

Title

Surviving at high elevations: an inter- and intraspecific analysis in a mountain bird community.

Authors

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This is the first study finding an interplay between intra- and interspecific survival strategies that may affect species distribution along elevational gradients.

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Abstract

1 Elevation represents an important selection agent on self-maintenance traits and
2 correlated life histories in birds, but no study has analysed whether life-history variation
3 along this environmental cline is consistent among and within species. In a sympatric
4 community of passerines, we analysed how the average adult survival of 25 open-
5 habitat species varied with their elevational distribution and how adult survival varied
6 with elevation at the intraspecific level. For such purpose, we estimated intraspecific
7 variation in adult survival in two mountainous species, the Water pipit (*Anthus*
8 *spinoletta*) and the Northern wheatear (*Oenanthe oenanthe*) in NW Spain, by means of
9 capture-recapture analyses. At the interspecific level, high-elevation species showed
10 higher survival values than low elevation ones, likely because a greater allocation to
11 self-maintenance permits species to persist in alpine environments. At the intraspecific
12 level, the magnitude of survival variation was lower by far. Nevertheless Water pipit
13 survival slightly decreased at high elevations while the proportion of transient birds
14 increased. In contrast, no such relationships were found in the Northern wheatear.
15 Intraspecific analyses suggest that living at high elevation may be costly, such as for the
16 Water pipit in our case study. Therefore, it seems that a species can persist with viable
17 populations in uplands, where extrinsic mortality is high, by increasing the investment
18 in self maintenance and prospecting behaviours.

19 **Key words:** adult survival, elevation, interspecific variation, capture-recapture analysis,
20 passerines.

Introduction

21 Species inhabiting distinct environments are expected to show different
22 combinations of life-history traits resulting from the different selective pressures they
23 experience (Promislow and Harvey 1990; Stearns 1992; Martin 1995; Hodkinson 2005;
24 Metz et al. 2010). Environment-driven differences in survival, fecundity or other life
25 history traits emerge even after controlling for other sources of variation, such as body
26 mass (e.g. Sibly and Brown 2007), phylogeny (e.g. Stearns 2000, Laiolo et al. 2015a),
27 behavior (e.g. Sandercock and Jaramillo 2002) and life history trade-offs (e.g. Ricklefs
28 and Wikelski 2002; Martin 1995). Food limitation and environmental mortality (e.g.
29 induced by predation or parasites) are the extrinsic factors that determine the relative
30 investment in self-maintenance of many animal species (Lack 1948; Crowl and Covich
31 1990; Martin 2004). Among self-maintenance traits, survival contributes to the residual
32 reproductive value of an organism and reflects individuals' optimal responses to
33 environmental selective pressures (Ghalambor and Martin 2001).

34 Although comparisons of survival values across species help to highlight the
35 macro-evolution of strategies for self-maintenance in relation to specific environmental
36 contexts (Bielby et al. 2007), intraspecific comparisons are also important (Owens and
37 Bennet 1995). The latter can discern the micro-evolutionary mechanisms acting at early
38 stages of differentiation that determine local adaptation (Grant & Dunham, 1990), but
39 also reveal adaptive phenotypic plasticity (Sears and Angilletta 2003) or the strength of
40 selection on traits (Martin et al. 2001). At an intra-specific level, in fact, survival varies
41 with several individual and population factors, e.g. sex, age, genetic quality, and/or
42 density-dependent processes (Forslund and Pärt 1995; Clutton-Brock 1991; Tavecchia
43 et al. 2001; Foerster et al. 2003; Lescroël et al. 2009) but also with the habitat, climate,

44 food availability, and with acquired experience (Doherty and Grubb 2002; Gosselink et
45 al. 2007; Coulson et al. 2008; Low et al. 2010; Fernández-Chacón et al. 2015).

46 Changes in environmental conditions found along latitudinal (Promislow and
47 Harvey 1990; Martin 1995) or elevational gradients allow for the investigation of the
48 survival-environment relationship (Badyaev and Ghalambor 2001; Bears et al. 2009;
49 Laiolo and Obeso 2015). Along elevational gradients, the major environmental shifts
50 involve a decrease of temperature and an increase of seasonality and, as a consequence,
51 a decrease also in breeding/growing season length (Laiolo et al. 2015b). These
52 conditions are argued to favour species with high investment in survival over
53 reproduction, as found in many taxa (e.g. anurans: Morrison et al. 2004; birds:
54 Tavecchia et al. 2002, Bears et al. 2009; small mammals: Zammuto and Millar 1985).
55 Nevertheless, there are several exceptions to the expected trend of increased survival
56 along elevational gradients, especially in birds (Badyaev and Ghalambor 2001;
57 Sandercock et al. 2005; Hille and Cooper 2015), which deserve further investigation. To
58 our knowledge, a simultaneous analysis of the interspecific and intraspecific variation in
59 survival along a geographical gradient has not been addressed so far. However, from an
60 evolutionary and ecological point of view, this approach is useful to scrutinize processes
61 of adaptation to a continuous environmental gradient with (interspecific level) or
62 without (intraspecific level) major phylogenetic constraints, and thus to illustrate the
63 link of macro-evolutionary processes with micro-evolutionary and demographic
64 processes (Muñoz et al. 2014; Vellend et al. 2014).

