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Original Research Article

Partial migration of White-winged snowfinches is correlated with winter weather conditions

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ABSTRACT

Seasonal movements are a response to variability in resource availability and result from a complex interaction between the behavioral and physiological traits of a species and its prevailing environment. A widespread bird migration strategy is partial latitudinal migration, where some proportion of the population moves from breeding to winter grounds, while the remaining individuals stay year-round on the breeding grounds. Deciphering how and why some individuals migrate while others stay is essential to understanding population and community structure and dynamics. Little is known about the drivers of partial migration strategies of high-mountain birds that are subjected to strong seasonal environmental fluctuations and count among the species most threatened by climate change. In this study, we investigated the migratory pattern of an alpine songbird, the White-winged Snowfinch (*Montifringilla nivalis nivalis*), through the analysis of stable hydrogen isotopes of feathers (δ^2H_f), and how it relates to weather factors. First, values of δ^2H_f were used to assess the probability that snowfinches wintering in the Spanish Pyrenees and Cantabrian Mountains have a breeding origin in the Alps. Second, we analysed whether winter weather conditions (ambient temperature and precipitation) in the Alps may play a role in migratory movements towards the southern wintering grounds. Overall, ca 98% and 86% of the individuals sampled in winter in the Spanish Pyrenees and Cantabrian Mountains, respectively, were likely to originate from breeding populations in the Alps. Snowfinches also had a higher propensity for large-scale movements to the South in winters where the average monthly temperature was particularly low in the Alps, typically $< -2\,^{\circ}C$ (i.e., in the 42% coldest winters). Our results suggest that snowfinches adopt a partial migratory strategy, with different patterns among and within populations that have important implications in terms of population connectivity, spatio-temporal dynamics and structuring. Considering the role of cold winter conditions in migration propensity of

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snowfinches, there is a risk of increased isolation of the southern populations under a scenario of global warming, insofar as the hypothetical settling of winter immigrants could no longer contribute to a demo-genetic rescue. Future research should decipher how these risks affect alpine species that are particularly exposed to climatic shifts, and how they adapt and evolve.

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1. Introduction

Animal migration consists of spatial movements that result from a complex interaction between the behavioral and physiological traits of a species and its prevailing environment (Newton, 2008). Migration is defined as a movement between geographically distant breeding and non-breeding areas that aims at tracking seasonally fluctuating environmental conditions, in particular food supplies, year-round (Berthold, 2001; Newton, 2008). Different factors such as age, sex, habitat quality, risk of predation or weather conditions may influence animal migration strategies (Berthold, 2001; Webster et al., 2002), which can differ not only among species (Chapman et al., 2011) but also between populations (Newton, 2008). Alpine populations can exhibit both latitudinal or elevational migration in order to moderate environmental stressors. Whereas latitudinal migration involves individuals moving relatively long distances from breeding to wintering grounds, elevational migration is often a very short distance movement along mountain slopes and can occur many times throughout the year in response to inclement weather and the strong inherent seasonality of these environments (Borras et al., 2010; Boyle, 2017; Hsiung et al., 2018; Newton, 2008).

A widespread migration strategy is partial latitudinal migration, where only a proportion of a population migrates from breeding to wintering grounds, whereas another subset remains in or next to the breeding areas throughout the year (Chapman et al., 2011; Newton, 2008). Partial latitudinal migration can be obligate (i.e., a specific proportion of individuals migrates every year), or irruptive/facultative (i.e., migration only occurs some years depending on prevailing environmental conditions on the breeding grounds). In obligate partial migration, the migratory strategy seems to be under endogenous control (Berthold and Helbig, 1992), with individuals from any given population adopting the same strategy (staying or migrating) every year. In irruptive or facultative partial migration, individuals may stay or migrate according to directly perceived environmental conditions at the time (Watts et al., 2018; Borras et al., 2010; Boyle, 2017; Newton, 2008).

