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**Evidence for intraspecific phenotypic variation in songbirds along elevation gradients in central Europe**

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(Article begins on next page)



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11 **Evidence for intra-specific phenotypic variation in songbirds along elevation**  
12 **gradients in central Europe**

13 **ABSTRACT**

14 Studying phenotypic variations along gradients may provide insights into mechanisms that drive species  
15 distributions, and thus can be useful indicators of environmental change. In mountains, the study of phenotypic  
16 variation along elevation gradients is of increasing relevance due to impacts of climate change. We analysed  
17 European ringing data to unravel the direction of phenotypic variation along elevation gradients in six common  
18 and resident songbird species occurring along a wide elevational range. We modelled intra-specific change in  
19 wing length, body mass and their ratio with elevation and found a significant increase in wing length and a  
20 decrease in body mass at high elevations. The results of our exploratory analysis show the potential that  
21 continent-wide ringing databases offer to describe patterns of phenotypic variation along environmental  
22 gradients.

23

24 **Keywords:** Alps, Bergmann's Rule, body mass, wing length.

25

26 **Running head:** Phenotypic variation in Alpine birds

## 27 INTRODUCTION

28 Species with high variability in traits may more readily adapt to environmental changes (Lehikoinen *et al.* 2018).  
29 Phenotypic variation within species is shaped by the spatial and temporal differences of the habitats in which  
30 different populations live and includes differences in morphological traits such as wing length (Poblete *et al.*  
31 2018). Studies of phenotypic variation in relation to the environment are important, as they may reveal  
32 fundamental drivers of variation within and between species. For example, Bergmann's Rule proposes that  
33 species of larger size tend to be found in colder climates (Bergmann 1847), a concept that has also been  
34 extended to variation within species, although support is not universal (Blackburn *et al.* 1999). Furthermore,  
35 studies of phenotypic variation may reveal sensitivity to environmental change. For example, recent studies  
36 have documented evidence that morphological changes in mountain birds (Delgado *et al.* 2019) and migratory  
37 passerines (Weeks *et al.* 2019) are correlated with climate change.

38 Along elevation gradients, numerous factors shape phenotypic adaptations. Variables that are causally related  
39 to elevation include ultraviolet radiation, oxygen levels, and (of particular relevance to phenotypic adaptation)  
40 temperature and air pressure. Bergmann's Rule is used to explain morphological differences across climate  
41 gradients, predominantly from warmer to colder environments (Meiri & Dayan 2003). There is some evidence  
42 for larger individuals (i.e. a higher body mass) with relatively shorter extremities, e.g. legs and wings, at high  
43 elevations (Laiolo & Rolando 2008, Meiri & Dayan 2003, Poblete *et al.* 2018). This may arise through selection  
44 for larger animals that have a lower surface area to volume ratio than smaller animals, so they radiate less  
45 body heat per unit of mass, in agreement with Bergmann's Rule. Conversely, a preponderance of smaller  
46 individuals (a combination of different length measurements and body mass) has been reported at higher  
47 elevations (Lundblad & Conway 2019), as have smaller individuals (body mass) with longer wings (Bears *et al.*  
48 2008, Lu *et al.* 2009). The latter seems reasonable as smaller bodies require lower energy intake, which might  
49 be a limiting factor in high elevation habitats with seasonally variable resource availability. For example,  
50 Freeman (2017) found little evidence for body size clines within tropical bird species, but where there were  
51 differences, they were inconsistent with Bergmann's Rule. Similarly, Boyce *et al.* (2019) found that body mass  
52 of Bornean mountain birds decreased with elevation whereas relative tarsus length increased. The authors  
53 argued that phenotypic adaptation is more likely to be driven by the foraging mode of high elevation species,  
54 rather than temperature (Boyce *et al.* 2019). In both of these studies, wing length was not related to elevation,

55 even though other studies have argued that longer wings reduce the cost of flying at lower air pressure (Scott  
56 2011) and may increase aerodynamic performance (Altshuler & Dudley 2006). Furthermore, flying in oxygen-  
57 thin environments requires physiological and morphological adaptations to enable the birds to cope with  
58 hypoxia and to reduce the metabolic cost of staying aloft (Barve *et al.* 2016, Scott 2011). A consensus on the  
59 association between phenotypic adaptations and elevation is therefore lacking, possibly because there have  
60 been few large-scale investigations on this topic.

61 We aimed to assess whether there was a trend in intra-specific morphological variation in songbird species  
62 along elevation gradients. We analysed the variation in two phenotypic traits (wing length, body mass) and  
63 their ratio (i.e. wing length relative to body mass) within six different songbird species that occur along  
64 elevation gradients in the breeding and post-fledging period (spring and summer). We used ringing data  
65 retrieved from the EURING Data Bank (du Feu 2019), the coordinating organisation for European bird ringing  
66 schemes, and collected mainly in the Alps and their foothills.