65 We focused on inter- and intraspecific variation of survival along an elevational
66 gradient in open- habitat passerines belonging to a sympatric assemblage in Northwest
67 Spain. At the interspecific level, we analysed whether the average adult survival is
68 affected by species elevational preferences, considering the latter as a proxy of species'

69 thermal niche (Price et al. 2014). For this, we analysed the relationship between survival
70 estimates in 25 species with two independent measures of species elevational
71 distributions (locally, in the Cantabrian Mountains, NW Spain, and at the continental
72 scale, across Europe). We controlled for allometry with body mass, phylogeny and
73 migratory status. We considered the variance of survival mean estimates in order to take
74 into account both the accuracy and the natural variation of such values by means of
75 weighted generalized least squared regressions. In a second analysis, we used
76 individual-based data to assess how adult apparent survival varied with elevation at the
77 intraspecific level, in two characteristic mountainous species: the Water pipit (*Anthus*
78 *spinoletta*) and the Northern wheatear (*Oenanthe oenanthe*). For this, we used data
79 collected over the course of a five-year mark-recapture study along an 1100 m
80 elevational gradient in the Cantabrian Mountains. Here both species have viable
81 populations along a broad elevational gradient (870 – 2500 m, Laiolo et al. 2015a). In
82 analyses, we controlled for other environmental descriptors, independent from
83 elevational changes, that may potentially affect survival patterns, such as aspects of the
84 climate (e.g., rainfall, Öberg et al. 2015) and habitat (Low et al. 2010).

85 If higher elevations favour slow life-history tactics, that is greater investment in
86 self-maintenance than in reproduction (Sandercock et al. 2005; Bears et al. 2009;
87 Wilson and Martin 2011), we expect species and individual survival to increase with
88 elevation. Since environmental pressures should act in a consistent way along the
89 gradient (Jetz et al. 2008; Hille and Cooper 2015), we also expect that inter and
90 intraspecific patterns of variation to be concordant.

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95 **Materials and methods**

96 **Interspecific survival clines**

97 We analysed the effect of the elevation on the adult survival of 25 passerine
98 species of open habitats distributed among 10 families and 18 genera (Appendix 1),
99 controlling for the effects of migratory status and of body mass, which have been
100 proven to affect survival at the interspecific level (Sæther 1989; Laiolo et al 2015a). We
101 used published information of birds of the western Palearctic to obtain the average and
102 variance of adult survival rate, average body mass and migratory status for each species
103 (i.e. trans-Saharan migrants and sedentary/short distance migrants) (Appendix 1). For
104 11 species, survival estimates were derived from capture-mark-recapture studies, while
105 for the other species only recovery data (percentage of adults present at the next year)
106 were available. In the former case, the variance refers to a single population, while in
107 the latter case we estimated the variance of the annual survival of several populations
108 (Appendix 1). This variance was considered as a measure of intraspecific variability (as
109 well as measurement error) of survival rate, to control for it in successive analyses.

110 In order to obtain a robust assessment of the influence of elevation on the
111 interspecific variation of survival, we used two alternative estimates of bird elevational
112 distribution, one considering local data obtained in our study area (Cantabrian
113 Mountains; NW Spain – hereafter called Cantabrian elevation) and the other using
114 literature data for the rest of variables. The Cantabrian elevation was derived from
115 survey data of the birds breeding in the Cantabrian Mountains during the 2009-2014
116 breeding seasons. We surveyed bird densities in an area of 16000 km² in the elevation
117 range of 120-2600 m a.s.l. (Appendix 2). Surveys began at the end of March in
118 lowlands and ended in July in highlands to track bird phenology. Each field day we
119 covered a 5-24 km route stopping every 400 m to survey bird species in plots of 100 m
120 radius, so that bird relative density was established over 3.14 ha. We recorded all visual

121 or acoustic detections in plots for 10-minutes, the first 5 minutes of which were spent in
122 the centre of the plot and the rest was spent walking around to flush possible hidden
123 birds (Laiolo et al. 2004). Each survey started at sunrise and ended at midday. Overall,
124 2347 survey plots were performed. Elevation of the target species was expressed in
125 terms of abundance-weighted average elevation (i.e. plot elevation \times species abundance
126 within the plot / overall species abundance). The alternative elevation value was
127 obtained from the literature (Cramp and Perrins 1977-1994) and consists of the average
128 of the elevational values reported for each species within their European range
129 (hereafter European elevation; Appendix 1). These two alternative estimates were
130 positively and significantly correlated ($r = 0.5$, $p = 0.02$).

131 Phylogenetic generalized least square regressions (hereafter PGLS regressions)
132 permitted us to test for the effect of elevational distribution on survival controlling for
133 body mass and migratory status and taking into account the potential phylogenetic
134 dependence of the data (Felsenstein 1985; Freckleton et al. 2002). PGLS regressions
135 were run entering either the Cantabrian elevation or the European elevation as an
136 estimate of bird elevational preference. In order to take into account the variability in
137 survival estimations, we weighted the regressions by the variance of survival. Survival
138 has higher variance than other biological traits (Laiolo et al. 2015a), thus controlling for
139 the variability of the most variable factor can be considered a conservative approach. As
140 phylogenetic control, we used an ultrametric maximum clade credibility (MCC) tree
141 obtained from 10,000 trees downloaded from www.bird.tree.org (Jetz et al. 2012) using
142 the Hackett backbone of species (Hackett et al. 2008) (Appendix 3). The MCC tree was
143 built with TreeAnnotator in BEAST (Drummond et al. 2007). We fitted each model
144 using Pagel's correlation structure (Paradis et al. 2004) in the generalized least squared
145 procedure in *nlme* package of R (Pinheiro and Bates 2014). We used Pagel's correlation