Migration strategies ultimately affect individual survival and reproduction (Chapman et al., 2011; Fudickar et al., 2013). Therefore, determining how and why animals migrate within their range is fundamental to a deeper understanding of population and community structures and dynamics (Morales et al., 2010). High mountain ecosystems are subject to strong seasonal fluctuations (Lloret, 2017) and species inhabiting such challenging environments have evolved complex life-history strategies to cope with extreme abiotic conditions (Hille and Cooper, 2015). For instance, some alpine animal populations remain as high as possible close to the breeding grounds for the competitive advantage of arriving and breeding earlier the following year (Winger et al., 2019), moving to wintering areas or lowlands only in the case of extreme disruption of food resources (Watts et al., 2018). Weather can indeed strongly impact food availability in these environments (e.g. while precipitation and temperature influence insect activity and abundance, snow and ice may cover seeds) and thus trigger large-scale movements (Mittelhauser et al., 2012). Therefore, in high mountain ecosystems, animal migration strategies may form a continuum from obligate to irruptive migratory movement behaviours that, together with elevational movements, may enhance the capability of individuals, populations and species to cope with seasonally varying environments (Fudickar et al., 2013; Newton, 2008; Reid et al., 2018).

Despite the information accrued from bird ringing and species monitoring programs, bird movement strategies in high mountain ecosystems remain poorly documented. Indeed, high elevations can be important over-wintering sites for short-distance migrants, as well as migration corridors and refueling sites for long-distance migrants (Boyle and Martin, 2015). Yet, little is known about how weather factors may influence the movements of alpine species (Laplante et al., 2019; Macdonald et al., 2016). This is particularly important since alpine ecosystems are forecasted to be among the most impacted by climate change, with temperature warming being double of what is estimated globally (Brunetti et al., 2009). The analysis of the stable hydrogen isotope ratios of feathers (δ^2H_f) has proven to be a useful tool for investigating the breeding origins of latitudinal and elevational migrants (Boyle et al., 2011; Hobson et al., 2003). This is facilitated by continental-scale gradients from lower δ^2H values in precipitation and surface waters with higher latitudes and elevations, which is transferred through the foodweb into animal tissues (Hobson, 2011). Metabolically inert tissues, such as feathers, integrate and maintain the hydrogen isotopic composition of the environment where they were grown (Rubenstein and Hobson, 2004). For most migratory bird species, the timing and extent of moulting is sufficiently well described (Jenni and Winkler, 1994) that the analysis of δ^2H_f values in targeted feathers may allow individuals to be assigned probabilistically to the regions where their feathers were grown, relative to their breeding grounds (Cardador et al., 2015; Rubenstein and Hobson, 2004). In recent years, a few studies analyzing δ^2H_f have elucidated seasonal elevational movements in both temperate and tropical bird species that would have been difficult to assess by conventional methods (Boyle et al., 2011; Gadek et al., 2018; Hobson et al., 2003). In the Western Palearctic, even fewer studies have investigated the applicability of δ^2H_f for the assessment of mountain songbird

migratory movements (but see Arizaga et al., 2015; Resano-Mayor et al., 2017). Compared with conventional migratory tracking methods, the analysis of δ^2H_f presents the advantage that an individual only needs to be captured and sampled once (Hobson, 2011).

Here, we investigated the migratory movement patterns of an emblematic songbird of high-alpine European ecosystems, the White-winged Snowfinch (*Montifringilla nivalis nivalis*; hereafter snowfinch), through the analysis of δ^2H_f. We aimed to elucidate whether snowfinches wintering on their southwesternmost European grounds (i.e., Spanish Pyrenees and the Cantabrian Mountains) may originate from breeding grounds in the Alps. More specifically, we investigated whether δ^2H_f measured in the most outer rectrices differed between breeding grounds in the Swiss Alps and those in other southwestern European populations such as the Spanish Pyrenees, Cantabrian Mountains and Italian central Apennines. Due to the general pattern of lower δ^2H with increasing latitude and elevation, we predicted that breeding individuals in the Swiss Alps should have distinctively lower δ^2H_f compared to those in the southwestern breeding populations. In addition, we assessed the pattern of δ^2H_f in several wintering populations and estimated the proportion of wintering birds with a high probability of having a breeding origin in the Alps. Finally, we investigated the extent to which weather factors, such as winter ambient temperature and precipitation in the Swiss alpine region might correlate with southward movement of snowfinches breeding in the Alps. We predicted that under harsh wintering weather conditions (lower temperature and greater snowfall) in the Alps, a greater proportion of the snowfinch breeding population in this mountain region would exhibit southward migration.

