isotope analysis by species, site, and sex.

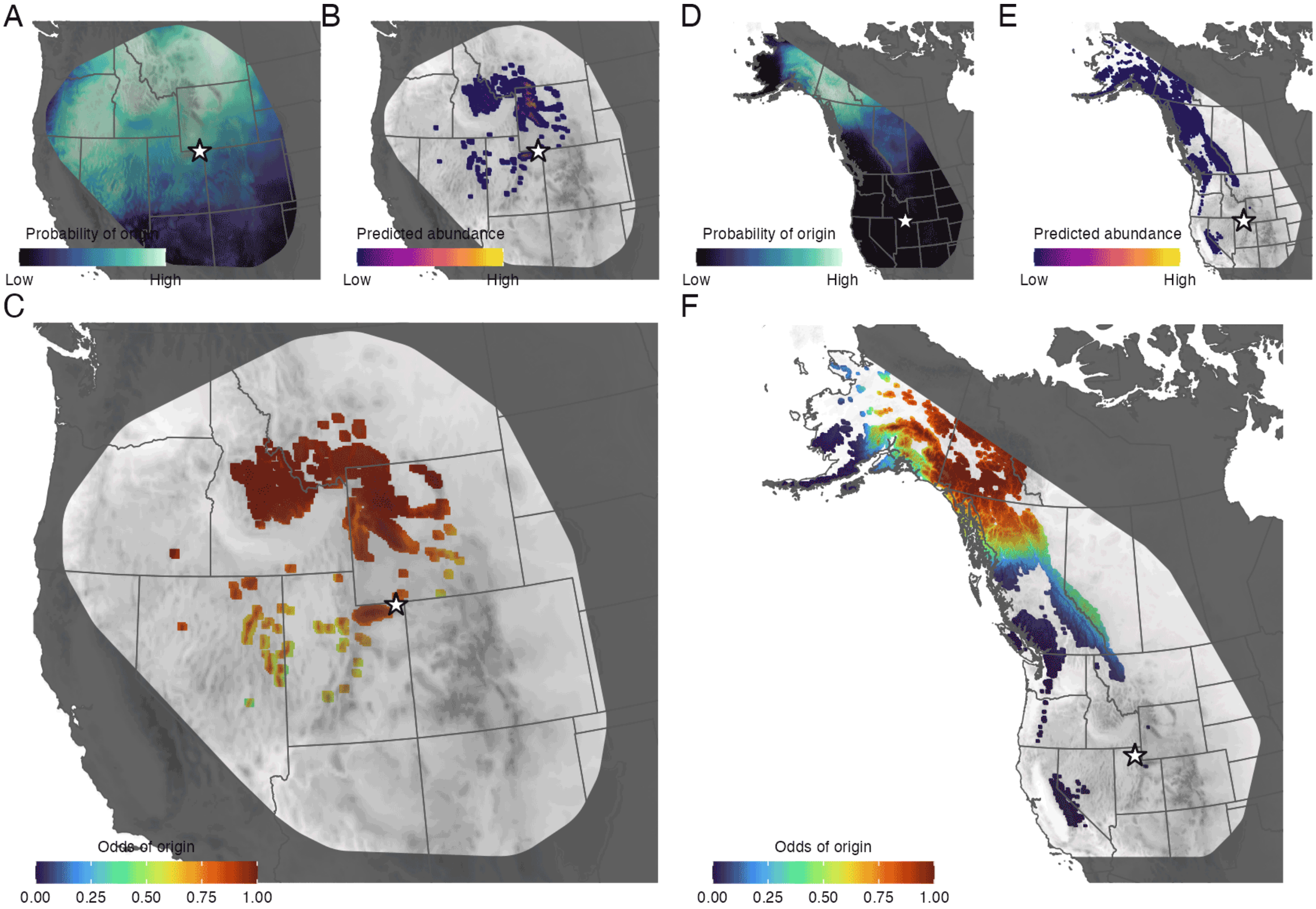
Species	Site	Sex		
		Female	Male	Unknown
Black Rosy-Finch	Alta	7	7	1
	Dutch John	10	10	0
	Powder Mountain	1	2	0
Subtotal		18	19	1
Gray-crowned Rosy-Finch	Alta	1	1	0
	Dutch John	0	0	0
	Powder Mountain	13	21	1
Subtotal		14	22	1