## 67 **METHODS**

68 We selected species breeding along a continuous elevation gradient from 0 to >2000 m.a.s.l. based on  
69 information in BirdLife International (2019), and from digital elevation maps available in [www.ornitho.it](http://www.ornitho.it).  
70 Furthermore, we selected species which are classified as residents and/or facultative short-distance migrants  
71 (del Hoyo & Christie 2006, Glutz von Blotzheim & Bauer 1991), as long-distance migration itself shapes wing  
72 morphology (Fiedler 2005). We requested all available ringing data of birds captured and recaptured frequently  
73 (Fasano *et al.* 2018) in our prior defined Alpine landscape (44°N - 48°N, 4°E - 16°E, Switzerland, France, Italy,  
74 Austria, Germany, Slovenia) from the EURING database. These data included captures from outside the defined  
75 area (e.g. northern France, northern Germany, Sweden) if birds were then recovered inside this area (Fig. 1).  
76 Within the data set of all 14 species, we selected only adults that were first captures (to exclude  
77 pseudoreplication). Although we restricted our species to those that are mainly resident in the study region,  
78 we cannot exclude altitudinal migration during winter (Barcante *et al.* 2017, Boyle 2017, Hsiung *et al.* 2018).  
79 Furthermore, some of our species are known to disperse over short distances within their ranges, including  
80 some longer distance movements within Europe, e.g. Black Redstart *Phoenicurus ochruros*, Eurasian Blackbird  
81 *Turdus merula* (del Hoyo & Christie 2006, Glutz von Blotzheim & Bauer 1991). We therefore excluded captures  
82 outside the period May to September to minimise the chances of including migrant individuals breeding at

83 other elevations than those expected from the ringing location (for brevity henceforth referred to as 'breeding  
84 birds'). After filtering the records following the above criteria, we selected those species for which we had  
85 sufficient records across the elevation gradient (10 % of all records per species had to be from locations above  
86 1200 m.a.s.l.) and which had biometric data, i.e. wing length (as measured by the length of 3<sup>rd</sup> primary) and  
87 body mass. They were Eurasian Blackbird, Eurasian Wren *Troglodytes troglodytes*, Coal Tit *Periparus ater*,  
88 Goldcrest *Regulus regulus*, Black Redstart and Willow Tit *Poecile montanus*.

## 89 **Statistical Analyses**

90 As wing length is allometrically correlated with body mass (i.e. that individuals with longer wings also have  
91 higher body masses, Fig. S1) and both may be a proxy for body size, we calculated the ratio of wing length to  
92 the cubic root of body mass ( $wing\ length / \sqrt[3]{body\ mass}$ , henceforth wing:mass ratio) to analyse the  
93 differences in relative wing length between individuals breeding at low and high elevations. To allow direct  
94 comparison of effect sizes across species, we scaled all biometrics at the species level (z-score). To assess how  
95 wing length, body mass and wing:mass ratio varied as a function of elevation, we used linear mixed effect  
96 models, using the 'lmer' function in R 3.4.2 (R Core Team 2019), assuming normally distributed errors. The  
97 models included elevation as an explanatory variable, which we considered in two different ways in separate  
98 models: first, as a continuous variable, and second as a categorical variable. Following the definition of  
99 mountain habitat for the Alps (Lehikoinen *et al.* 2018), we defined locations <1200 m.a.s.l. as low and >1200  
100 m.a.s.l. as high elevations. Grouping the birds according to high and low elevations reflects the ecological  
101 context of this study, whereas showing the effect along a continuous gradient gives information about the  
102 distribution of our data.

103 Wing length, body mass and wing:mass ratio (all scaled) were analysed as response variables in three separate  
104 models in relation to elevation. We were interested in general trends with elevation across Alpine birds, hence  
105 we pooled all species for the analysis and set species as a random effect in all six models (i.e. three different  
106 response variables in relation to two different measures of elevation) to account for the fact that variation in  
107 scaled traits may be species-specific. However, we also ran the same models for each individual species  
108 (without the random term) to determine the extent to which individual species associations were consistent  
109 with the overall trends. There is evidence that biometrics of birds have changed over time in relation to  
110 increasing global temperatures due to climate change (Delgado *et al.* 2019, Weeks *et al.* 2019). To account for

111 possible temporal trends over our time period of 36 years, we tested the effect year by including it as a fixed  
112 effect in the overall model and comparing AIC values for models with and without year. Additionally, we  
113 performed linear models for each species including year.

114 Analysis of model residuals did not show any violation of the model assumptions. We used Bayesian methods  
115 to obtain uncertainty estimates of the model parameters (Korner-Nievergelt *et al.* 2015) and therefore to  
116 account for the uncertainty of the model estimates and model predictions. Following Korner-Nievergelt *et al.*  
117 (2015), we used improper prior distributions, namely  $p(\beta) \sim 1$ , for the coefficients and  $p(\sigma) \sim 1/\sigma$  for the  
118 variance parameters and furthermore obtained posterior distributions of the respective models by simulating  
119 5000 values from the joint posterior distributions of each model's parameter, applying the function 'sim'  
120 included in the package 'arm' (Gelman & Hill 2007). For the respective model estimates, we used the means of  
121 the simulated values from the joint posterior distributions of each model's parameter and the 2.5% and 97.5%  
122 quantiles as limits for the 95% credible intervals (CrI; Korner-Nievergelt *et al.* 2015). The effect of a variable was  
123 declared as significant if the corresponding 95% CrI did not include zero or if the 95% CrIs of the comparative  
124 groups (low and high elevation) did not overlap.