2. Materials and methods

2.1. The species

The snowfinch is an emblematic, high-alpine bird. In Western Europe, the subspecies *M. n. nivalis* has a patchy breeding distribution, ranging from the Cantabrian Mountains in northwestern Spain, through the Pyrenees, the Alps, Corsica and the Apennines east to northern Greece (Brambilla et al., 2020; Cramp and Perrins, 1994). Snowfinch occurs above the tree-line, in barren rocky habitat interspersed with grasslands. During the breeding season (May–August), it commonly forages on invertebrates next to patches of melting snow (Bettega et al., 2020; Resano-Mayor et al., 2019; Strinella, 2007). Snowfinch breeds in cliffs, buildings and skilift pylons. After fledging, family groups gather in large flocks, ascending above breeding grounds up to glaciers. They move to lower elevations with first snow falls (Cramp and Perrins, 1994). The species has long been considered as resident in Europe with only elevational downward movements depending on weather severity (Géroudet and Cousin, 1998); yet, individuals have been sighted in winter a few hundred kilometers away from their breeding grounds (Cramp and Perrins, 1994) and the origin of these birds has long remained a mystery. For instance, the French Central Massif, situated midway between the Alps and the Pyrenees, is regularly visited in winter (Cheylan, 1973), suggesting that birds from the Alps may move south towards the Pyrenees (Albouy and Riols, 2018). A few ring recoveries in the Spanish Pyrenees have established that some snowfinches wintering in Spain actually come from the Alps (Resano-Mayor et al., 2017). Nonetheless, the magnitude and frequency of this partial latitudinal migration is still poorly understood, especially given the limited ringing effort deployed so far in the difficult mountainous terrain and often adverse weather conditions.

2.2. Study sites and feather collection

Between 2006 and 2018, we collected primary and tail feathers from 382 snowfinches in four populations across Western Europe (Fig. 1). Between May and August, we captured and sampled 109 individuals on their breeding grounds in the Cantabrian Mountains (CM, northwestern Spain; $n = 63$, 1800–2100 m a.s.l), Spanish Pyrenees (SP, northern Spain; $n = 8$, 2500 m), Swiss Alps (SA, southwestern Switzerland; $n = 27$, 2200–2800 m) and Italian central Apennines (AP; $n = 11$, 2200 m). Individuals were mist-netted either on passes, while commuting from their foraging grounds to nesting cliffs (CM and SP), or next to breeding sites in buildings and skilift pylons (SA), and near nestboxes (AP). All winter captures (January–March; $n = 273$) resulted from mist-netting (CM: $n = 9$, 1400 m; SA: $n = 100$, 1500 m) or whoosh-netting (SP: $n = 164$, 1850 m) at foraging sites, often next to artificial seed feeders. Every individual was ringed and we collected either the innermost primary (wing feather P1; $n = 227$) or the outermost rectrice (tail feather R6; $n = 244$) for subsequent isotopic analysis. Feathers were stored in sealed plastic or paper bags at −20 °C until analysed. From 89 individuals we collected both a P1 and a R6 each to run tests of variation in δ^2H_f between primaries and rectrices. As the difference in δ^2H_f values between the SA population and all other populations was more pronounced for R6 than P1, we conducted all the analyses with rectrix material (Supporting Information Fig. S1 and Table S1). The reason is probably that snowfinches moult their R6 later in the season (generally, September to October) than P1 (July to August, Strinella et al., 2011; Winkler and Winkler, 1985), typically when social flocks aggregate at the highest elevations. Indeed, in the Alps, these late summer gatherings can take place at much higher elevation than in the other mountain massifs investigated because the Alps are much higher, potentially leading to more negative δ^2H_f.

2.3. Stable isotope analysis

A total of 471 feathers (including both P1 and R6) were prepared and analysed for δ^2H following standard procedures. All samples were cleaned using a 2:1 chloroform-methanol solvent soak (24 h) and rinsed, followed by drying in a fume

