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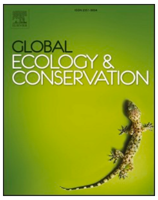

Original research article

Wing morphology changes with habitat availability and elevation in an alpine-specialist bird

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ABSTRACT

Intraspecific morphological variation of organisms is known to be influenced by several factors, but the role of habitat availability has been scarcely investigated. Studying bird wing morphology is ideal to explore this topic, given the usually rapid response of birds to environmental changes, but other factors such as sexual dimorphism, habitat structure, climate and elevation need to be considered. Here, we investigated the effects of habitat availability, local climate and elevation on the wing morphology of a high-elevation specialist bird (*Montifringilla nivalis*), while accounting for sexual dimorphism. We hypothesized that birds relying on less extended suitable areas around their breeding sites show wing traits allowing a more energy-efficient flight, given their need of more frequent and longer movements to find foraging areas in the post-breeding period and the longer dispersal distances. We also expected that individuals breeding at higher elevations show wings traits allowing higher flight efficiency, given the higher hypoxia risk. We derived wing traits (isometric size, pointedness and concavity) by measuring primary feathers of individuals from 7 breeding sites in the European Alps, and we obtained habitat availability from detailed habitat suitability maps. Consistently with the need for a more energy-efficient flight, birds relying on less extended suitable habitat showed larger and more concave wings, and individuals breeding at higher elevations showed more concave wings. Local climate had a less clear effect. The observed patterns may result from local adaptations and could represent one of the ways mountain birds cope with the harsh and unpredictable environment they inhabit.

1. Introduction

Intraspecific morphological variation of organisms is known to be subject to a variety of selective pressures such as predation,

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climate, sexual selection, and habitat structure (e.g., Bourdeau and Johansson, 2012; Eklöv and Svanbäck, 2006; Ficetola et al., 2016; Greene and Funk, 2009; Ryding et al., 2021; Svensson et al., 2006; Vanhooydonck et al., 2009; Yom-tov et al., 2010). A poorly investigated and still unclear aspect is the relationship between morphological variation and habitat availability (Desrochers, 2010; Hermes et al., 2016; Wood and Cousins, 2023). Morphological changes may potentially help species to adapt to environmental changes such as anthropogenic land use and land cover modifications, but evidence for this is still scarce. As an example, several North American songbird species showed changes in wing morphology across a short time frame (100 years) according to anthropogenic changes in the amount of available habitat, evolving towards a higher flight efficiency in regions where they experienced habitat loss and fragmentation, consistently with the need for more frequent and longer movements and crossing of larger habitat gaps (Desrochers, 2010). Other studies have further supported the occurrence of changes in avian wing morphology also over relatively limited time frames (Brown and Brown, 2013) and spatial scales (Hermes et al., 2016; Senar et al., 2006), according to environmental stressors or habitat configuration. This is consistent with the strong selective pressures acting on wing morphology (also due to the high energetic costs of flight; Norberg, 1996), their frequently rapid changes in space and time (e.g., vegetation structure, predation), and the fast response of many birds to environmental changes (e.g., Hallman et al., 2022; Lantz and Karubian, 2017). Investigating bird wing morphology is therefore ideal for exploring the relationships between habitat availability and morphological variation.

However, a variety of other factors can affect such a relationship; wing morphology of birds can indeed vary at the intraspecific level according to sex (Szekely et al., 2007), age (Alatalo et al., 1984), differences in migration habits (Rolshausen et al., 2009), habitat structure (Ceresa et al., 2022; Saino et al., 2017; Vanhooydonck et al., 2009) or elevation (e.g., Hernández-Téllez et al., 2023). For example, migration selects for longer, more pointed, and more concave wings, as these characteristics allow a more energy-efficient and sustained flight (Leisler and Winkler, 2003; Lockwood et al., 1998; Saino et al., 2010). In contrast, dense vegetation implies the need for higher flight manoeuvrability, selecting for more rounded wings (Lockwood et al., 1998; Saino et al., 2017). Differences in wing morphology among sexes are widespread among birds (Szekely et al., 2007) and can be connected, e.g., to the specific requirements derived from males' song flights (Hedenström and Møller, 1992), to intersexual differences in migration distances (e.g., Fernández and Lank, 2007), or to higher exposure to predation of females during incubation, which could select for wing characteristics allowing higher escape abilities (e.g., Minias et al., 2013).

Within this context, another poorly understood potential pressure is the influence of elevation on avian wing morphology, as several studies dealing with this topic provided partly contradictory results, including both a total lack of effects (Boyce et al., 2019; Ceresa et al., 2022), a positive relationship with wing length (e.g., Hernández-Téllez et al., 2023; Lu et al., 2009), or both of these patterns, depending on the species or the geographic area considered (Laiolo and Rolando, 2001; Sander and Chamberlain, 2020; Wilson et al., 2010). The reported cases of positive relationships could be explained by the need for a more energy-efficient flight due to the lower air pressure and higher hypoxia risk associated with higher elevations (Altshuler and Dudley, 2006; Sander and Chamberlain, 2020; Scott, 2011). As a further limit to the current knowledge, as most studies considered wing length only, the effects of elevation on wing shape have been very rarely investigated (but see Ceresa et al., 2022; García et al., 2021; Hernández-Téllez et al., 2023). In addition, only a few studies on this topic have accounted for the potential influence of other environmental factors, such as vegetation structure (Ceresa et al., 2022; García et al., 2021; Hernández-Téllez et al., 2023). Therefore, to better understand the effects of elevation on wing morphology, studies considering both wing shape and size and accounting for other potentially relevant environmental factors are necessary.

In this study, we investigated the effects of habitat availability, local climate, and elevation on avian wing morphology, using as a model a high-elevation specialist, the white-winged snowfinch (*Montifringilla nivalis*). Based on current knowledge of the relationships between the environment (i.e., habitat availability, climate and elevation) and avian wing morphology, we formulated the following, non-alternative, hypotheses:

1. Habitat isolation: Birds can show wing traits allowing a more energy-efficient flight (longer and more pointed/concave wings) where the extension of suitable habitat is lower, because of the need to reach other and more distant areas for foraging opportunities after reproduction, as well as the longer natal and breeding dispersal distances required to find settlement opportunities ('habitat isolation hypothesis'; Desrochers, 2010);
2. Winter climate: Longer and more pointed/concave wings can be expected in areas with harsher winter climates (lower temperature, higher precipitation). For a species facing the challenging conditions of winters at high elevations (scarce food, harsh climate), local winter climate may also affect the length and frequency of erratic movements: birds breeding at sites that become colder and have stronger precipitation in winter may more likely be forced to move towards mountain sectors with milder climates. A high snow cover makes access to food resources (mainly seeds in our model species, Summers-Smith and Bonan, 2020) more difficult, and low temperatures imply a high energy demand for thermoregulation;
3. Elevation: Birds can have longer and more pointed/concave wings at higher elevations, given the need for a more energy-efficient flight (Altshuler and Dudley, 2006; Scott, 2011).

These three hypotheses are not necessarily mutually alternative; in the case of co-occurrence of effects, we aimed to assess which is the prevailing one, especially by comparing the effects of habitat availability and winter climate while taking into account the effect of elevation. To our best knowledge, while some highly valuable studies cited above investigated the effects of elevation or (in very few cases) habitat availability on avian wing morphology, the potential effects of these factors have never before been simultaneously tested, for wings of birds or of any other taxa.

2. Material and methods

2.1. Model system

Our study area spans a wide area of the European Alps (Fig. 1). In this mountain chain, the snowfinch inhabits island-like patches of high mountain open areas surrounded by unsuitable habitats, such as forested mountain slopes and anthropized valley bottoms (Brambilla et al., 2022a; Ceresa et al., 2024). Based on detailed species distribution models, these patches greatly vary in extension according to land cover, and climatic and topographic variables (Brambilla et al., 2022a; Ceresa et al., 2024). This provides an ideal study system to investigate the habitat availability - wing morphology relationship at a regional scale. An advantage of such a scale is to control for factors that could influence wing morphology when considering larger areas (e.g., the entire Alpine range or multiple mountain chains), such as latitudinal effects or possible population genetic clustering (see, e.g., García et al., 2021; genetic clustering is absent in our study area, Ceresa et al., 2024). This allowed a less complex and more interpretable testing of our hypotheses.