125

## 126 **RESULTS**

127 After selecting six target species with sufficient sample sizes, the raw data from EURING contained 79,653  
128 records, of which 30,426 were first captures and 12,805 fitted our time period of May to September. Of these,  
129 only 1,445 records contained biometrics (11% of all first captures during the breeding season; see Table S1 for  
130 sample sizes according to species), and, despite having considered data from a total of six countries, only data  
131 from the Swiss Ringing Scheme were usable. The records spanned a 36 year period (1982 – 2018, mean: 2010,  
132 1<sup>st</sup> quartile: 2008, 3<sup>rd</sup> quartile: 2015), and presented an overall elevation gradient from 95 m.a.s.l. to 1,900  
133 m.a.s.l (mean: 962 m.a.s.l., 1<sup>st</sup> quartile: 462 m.a.s.l., 3<sup>rd</sup> quartile: 1,233 m.a.s.l.). The locations of first captures  
134 were widely distributed across Europe, but the majority of the records was located within or close to the Alps  
135 (Fig. 1; see Fig. S2 for heatmaps).

136 When considering the two elevation categories, there were  $n= 908$  records for the low elevation group and  $n =$   
137 534 records for the high elevation group. In the overall model, the year had no significant effect on the

138 biometrics and did not improve the model in terms of AIC, hence it was not considered further (Table S2). We  
139 additionally tested the effect of year on the wing:mass ratio in single-species models and found a positive  
140 effect in Coal Tit, indicating their wings increased in length relative to body mass over a period of 30 years (Fig.  
141 S3), but not in any other species, nor in the combined-species model.

142 We found a significant positive effect of elevation (continuous) on scaled wing length, which increased by 0.15  
143 mm (95% CrI: 0.04 – 0.27) per 1000m increase in elevation. Body mass was found to decrease significantly with  
144 elevation ( $\beta = -0.11$ , 95% CrI: -0.21 – -0.01). The wing:mass ratio also increased significantly with elevation ( $\beta =$   
145 0.14, 95% CrI: 0.09 – 0.20). When records were grouped into high and low elevation, the results were similar,  
146 with a positive effect on wing length ( $\beta = 0.15$ , 95% CrI: 95% CrI: 0.02 – 0.28) and wing:mass ratio ( $\beta = 0.20$ ,  
147 95% CrI: 0.12 – 0.28; Table 1, Fig. 2). In all models, a lot of variation was unexplained, resulting in very low  $R^2$ -  
148 values (<0.1, Table 1). For single-species models, parameter estimates were in general in accord with those of  
149 the combined-species model in terms of direction of effect. There was stronger support (i.e. a significant effect)  
150 for longer wings in Blackbird and Willow Tit), lower body masses in Coal Tit and increasing wing:mass ratio in  
151 Blackbird and Coal Tit, with increasing elevation. However, Willow Tit body mass showed the opposite trend to  
152 the overall model, significantly increasing with elevation (Table S3).

153

## 154 **DISCUSSION**

155 Individuals breeding at high elevations were generally smaller and had longer wings. Wing:mass ratio increased  
156 with higher elevations, i.e. wing length increased relative to body size along the gradient, which was driven by  
157 both increases in wing length and decreases in body mass (Table 1, Fig. 2). These associations were, however,  
158 fairly weak in terms of the variation explained by the models, and for body mass, in terms of the consistency of  
159 results at the species level.

160 Interestingly, our results do not provide much support for Bergmann's rule, which predicts shorter wings and  
161 larger bodies in colder (therefore higher elevation) environments (as shown by Laiolo & Rolando 2008, Meiri &  
162 Dayan 2003, Poblete *et al.* 2018). The combined-species model suggested a general decrease in body mass with  
163 elevation, although at the individual species level (Table S3), there was a single species, Willow Tit, that showed  
164 an increase in body mass. There was more consistency in associations between wing length and elevation,



165 longer wings being evident in combined-species models and in most individual species (although only two were  
166 significant). Similar results have been found in individual species. For example, female Dark-eyed Juncos *Junco*  
167 *hyemalis* breeding at high elevations had longer wings and shorter tarsi (a measure of body size; Bears *et al.*  
168 2008), and snowfinch *Montifringilla* species were smaller (in terms of body length, bill length, body mass,  
169 tarsus length) with longer wings and a higher ratio of wing length and body size at high elevation sites (Lu *et al.*  
170 2009).

171

172 Along an elevation gradient, temperature (the variable hypothesized to explain Bergmann's Rule) might not be  
173 the only determining factor shaping bird morphology. Indeed, in tropical mountain systems, it has been shown  
174 to be of lower importance for trait variations along elevation gradients (Boyce *et al.* 2019, Freeman 2017);  
175 instead, flying in thin air (lower air pressure at high elevations) and the necessity to increase flight performance  
176 (due to stronger winds) might select for longer wings (Altshuler & Dudley 2006, Bears *et al.* 2008). The  
177 seasonality of resource availability in higher elevation habitats, e.g. the later peak in insect abundance due to  
178 snow cover (Bears *et al.* 2003), hypoxia and climate severity (Bears *et al.* 2008) may further lead to an  
179 advantage of having a small body in order to reduce the amount of energy needed. It is possible that these  
180 factors selected for smaller body sizes in high elevation habitats, but there may also be direct effects that  
181 restrict the growth of morphological traits, such as body mass, during the individual's lifetime.