The modeled relationship between each individual rosy-finch, adjusted to the VSMOW-SLAP reference scale, was $\delta^2H_f = (0.722)\,\delta^2H_p - 10.334$ (standard deviation of residuals = 17.57). We then used the feather isoscapes and deviation of residuals to generate probability-of-origin maps for each individual, which were then combined with eBird breeding abundance maps. Figure 2 illustrates the origins of the individual with the median δ^2H_f value for each species. The predicted breeding abundance for each species is highlighted in Figure 2B and 1D; for Black Rosy-Finches, it was highest in the Sawtooth Mountains of central Idaho; the Beartooth Mountains of southwestern Montana; the Absaroka, Wind River, and Teton Mountains of Wyoming; and the Uinta Mountains of Utah (Fig. 2B). For Gray-crowned Rosy-Finches, predicted abundance was highest in the coastal and interior mountain ranges of Alaska, the Yukon Territory, and British Columbia (Fig. 2F). Incorporating smoothed breeding abundance significantly refined the region of likely origin for each species relative to stable hydrogen markers alone.

The 5th and 95th percentiles of likely distances traveled by Black Rosy-Finches ranged 68–658 km (Fig. 3A), with the 50th percentile estimates ranging 343–507 km (the median 50th percentile distance was 428 km, with a standard deviation of 40 km, across all samples). For Gray-crowned Rosy-Finches, the 5th and 95th percentiles ranged 980–3777 km (Fig. 3B). The 50th percentile estimates ranged 2329–2788 km (median 2688 km, standard deviation 77 km). Most (78.9%, n = 30) of Black Rosy-Finches had mean directions of travel clearly north of the sample site (i.e., between the northwest and the northeast, bearings -45° – 45°). Five individuals had mean directions of origin west of the sampling location (bearings -135° – -45°), with the remaining three individuals having mean likely origins to the south or east (bearings -135° – -180° and 45° – 180°). All Gray-Crowned Rosy-Finches had mean likely origins north of their sampling locations (bearings -45° – 45°).

Black Rosy-Finches origins overlapped with the Northern Rockies, Great Basin, Colorado Plateau, and Badlands and Prairies Bird Conservation Regions (Bird Studies Canada and North American Bird Conservation Initiative 2014), as well as the states of Montana, Idaho, Utah, and Wyoming, and Utah. Four individuals had likely origins that fell almost entirely within the Northern Rockies (bottom four rows of Fig. 4B), with > 90% of likely origins overlapping with the state of Montana (bottom four rows of Fig. 4D). Four different individuals had high probabilities of origin overlapping with the Colorado Plateau and the Great Basin (top rows of Fig. 4B), reflecting origins likely in Utah or Nevada (top four rows of Fig. 4D). These individuals also represented generally westerly and southerly origins in the direction model (Fig. 3B). The remaining 30 Black Rosy-Finches had likely origins that overlapped the most with the Northern Rockies, but with varying levels of overlap with the Colorado Plateau and Great Basin that prevent confident assignment to one

Fig. 2. A representative workflow for combining δ²H-based origin maps with eBird abundance maps, here illustrated with two example individual rosy-finches. At left, panels A-C show an example assignment for a Black Rosy-Finch (*Leucosticte atrata*) feather; at right, panels D-F show the same for a Gray-crowned Rosy-Finch (*Leucosticte tephrocotis*) feather. Panels A and D show a δ²H-based assignments only, with lighter areas representing regions of higher probability of origin; panels B and E show eBird abundance maps for the breeding season (24 May–27 July; Fink et al. 2022). The bottom row, containing panels C and F, show the results of the combined models, wherein the δ²H-derived surface was combined with a smoothed eBird abundance surface, representing combined likelihood of origins. The white stars indicate sample location for each individual.



region or another. Their likely origins also overlapped with four to five states, also preventing confident assignment to a particular one. Gray-Crowned Rosy-Finch feathers broadly reflected likely origins restricted to states and provinces contained in their breeding range: Alaska, Yukon, British Columbia, and Alberta (Appendix 2).