146 structure to estimate the λ parameter through maximum likelihood. This parameter
147 indicates the influence of phylogeny on the relationship, in particular how similar the
148 covariances are to those in a Brownian motion model of trait evolution (species'
149 differences increasing proportionally to divergence time, $\lambda = 1$) and in the case of no
150 influence of phylogeny ($\lambda = 0$). We standardized the average elevation and body mass
151 predictors. We built several alternative models starting from a null model considering
152 only the effect of body mass, and adding the rest of the predictors (migratory status and
153 elevation, either Cantabrian or European elevation), as well as the interaction between
154 body mass and elevation (Table 1). We checked for outliers, i.e. those data points that
155 differed by > 2 SD of the total range of values (Freckleton et al. 2002), but no species
156 value could be considered as such. We compared models using the AICc value
157 (Burnham and Anderson 2002, see also below). AICc values were obtained by
158 maximum likelihood while the estimate of the parameters included in the best models
159 was obtained by restricted maximum likelihood (Pinheiro and Bates 2000).

160 **Intraspecific survival clines**

161 We collected capture-mark-recapture data of individuals of two species included
162 in the above dataset, the Water pipit (*Anthus spinoletta*) and the Northern wheatear
163 (*Oenanthe oenanthe*). The survey area was located in four massifs of the eastern
164 Cantabrian Mountains, in the Picos de Europa range (NW Spain; Appendix 2). The area
165 covered 169.25 km², the habitat is characterized by homogeneous alpine and pseudo-
166 alpine meadows with variable coverage of dispersed rocks and shrubs, and is located
167 between 870 and 2040 m a.s.l. (Meléndez et al. 2014). This habitat is the favourite
168 breeding habitat of both species in the Cantabrian area, which display maximum
169 densities around 1600 and 1700 m a.s.l. (Meléndez and Laiolo 2014; Meléndez et al.
170 2014; COA 2014). In winter, the Water pipit performs short displacements toward

171 lowlands and returns to its breeding area following the snow line in April-May, while
172 the Northern wheatear is a trans-Saharan migrant that settles in its breeding area from
173 the middle of April to August (COA 2014; Bastianelli et al. 2015).

174 Data were originally collected on 12 sites, but we retained for the analysis only
175 those where at least 15 adult individuals were captured (10 sites for Water pipit and 9
176 sites for Northern wheatear, Appendix 4). As we did for the survey, we tracked bird
177 phenology, starting the capture-recapture sampling at lowland sites and ending in the
178 high elevation sites (Appendix 4). In each site, we performed capture-mark-recapture
179 sessions once per year from April to July across five consecutive years (2009-2013 –
180 except for two sites at 1050 m and 1600, respectively, where the capture-recapture
181 sessions began in 2010 and one site at 1570 where they began in 2011, see also
182 Appendix 4). Capture-mark-recapture sessions commonly lasted 3-4 days. Birds were
183 lured by playbacks of their songs and captured using mist nets and bird mesh traps.
184 Once captured, individuals were marked with a metal ring with a unique alphanumeric
185 code and a combination of three colour rings to allow identification from distance. The
186 adult status was determined from plumage characteristics. All birds were released at
187 capture sites. All recapture occurred at the marking site and we never witness
188 movements from one capture-recapture site to another. The geographical coordinates
189 (longitude and latitude) of the site where animals were captured were noted, to be used
190 in subsequent analyses.

191 We obtained average annual and monthly temperatures (corresponding to the
192 breeding season, April-August) and accumulated rainfall from layers of the Climatic
193 Atlas of the Iberia Peninsula (resolution 200 m, Ninyerola et al. 2005). The climatic
194 Atlas results from a model of 15 years of meteorological data from the National
195 Metereological Institute stations. We found a high negative correlation between

196 elevation and yearly and monthly temperature ($-0.98 \leq r \leq -0.95$, $p < 0.01$), confirming
197 that elevation is a good surrogate of thermal conditions at the survey site. We
198 considered the average accumulated annual rainfall as an indicator of the rainfall
199 abundance of the site also during breeding season since this value was significantly
200 correlated with average rainfall from April to August ($r = 0.75$, $p < 0.01$), although it
201 was not correlated with elevation ($r = 0.10$; $p = 0.77$). We measured the percent
202 coverage of rocks and shrubs within an area of 1 km radius around the trapping area
203 using orthophotos available at <http://www.ign.es/iberpix2/visor>.

204 Observations of marked birds were coded into encounter histories, a series of
205 “0” and “1” denoting a non-encounter and an encounter (seen or physically recaptured),
206 respectively. We used capture-recapture models (Cormack-Jolly-Seber models – here
207 after CJS) to estimate annual survival (S) and probability of re-encounter, or recapture,
208 (p) of each species with the Program MARK 8.0 (White and Burnham 1999). These
209 models confound mortality with permanent emigration and survival should be
210 considered as local.