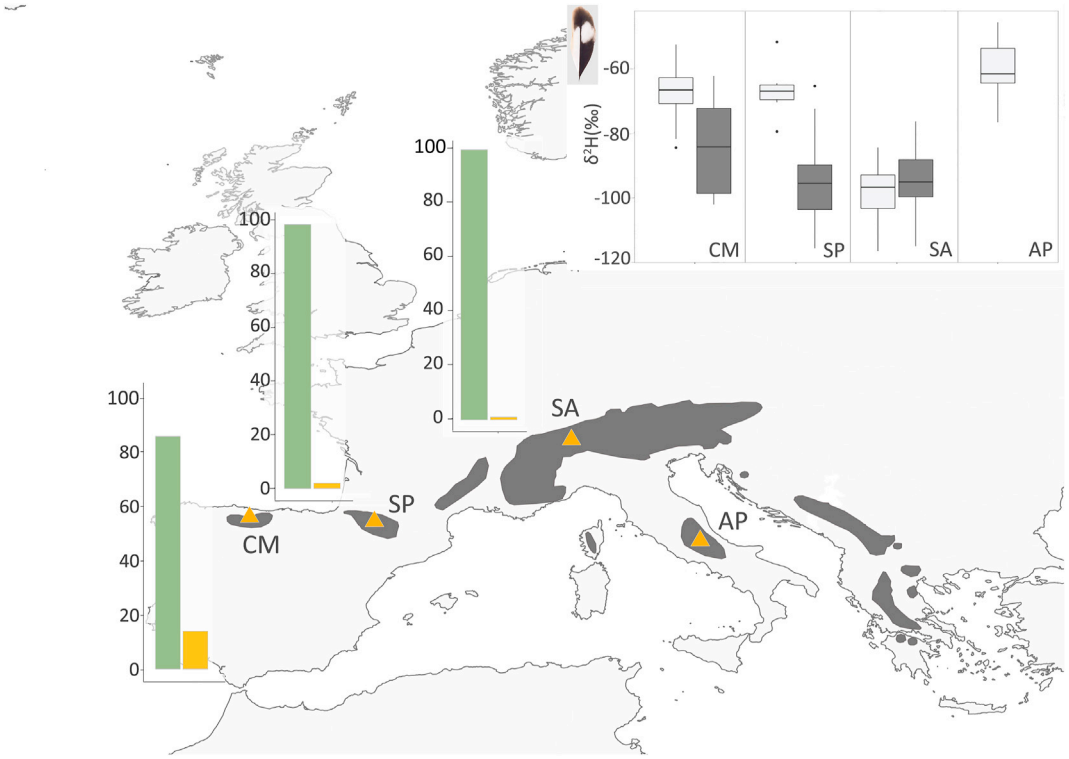

Fig. 1. Distribution (grey shaded area) of the subspecies *Montifringilla nivalis nivalis* (Birdlife International, 2017). Monitored snowfinch breeding populations (orange triangles) in the Cantabrian Mountains (CM), Spanish Pyrenees (SP), Swiss Alps (SA) and Italian central Apennines (AP). The investigated wintering populations are in CM, eastern SP and SA. Insert: differences in δ^2H_f values of rectrices per population during the breeding (light grey boxes) and wintering (dark grey boxes) seasons. The bar charts show the probability of a breeding origin from the Alps (green bar) or other than the Alps (orange bar) for wintering birds sampled at CM, SP and SA. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hood for 48 h. We corrected for "exchangeable" hydrogen by conducting δ^2H analyses with the comparative equilibration method described by Wassenaar and Hobson (2003), thus using three calibrated keratin hydrogen isotope reference materials (CBS:- 197‰, SPK:- 121‰, KHS:- 54.1‰). Approximately 0.35 mg of feather material was weighed into a silver cup, crushed, and then loaded into a zero-blank carousel. Pyrolytic combustion of samples under helium flow (1350 °C) produced H_2 gas that was separated in an elemental analyser (Eurovector, Milan, Italy) and analysed using continuous-flow isotope-ratio mass spectrometry (Isoprime, Manchester, UK). Isotope measurements are expressed in the delta (δ) notation as parts per thousand (‰) relative to Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP). Within-run analytical precision was estimated to be ±2‰ based on 5 replicate measurements from each of the three keratin reference standards for every 84 sample unknowns. Measurements of δ^2H were performed at the National Hydrology Research Centre of Environment Canada in Saskatoon, Canada. Note that for individuals captured at artificial feeders during the winter, supplemental feeding would not influence isotope measurements because feather growth was already completed.

2.4. Weather data

To test the hypothesis that the movements of snowfinches from the Alps to SP in winter might correlate with the prevailing winter weather conditions in the Alps in a given year, we correlated our proxy for an apparent yearly influx of snowfinches from the Alps into SP with mean monthly ambient temperature (°C) and monthly total precipitation (mm) in SA and in SP, recorded from October to March 2004–2015 (for SA: MeteoSwiss, data were averaged from n = 24 weather stations, 1300–2300 m a.s.l., Fig. S2; for SP: AEMET, data averaged from n = 11 weather stations, 1300–2300 m a.s.l.).