182

183 Although our results give some support to phenotypic adaptation to lower air pressure at higher elevations, it  
184 must be acknowledged that there are many potentially important drivers that vary along the gradient which  
185 were unable to take into account. For example, it is known that variation in wing morphology within species  
186 may be influenced by the degree of forest fragmentation (e.g. Fiedler 2005, Desrochers 2010) which could vary  
187 from more anthropogenically disturbed lowlands to mountain forests. Additionally, wing morphology may vary  
188 according to foraging habitat, as round-winged species have been shown to forage closer to the ground,  
189 whereas species with more pointed wings forage more commonly in trees (Marchetti *et al.* 1995).

190 Furthermore, the influence of environmental factors such as forest cover and fragmentation may vary at large  
191 geographical scales. Our sample was derived from a relatively large area in order to maximize sample size. The  
192 availability of a larger sample of biometrics from ringed birds (see below) would also allow habitat and  
193 geographical influences (e.g. latitude) to be estimated.

194

195 Unfortunately, the data were not sufficient to account for sex and age. In addition to effects of environmental  
196 variables (see above), we assume that a large proportion of the unexplained variation in our models comes  
197 from morphological differences between males and females, as shown for songbirds in similar studies (Bears *et al.*  
198 *al.* 2008, Lu *et al.* 2009). Furthermore, our measure of body size (body mass) is likely to vary between  
199 individuals and may be sensitive to fine-scale seasonal and even diel variations that we were not able to take  
200 into account. Nevertheless, we would expect that body mass represents a reasonable, although fairly  
201 approximate, measure of body size. A better measure of body size would be one related to skeletal growth,  
202 such as relative tarsus length, which is likely to be less temporally variable (Bears *et al.* 2008), but which was  
203 not available on the EURING Data Bank. Another reason for the relatively weak effect of elevation on the  
204 morphological traits is that we used species occurring across the entire elevation gradient instead of comparing  
205 subspecies of low and high elevation. Additionally, due to the habitat requirements of the species we have  
206 chosen (mostly forest species), we do not have data from very high elevation habitats above the tree-line,  
207 where environmental cues may exert stronger pressures on the breeding and survival of birds (Lu 2005), in  
208 particular to cope with hypoxia (Barve *et al.* 2016), although within the studied region, possibly only Black  
209 Redstart would occur at these elevations in addition to lower elevation habitats.

210 This study has used a continental-scale database to analyse phenotypic variability in passerine species across  
211 elevation gradients. Whilst we find some intriguing results, in particular individuals at higher elevations having  
212 lower body mass and relatively longer wings, we were restricted in the conclusions that we were able to draw  
213 due to the availability of the data. To better understand phenotypic adaptations of birds to elevation, we  
214 highlight the importance of the collection of biometric ringing data, especially for high elevation populations,  
215 where data from breeding periods is lacking for many species. We suggest that ringers always record wing  
216 length (both, 3<sup>rd</sup> primary and maximum wing length) and tarsus length, as well as body mass. Furthermore, the  
217 scientific potential of standardised bird ringing could be higher if we were able to improve the data transfer  
218 from national ringing schemes to the EURING Data Bank. Even though measurements are commonly taken  
219 within the standard protocols in all European ringing schemes, we only located usable data from the Swiss  
220 Ringing Scheme. Enhancing biometric data availability at the European scale would greatly enhance our ability  
221 to study species adaptations.

222 The current literature covers almost exclusively tropical mountain ecosystems, and comparative within-species  
223 studies in temperate regions are lacking, which might be an additional reason for the inconsistency in the  
224 results. European-wide or even global ringing datasets have a huge potential to address questions regarding  
225 the phenotypic adaptations to different environments within the same species and their response to climate  
226 change (as there are indications for changes in morphology within the last decades, e.g. Fig. S3, and Delgado *et*  
227 *al.* 2019, Weeks *et al.* 2019). Further studies with larger biometric datasets (especially for high elevation  
228 populations of species) may even enable us to analyse differences in morphological variability between  
229 specialists and generalists, species of different habitat types (open grassland vs. forest), or differences in the  
230 degree of phenotypic plasticity between single species or subspecies (see Fig. S4 for visual comparison of the  
231 variability in traits between the study species, showing slightly higher variability in the data of Blackbirds and  
232 Coal Tits). Ultimately, we might be able to use phenotypic traits as predictors for the ability of a species to shift  
233 their range, and to assess whether they are more resilient and/or resistant to environmental changes.