The strength of migratory connectivity was relatively low in both species. For Black Rosy-Finches, MC was 0.14 (95% confidence interval: 0.03–0.38) while in Gray-crowned Rosy-Finches MC was 0.15 (0.003–0.51). Comparison of MC values from each species revealed no significant difference in the strength of connectivity (-0.018, 95% CI: -0.42–0.28).

DISCUSSION

Stable hydrogen isotope analysis showed that northern Utah's wintering Black Rosy-Finches travel hundreds of kilometers and are not making local altitudinal migrations downslope from their breeding sites. The birds in our study have the highest probabilities of breeding and molting origins that correspond to mountain ranges in Idaho, Wyoming, and Montana (Fig. 4C, D) and, on average, travel 428 km between their breeding and non-breeding ranges. Overall migratory connectivity was low, indicating that Rosy-Finches may mix spatially between breeding and non-breeding sites and highlighting the presence of latitudinal (as opposed to strictly elevational) migration.

Northern Utah contains suitable breeding and non-breeding habitat for Black Rosy-Finches, however the birds sampled in this study do not appear to represent the local breeding population. The Uinta Mountains, located within 40 km west of Dutch John, contains the largest continuous area of Black Rosy-Finches breeding habitat in the state (Paprocki and Pope 2019, Fink et al. 2022). Black Rosy-Finches also breed in the Central Wasatch Mountains, and occupied breeding habitat that occurs within 2 km from the Alta research site (Farr et al. 2017, Fink et al. 2022). However, only four Black Rosy-Finches sampled in this study showed a > 0.50 probability of Utah origins (Fig. 4C, D), and the

Fig. 3. A summary of distance and direction of travel results for feathers analyzed in this study. The top row (panels A-B) show results for Black Rosy-Finch (*Leucosticte atrata*) feathers (n = 38); the bottom (panels C-D) for Gray-crowned Rosy-Finch (*Leucosticte tephrocotis*; GCRF, n = 29); Hepburn's subspecies (GCRF-Hep., n = 8) are highlighted in yellow. Panels A and C show the ranges of potential distances traveled by individual rosy-finches (each row being an individual, arranged by increasing δ^2H_f values). Lines indicate the range between the 5th and 95th distance percentiles in a probability-weighted sampling of potential origins; boxes 25th to 75th; and dark circles 50th. Panels B and D show radial histograms representing the likely northerly direction of origin for all rosy-finch feather samples relative to the sample site (star), with the horizontal axis representing the mean bearing of potential origins in a 10000-fold sampling of potential origins, weighted by probability of origin; the vertical axis indicates number of individuals with mean bearings falling within an 22.5-degree bin.

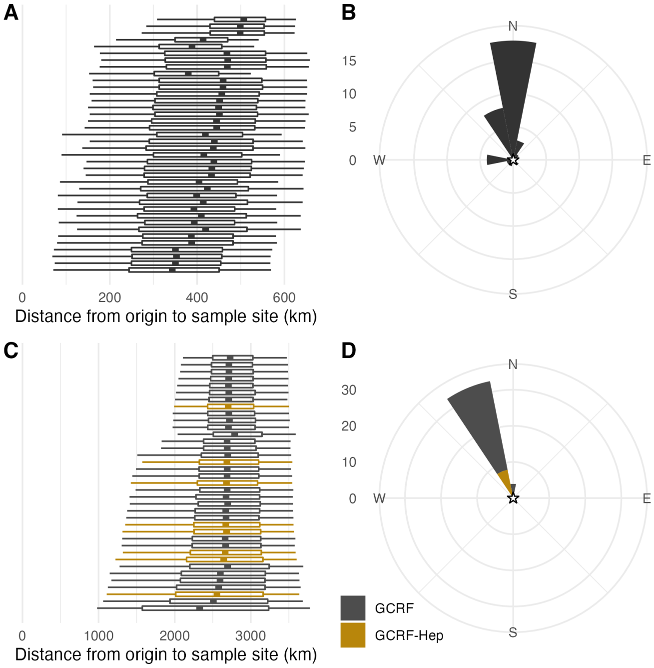
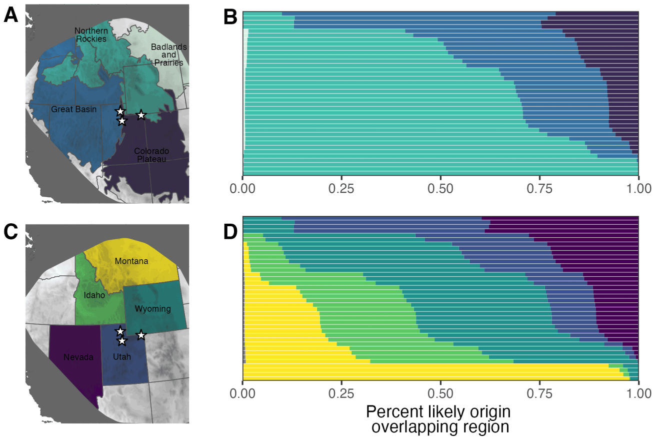