2.5. Statistical analysis

To investigate the differences in δ^2H_f between breeding populations, we performed a linear regression model, including δ^2H_f as the response variable and two predictors, population and season, as well as their interaction. Note that the AP

population could not be included in this model because it lacked data for wintering birds. Once we generated sets of competing models, we applied the Akaike information criterion (AIC), using the values of $\Delta AIC < 2$ as the criterion for selecting the most parsimonious models (Burnham and Anderson, 2002). Following standard procedures, we calculated the Akaike weight for each candidate model (*wi*) as the relative strength of evidence, i.e., the probability of model *i* being the best-approximating model from the entire set of candidate models, and evidence ratios of the best models as the ratio of model weights.

The previous linear regression model showed that δ^2H_f differed between SA and the other breeding populations to an extent that allowed us to estimate the proportion of individuals captured on the wintering grounds in CM, SP and even SA having a breeding origin in the Alps. To do so, we used a finite mixture model for the stable isotope measures y_i. We defined the likelihood $p(y_i|\lambda) = \lambda * Normal(-98.11, 8.70) + (1-\lambda) * Normal(-67.05, 7.79)$, where λ is the proportion of birds originating from the Alps. The first normal density function is defined by the mean and standard deviation of the stable isotope measurements of the breeding population in the Alps and the second one by the combined measurements from the Pyrenees and the Cantabrian Mountains. We fitted the model to each data from the three mountains (Cantabrian, Pyrenees and Alps) separately by Hamiltonian Monte Carlo as implemented in Stan (Carpenter et al., 2017) using the R-interface rstan (Stan Development Team, 2019). We simulated 4 chains with 4000 iterations of which the last 2000 were used to describe the posterior distribution of λ. We assessed convergence by diagnostic statistics and graphical exploration of the Markov chains using shinystan (Gabry, 2018).

To test whether harsh winter weather conditions in the Alps may be associated with more snowfinches moving from the Alps to SP, we used bird ringing data obtained at one station in the Pyrenees from 2005 to 2015 (Supporting Information Table S2). We first performed a logistic regression where the response variable was binary: 1 meaning snowfinches were captured during a single capturing attempt in the Pyrenees, and 0 meaning no capture, in relation to the weather conditions in the Swiss Alps and in the Pyrenees (i.e., mean temperature and mean precipitation) during the two months preceding each capture attempt. We also modelled weather conditions during the three preceding months, but the results did not qualitatively differ (Table S3). Correlations between monthly mean temperature and total precipitation, both in the Alps and in the SP, and over the years, are shown in Supporting Information (Fig. S3). Based on field observations, we assumed that the probability of snowfinch capture is a good measure of snowfinch presence/absence at this particular wintering site (in most cases when snowfinches were not captured, they were also not observed), which was visited regularly and under different weather conditions. As a second step, we built a further model, in which we included the number of snowfinches captured as a function of the above weather variables. We treated the number of snowfinches captured as a count data. As we had overdispersion in our data, we fitted a negative binomial model. Model selection followed the same criteria as for δ^2H_f ($\Delta AICc < 2$). We could not include the variable year as a random factor in these last two models because of singularity problems.

All analyses were performed in R 3.4.4 (R Core Team, 2018), using the *lme4* package (Bates et al., 2015). Multimodel inference and model selection were run using the *MuMIn* package (Bartoń, 2009).

3. Results

3.1. Among population δ^2H_f differences and breeding origins of snowfinches

Breeding individuals of the SA population had significantly lower δ^2H_f (mean ± SD = −98.2 ± 8.4‰; range = −116.6‰, −84.6‰) compared to individuals from the breeding grounds in SP (−66.9 ± 9.0‰; range = −79.7‰, −52.0‰), CM (−67.1 ± 7.5‰; range = −84.6‰, −52.8‰) and AP (−60.6 ± 10.1‰; range = −76.8‰, −45.9‰; Fig. 1 and Table S1). However, a different pattern emerged in the values of δ^2H_f of wintering individuals. Snowfinches captured in the SA during winter had similar values to those captured during the breeding period (−94.9 ± 8.9‰; range = −130.2‰, −76.5‰), while individuals at both SP (−95.7 ± 10.7; range = −115.7, −65.6) and CM (−85.9 ± 15.0‰; range = −102.2‰, −62.5‰) showed the widest ranges of δ^2H_f. That is, wintering individuals at the SP and CM encompassed the entire isotopic values of all breeding populations, although their δ^2H_f values were closer to the SA breeding birds than to the breeding individuals of the two Iberian populations. There were also larger differences in δ^2H_f between breeding and wintering individuals in the SP population compared to the CM population (Table 1A, Fig. 1 and Supporting Information Fig. S4).