Snowfinches are strictly connected to high-elevation, open habitats all year round (Bettega et al., 2020). During the non-breeding period, they are highly mobile, performing erratic movements in search of food, often in large flocks, and also occasional short-distance migrations (e.g., among different mountain systems; Resano-Mayor et al., 2020). We accounted for sex in the analyses, given that male snowfinches show longer wings than females (Demongin, 2016); we expected sexual dimorphism also in wing shape, as a possible consequence of specific requirements connected to the song flights performed by males. We did not consider vegetation structure because the species strictly inhabits open habitats with grassland and rocks (Bettega et al., 2020; Summers-Smith and Bonan, 2020), where vegetation height is so low that it does not affect flight or take-off, and therefore wing traits related to manoeuvrability are extremely unlikely to be affected.

2.2. Data collection

We captured and measured snowfinches during the years 2021 and 2022, at seven breeding sites located in the central-eastern Italian Alps (Fig. 1). The study area spanned from peripheral breeding areas in the south, where the species distribution is highly scattered, to the main Alpine watershed in the north, where the distribution is more continuous (Fig. 1). Sampling sites ranged between c. 2350 and 2750 m asl, covering most of the elevational range occupied by the species in this region. We captured birds during the breeding period (mid-May – mid-July), in order to avoid sampling birds during their erratic or short-distance migratory periods. Birds were captured by mist nets and were marked with metal rings of the Italian ringing scheme. We determined age and sex following Demongin (2016) and Strinella et al. (2013). We then measured the lengths of all primary feathers except the vestigial outermost one using a metal ruler (± 0.5 mm). We based our study on measurements of primary feathers instead of distances between feather tips (e.g., the Kipps's distance) because they allow a lower measurement error (feathers are notably larger than the distances between their tips) and higher repeatability (Swaddle and Witter, 1997; Lockwood et al., 1998). Measurements were taken based on the same protocol by two of the authors, who are long-experienced bird ringers. We also assessed the lack of differences between the two ringers by comparing their measurements of a primary feather (P8) of the same individuals of passerine species with wing sizes very similar to the snowfinch (measurements taken at a ringing station in the Italian Pre-Alps located at Passo di Spino, Lombardy; details in the Supplementary material). We obtained measures of all primary feathers from 67 snowfinches, including 62 adults and 5 juveniles. Details about the number of birds per sampling site as well as their sexes and ages are reported in the Supplementary material (Tab. S1).

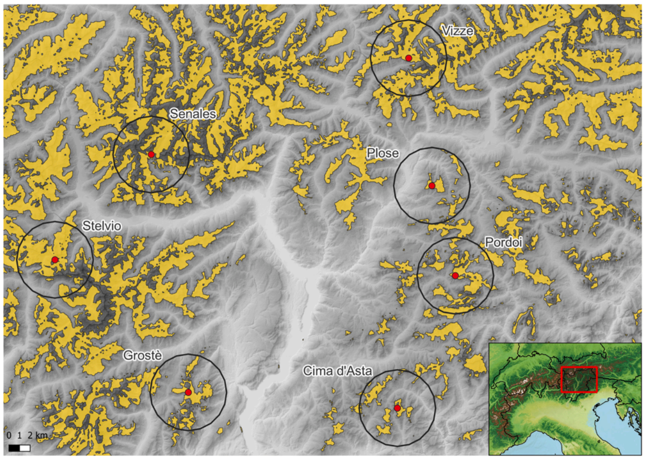

Fig. 1. Study area in the central-eastern European Alps, with areas suitable for the snowfinch according to MaxEnt modelling (based on the 10th percentile threshold; in yellow) and snowfinch sampling sites (red dots). Black circles are 10 km radius buffers used to measure the extension of suitable habitat around each sampling site.

2.3. Statistical analysis

2.3.1. Morphological indexes

Primary feather lengths were analyzed by means of size-constrained component analysis (SCCA; Lockwood et al., 1998; Somers, 1986). Unlike a standard principal component analysis, this approach allows to separate size from shape, i.e., to obtain wing shape indexes that are not affected by allometry (Lockwood et al., 1998), a crucial aspect in morphological studies. Performing a SCCA using all 9 measured primary feathers allowed a detailed description of the morphological variation of the entire wingtip, unlike more simple methods based on distances between tips of two feathers only (e.g., the Kipp's distance; Kipp, 1959) and related indexes like the Hand Wing Index (HWI), that combines Kipps' distance and wing chord (e.g., Sheard et al., 2020). This is crucial when investigating the subtle differences occurring at the intraspecific level (within the same population in our case), while less detailed methods like the HWI are general proxies of flight efficiency and are mostly used in interspecific comparisons, where morphological differences are far larger (e.g., Fan et al., 2024; Sheard et al., 2020; Weeks et al., 2022).

We performed SCCA with the program sizepca (Somers, 1993) and we used the first three components as wing trait indexes, overall accounting for 96 % of variability in wing morphology within our sample (Table 1). By definition, the first component C1 of sizepca output represents isometric size, i.e., the wing size without the influence of shape. Component loadings (Table 1) identified the other two components, C2 and C3, as shape indexes describing wing pointedness and wing concavity, respectively. Wing pointedness describes the shift in the position of the wingtip feather towards the wing leading edge, while concavity measures the increase in the acuteness of the wingtip (Lockwood et al., 1998). The ranges of these three wing traits within our sample are represented in Fig. 2.

2.3.2. Habitat suitability and climatic factors

To estimate the extension of suitable habitat around each sampling site, we used a detailed habitat suitability model developed by Ceresa et al. (2024) for the same area of the Alps considered in the present study. This model was constructed according to a maximum entropy approach, by relating recent occurrence data for the species with land cover, and topographic and climatic factors (Ceresa et al., 2024). Although snowfinches are tightly connected to high-elevation open habitats all year round, their habitat preferences are slightly less specialized during the non-breeding period than during reproduction (Bettega et al., 2020). Therefore, given that the model described habitat suitability for breeding, we used a relatively low (compared to other commonly adopted thresholds) presence threshold (10th percentile) to reflect the partly less strict habitat requirements during the non-breeding period. The resulting suitable areas (Fig. 1) covered a large part of the open areas above the treeline, consistently with the species ecology. Valley bottoms are visited by snowfinches only occasionally when there are extremely adverse weather conditions at high elevations (Heiniger, 1991a). Importantly, the suitable areas depicted in Fig. 1 should be interpreted as the areas available to snowfinches to be explored in search of food resources during the non-breeding period, rather than areas statically and permanently occupied by the species throughout that period. Outside the reproductive season, snowfinch distribution within high-mountain areas is highly dynamic, due to erratic movements that are likely influenced by the patchy and heterogeneous distribution of food resources and their temporal variation, as well as by the frequent and abrupt weather changes typical of this environment (e.g., Bettega et al., 2020; del Mar Delgado et al., 2021). We then calculated the extension of suitable habitat within a 10 km radius around each of the seven sampling sites (Fig. 1). We chose this arbitrary distance to include areas that can be reached by snowfinches with short movements from the starting point (breeding/natal site), given their high flight capability (Heiniger 1991b; Resano-Mayor et al., 2020). Increasing the radius to 15 km led to very similar results in the downstream analysis, indicating that our approach is robust to moderate changes in the considered radius.

To describe winter climatic conditions across sampling sites, we used winter mean temperatures (BIO11) and mean winter precipitation (BIO19) for the years 1981–2010 downloaded from the CHELSA database V2.1 (Karger et al., 2017). We averaged temperature and precipitation values within each of the seven 10-km buffers but considered only values (pixels) above 2000 m asl, to better represent the conditions experienced by snowfinches. Temperature and precipitation mean values calculated for each 10-km buffer are reported in Tab. S2.

The elevation considered in the analysis is referred to the precise capture location of each bird (i.e., the location of the mist nets transect, Tab. S2). At three sampling sites, we placed mist-nets at a few different locations at very short distances from each other, resulting in 14 capture locations across the seven sampling sites.