Fig. 4. A summary of likely regions of origin for Black Rosy-Finch (*Leucosticte atrata*) feathers analyzed in this study. The top row shows the proportions by which each feather samples' abundance-weighted likely origin (panel B) overlaps North American Bird Conservation Initiative's Bird Conservation Regions (mapped in panel A; Bird Studies Canada and North American Bird Conservation Initiative 2014). As above, each row represents an individual, arranged by increasing δ^2H_f values. In the bottom row, likely origins (panel D) are mapped over U.S. states (panel C).



lowest potential (between the 5th and 95th distance percentiles) distance traveled by Black Rosy-Finches was approximately 75 km. There were also few easterly or westerly origin probabilities that would correspond to potential movement between the Alta and Dutch John research sites and the Uinta Mountains. Black Rosy-Finches have been observed in the winter at lower elevation sites adjacent to high elevation breeding sites throughout much of their range, as well as habitats in desert regions in northern Arizona and New Mexico, which are at a minimum 400 km from the nearest breeding location (Paprocki and Pope 2019, Fink et al. 2022). Thus, there are likely both local (elevational) and short distance (regional) migratory individuals or populations of Black Rosy-Finches. Occupied Black Rosy-Finch breeding habitat occurs within close proximity to our winter study sites, however few samples had high probability of origins from Utah, suggesting those birds wintering in Utah are regional migrants.

Our results suggested a predominately southern migratory route between breeding and non-breeding habitats of sampled Black Rosy-Finches. If Black Rosy-Finches across their range follow a similar pattern, Utah's breeding population may overwinter in the southern and central portions of Utah or northern Arizona, where they are known to use lower-elevation rangelands across these areas (Fink et al. 2022). Encounter rates of rosy-finches in these areas are low and likely limited by both lower observation effort as well as low occupancy and abundance in such expansive habitats. Additionally, few bird feeders exist in these areas and rosy-finches in these low elevation and desert habitats tend to exhibit higher tendency toward nomadic behaviors. These factors make such individuals difficult to locate and present additional challenges to capture and study.

Our findings of Black Rosy-Finch geographic origins broadly align with the species-wide estimated breeding bird abundances of Fink et al. (2022), supporting our findings of broad mixing / low connectivity in the sampled population. Of our sampled Black Rosy-Finches, 89% (34 of 38) had origins that most likely reflected origins with the Northern Rockies bird conservation region (Fig. 1). The proportion of the breeding Black Rosy-Finch population found in that region is 83%. The remaining 11% (4 of 34) individuals had origins that most likely reflected likely origins in the Great Basin or Colorado Plateau, which collectively represent an expected 17% of the breeding population. This generally supports our findings that the sampled population of

Black Rosy-Finches in Utah are unlikely to reflect a local population of altitudinal migrants, but more likely reflects the range-wide migratory patterns of the species.

Although we sampled all Black Rosy-Finch individuals captured at our study sites, our results may not reflect the full diversity of migratory strategies within individuals wintering in Utah or within Black Rosy-Finches more generally. Birds that bred in close proximity to our sampling sites may have been present during the winter period and not captured. This study was also limited to samples of rosy-finches that were wintering at high elevation sites, and we did not target individuals in flocks at locally lower elevations. These individuals may have been mixing with those we targeted at higher elevations, but may have represented a different segment of the local wintering population.