211 As we found no movement across sites, we treated individuals captured in the
212 same site as a separate group (10 groups for Water pipit and 9 groups for Northern
213 wheatear) and we used the site-dependent variables as predictors of survival. We began
214 the analysis by assessing the assumption of CJS models by means of contingency tables
215 using the program U-CARE (Choquet et al. 2009). In Water pipit data set, the Test3.SR
216 (assuming that new and already marked animals share the same survival probability)
217 was significant and indicated a difference in survival between these two groups. This
218 suggested the presence of transient birds, i.e. an excess of animals seen only at marking.
219 The presence of transients should be accounted for to avoid underestimating survival,
220 because by definition survival of transient birds is zero (Pradel et al. 1997). Therefore,

221 for the Water pipit data set, we built a “time since marking models” (Oro et al. 1999;
222 Tavecchia et al. 2007) considering three different parameters for each species in each
223 site. The first was the survival for newly caught animals (e.g. the survival probability
224 estimated over the first year after marking, hereafter noted S^*), the second was the
225 annual survival probability of already marked animals (e.g. annual survival probability
226 two or more years after marking - hereafter, S). The proportion of transient birds can be
227 estimated as $1-(S^*/S)$ (Pradel et al. 1997). The third parameter was the probability of re-
228 encounter (hereafter p). In Northern wheatear S^* was not considered because the
229 Test3.SR did not detect an excess of transient animals. Preliminary model selections
230 indicated that models assuming constant survival and capture probabilities described the
231 data adequately. As a consequence we did not consider a possible variation of the
232 parameters over time to avoid over-parameterized models.

233 We assessed the effect of site and also of linear as well as quadratic effects of
234 the elevation on S^* , S and p . Model selection was based on AICc and consisted of two
235 subsequent modelling steps. We began by modelling the probability of recapture
236 keeping S^* and/or S as site-dependent (the first step - Appendix 5). Once we found the
237 most parsimonious structure for the re-encounter probability, we proceeded to model S^*
238 and/or S (the second step, Table 3). When necessary we re-tested for some effects on
239 the probability p once a more parsimonious structure of S^* and/or S was reached (Table
240 3b). The effect of the site on model parameters was tested by means of 3 alternative
241 relations with site-dependent covariates: (a) as a categorical variable (10 levels in Water
242 pipit analysis and 9 levels in Northern wheatear analysis), (b) as a function of the
243 geographical position of each sampling site (longitude, latitude and their interaction)
244 and (c) as a function of site environmental conditions independent from elevational
245 changes such as abundance of rainfall and percentage covers of shrubs and rocks in the

246 meadows. The two last approaches considered site variables as continuous as done with
247 elevation, to avoid problems associated with differences in the number of levels of
248 predictors when considering categorical or continuous variables. We did not consider a
249 possible association between encounter probability and rainfall as we had no hypothesis
250 on such relationship.

251 The influence of the continuous environmental predictors on S^* , S and p was
252 assessed using a model in which a given parameter θ (with $\theta = S^*$, S , or p) was
253 expressed as a function of each predictor as: $\text{logit}(\theta) = B_0 + B_1 \times X_i$; where B_0 and B_1 are
254 the intercept and slope of the linear regression between the parameter and the predicting
255 variable X , respectively. For the Water pipit data set, we tested the effects of each
256 environmental variable on survival by considering either a common slope or different
257 slopes for S^* and S . Continuous predictors were standardized. The model with the
258 lowest AICc value was considered as the most appropriate model, optimizing the
259 compromise between the deviance explained and the number of parameters in the
260 model. We considered as plausible all models at $\Delta\text{AIC} \leq 2$ (Burnham and Anderson
261 2002). We also calculated model support using Akaike weights (AICc weight, ranging
262 from 0 to 1, with larger numbers indicating greater support; Anderson 2007).

263 The goodness-of-fit of the general and simplest model with constant parameters
264 (that is $S^*(.)$ $S(.)$ $p(.)$ for Water pipit and $S(.)$ $p(.)$ for Northern wheatear) was assessed
265 using the bootstrap technique in software MARK 8.0 (White and Burnham 1999). The
266 overdispersion coefficient (\hat{c}) was estimated as the deviance of the model divided by the
267 mean deviance of the bootstrap simulations. The bootstrap test (1000 simulations) did
268 not detect overdispersion ($\hat{c} \approx 1$) in either species data sets (for Water pipit: deviance
269 model = 25.53; mean deviance of the simulations \pm SE = 24.79 \pm 0.18, $\hat{c} = 1.03$; for
270 Northern wheatear: deviance model = 24.43; mean deviance of the simulations \pm SE =

271 20.28 ± 0.17 , $\hat{c} = 1.16$). The variance of the proportions of transients was estimated
272 using the δ -method (Morgan 2000).

273 **Results**

274 **Interspecific survival clines**

275 The most plausible model explaining variation in species survival included the
276 effect of body mass and elevation (either in the Cantabrian Mountains or in species
277 European distribution) (Table 1). The model considering only the effect of body mass
278 was also selected although its weight was lower, and the effect of this variable was not
279 significant (slope = -0.03; SE = 0.03; $p = 0.28$) (Table 1). Species adult survival was
280 instead significantly and positively associated with elevation: species breeding at higher
281 elevations had on average higher survival than lowland species (Table 2, Fig. 1).
282 Notably, the slopes of the regressions of survival on elevation were identical when
283 using literature or local data of elevation (Table 2), highlighting the robustness of the
284 relationship even when obtained with different sources of information.