Table 1
Loadings of SCCA components and variance explained by each component.

	SCCA component		
Primary feather	C1	C2	C3
P9	0.941	0.238	0.091
P8	0.941	0.281	0.142
P7	0.941	0.270	−0.001
P6	0.941	0.244	−0.115
P5	0.941	0.177	−0.151
P4	0.941	0.003	−0.186
P3	0.941	−0.148	−0.251
P2	0.941	−0.191	−0.111
P1	0.941	−0.282	0.229
R^2	*88.57*	*4.86*	*2.53*

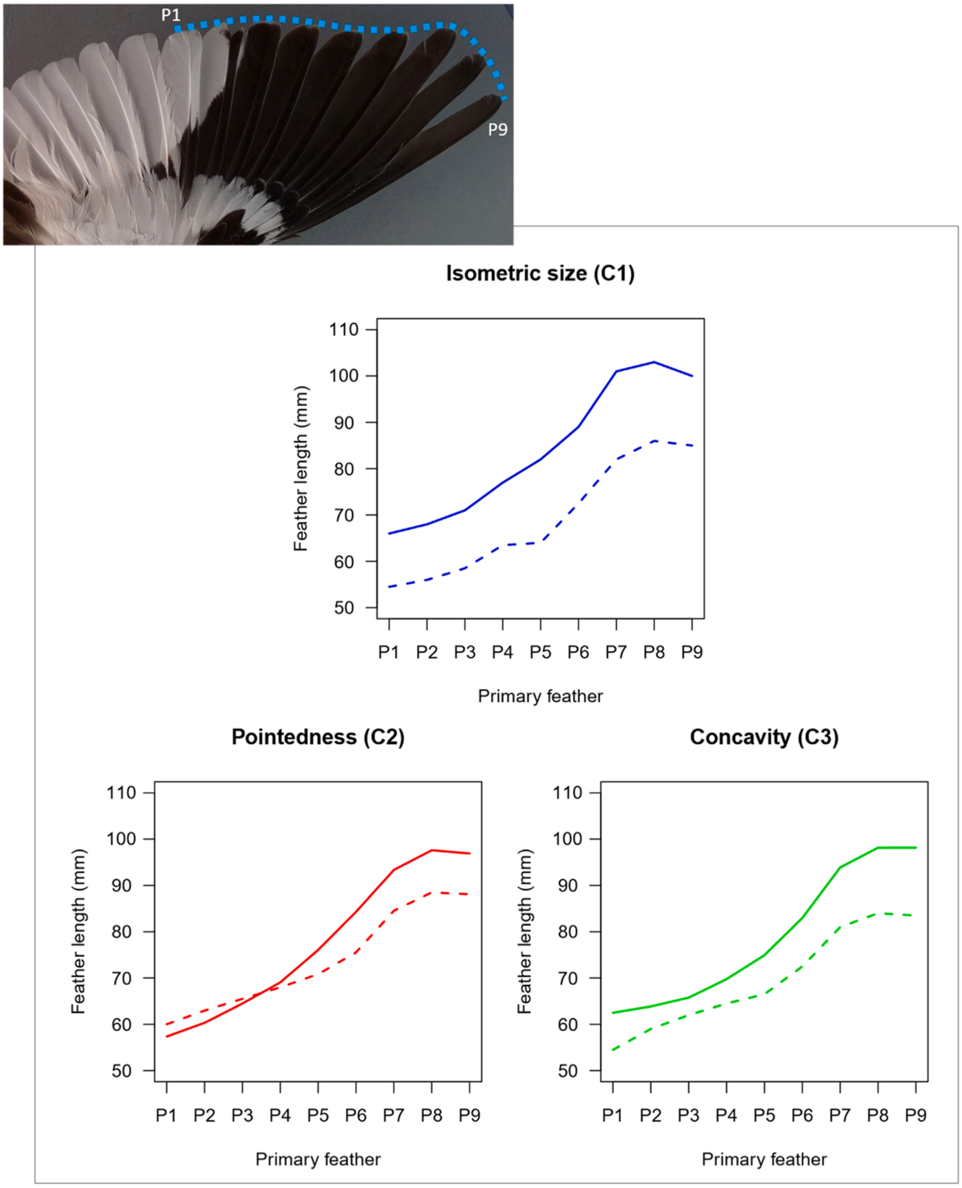

Fig. 2. Ranges of wing traits within the sample of measured individuals, depicted by primary feathers lengths. In the plots, solid lines refer to the individuals with the higher values of wing trait index (larger, more pointed, and more concave wings), while dashed lines refer to the individuals with the lower values (shorter, more rounded, and more convex wings). Measured primary feathers are highlighted in the wing photograph by the dashed line and are numbered ascendingly excluding the vestigial outermost one (P10).

2.3.3. *Hypotheses testing*

We investigated the effects of habitat availability, winter climate (temperature and precipitation), and elevation on snowfinch wing morphology using multiple linear regression analysis, carried out through the *lm* function in program R 4.3.1 (https://cran.r-project.org/). We assessed the influence of these factors while controlling for sex, whereas age was not included as we only considered the 62 adult birds. Including the 5 juveniles would have led to unnecessarily more complex models, without a sufficient sample of juveniles to properly describe morphological differences between age classes. Continuous predictors were standardized to allow comparisons among the predictors' effects.

Data exploration showed strong correlations between habitat availability and the two climatic variables ($r = -0.88$ and 0.78 with temperature and precipitation, respectively), resulting in high variance inflation factors ($VIF > 10$) in models including both types of variables. Thus, we compared the effect of habitat and climate on each wing trait by fitting two sets of alternative models, i.e. climate and habitat models, including sex and elevation in both cases. For each wing trait and model category, we ranked all possible models based on their Akaike Information Criterion corrected for low sample sizes (AICc), using the *dredge* function of R package MuMIn

(Bartoń, 2020) and removed uninformative parameters (Arnold, 2010). We considered models within ΔAICc < 2 to be substantially supported (Burnham and Anderson, 1998). In this way, we identified the most supported models within each of the two model sets (habitat and climate). To assess whether habitat availability or climate better described the variation in wing morphology, we compared the AICc values of the best habitat and the best climate model, and we considered differences in AICc larger than 2 to indicate a substantially different support. To assess the predictors' effects for each of the two model sets, we performed a full model averaging across all substantially supported models (Burnham and Anderson, 1998). We considered an effect to be significant when 95 % confidence intervals did not include 0. We then checked for possible spatial autocorrelation in the residuals of the best models using the *Moran.I* function of R package ape 5.7 (Paradis and Schliep, 2019). To check for the possible effect of potential lack of independence between data collected at the same location, in addition to the evaluation of spatial autocorrelation patterns, we also re-run the models by adding the study site as a random factor in the best models, fitting them as mixed effect models (GLMM). The results were fully confirmed or remained qualitatively similar, according to the wing trait considered, and the random factor explained a null or limited amount of variation, confirming the lack of relevant effects related to the sampling location (details not shown).

We further deepened our approach by using variation partitioning to assess the proportion of variability in wing traits explained by each explanatory variable, considering only those variables included in the best linear models (i.e., informative parameters). We carried out variation partitioning using the *varpart* function of R package vegan (Oksanen et al., 2020).

3. Results

For wing isometric size, the most supported models included the extension of suitable habitat in the habitat models set (Table 2a) and mean winter temperature in the climate models set (Table 2b). Sex was also included in both sets, with males showing larger wings. Suitable habitat showed a significant negative effect on isometric size (β = −0.674; CI 95 % −1.084 to −0.264; Fig. 3), while winter temperature had a significant positive effect (β = 0.570; CI 95 % 0.147 to –0.994; Fig. 4). The difference in AICc clearly indicated that the best habitat model was more supported than the best climate model (ΔAICc = 3.10; Table 2c). Wing pointedness was not influenced by any of the considered predictors, as the null model was the most supported one in both models sets (Tables 2a and 2b). For wing concavity, the most supported models included the extension of suitable habitat and elevation in the habitat models set (Table 2a) and winter temperature, precipitation, and elevation in the climate models set (Table 2b). For this wing trait, we found no clear difference in support between the best habitat model and the best climate model (ΔAICc = 0.5, Table 3). However, the extension of suitable habitat showed a significant negative effect (β = −0.136; CI 95 % −0.263 to −0.009; Fig. 3) while the effects of the climatic predictors were non-significant (Table 3). Elevation showed a positive effect, significant and stronger than the other considered predictors (Table 3, Figs. 3 and 4). For both isometric size and concavity, residuals of the best models were normally distributed and were not spatially autocorrelated (Moran's I range: −0.003 to −0.018; p-values range: 0.308–0.897).