234

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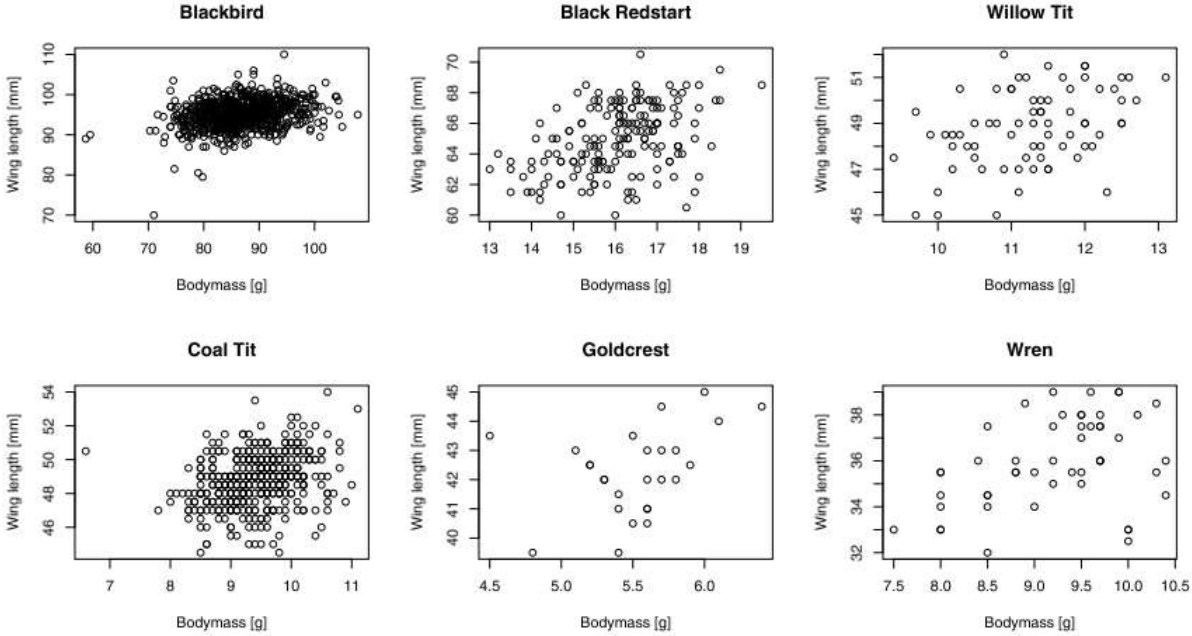
**Table 1.** Effect of elevation (continuous in  $m \times 10^3$ , and categorical) on the bird's scaled (z score) wing length, body mass and wing:mass ratio, modelled with linear mixed effect models (LMMs). The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects of elevation are given in bold.  $N = 1442$  in each case.

LMM	Intercept	Estimate (elevation)	Marginal $R^2$	Conditional $R^2$
Wing length ~ elevation (continuous) + (1 Species)	-0.157 (95% CrI: -0.292 – -0.022)	<b>0.153</b> <b>(95% CrI: 0.040 - 0.270)</b>	0.007	0.010
Body mass ~ elevation (continuous) + (1 Species)	0.119 (95% CrI: 0.002 – 0.238)	<b>-0.111</b> <b>(95% CrI: -0.210 - -0.010)</b>	0.004	0.005
Ratio ~ elevation (continuous) + (1 Species)	-0.23 (95% CrI: -1.44 – 1.01)	<b>0.140</b> <b>(95% CrI: 0.09 – 0.20)</b>	0.002	0.930
Wing length ~ elevation (categorical) + (1 Species)	-0.061 (95% CrI: -0.153 – 0.031)	<b>0.145</b> <b>(95% CrI: 95% CrI: 0.017 – 0.279)</b>	0.005	0.008
Body mass ~ elevation (categorical) + (1 Species)	0.058 (95% CrI: -0.020 – 0.140)	-0.120 (95% CrI: -0.241 – 0.004)	0.004	0.005
Ratio ~ elevation (categorical) + (1 Species)	-0.160 (95% CrI: -1.38 – 1.060)	<b>0.198</b> <b>(95% CrI: 0.120 – 0.277)</b>	0.004	0.930

**Figure 1.** Locations of all first captures during breeding season (May – September) for each species. Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the whole dataset are given in Table S1.

**Figure 2.** Intra-specific morphological variation of passerines along an elevation gradient. Plots show combined data of six species. Scaled measures wing length, body mass and wing:mass ratio along a continuous elevation gradient were analysed. Regressions are black solid lines and the corresponding 95% CrI are in grey, when the effect was significant. Right below: Differences in scaled measures wing length (filled circle), body mass (circle) and wing:mass ratio (square) between captures from low (<1,200 m.a.s.l.) and high (>1,200 m.a.s.l.) breeding grounds. Results of the appropriate LMMs are provided in Table 1.