Our findings that Utah contains non-breeding habitat for Black Rosy-Finches that appear to breed primarily in Idaho, Wyoming, and Montana (Fig. 1) underscore the importance of coordinating conservation and management of this species across the full annual and geographic cycle of this species. To date, wildlife researchers and managers of Black Rosy-Finches have been less focused on non-breeding habitats, as the impacts of climate change on the alpine habitats used during the breeding season are considered a primary threat (Utah Wildlife Action Plan Joint Team 2015, Rosenberg et al. 2016, Idaho Department of Fish and Game 2017, Wyoming Game and Fish Department 2017, Nevada Department of Wildlife 2022). There is a disproportionate rate of temperature increase in the alpine that has cascading effects on hydrology, vegetation, and wildlife (Mountain Research Initiative EDW Working Group 2015, Hotaling et al. 2024). In the Brown-capped Rosy-Finch (*Leucosticte australis*), strong predictors of suitable breeding habitat include how much precipitation falls as snow and the average temperature of the warmest month (DeSaix et al. 2022). Direct effects, including loss of alpine habitat due to tree line encroachment (Formica et al. 2014, Scharnagl et al. 2019, Verrall and Pickering 2020) may threaten Rosy-Finches as global temperatures warm.

In identifying the locations where Black Rosy-Finches winter and breed, we can focus potential collaborative conservation efforts with important states and land management agencies across the annual cycle. The Rosy-Finch Working Group (Gardner 2022) used Structured Decision Making (Rushing et al. 2020, Smith 2020) to prioritize research based on management actions that could improve rosy-finch abundance and survival. Management actions that could improve abundance and survival during the non-breeding season include restoring wild seed-producing vegetation in wintering habitats, protecting winter roost sites (e.g., caves, cliffs, buildings), and ensuring the conditions at bird feeders are not negatively impacting birds (Gardner 2022). During the breeding season, priority actions are responding to tree line advancement in the alpine, ceasing trout stocking in alpine lakes, and restoring important seed bearing plants in the alpine.

Using stable hydrogen isotope analysis, we demonstrated that Gray-crowned Rosy-Finch had higher probability of origin in northern latitudes of Alaska, Alberta, British Columbia, and Yukon (Fig. 2D, F). These results support the use of stable hydrogen isotope analysis for understanding the origins of rosy-finch species. However, stable hydrogen isotope analysis cannot provide precise origins for these species. The continental isoscape for hydrogen isotopes provides broad latitudinal clines, but has much poorer longitudinal resolution (Bowen et al. 2005), often resulting in broad geographic assignments of origin (Wunder et al. 2005). Isoscapes in high-relief terrain, like the mountain ranges in this study, also have poorer resolution (Clark and Friz 1997). There are methods available that may increase precision when assigning geographic origins of rosy-finch feathers. Analyzing feather samples with known origins can improve the accuracy of the geographic assignment models (Tonra et al. 2015, Reese et al. 2019). Similar to Reese et al. (2019) and Rushing et al. (2017), we found utility in refining isoscape boundaries using eBird distribution mapping products (Fink et al. 2022).

This study underscores that managers and stakeholders from different management units must coordinate conservation and tracking efforts to conserve the Black Rosy-Finch as its alpine breeding habitat is expected to shrink and degrade with ongoing climate change. The United States Forest Service has management authority on nearly all of the alpine habitat where Black Rosy-Finch breed. Conversely, during the non-breeding season, Black Rosy-Finches can be found on nearly every land ownership type in the region. Given that we found this species migrates regionally, interventions benefiting a local non-breeding population might not bestow corresponding benefits on a nearby breeding population. Future research expanding our understanding of rosy-finch migration ecology under the context of potential management actions (Gardner 2022), as well as targeting populations that may be particularly vulnerable to warming temperatures, is needed.

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All research activities were performed under protocols approved by Utah State University's Animal Care and Use Committee of the authors' institution, permitted by the relevant federal and state authorities (U.S. Geological Survey banding permits 21673 and 24181), and in compliance with the Guidelines to the Use of Wild Birds in Research (Fair et al. 2023).