According to variation partitioning, informative parameters from the best habitat models explained 51 % of variability in overall wing isometric size, with 8 % of variability explained by the extension of suitable habitat. Climate models performed slightly worse,

Table 2

Best linear regression models for each wing trait (ΔAICc < 2), based (a) on the extension of suitable habitat and (b) on winter climatic conditions, and (c) comparison between the best habitat and the best climate models. t = temperature and prec = precipitation. Full models are reported in italics.

a) Habitat models

Response variable	Predictor	AICc	ΔAICc
Isometric size (C1)	Suitable area + sex	241.9	0.00
	Suitable area + elevation + sex	*244.1*	*2.22*
Pointedness (C2)	[intercept only]	104.0	0.00
	Suitable area + elevation + sex	*110.0*	*6.02*
Concavity (C3)	Suitable area + elevation	69.4	0.00
	Suitable area + elevation + sex	*71.3*	*1.94*

b) Climate models

Response variable	Predictor	AICc	ΔAICc
Isometric size (C1)	Winter mean t + sex	245.0	0.00
	Winter mean t + winter prec + elevation + sex	*247.6*	*2.53*
Pointedness (C2)	[intercept only]	104.0	0.00
	Winter mean t + winter prec + elevation + sex	*112.2*	*8.20*
Concavity (C3)	Winter mean t + elevation	69.9	0.00
	Winter prec + elevation	71.5	1.62
	Elevation	71.6	1.71
	Winter mean t + winter prec + elevation + sex	*73.7*	*3.84*

c) Comparison between best habitat vs best climate models

Response variable	Model	Predictor	AICc	ΔAICc
Isometric size (C1)	Habitat	Suitable area + sex	241.9	0.00
	Climate	Winter mean t + sex	245.0	3.10
Pointedness (C2)	Habitat	[intercept only]	104.0	0.00
	Climate	[intercept only]	104.0	0.00
Concavity (C3)	Habitat	Suitable area + elevation	69.4	0.00
	Climate	Winter mean t + elevation	69.9	0.50

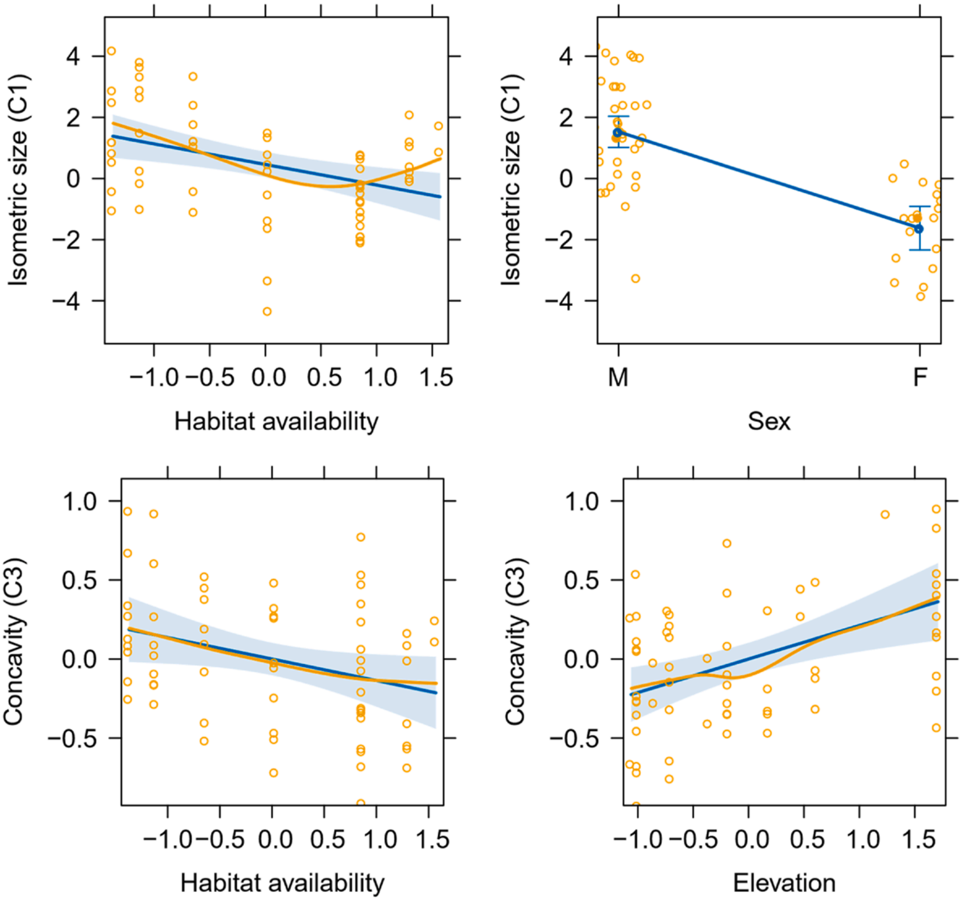

Fig. 3. Effects of informative predictors on wing traits according to the most supported habitat models (see Table 2a). Dots represents partial residuals and the yellow line is a smoothing spline interpolating the data. All the depicted effects are significant.

with 49 % of the overall variability explained, of which 5 % was explained by winter temperature. For wing concavity, within the best habitat model, elevation and habitat availability explained 14 % and 5 % of data variability, respectively. For climate models, elevation explained 13 % of the variability in wing concavity while temperature and precipitation explained 1 % and 0 % of variability, respectively (R^2_{adj} of precipitation was negative, which can sometimes happen with this statistic and should be interpreted as 0; Legendre, 2008). The results of variation partitioning are summarized in Fig. 5.

4. Discussion

Our work represents the first attempt to model intraspecific morphological variation in wings in relation to habitat availability, climate and elevation. The results clearly indicate that, consistently with our first hypothesis, snowfinches with lower availability of suitable habitat around their breeding sites have longer wings. On the one hand, such a pattern may be linked to the larger erratic movements that such individuals need to find foraging areas outside the breeding period, and the consequent need for a more energy-efficient flight, compared to those that can rely on larger suitable areas near their breeding sites when starting their erratic movements after reproduction. On the other hand, differences in natal and breeding dispersal distances related to the extent of suitable habitat may be involved in the observed pattern, given the connection between dispersal and wing morphology (e.g., Chu and Claramunt, 2023; Weeks et al., 2022). Less suitable habitat near a breeding site implies longer movements to find settlement opportunities, and that immigrants arrive from proportionally farther areas, selecting for individuals with higher movement capability (e.g., Fahrig, 2003). Whatever the relative contribution of erratism and dispersal, in both cases the longer movements imply the need for a more energy-efficient flight, which is crucial in determining the birds' ability to cross habitat gaps (Claramunt et al., 2022; Ibarra-Macias et al., 2011; Naka et al., 2022). The observed more concave wings with lower habitat availability is also consistent with this interpretation, as higher concavity implies higher flight efficiency (Leisler and Winkler, 2003; Hernández-Téllez et al., 2023). For this wing trait, the difference between habitat and climate models was small, but the stronger effects and the larger variation explained by habitat extension than by climate suggest that habitat availability actually influences wing concavity. The non-significant effect of climate could be partly spurious, and it may be due to the correlation between climate and habitat availability. The effect of