The breeding origin assignment of wintering birds suggests that 99% (CI: 96–100%) of the individuals sampled during the winter in SA had a high probability to belong to the SA breeding population, with the remaining 1% (CI: 0–3%) showing a breeding origin other than SA (Fig. 1). Similarly, 98% (CI: 92–99.8%) of the wintering birds from SP were assigned to a breeding origin from the Alps, compared to 2% (CI: 0.2–8%) for which a breeding origin other than SA was obtained (Fig. 1). The 86% (CI: 55–99%) of the wintering birds captured in the CM had a high probability to belong to the breeding population from the Alps, while for 14% (CI: 1–45%) a breeding origin other than the Alps was assigned (Fig. 1). It is important to note, however, that with only 9 individuals captured in winter in the Cantabrian Mountains, these estimates should be taken with caution.

3.2. Winter weather conditions and migratory propensity

Finally, the probability of capturing snowfinches at the SP wintering site was related to the mean temperature in the Alps and to the mean precipitation in the SP during the previous two months: the lower the temperature in the Alps and the higher

Table 1
AICc, ΔAICc, AICc weight and goodness-of-fit values of the most parsimonious models (for which coefficients and confidence intervals are shown), for: (A) comparing pattern of δ^2H for the outer rectrix in breeding vs. wintering populations; and (B) investigating the influence of weather variables on the success (i.e., binary response variable, with 1 = snowfinches were captured during one session, and 0 = no snowfinches were captured; total number of capture attempts = 49) of capturing snowfinches in SP during every winter capturing attempt (predictor variables: MeanTemp_CH = mean ambient temperature in the Swiss Alps of the two months preceding each capture; MeanPrec_CH = mean precipitation in the Swiss Alps of the two months preceding each capture; MeanPrec_SP = mean precipitation in the Spanish Pyrenees of the two months preceding each capture). Models shown here are those with ΔAICc <2 (see all other alternative models in the Supporting Information Table S5).

A	Models	AICc	ΔAICc	AICc weight	Adjusted-R^2	β	SE	RIV	Confidence Interval	
									2.5%	97.5%
	Season + Population + Season*Population	**1719.76**	**0.00**	**1**	**0.56**					
	Intercept					−67.09	1.66		−70.36	−63.81
	Season: Winter					−18.84	3.50	1	−25.74	−11.95
	Population: SP					0.21	4.12	1	−7.92	8.33
	Population: SA					−31.07	2.61	1	−36.22	−25.92
	Winter * Population SP					−9.92	5.27	1	−20.31	0.47
	Winter * Population SA					22.43	4.15	1	14.26	30.60

B	Models	AICc	ΔAICc	AICc weight	Deviance	β	SE	Confidence interval	
								2.5%	97.5%
	MeanTemp_CH + MeanPrec_SP	**51.55**	**0.00**	**0.42**	**0.33**				
	MeanTemp_CH + MeanPrec_CH + MeanPrec_SP	**53.40**	**1.85**	**0.17**					
	Intercept					0.13	0.38	−0.66	0.89
	MeanTemp_CH					−2.25	0.73	−4.07	−1.06
	MeanPrec_SP					1.34	0.62	0.26	2.75

the precipitation in the SP, the greater the number of snowfinch were captured (Table 1B). Combining the information on δ^2H_f and captures, this suggests that snowfinches from SA may be more prone to move to SP when low winter ambient temperature prevailed in the Alps (<−2 °C, i.e., in the 42% coldest winters. Table 1B and Fig. 2) and high level of precipitation in the SP (Table 1B). Mean precipitation of the previous two months in the Alps also entered the most parsimonious models but with no significative effect. In contrast, the number of wintering snowfinches captured per capturing attempt in SP was not related to any weather variables: correlations with weather variables could not be measured due to large uncertainty and/or low sample size (Table S4).