Data Availability:

https://github.com/cjcampbell/RosyFinchesdD

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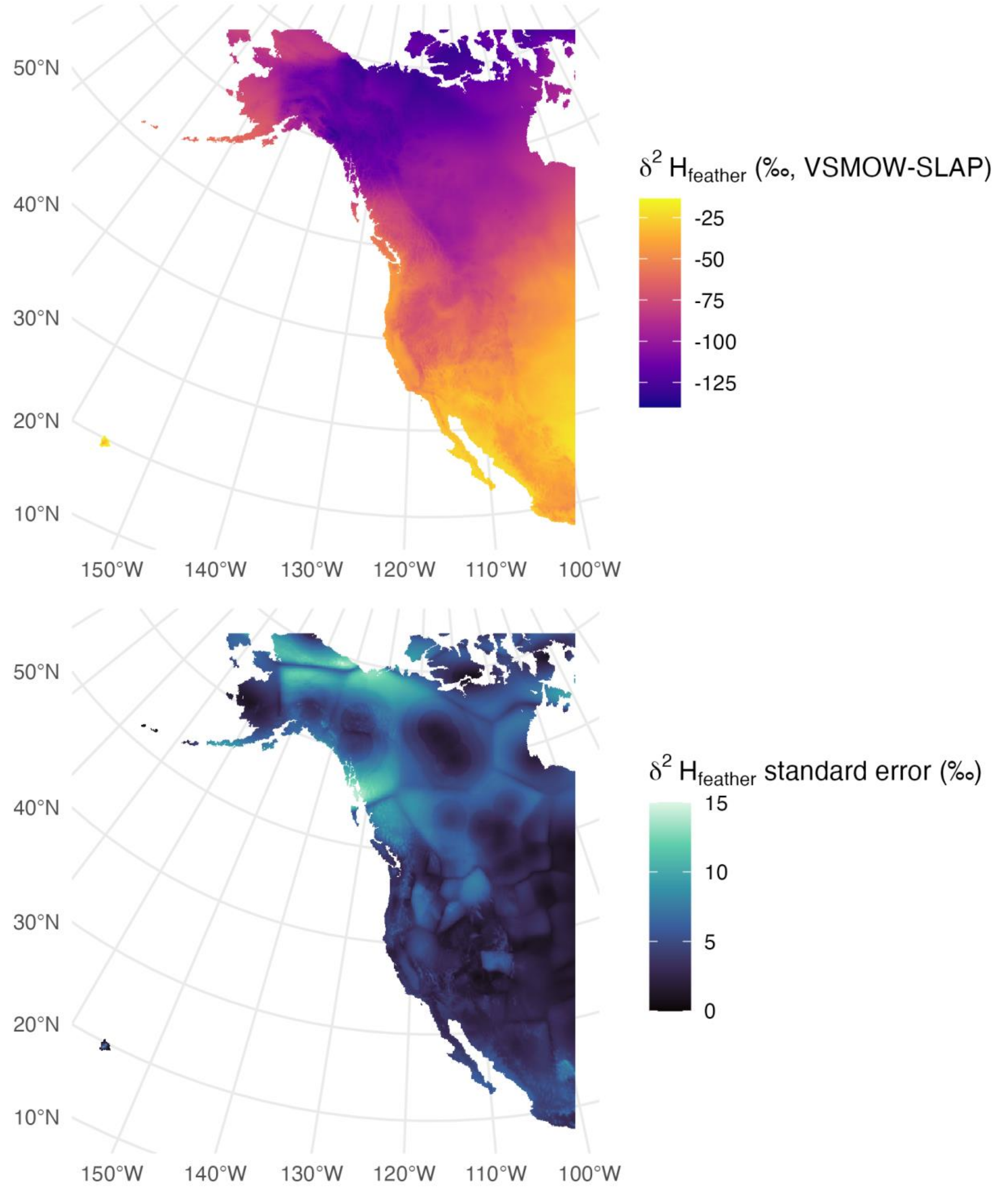
Appendix 1. The selected feather isoscape and isoscape standard error.



Appendix 2. Gray-crowned rosy-finch likely origins.