285 **Intraspecific survival clines**

286 We analysed the re-encounter histories of 369 Water pipit adults and 289
287 Northern wheatear adults. The re-encounter model selection identified, as the most
288 parsimonious model, one with re-encounter probability constant across site for both
289 species (Appendix 5). As a consequence, the survival model began from a complex
290 model where survival was dependent on the site (group) while re-encounter
291 probability was kept constant (Table 3a-b, model 1).

292 For Water pipit residents, average annual survival rate (S) was 0.76 ± 0.07 SE
293 (survival value used for the interspecific analysis), average annual S^* was 0.26 ± 0.04
294 SE (average proportion of transients was 0.66) and the average annual p was 0.55 ± 0.07
295 SE, as derived from the model where all the parameters were constant (model 25). In

296 Water pipit the set of best models (i.e. models with $\Delta AIC \leq 2$) considered an effect of
297 elevation on the average annual survival parameters (Table 3a, models: 16-17-20-23-
298 24). This finding suggests that differences in the average annual survival parameters
299 across sites were explained by site elevation rather than by site *per se* or by geographic
300 or environmental characteristics of the sites (Table 3a, from model 1 to model 14). The
301 best supported model (AICc weight = 0.19) considered an additive effect of elevation
302 on the survival of newly and already marked Water pipit (Table 3a, model 16). Water
303 pipit average annual adult survival decreased with elevation and the percentage of
304 transients increased. The estimated decline along elevation gradient for S and S^* on a
305 logit scale was -0.40 ± 0.15 SE (95% CI: -0.72 to -0.08) (Fig. 2). Notably, the effect of
306 elevation was more evident on transient birds since the second best model considered
307 the effect of elevation only on S^* (Table 3a, model 17, the estimate on a logit scale was
308 -0.43 ± 0.19 ; 95% CI: -0.19 to -0.0012), while the model considering the effect of
309 elevation only on S was not supported (Table 3a, model 18). The model considered a
310 quadratic effect of elevation on both S and S^* (Table 3a, model 20) was selected among
311 plausible models but the slope estimates of the quadratic predictors were not
312 significantly different from zero. Also the slope estimates of the shrub cover on the
313 probability of re-encounter p were not significantly different from zero (Table 3a,
314 Models 23-24).

315 We found that average annual survival estimates in the Northern wheatear were
316 constant over site with no relationship with any of the covariates considered (Table 3b,
317 model 8, AICc weight = 0.26). Some models with environmental factors were selected
318 among plausible models but the slope estimates were not significantly different from
319 zero (Table 3b, models: 3-4-5-9). For Northern wheatear adults, the average annual
320 survival rate was 0.44 ± 0.06 SE (survival value used for the interspecific analysis) and

321 the probability of re-encounter was 0.41 ± 0.08 SE as derived from the model where all
322 the parameters were constant (model 8).

323 **Discussion**

324 This study suggests a complex pattern of variation in birds' adult survival along
325 an elevational gradient. Consistent with our first prediction, high-elevation specialists
326 had an higher survival than species dwelling in lowlands, a result that confirms the
327 hypothesis that high elevation species share a life-history strategy of high investment in
328 self-maintenance (Morrison et al. 2004; Hille and Cooper 2015; Laiolo et al. 2015a).
329 Indeed, the Water pipit and Northern wheatear, which have larger population sizes at
330 mid-high elevation, have high survival rates compared to other passerines of similar size
331 and migration status (see Laiolo et al. 2015a). Our second prediction, of similarity
332 between intra and interspecific patterns, was not supported, and the effect of elevation
333 on intraspecific survival was not as strong as among species. This may be explained
334 both by a reduced magnitude of the effect of elevation among populations, and an
335 insufficient sample size to reveal it. The sample was however big enough to detect that
336 the survival of Water pipits slightly decreased, and that the proportion of Water pipit
337 transients increased at high elevations.

338 The interspecific patterns of variation we found suggests that at macro-
339 evolutionary scales birds that occur at high elevations converge in their strategy of high
340 investment in self-maintenance (Jetz et al. 2008; Hille and Cooper 2015). An increase in
341 investment in self- maintenance may be favored by the specific conditions of high
342 elevation, such as low temperature and shorter growth and breeding seasons, which in
343 parallel favor a reduced reproductive allocation. In our study area, for instance, a
344 concurrent reduction of the number of eggs laid per year has been reported in upland
345 species (Laiolo et al. 2015a), which allows saving resources for self-maintenance

346 (Stearns 1992). Thus, the observed pattern strengthens the idea of a shift to a “slow”
347 pace of life for birds at high elevations (high survival -this study- and low annual
348 allocation in reproduction - Laiolo et al. 2015a). This life-history strategy fits the
349 particular conditions of this habitat and, remarkably, of tropical habitats as well
350 (Sandercock et al. 2005, Hille and Cooper 2015; Boyle et al. 2016; Versteegh et al.
351 2012; Wiersma et al. 2007) and may also involve changes in other behaviours. Among
352 these, intense parental care and investment in offspring quality rather than quantity and
353 less marked sexual ornaments have been observed (Badyaev 1997a and b; Badyaev and
354 Ghalambor 2001).