4. Discussion

The breeding population of snowfinch in the Swiss Alps (SA) showed a distinctive lower δ^2H_f in rectrices compared to southern populations such as those in the Apennines (AP), Spanish Pyrenees (SP) and Cantabrian Mountains (CM), which did

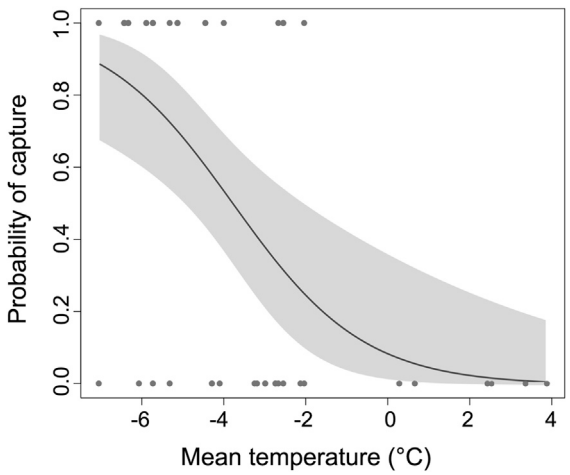

Fig. 2. Model prediction for the probability of capturing wintering snowfinches in SP from 2005 to 2015 in relation to the mean ambient temperature (°C) of the two months preceding each capture, recorded in the Swiss Alpine massif.

not differ between them. Here, we assume that δ^2H_f of the sampled breeding populations were representative of the respective breeding population. This isotopic pattern allowed us to estimate the probability of a breeding origin (Alps *vs*. other) for wintering birds in the SA, SP and CM. When assessing the probabilities of having a breeding origin from the Alps within a wintering snowfinch population in the SA, not surprisingly we found that *ca* 100% of the individuals were estimated to be local breeders. Astonishingly, as many as 98% and 86% of the individuals sampled in winter in the SP and CM, respectively, also had a high probability of originally stemming from the breeding population in the Alps. These results not only support previous evidence suggesting that latitudinal wintering movements exist in the European snowfinch (Albouy and Riols, 2018; Cheylan, 1973; Resano-Mayor et al., 2017) but also suggest that such wintering movements from the Alps to the SP could reach the westernmost distribution limit represented by the CM massif.

Snowfinches from the Alps apparently adopt a partial latitudinal migratory strategy, which leads to southern, resident populations potentially merging with northern populations in winter. Among extrinsic drivers, winter ambient temperature seems to play a role in partial migratory movements of snowfinches from the Alps, as documented for other species (Watts et al., 2018). For instance, in Europe some northern populations of the European robin (*Erithacus rubecula*) migrate longer distances when winter temperatures in the breeding areas are cold, although large geographical variation in response to climate seems to exist (Ambrosini et al., 2016). Interactions between an individual's physiological balance (homeostasis *sensu* Arlettaz et al., 2015; Wingfield et al., 2017) and its ability to acquire food (social status, Mckinnon et al., 2019) are likely to be the mechanisms at play when deciding whether to stay or move in non-obligate migrants (Singh et al., 2012). Our results raise the question of which are the key triggering factors determining the snowfinch flexible partial migration from the Alps towards southern Iberian populations. Snowfinches might move in response to low temperatures because of allostatic stress, or because low temperatures prevent snow melting and thus reduce food availability, or as a combination of both. Yet, factors other than extrinsic (e.g. food availability and weather) can motivate birds to migrate. Intrinsic factors linked to social rank and/or physiological performance may constrain subordinate individuals to leave breeding territories in the cold season (Chapman et al., 2011; Macdonald et al., 2016; Reid et al., 2018). In this regard, migration propensity in partially migratory populations may be dependent on the sex, age, size or individual internal state (Chapman et al., 2011; Fudickar et al., 2013; Hegemann et al., 2015). However, more research is still needed to better understand how extrinsic and intrinsic factors may determine migratory strategies, and whether different movement patterns may ultimately affect population viability.