SUPPLEMENTARY ONLINE MATERIAL

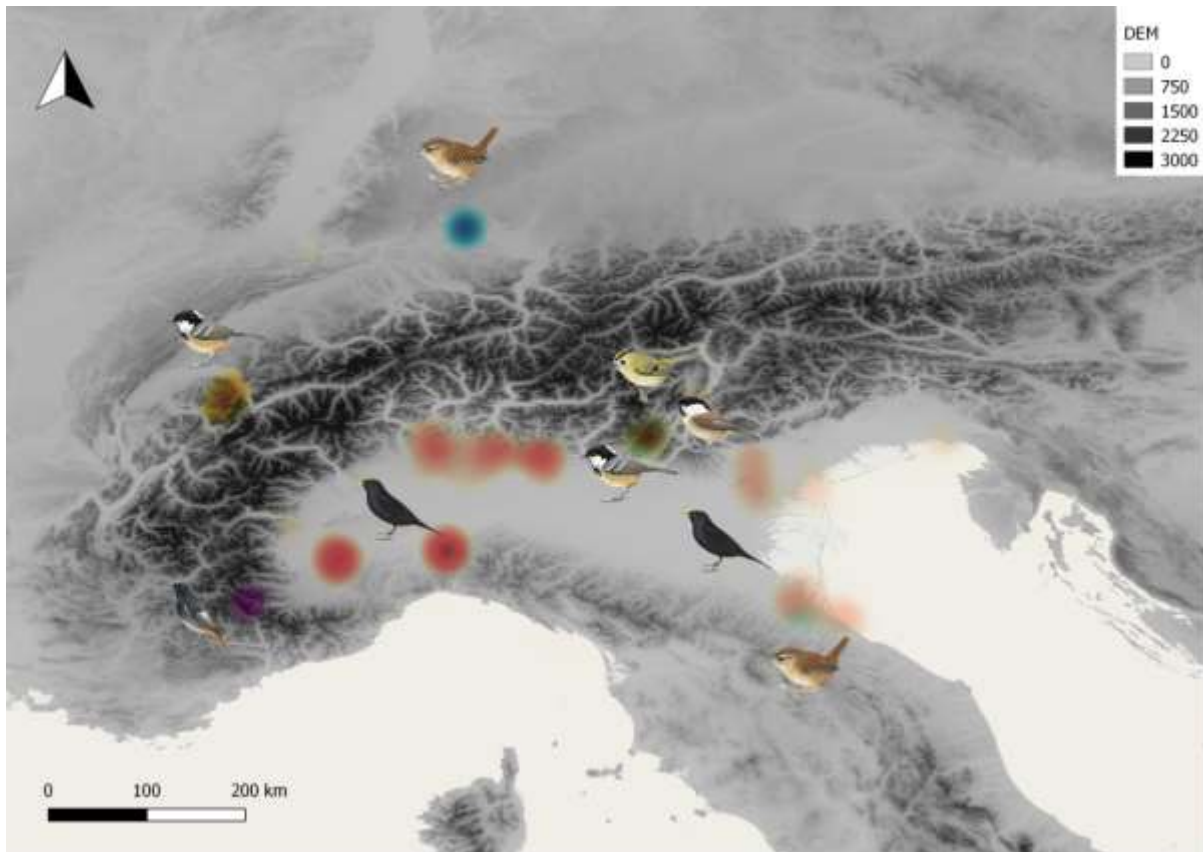


**Figure S1.** Associations between wing length and body mass for all six study species. The unscaled raw data are shown. Sample sizes for each species are given in Table S1.



**Table S1.** Sample sizes of each species included in the analysis (Number of records with biometrics). Number of records from birds captured above 1,200 m.a.s.l. are given in brackets. Ringing records were included if, for each individual (first capture during breeding season), location, date, wing length and body mass was available (% of records with biometrics).