355 Intraspecific patterns reveal a less straightforward scenario. First, we found a
356 high proportion of transients (0.65) in the Water pipit, a fact that suggests that
357 emigration (i.e. dispersal) is an important phenomenon in this species, especially at high
358 elevation. The conditions of highlands, involving a reduced time frame of high resource
359 availability and the unpredictable occurrence of unfavorable weather events, may
360 promote a plastic and flexible spatial behavior, with high inter-annual mobility and
361 emigration, and greater territorial turnover after food depletion or nest losses (Santoro et
362 al. 2013). On the other hand, the warmer and more stable thermal conditions of lowland
363 may foster the return of the individual to the same site during the reproduction period
364 and, consistent with this, the territorial behavior of Water pipit males is more
365 pronounced at low (1000 m) than at high elevations (1700-2000 m) (Bastianelli et al.
366 2015).

367 When considering intraspecific patterns of survival, we found that it decreased
368 slightly with elevation in this species, with a population cline that contrasts with the
369 interspecific pattern above discussed. However, it should be noted that the survival rate
370 also includes a component determined by the environment, i.e. extrinsic survival, apart

371 from an intrinsic component corresponding to a selected (adaptive) life-history strategy.
372 Intraspecific patterns, in this sense, may serve to reveal the strength of selection on traits
373 (proximate causes), which ultimately leads to the responses of species measured at the
374 interspecific level (Martin et al. 2001). Hence, the conditions of high elevation might
375 represent a source of extrinsic mortality, and only species characterized by high
376 allocation in self-maintenance as a life-history strategy may deal with this cost and
377 occupy highlands, thus explaining the interspecific trend. A species characterized by a
378 low survival strategy might not persist with viable populations where extrinsic mortality
379 is too high. Indeed, Water pipit abundances peak between 1200-1600 m a.s.l. and, as for
380 survival, they also decline at higher elevations (Meléndez and Laiolo 2014). Therefore,
381 at least in our Water pipit study populations, the hypothesis that survival reflects
382 extrinsic mortality seems more likely than the alternative of local adaptations.
383 Subpopulations at different elevations occur in fact at close distances (see Appendix 2),
384 shorter than the distance between wintering and breeding grounds of the species
385 (Meléndez and Laiolo 2014) and likely not enough to permit the full isolation and
386 development of local adaptations among populations (Kawecki and Ebert 2004). The
387 high proportion of transients is also poorly compatible with the occurrence of dispersal
388 barriers among subpopulations. As a further step, field studies tracking individual
389 movements as well as common-garden experiments are needed to evaluate
390 environmental and micro-evolutionary effects on life-history variation.

391 We did not detect an effect of elevation and of the other environmental
392 characteristics on Northern wheatear survival. The low sample size may have limited
393 the power of the tests, but unfortunately sample size cannot be easily augmented in
394 mountain ecological scenarios where sites have to be reached by long treks and
395 populations under study are typically sparse. As for the Water pipits, we stress that our

396 study design did not permit us to highlight the influence of other factors. Among these,
397 we think that historical characteristics of the population of each site or meta-population
398 dynamics (sink-source meta-population) may have played a role in determining the
399 observed intraspecific patterns. Furthermore, the overall scarce variation in survival
400 might also represent a case of demographic buffering against environmental changes
401 (Doak and Morris 2010), which reduces the variability of crucial vital rates (e.g.,
402 survival) for population growth. Alternatively, the limited extent of elevational gradient,
403 and thus the reduced extent of environmental variation could have contributed to the
404 reduced variation in survival rates among populations. For instance, along such gradient
405 (800- 2000 m a.s.l.), the intensity of predation and parasitism does not vary to a great
406 extent (Bastianelli, Illera and Laiolo in prep.).

407 To our knowledge, this is the first study that focuses on both inter- and
408 intraspecific variation of survival along a geographical gradient. We found that high-
409 elevation species have higher survival rates than low-elevation species, supporting the
410 idea of a slow pace of life at high elevations. At intra-specific level, a low sample size
411 combined with a low magnitude of the elevational effect could have limited our
412 capability of detecting significant trends. However, we contend that the idiosyncratic
413 relationships between survival and elevation within and among species have a
414 biological interpretation, and indicate that life-history strategies of species influence the
415 costs (in terms of fitness) the species can deal with, and this in turn influences the
416 occupancy of different environments and geographic areas (Vellend et al. 2014). In the
417 case of the Water pipit, for instance, the greater investment in self maintenance and high
418 levels of mobility may facilitate the presence of this passerine at high elevation. The
419 results obtained at the two levels of study (inter- and intraspecific) stress the importance

420 and usefulness of looking at both macro and micro- evolutionary scales in the same
421 environmental gradients, in order to better understand patterns of life history variation.

422

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435 **Ethical approval**

436 All procedures performed in studies involving human participants were in accordance
437 with the ethical standards of the institutional and/or national research committee and
438 with the 1964 Helsinki declaration and its later amendments or comparable ethical
439 standards.