We do not really know from our results whether the sampled wintering individuals at the southern populations with high probability of a breeding origin from the Alps are migrating or dispersing (i.e., we do not know if they return). Based on ring recoveries, both SW movements in autumn-winter and NE movements in spring indicate that migrating individuals move in both directions (from and to the breeding grounds in the Alps, although quantitative analyses are still missing). Our results could also indicate a case of irruption, which is common for many North American finches, particularly during harsh winters, when birds that are unable to stay farther North migrate South (Strong et al., 2015). Snowfinches' movements between the Alps and the Spanish Pyrenees and Cantabrian Mountains, as well as the exchanges of individuals between different sectors of the Alps described earlier (Scridel, 2019), may be important for the overall genetic structure of the snowfinch west European metapopulation (see Resano-Mayor et al., 2017). If we assume that winter migrants from the Alps settle from time to time to breed in the Iberian populations, then gene flow could help to maintain genetic diversity across the western European range of the snowfinch. This would help preventing the potential negative impacts of a demo-genetic isolation due to habitat loss (Cote et al., 2017; Jacob et al., 2017; Procházka et al., 2008), which will be more acute in high-alpine ecosystems than anywhere else because of both the pyramid shape of mountains and rapid climate warming (Brunetti et al., 2009; Urban, 2018). In our case this concerns, in particular, the small CM population for which an occasional settling of winter immigrants might represent a unique demo-genetic rescue option. Although according to our findings a good proportion of birds wintering in the CM may come from the Alps, we need to point out that our sample size was low, what might have overestimated the result. In effect, this population shows signs of genetic isolation, having a specific and predominant haplotype not shared by other European populations (Resano-Mayor et al., 2017). Nevertheless, further genetic studies would be needed to better understand if the CM snowfinch population became more isolated since the last ice age because of the use of a different refuge compared to the other populations, or whether the higher genetic isolation currently observed has increased overtime. Future studies employing individual tracking devices (e.g., GPS-based system) and high-resolution genetic markers would help to test the hypotheses raised in this study to better understand whether or not, and to what extent, wintering birds in the SP and the CM are actually residents, migrants or dispersers.

Climate change influences movement strategies in different ways. For instance, in long-distance migrants, it can affect the onset of migration and the arrival date on the breeding grounds (Bókony et al., 2019). In short-distance migrants, milder winters may induce a progressive reduction of seasonal journeys (Singh et al., 2012), which may eventually lead to permanent residency (Pulido and Berthold, 2010). Alpine ecosystems are particularly vulnerable to climate change (Brunetti et al., 2009). Warmer temperatures cause an upwards elevational shift of the treeline, resulting in higher fragmentation and isolation of alpine habitats (Holtmeier and Broll, 2007). For species adapted to live in such environments, this could have detrimental effects on population connectivity. An upward shifting treeline can lead to the shrinkage of alpine habitat so animals would need to move farther to find suitable patches, with such movements having the importance of enhancing metapopulation functioning (Cote et al., 2017; Roland et al., 2000). In species like the snowfinch, if the decision to migrate is triggered by adverse climatic conditions, warmer winters might reduce the frequency of latitudinal migration. If the latter occurs in the long run with snowfinches breeding in the Alps (i.e., if they progressively reduce migration propensity), and the viability of the smaller, potentially more isolated populations (e.g. CM) relies on immigrants from the Alps, then those populations may

eventually become extinct. In effect, the latter would not only be massively impacted by global warming given their southern latitude, but they may in addition lose the demo-genetic rescue benefits provided by potential immigrants coming from the North for overwintering. Conversely, the migrant portion of the breeding population in the Alps, by becoming less mobile, might experience an increase in competition. As the dynamics of migrant and non-migrant subpopulations might be linked through density-dependent effects (Griswold et al., 2011), warming conditions might affect population demography, structure and heterogeneity of species living in alpine environments. More generally, future research should decipher how these sorts of risks affect high-alpine species that are particularly exposed to climatic shifts, but show flexible migration behaviour in space and time, to better understand how they may respond to rapidly changing environments.

5. Conclusions

Our study suggests that snowfinches adopt a partial latitudinal migratory strategy probably determined by climatic conditions such as the temperature in the Alps over the winter. The different movement patterns suggested by the analysis of δ^2H_f could have important implications in terms of population connectivity, spatio-temporal population dynamics and structuring. The consequent eco-evolutionary responses to environmental perturbations might be similarly multi-faceted, especially under uncertain future climate change scenarios. Long-term studies, considering the metapopulation structure of the species in western Europe, are thus required to better disentangle the complexity of the movement strategies of alpine species, and its potential consequences in the light of global warming for conservation purposes. The analysis of δ^2H_f may thus offer unique opportunities for research about migratory strategies and population connectivity in high-alpine birds.

Authors' contributions

JRM conceived the project; JRM, CB, MMD, AFM, SHG, IT, AE, MG, IRA, JAG and ES collected the data; KAH performed the isotopic analysis; JRM and MMD analysed the data; JRM, CB, MMD, KAH and RA wrote the manuscript. RA funded part of the research. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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