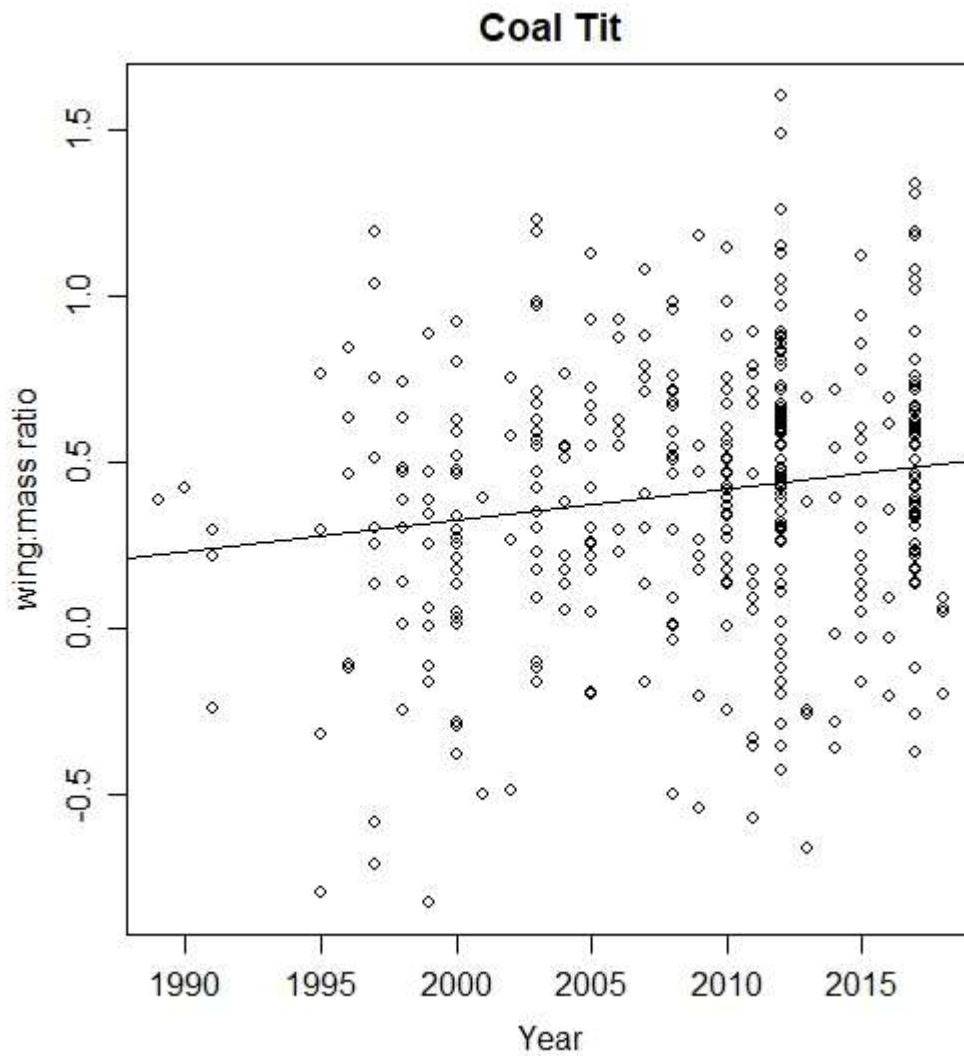
Species	Total no. of records in Data bank	No. of adult first captures	No. of first captures during breeding season	No. of records with biometrics	% of records with biometrics
All species	79,653	30,426	12,805	1,442 (908)	11
Blackbird <i>Turdus merula</i>	53,811	20,039	8,844	739 (61)	8
Eurasian Wren <i>Troglodytes troglodytes</i>	8,285	3,195	485	50 (13)	10
Coal Tit <i>Periparus ater</i>	7,633	3,210	1,936	388 (364)	20
Goldcrest <i>Regulus regulus</i>	5,437	2,272	441	26 (21)	6
Black Redstart <i>Phoenicurus ochruros</i>	3,026	1,168	706	170 (15)	24
Willow Tit <i>Poecile montanus</i>	1,461	542	393	72 (62)	18



**Figure S2.** Species-specific heatmaps for locations of first captures (Blackbird: red, Eurasian Wren: blue, Coal Tit: orange, Goldcrest: green, Black Redstart: purple, Willow Tit: yellow). Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the dataset used in the analysis are given in Table S1 and their distribution across the whole area in Figure 2 (main text).

**Table S2.** Effect of elevation (continuous (in  $m \times 10^3$ )) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio between both, modelled with linear mixed effect models (LMMs, function 'lmer'), including year as fixed effect. The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects are given in bold.  $\Delta$ AIC is the difference between the model without year (that used in the main text) and the model including year as a fixed effect (that presented here).  $N = 1442$ .

LMM	Intercept	Estimate (elevation)	Estimate (year)	Marginal $R^2$	Conditional $R^2$	$\Delta$ AIC
Ratio ~ elevation + year + (1 Species)	-4.86 (95% CrI: -12.19 – 2.54)	<b>0.136</b> <b>(95% CrI: 0.080 – 0.190)</b>	0.002 (95% CrI: -0.001 – 0.006)	0.002	0.930	0.5