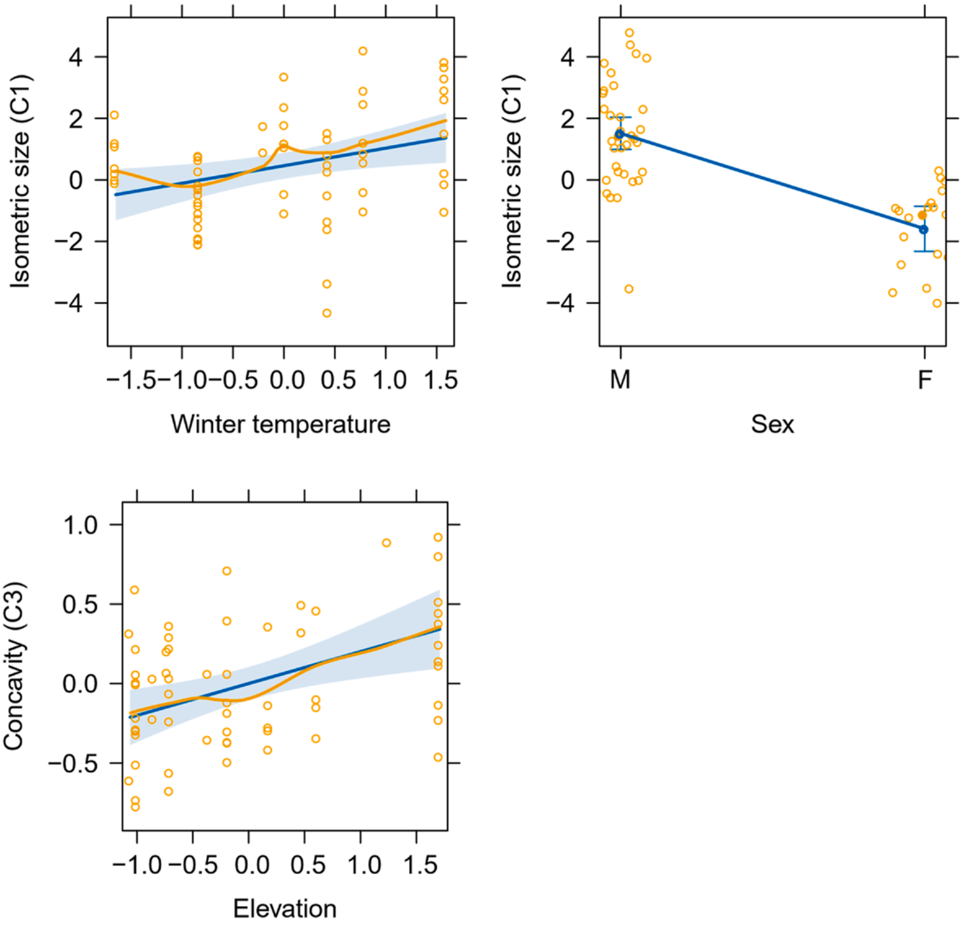

Fig. 4. Effects of informative predictors on wing traits according to the most supported climate models (see Table 2b). Dots represents partial residuals and the yellow line is a smoothing spline interpolating the data. Only significant effects are reported.

Table 3

Effects of predictors on wing traits based on multi model averaging on the most supported (a) Habitat and (b) Climate models. t= temperature.

a)				
Response variable	Predictor	Effect (SE)	−95 % CI	+95 % CI
Isometric size (C1)	Sex (female)	−3.151 (0.438)	−4.010	−2.292
	Suitable area	−0.674 (0.209)	−1.084	−0.264
Concavity (C3)	Elevation	0.212 (0.065)	0.085	0.339
	Suitable area	−0.136 (0.065)	−0.263	−0.009
b)				
Response variable	Predictor	Effect (SE)	−95 % CI	+95 % CI
Isometric size (C1)	Sex (female)	−3.101 (0.453)	−3.988	−2.214
	Winter mean t	0.570 (0.216)	0.147	0.994
Concavity (C3)	Elevation	0.175 (0.068)	0.042	0.309
	Winter mean t	0.068 (0.079)	−0.087	0.223
	Winter precipitation	−0.020 (0.044)	−0.083	0.044

temperature on isometric size could also be at least partly spurious and it showed the opposite direction than we expected, indicating that there is apparently no selection for higher flight efficiency in colder mountain sectors, at least at this spatial scale. However, the role of winter temperatures may be different over larger scales, encompassing a larger climatic variability. As a further possible explanation, the correlation between winter climatic conditions and foraging opportunities is weak, or it is largely influenced by other factors such as geomorphology. As an example, steep and/or south-facing slopes might offer snow-free patches suitable for foraging even in areas with the harshest winter climate.

The observed relationship between wing morphology and habitat availability could represent a previously undescribed example of the way mountain birds cope with the harsh and unpredictable environment they inhabit, jointly with the specific physiological (Barve

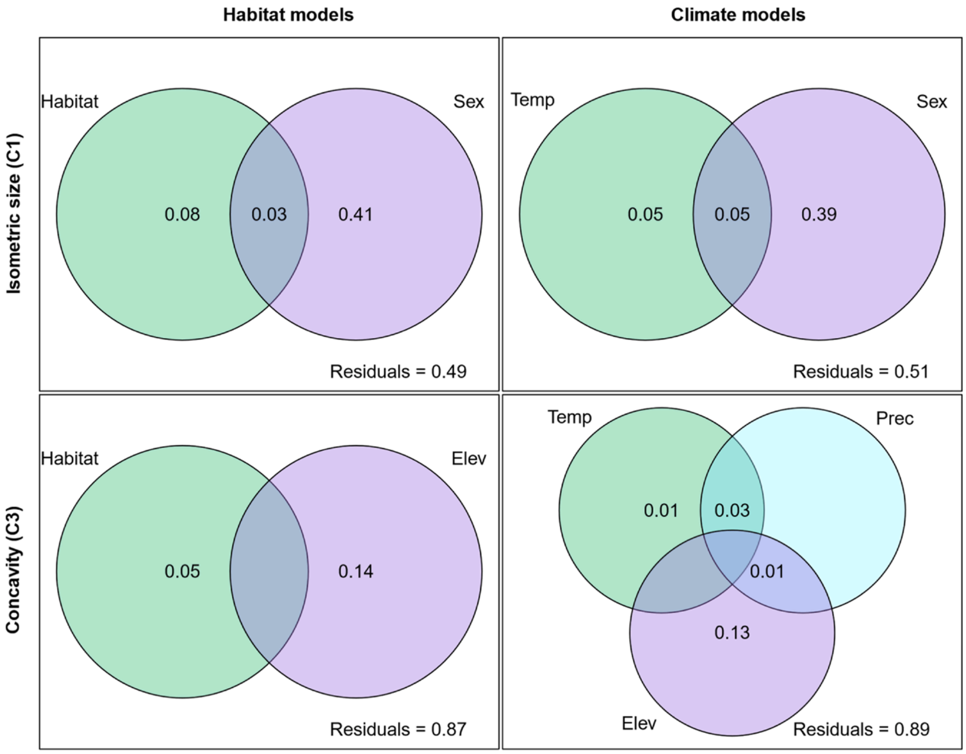

Fig. 5. Venn diagrams showing the individual and shared proportion of variation in wing traits explained by the predictors (Habitat: habitat availability; Temp: mean winter temperature; Prec: accumulated winter precipitation; Elev: elevation).

et al., 2016) and behavioural adaptations of these species (e.g., Altamirano et al., 2023; Ceresa et al., 2020; de Zwaan et al., 2019; Rime et al., 2023). To our best knowledge, regional-scale variation in wing morphology according to habitat availability has been previously described only for forest species with very low movement capability (Hermes et al., 2016). As suggested by Hermes et al. (2016), such a morphological adaptation may partly mitigate the negative effects of habitat loss on bird populations. This would be very relevant for a species like the snowfinch, which is currently threatened by habitat loss and fragmentation due to climate change and anthropogenic land use changes (Brambilla et al., 2022b). While we cannot exclude an influence of phenotypic plasticity in determining the patterns we observed, it is plausible that they are a result of local adaptations, given the high heritability of wing length in birds (Desrochers, 2010), the restrictions to gene flow, and signs of high philopatry reported for the snowfinch across the same area as in the present study (Ceresa et al., 2024); high gene flow can limit the capability of local populations to adapt to the local environment (e.g., Storfer, 1999). Signs of high philopatry have been detected also in other high-elevation specialist bird species (Bech et al., 2009; Ceresa et al., 2023) and, while this can limit population connectivity, it also may improve the capability of these species to develop local adaptations in harsh environments. Senar et al. (2006) found strong genetic differentiation between two breeding sites very close to each other, as well as significant morphological differences in another mountain specialist bird, the citril finch *Carduelis citrinella*, that however breeds in wooded and semi-open areas. The differentiation was probably related to variation in vegetation structure and predation intensity between the two habitat patches. This further suggests that mountain bird populations can develop strong differentiation across limited spatial scales, possibly because of the strong variation of biotic and abiotic factors within short distances occurring in mountain areas (e.g., Körner and Oshawa, 2006).