440 **References**

441 Anderson DR (2007) Model Based Inference in the Life Sciences: A Primer on
442 Evidence. Springer, New York
443 Badyaev A V (1997a) Altitudinal variation in sexual dimorphism: a new pattern and

444 alternative hypotheses. *Behav Ecol* 8:675–690. doi: 10.1093/beheco/8.6.675

445 Badyaev A V (1997b) Covariation between Life History and Sexually Selected Traits:
446 An Example with Cardueline Finches. *Oikos* 80:128–138. doi: 10.2307/3546524

447 Badyaev A V, Ghalambor CK (2001) Evolution of life histories along elevational
448 gradients: trade-off between parental care and fecundity. *Ecology* 82:2948–2960.
449 doi: 10.1890/0012-9658(2001)082[2948:EOLHAE]2.0.CO;2

450 Bastianelli G, Seoane J, Álvarez-Blanco P, Laiolo P (2015) The intensity of male-male
451 interactions declines in highland songbird populations. *Behav Ecol Sociobiol*
452 69:1493–1500. doi: 10.1007/s00265-015-1961-6

453 Bears H, Martin K, White GC (2009) Breeding in high-elevation habitat results in shift
454 to slower life-history strategy within a single species. *J Anim Ecol* 78:365–375.
455 doi: 10.1111/j.1365-2656.2008.01491.x

456 Bielby J, Mace G M, Bininda-Emonds O R P, Cardillo M, Gittleman J L, Jones K E,
457 Purvis A (2007) The fast-slow continuum in mammalian life history: an empirical
458 re-evaluation. *Am Nat* 169: 748-757

459 Boyle AW, Sandercock BK, Martin K (2016) Patterns and drivers of intraspecific
460 variation in avian life history along elevational gradients: a meta-analysis. *Biol*
461 *Rev* 91:469–482. doi: 10.1111/brv.12180

462 Burnham KP, Anderson DR (2002) *Model Selection and Inference. A Practical*
463 *Information-Theoretic Approach*, 2nd edn. Springer, New York

464 Choquet R, Lebreton J-D, Gimenez O, et al (2009) U-CARE: Utilities for performing
465 goodness of fit tests and manipulating CAPture–REcapture data. *Ecography (Cop)*

466 32:1071–1074. doi: 10.1111/j.1600-0587.2009.05968.x

467 Clutton-Brock T H (1991) The evolution of parental care, Princeton University Press,
468 USA

469 COA. Coordinadora Ornitológica D’Asturies, Indurot (2014) Atlas de las aves
470 nidificantes de Asturias 1990-2010, Coordinadora Ornitológica D’Asturies

471 Coulson T, Ezzard THG, Pelletier F, et al (2008) Estimating the functional form for the
472 density dependence from life history data. *Ecology* 89:1661–1674. doi:
473 10.1890/07-1099.1

474 Cramp S, Perrins CM (eds) (1977–1994). The Birds of the Western Palearctic, Vols 1–
475 9. Oxford University Press, Oxford, UK

476 Crowl T A and Covich A P (1990) Predator-induced life-history shifts in a freshwater
477 snail. *Science* 247: 949-951

478 Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-
479 induced range shifts. *Nature* 467:959–962.

480 Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented
481 forested landscape. *Ecology* 83:844–857. doi: 10.1890/0012-
482 9658(2002)083[0844:SOPRBI]2.0.CO;2

483 Drummond AJ, Ho SY, Rawlence N, Rambaut A (2007) A rough guide to BEAST 1.4

484 Felsenstein J (1985) Phylogenies and the Comparative Method. *Am Nat* 125:1–15.

485 Fernández-Chacón A, Genovart M, Álvarez D, et al (2015) Neighbouring populations,
486 opposite dynamics: influence of body size and environmental variation on the
487 demography of stream-resident brown trout (*Salmo trutta*). *Oecologia* 178:379–

488 389. doi: 10.1007/s00442-015-3222-9

489 Foerster K, Delhey K, Johnsen A, et al (2003) Females increase offspring
490 heterozygosity and fitness through extra-pair matings. *Nature* 425:714–717.

491 Forslund P, Pärt T (1995) Age and reproduction in birds — hypotheses and tests.
492 *Trends Ecol. Evol.* 10:374–378.

493 Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative
494 data: a test and review of evidence. *Am Nat* 160: 712-726

495 Ghalambor CK, Martin TE (2001) Fecundity-Survival Trade-Offs and Parental Risk-
496 Taking in Birds. *Science* (80-) 292:494 LP-497.

497 Gosselink TE, Van Deelen TR, Warner RE, Mankin PC (2007) Survival and cause-
498 specific mortality of red foxes in agricultural and urban areas of Illinois. *J*
499 *Wildlife Manage* 71: 1862-1873

500 Grant BW, Dunham AE (1990) Elevational Covariation in Environmental Constraints
501 and Life Histories of the Desert Lizard *Sceloporus Merriami*. *Ecology* 71:1765–
502 1776. doi: 10.2307/1937584

503 Hackett SJ, Kimball RT, Reddy S, et al (2008) A Phylogenomic Study of Birds Reveals
504 Their Evolutionary History. *Science* (80-) 320:1763 LP-1768.

505 Hille SM, Cooper CB (2015) Elevational trends in life histories: revising the pace-of-
506 life framework. *Biol Rev* 90:204–213. doi: 10.1111/brv.12106

507 Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and
508 community responses to altitude. *Biol Rev* 80:489. doi:
509 10.1017/S1464793105006767

510 Jetz W, Sekercioglu CH, Böhning-Gaese K (2008) The Worldwide Variation in Avian
511 Clutch Size across Species and Space. *PLoS Biol* 6:e303.