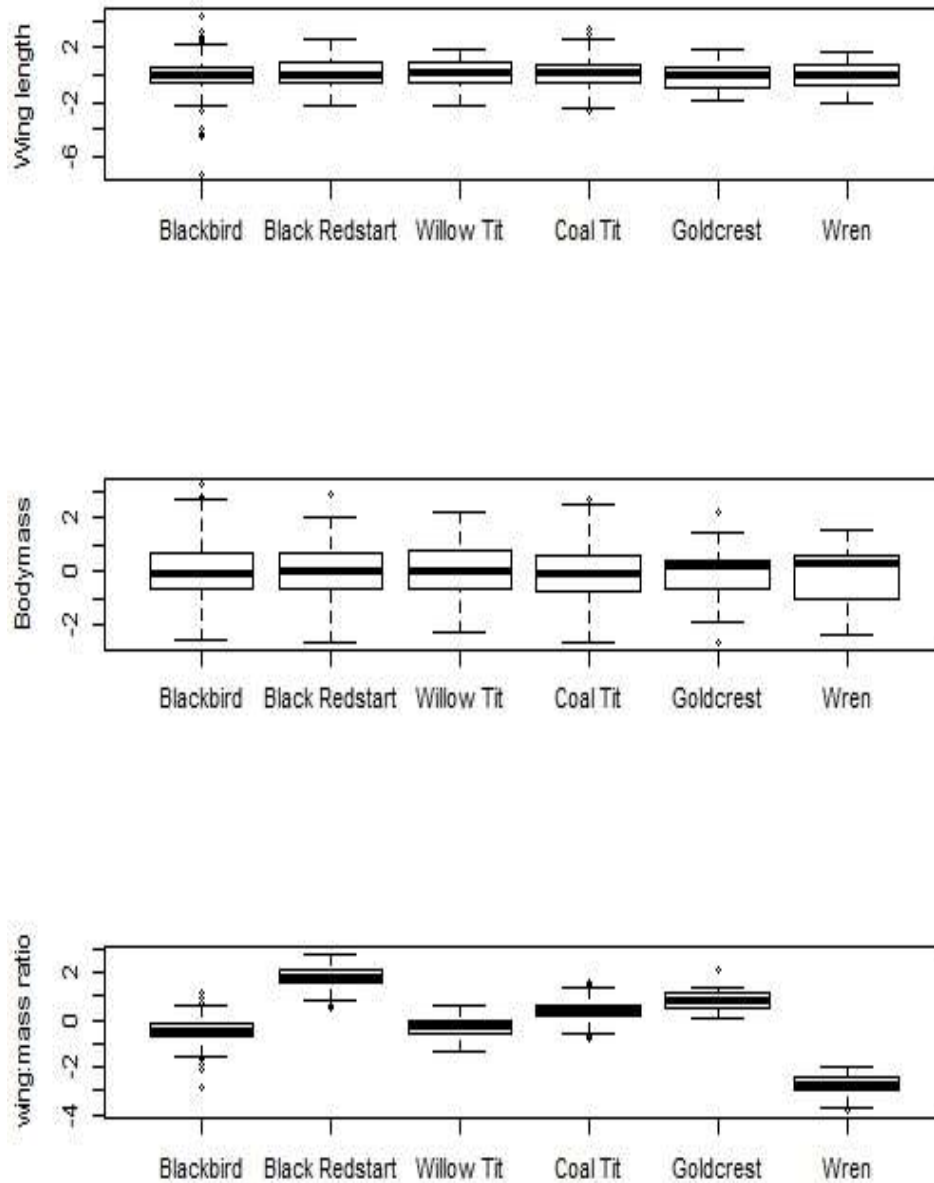


**Figure S3.** Significant effect of year on the scaled wing:mass ratio in Coal Tits ( $y = 0.009x - 18.63$ ,  $df = 385$ ,  $P < 0.01$ ) using a linear model (response variable: wing:mass ratio, explaining variable: year) with the function 'lm'.

**Table S3.** Single-species models for the effect of elevation (continuous (in m x 10<sup>3</sup>)) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio (ratio), modelled with linear models (function 'lm').

Species	LM	Intercept ± se	Estimate (elevation) ± se	Sample size (No. of individuals)	P-value	R <sup>2</sup>
Blackbird <i>Turdus merula</i>	Wing length ~ elevation	-0.173 ± 0.069	<b>0.266 ± 0.091</b>	734	<b>0.004</b>	0.010
	Body mass ~ elevation	0.037 ± 0.068	-0.031 ± 0.090	734	0.72	-0.001
	Ratio ~ elevation	-0.518 ± 0.030	<b>0.120 ± 0.039</b>	734	<b>0.002</b>	0.012
Eurasian Wren <i>Troglodytes troglodytes</i>	Wing length ~ elevation	-0.127 ± 0.263	0.152 ± 0.264	49	0.57	-0.014
	Body mass ~ elevation	0.068 ± 0.264	-0.081 ± 0.265	49	0.76	-0.019
	Ratio ~ elevation	-2.840 ± 0.116	0.100 ± 0.117	49	0.42	-0.007
Coal Tit <i>Periparus ater</i>	Wing length ~ elevation	0.008 ± 0.225	-0.007 ± 0.144	386	0.96	-0.003
	Body mass ~ elevation	1.380 ± 0.207	<b>-0.904 ± 0.133</b>	386	<b>&lt; 0.001</b>	0.105
	Ratio ~ elevation	0.044 ± 0.089	<b>0.238 ± 0.057</b>	386	<b>&lt; 0.001</b>	0.040
Goldcrest <i>Regulus regulus</i>	Wing length ~ elevation	-0.895 ± 1.131	0.700 ± 0.904	24	0.48	-0.017
	Body mass ~ elevation	-0.413 ± 0.978	0.421 ± 0.781	24	0.60	-0.030
	Ratio ~ elevation	0.560 ± 0.407	0.188 ± 0.325	24	0.57	-0.029
Black Redstart <i>Phoenicurus ochruros</i>	Wing length ~ elevation	-0.120 ± 0.226	0.146 ± 0.241	167	0.55	-0.004
	Body mass ~ elevation	0.053 ± 0.218	-0.026 ± 0.233	167	0.91	-0.006
	Ratio ~ elevation	-1.751 ± 0.099	0.070 ± 0.106	167	0.51	-0.003
Willow Tit <i>Poecile montanus</i>	Wing length ~ elevation	-1.228 ± 0.397	<b>0.857 ± 0.266</b>	71	<b>0.002</b>	0.12

Body mass ~ elevation	-0.933 ± 0.409	<b>0.651 ± 0.274</b>	71	<b>0.02</b>	0.06
Ratio ~ elevation	-0.516 ± 0.161	0.156 ± 0.107	71	0.15	0.015



**Figure S4.** Boxplots show a similar variability in the scaled biometrics across the study species. All available data across all elevations included. Slightly higher variability seems to occur in Blackbirds and Coal Tits. Inter-species variability is highest in the wing:mass ratio.