The observed variation in wing concavity along the elevational gradient is consistent with our third hypothesis and is likely related to the need for a more energy-efficient flight at a higher elevation, given the thinner air and the higher hypoxia risk (Altshuler and Dudley, 2006). Of course, the elevation range of the breeding sites we considered in the analyses may not be fully representative of the elevational ranges used by individuals throughout the entire year. However, areas other than breeding sites are likely used for much shorter periods during the erratic movements, when the birds need to frequently adjust for changing local conditions and food availability. On the other hand, reproduction involves approximately a third of the year, and it is a crucial and energetically challenging period. Therefore, factors related to energetic costs during this period are likely to exert a strong selective pressure. Studies about the elevation-wing shape relationship are especially scarce; however, more concave wings at higher elevations have been reported also within a set of forest songbirds, but not for all studied species (Hernández-Téllez et al., 2023). The water pipit *Anthus spinoletta*, a high-elevation specialist like the snowfinch, showed no elevational effects on wing concavity, and generally no clear effect of elevation on wing shape (Ceresa et al., 2022). In comparison to the snowfinch, the water pipit inhabits sites that are located at lower elevations (Brambilla et al., 2022a), and it overwinters in lowland areas (Tyler, 2020). Even if elevation influenced snowfinch wing shape, we found no effect on wing size, contrasting our expectations. Several previous studies provided mixed evidence about the elevation-wing size relationship, with no clear generalized patterns (e.g., Boyce et al., 2019; Ceresa et al., 2022; Sander and Chamberlain, 2020; Hernández-Téllez et al., 2023; Wilson et al., 2010). This suggests, with the further contribution of our study, that this relationship may be species- and possibly context-specific, but also that the study scale and the choice of environmental predictors to account for in the analyses are very likely influential. Multi-scale studies on many bird species across different mountain ranges will be necessary to better understand how wing size changes along elevation gradients.

While we observed changes in wing size and concavity according to some of the considered predictors, the same did not happen for wing pointedness, differently from our expectations. This suggests that within the study population, this wing trait may be subjected to strong constraints (e.g., specific requirements in high-mountain conditions), with a consequent lack of spatial variation, while the balance between flight efficiency and manoeuvrability based on local conditions is apparently reached through adjustments in wing concavity. As a further possible explanation, snowfinch wing pointedness varies at a different, larger scale than considered in our study. Larger spatial variation in wing concavity than in wing pointedness has been observed also by Hernández-Téllez et al. (2023) for a set of forest species. Interestingly, sexual dimorphism did not include differences in wing pointedness or in concavity, and was limited to the known difference in wing size (Demongin, 2016). Larger wings in snowfinch males are probably linked to the song flights they perform, and the consequent need for a more energy-efficient flight (Hedenström and Møller, 1992). Other species performing song flights also show sexual dimorphism in wing shape (e.g., Ceresa et al., 2022; Minias et al., 2013). The lack of effects of sex to wing pointedness and concavity in our results further suggests the occurrence of constraints acting on snowfinch wing shape; putative advantages of changes in wing shape related to song flights are likely overridden by other requirements.

The lack of spatial autocorrelation in the model residuals (see Results) and the lack of relevant effect of the random factor when added to the model (see Methods) strongly suggest that, within our study system, there are no further and unaccounted spatially varying factors (among sampling sites) that could influence the wing traits we considered. Therefore, the patterns we observed are unlikely to be affected by the relatively clustered sampling design, which reflected the patchy distribution of the species and the difficult accessibility to many breeding sites.

In conclusion, our results provide one of the very few assessments of the relationship between intraspecific morphological variation and habitat availability, and confirm that avian wing morphology can vary according to habitat extension also across relatively limited (regional) spatial scales.

Ethics statement

This work includes standard wild birds ringing procedures (capture, measurements and release, i.e., no experiments) in accordance with the Italian laws and regulated by ISPRA (Istituto Superiore per la Protezione e Ricerca Ambientale), all the procedure and the permits released by local and national authorities are already directly listed in the manuscript for higher transparency.

CRediT authorship contribution statement

Francesco Ceresa: Conceptualization, Formal analysis, Investigation, Funding acquisition, Writing - Original Draft. **Mattia Brambilla**: Formal analysis, Funding acquisition, Writing - Review & Editing. **Laura Kvist**: Funding acquisition, Writing - Review & Editing. **Severino Vitulano**: Investigation, Writing - Review & Editing. **Michele Pes**: Investigation, Writing - Review & Editing. **Laura Tomasi**: Investigation, Writing - Review & Editing. **Paolo Pedrini**: Funding acquisition, Writing - Review & Editing. **Chiara Bettega**: Investigation, Writing - Review & Editing. **Matteo Anderle**: Investigation, Writing - Review & Editing. **Andreas Hilpold**: Funding acquisition, Writing - Review & Editing. **Petra Kranebitter**: Project administration, Funding acquisition, Writing - Review & Editing.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03276.

Data availability

Data used in this paper are available in the Figshare Digital Repository (Data for paper "Wing morphology changes with habitat availability and elevation in an alpine-specialist bird", Global Ecology and Conservation).

References

Alatalo, R.V., Gustafsson, L., Lundbkrg, A., 1984. Why do young passerine birds have shorter wings than older birds? Ibis 126, 410–415. https://doi.org/10.1111/j.1474-919X.1984.tb00264.x.

Altamirano, T.A., de Zwaan, D.R., Scridel, D., Wilson, S., Martin, K., 2023. Rock cavity nesting as the norm: breeding songbirds of the temperate High Andes. Ecology 104 (2). https://doi.org/10.1002/ecy.3931.

Altshuler, D.L., Dudley, R., 2006. The physiology and biomechanics of avian flight at high altitude. Integr. Comp. Biol. 46, 6271. https://doi.org/10.1093/icb/icj008.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manag. 74, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x.

Bartoń, K., 2020. MuMIn: Multi-Model Inference. – <https://cran.r project.org/web/packages/MuMIn/index.html>.

Barve, S., Dhondt, A.A., Mathur, V.B., Cheviron, Z.A., 2016. Life-history characteristics influence physiological strategies to cope with hypoxia in Himalayan birds. Proc. R. Soc. B 283 (1843), 20162201. https://doi.org/10.1098/rspb.2016.2201.

Bech, N., Boissier, J., Drovetski, S., Novoa, C., 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. Anim. Conserv. 12 (2), 138–146. https://doi.org/10.1111/j.1469-1795.2008.00233.x.

Bettega, C., Fernández-González, Á., Ramon Obeso, J., Delgado, M.D.M., 2020. Circannual variation in habitat use of the White-winged Snowfinch *Montifringilla nivalis nivalis*. Ibis 162 (4), 1251–1261. https://doi.org/10.1111/ibi.12829.

Bourdeau, P.E., Johansson, F., 2012. Predator-induced morphological defences as by-products of prey behaviour: a review and prospectus. Oikos 121 (8), 1175–1190. https://doi.org/10.1111/j.1600-0706.2012.20235.x.

Boyce, A.J., Shakya, S., Sheldon, F.H., Moyle, R.G., Martin, T.E., 2019. Biotic interactions are the dominant drivers of phylogenetic and functional structure in bird communities along a tropical elevational gradient. Auk 136, ukz054. https://doi.org/10.1093/auk/ukz054.

Brambilla, M., Bettega, C., Delgado, M.M., Gabriel-Hernando, D., Päckert, M., Arlettaz, R., Dirren, S., Fontanilles, P., Gil, J.A., Herrmann, M., Hille, S., Korner-Nievergelt, F., Pedrini, P., Resano-Mayor, J., Schano, C., Scridel, D., 2022b. Insufficient considerations of seasonality, data selection and validation lead to biased species–climate relationships in mountain birds. J. Avian Biol. 2022 (9), e03015. https://doi.org/10.1111/jav.03015.

Brambilla, M., Rubolini, D., Appukuttan, O., Calvi, G., Karger, D.N., Kmecl, P., Mihelič, T., Sattler, T., Seaman, B., Teufelbauer, N., Wahl, J., Celada, C., 2022a. Identifying climate refugia for high-elevation Alpine birds under current climate warming predictions. Glob. Chang. Biol. 28, 4276–4291. https://doi.org/10.1111/gcb.16187.

Brown, C.R., Brown, M.B., 2013. Where has all the road kill gone? Curr. Biol. 23 (6), R233–R234. https://doi.org/10.1016/j.cub.2013.02.023.

Burnham, K.P., Anderson, D.R., 1998. Practical use of the information-theoretic approach. Model selection and inference. Springer, pp. 75–117.

Ceresa, F., Brambilla, M., Kvist, L., Vitulano, S., Pes, M., Tomasi, L., Pedrini, P., Hilpold, A., Kranebitter, P., 2023. Landscape characteristics influence regional dispersal in a high-elevation specialist migratory bird, the water pipit *Anthus spinoletta*. Mol. Ecol. 32, 1875–1892. https://doi.org/10.1111/mec.16853.

Ceresa, F., Brambilla, M., Kvist, L., Vitulano, S., Pes, M., Tomasi, L., Pedrini, P., Bettega, C., Anderle, M., Hilpold, A., Kranebitter, P., 2024. Restricted dispersal and inbreeding in a high-elevation bird across the 'sky islands' of the European Alps. J. Biogeogr. 51 (5), 853–868. https://doi.org/10.1111/jbi.14787.

Ceresa, F., Brambilla, M., Monrós, J.S., Rizzolli, F., Kranebitter, P., 2020. Within-season movements of Alpine songbird distributions are driven by fine-scale environmental characteristics. Sci. Rep. 10 (1), 5747. https://doi.org/10.1038/s41598-020-62661-0.

Ceresa, F., Vitulano, S., Pes, M., Tomasi, L., Brambilla, M., Kvist, L., Pedrini, P., Anderle, M., Hilpold, A., Kranebitter, P., 2022. Variation in wing morphology is related to breeding environment in a high-elevation specialist bird. J. Avian Biol. 2022 (11-12), e03007. https://doi.org/10.1111/jav.03007.

Chu, J.J., Claramunt, S., 2023. Determinants of natal dispersal distances in North American birds. Ecol. Evol. 13 (2), e9789. https://doi.org/10.1002/ece3.9789.

Claramunt, S., Hong, M., Bravo, A., 2022. The effect of flight efficiency on gap-crossing ability in Amazonian forest birds. Biotropica 54 (4), 860–868. https://doi.org/10.1111/btp.13109.

Demongin, L., 2016. Identification guide to birds in the hand. Péronnas: Beauregard-Vendon.

Desrochers, A., 2010. Morphological response of songbirds to 100 years of landscape change in North America. Ecology 91 (6), 1577–1582. https://doi.org/10.1890/09-2202.1.

Eklöv, P., Svanbäck, R., 2006. Predation risk influences adaptive morphological variation in fish populations. Am. Nat. 167 (3), 440–452. https://doi.org/10.1086/499544.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34 (1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419.

Fan, H., Guo, W., Lin, B., Hu, Z., Wang, C., Li, S., 2024. The influence of wing morphology upon intraspecific divergence in birds: a global study of subspecies richness. Avian Res., 100188 https://doi.org/10.1016/j.avrs.2024.100188.

Fernández, G., Lank, D.B., 2007. Variation in the wing morphology of Western Sandpipers (*Calidris mauri*) in relation to sex, age class, and annual cycle. Auk 124 (3), 1037–1046. https://doi.org/10.1093/auk/124.3.1037.

Ficetola, G.F., Colleoni, E., Renaud, J., Scali, S., Padoa-Schioppa, E., Thuiller, W., 2016. Morphological variation in salamanders and their potential response to climate change. Glob. Chang. Biol. 22 (6), 2013–2024. https://doi.org/10.1111/gcb.13255.

García, J., Arizaga, J., Rodríguez, J.I., Alonso, D., Suárez-Seoane, S., 2021. Morphological differentiation in a migratory bird across geographic gradients in mountains of southern Europe. J. Biogeogr. 48 (11), 2828–2838. https://doi.org/10.1111/jbi.14242.

Greene, A.E., Funk, W.C., 2009. Sexual selection on morphology in an explosive breeding amphibian, the Columbia spotted frog (*Rana luteiventris*). J. Herpetol. 43 (2), 244–251. https://doi.org/10.1670/08-112R.1.

Hallman, T.A., Guélat, J., Antoniazza, S., Kéry, M., Sattler, T., 2022. Rapid elevational shifts of Switzerland's avifauna and associated species traits. Ecosphere 13 (8), e4194. https://doi.org/10.1002/ecs2.4194.

Hedenström, A., Møller, A.P., 1992. Morphological adaptations to song flight in passerine birds: a comparative study. Proc. Royal Soc. B 247(1320), 183–187. https://doi.org/10.1098/rspb.1992.0026.

Heiniger, P.H., 1991b. Anpassungsstrategien des Schneefinken (*Montifringilla nivalis*) an die extremen Umweltbedingungen des Hochgebirges. Ornithol. Beob. 88, 193–207.

Heiniger, P.H., 1991a. Ecology of the snowfinch (*Montifringilla nivalis*) – Use of home range in winter and summer with special reference to the winter roosting sites. Rev. Suisse Zool. 98, 897–924.

Hermes, C., Döpper, A., Schaefer, H.M., Segelbacher, G., 2016. Effects of forest fragmentation on the morphological and genetic structure of a dispersal-limited, endangered bird species. Nat. Conserv. 16, 39–58. https://doi.org/10.3897/natureconservation.16.10905.

Hernández-Téllez, I., Aguirre, J.I., de la Hera, I., Onrubia, A., Tellería, J.L., 2023. Highland and lowland forest birds differ in their feather growth rates: a multispecies test in the southwestern Palaearctic. Ibis 166, 909–924. https://doi.org/10.1111/ibi.13286.

Ibarra-Macias, A., Robinson, W.D., Gaines, M.S., 2011. Experimental evaluation of bird movements in a fragmented Neotropical landscape. Biol. Conserv. 144 (2), 703–712. https://doi.org/10.1016/j.biocon.2010.08.006.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, N.E., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4 (1), 1–20. https://doi.org/10.1038/sdata.2017.122.

Kipp, F., 1959. Der Handflügel-Index als flugbiologische Maß. Vogelwarte 20, 77–86.

Körner, C., Ohsawa, M., 2006. Mountain systems, ecosystem and human well-being: current state and trends. In: Hassan, R., Scholes, R., Ash, N. (Eds.), Millennium Ecosystem Assessment, 1. Island Press, Washington, D.C, pp. 681–716.

Laiolo, P., Rolando, A., 2001. Ecogeographic correlates of morphometric variation in the red-billed Chough *Pyrrhocorax pyrrhocorax* and the Alpine Chough *Pyrrhocorax graculus*. Ibis 143, 602–616. https://doi.org/10.1111/j.1474-919X.2001.tb04888.x.

Lantz, S.M., Karubian, J., 2017. Environmental disturbance increases social connectivity in a passerine bird. Plos One 12 (8), e0183144. https://doi.org/10.1371/journal.pone.0183144.

Legendre, P., 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. J. Plant Ecol. 1 (1), 3–8. https://doi.org/10.1093/jpe/rtm001.

Leisler, B., Winkler, H., 2003. Morphological consequences of migration in passerines. In Avian migration. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 175–186. https://doi.org/10.1007/978-3-662-05957-9_11.

Lockwood, R., Swaddle, J.P., Rayner, J.M., 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. J. Avian Biol. 273–292. https://doi.org/10.2307/3677110.

Lu, X., Ke, D.H., Zeng, X.H., Yu, T.L., 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: response to more stressful environments. J. Arid Environ. 73 (12), 1103–1108. https://doi.org/10.1016/j.jaridenv.2009.06.011.

del Mar Delgado, M., Arlettaz, R., Bettega, C., Brambilla, M., de Gabriel Hernando, M., España, A., Fernández-González, Á., Fernández-Martín, Á., Antonio Gil, J., Hernández-Gómez, S., Laiolo, P., Resano-Mayor, J., Obeso, J.R., Pedrini, P., Roa-Álvarez, I., Schano, C., Scridel, D., Strinella, E., Toranzo, I., Korner-Nievergelt, F., 2021. Spatio-temporal variation in the wintering associations of an alpine bird. Proc. R. Soc. B 288 (1951), 20210690. https://doi.org/10.1098/rspb.2021.0690.

Minias, P., Kaczmarek, K., Włodarczyk, R., Janiszewski, T., 2013. Wing shape influences stopover strategies in a migratory shorebird, the common snipe. Condor 115 (3), 535–542. https://doi.org/10.1525/cond.2013.120137.

Naka, L.N., Costa, B.M., Lima, G.R., Claramunt, S., 2022. Riverine barriers as obstacles to dispersal in Amazonian birds. Front. Ecol. Evol. 10, 846975. https://doi.org/10.3389/fevo.2022.846975.

Norberg, U.M., 1996. Energetics of Flight. In: Carey, C. (Ed.), Avian Energetics and Nutritional Ecology. Springer, Boston, MA. https://doi.org/10.1007/978-1-4613-0425-8_7.

Oksanen et al. 2020. vegan: Community Ecology Package. – <https://cran.r-project.org/web/packages/vegan/index.html>.

Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35 (3), 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Resano-Mayor, J., Bettega, C., del Mar Delgado, M., Fernández-Martín, Á., Hernández-Gómez, S., Toranzo, I., España, A., de Gabriel, M., Roa-Álvarez, I., Gil, J.A., Strinella, E., Hobson, K.A., Arlettaz, R., 2020. Partial migration of White-winged snowfinches is correlated with winter weather conditions. Glob. Ecol. Conserv. 24, e01346. https://doi.org/10.1016/j.gecco.2020.e01346.

Rime, Y., Nussbaumer, R., Briedis, M., Sander, M.M., Chamberlain, D., Amrhein, V., Helm, B., Liechti, F., Meier, C.M., 2023. Multi-sensor geolocators unveil global and local movements in an Alpine-breeding long-distance migrant. Mov. Ecol. 11 (1), 1–13. https://doi.org/10.1186/s40462-023-00381-6.

Rolshausen, G., Segelbacher, G., Hobson, K.A., Schaefer, H.M., 2009. Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. Curr. Biol. 19, 2097–2101.

Ryding, S., Klaassen, M., Tattersall, G.J., Gardner, J.L., Symonds, M.R., 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. Trends Ecol. Evol. 36 (11), 1036–1048. https://doi.org/10.1016/j.tree.2021.07.006.

Saino, N., Ambrosini, R., Caprioli, M., Liechti, F., Romano, A., Rubolini, D., Scandolara, C., 2017. Wing morphology, winter ecology, and fecundity selection: evidence for sex-dependence in barn swallows (*Hirundo rustica*). Oecologia 184, 799–812. https://doi.org/10.1007/s00442-017-3918-0.

Saino, N., Rubolini, D., Von Hardenberg, J., Ambrosini, R., Provenzale, A., Romano, M., Spina, F., 2010. Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds. Funct. Ecol. 24 (3), 658–669. https://doi.org/10.1111/j.1365-2435.2009.01659.x.

Sander, M.M., Chamberlain, D., 2020. Evidence for intraspecific phenotypic variation in songbirds along elevation gradients in central Europe. Ibis 162, 1355–1362. https://doi.org/10.1111/ibi.12843.

Scott, G.R., 2011. Elevated performance: the unique physiology of birds that fly at high altitudes. J. Exp. Biol. 214, 2455–2462. https://doi.org/10.1242/jeb.052548.

Senar, J.C., Borras, A., Cabrera, J., Cabrera, T., Björklund, M., 2006. Local differentiation in the presence of gene flow in the citril finch *Serinus citrinella*. Biol. Lett. 2 (1), 85–87. https://doi.org/10.1098/rsbl.2005.0412.

Sheard, C., Neate-Clegg, M.H., Alioravainen, N., Jones, S.E., Vincent, C., MacGregor, H.E., Bregman, T.P., Claramunt, S., Tobias, J.A., 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat. Commun. 11 (1), 2463. https://doi.org/10.1038/s41467-020-16313-6.

Somers, K.M., 1986. Multivariate allometry and removal of size with principal components analysis. Syst. Biol. 35 (3), 359–368. https://doi.org/10.1093/sysbio/35.3.359.

Somers, K.M., 1993. sizepca v6. http://www.life.bio.sunysb.edu/morph/soft-mult.html.

Storfer, A., 1999. Gene flow and endangered species translocations: a topic revisited. Biol. Conserv. 87 (2), 173–180. https://doi.org/10.1016/S0006-3207(98)00066-4.

Strinella, E., Catoni, C., de Faveri, A., Artese, C., 2013. Ageing and sexing of the snow finch *Montifringilla nivalis* by the pattern of primary coverts. Avocetta 37, 9–14.

Summers-Smith, D., Bonan, A., 2020. White-winged Snowfinch (Montifringilla nivalis), version 1.0. In Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whwsno1.01.

Svensson, E.I., Eroukhmanoff, F., Friberg, M., 2006. Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. Evolution 60 (6), 1242–1253. https://doi.org/10.1554/06-036.1.

Swaddle, J.P., Witter, M.S., 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. Can. J. Zool. 75, 1135–1146. https://doi.org/10.1139/z97-136.

Szekely, T., Lislevand, T., Figuerola, J., 2007. Sexual size dimorphism in birds. In: Fairbairn, D.J., Blanckenhorn, W.U., Székely, T. (Eds.), Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, pp. 27–37. https://doi.org/10.1093/acprof:oso/9780199208784.003.0004.

Tyler, S., 2020. Water Pipit (*Anthus spinoletta*), version 1.0. In: Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World (J. del Hoyo. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.watpip1.01.

Vanhooydonck, B., Herrel, A., Gabela, A.N.A., Podos, J., 2009. Wing shape variation in the medium ground finch (*Geospiza fortis*): an ecomorphological approach. Biol. J. Linn. Soc. Lond. 98, 129–138. https://doi.org/10.1111/j.1095-8312.2009.01269.x.

Weeks, B.C., O'Brien, B.K., Chu, J.J., Claramunt, S., Sheard, C., Tobias, J.A., 2022. Morphological adaptations linked to flight efficiency and aerial lifestyle determine natal dispersal distance in birds. Funct. Ecol. 36 (7), 1681–1689. https://doi.org/10.1111/1365-2435.14056.

Wilson, R.E., Valqui, T.H., McCracken, K.G., 2010. Chapter 12: ecogeographic Variation in Cinnamon Teal (*Anas cyanoptera*) Along Elevational and Latitudinal Gradients. Ornithol. Monogr. 67, 141–161. https://doi.org/10.1525/om.2010.67.1.141.

Wood, H., Cousins, S.A., 2023. Variability in bat morphology is influenced by temperature and forest cover and their interactions. Ecol. Evol. 13 (1), e9695. https://doi.org/10.1002/ece3.9695.

Yom-Tov, Y., Leader, N., Yom-Tov, S., Baagøe, H.J., 2010. Temperature trends and recent decline in body size of the stone marten *Martes foina* in Denmark. Mamm. Biol. 75, 146–150. https://doi.org/10.1016/j.mambio.2008.10.005.

de Zwaan, D.R., Wilson, S., Gow, E.A., Martin, K., 2019. Sex-specific spatiotemporal variation and carry-over effects in a migratory alpine songbird. Front. Ecol. Evol. 7, 285. https://doi.org/10.3389/fevo.2019.00285.