512 Jetz W, Thomas GH, Joy JB, et al (2012) The global diversity of birds in space and
513 time. *Nature* 491:444–448.

514 Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7:1225–
515 1241. doi: 10.1111/j.1461-0248.2004.00684.x

516 Lack D (1948) The significance of clutch-size. Part III.-Some Interspecific
517 Comparisons. *Ibis (Lond 1859)* 90:25–45. doi: 10.1111/j.1474-
518 919X.1948.tb01399.x

519 Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral
520 abandonment for the structure and diversity of the alpine avifauna. *J Appl Ecol*
521 41:294–304. doi: 10.1111/j.0021-8901.2004.00893.x

522 Laiolo P, Obeso JR (2015) Plastic Responses to Temperature Versus Local Adaptation
523 at the Cold Extreme of the Climate Gradient. *Evol Biol* 42:473–482. doi:
524 10.1007/s11692-015-9341-8

525 Laiolo P, Seoane J, Illera JC, et al (2015a) The evolutionary convergence of avian
526 lifestyles and their constrained coevolution with species' ecological niche. *Proc R*
527 *Soc B Biol Sci* 282:20151808. doi: 10.1098/rspb.2015.1808

528 Laiolo P, Illera JC, Meléndez L, et al (2015b) Abiotic, Biotic, and Evolutionary Control
529 of the Distribution of C and N Isotopes in Food Webs. *Am Nat* 185:169–182. doi:
530 10.1086/679348

531 Lescroël A, Dugger KM, Ballard G, Ainley DG (2009) Effects of individual quality,

532 reproductive success and environmental variability on survival of a long-lived
533 seabird. *J Anim Ecol* 78:798–806. doi: 10.1111/j.1365-2656.2009.01542.x

534 Low M, Arlt D, Eggers S, Pärt T (2010) Habitat-specific differences in adult survival
535 rates and its links to parental workload and on-nest predation. *J Anim Ecol*
536 79:214–224. doi: 10.1111/j.1365-2656.2009.01595.x

537 Martin TE (1995) Avian Life History Evolution in Relation to Nest Sites, Nest
538 Predation, and Food. *Ecol Monogr* 65:101–127. doi: 10.2307/2937160

539 Martin TE (2004) Avian life-history evolution has an eminent past: does it have a bright
540 future? *Auk* 121:289–301. doi: 10.1642/0004-
541 8038(2004)121[0289:ALEHAE]2.0.CO;2

542 Martin TE, Møller AP, Merino S, Clobert J (2001) Does clutch size evolve in response
543 to parasites and immunocompetence? *Proc Natl Acad Sci* 98:2071–2076. doi:
544 10.1073/pnas.98.4.2071

545 Meléndez L, Laiolo P (2014) The role of climate in constraining the elevational range of
546 the Water Pipit *Anthus spinoletta* in an alpine environment. *Ibis (Lond 1859)*
547 156:276–287. doi: 10.1111/ibi.12127

548 Meléndez L, Laiolo P, Mironov S, et al (2014) Climate-Driven Variation in the
549 Intensity of a Host-Symbiont Animal Interaction along a Broad Elevation Gradient.
550 *PLoS One* 9:e101942.

551 Metz J, Liancourt P, Kigel J, et al (2010) Plant survival in relation to seed size along
552 environmental gradients: a long-term study from semi-arid and Mediterranean
553 annual plant communities. *J Ecol* 98:697–704. doi: 10.1111/j.1365-
554 2745.2010.01652.x

555 Morgan BJT (2000) *Applied Stochastic Modelling*. Arnold, London.

556 Morrison C, Hero J-M, Browning J (2004) Altitudinal variation in the age at maturity,
557 longevity, and reproductive lifespan of anurans in subtropical queensland.
558 *Herpetologica* 60:34–44. doi: 10.1655/02-68

559 Muñoz MM, Wegener JE, Algar AC (2014) Untangling intra- and interspecific effects
560 on body size clines reveals divergent processes structuring convergent patterns in
561 *Anolis* lizards. *Am. Nat.* 184: 636-646

562 Ninyerola M, Pons X, Roure JM (2005) *Atlas Climático Digital de la Península*
563 *Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica* (ed)
564 Bellaterra. Universidad Autónoma de Barcelona.

565 Öberg M, Arlt D, Pärt T, et al (2015) Rainfall during parental care reduces reproductive
566 and survival components of fitness in a passerine bird. *Ecol Evol* 5:345–356. doi:
567 10.1002/ece3.1345

568 Oro D, Pradel R, Lebreton J-D (1999) Food availability and nest predation influence life
569 history traits in Audouin’s gull, *Larus audouinii*. *Oecologia* 118:438–445. doi:
570 10.1007/s004420050746

571 Owens IPF, Bennett PM (1995) Ancient Ecological Diversification Explains Life-
572 History Variation among Living Birds. *Proc R Soc London Ser B Biol Sci* 261:227
573 LP-232.

574 Paradis E, Claude J, Strimmer K (2004) *APE: Analyses of Phylogenetics and Evolution*
575 in R language. *Bioinforma* 20:289–290. doi: 10.1093/bioinformatics/btg412

576 Pinheiro JC, Bates DM (2000) Linear mixed-effects models: basic concepts and
577 examples. *Mixed-effects models in S and S-Plus*: 3-56.

578 Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) R Core Team (2014) nlme: linear and
579 nonlinear mixed effects models. R package version 3.1-117. [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)
580 [project.org/package= nlme](http://CRAN.R-project.org/package=nlme).

581 Pradel R, Hines JE, Lebreton J-D, Nichols JD (1997) Capture-Recapture Survival
582 Models Taking Account of Transients. *Biometrics* 53:60–72. doi:
583 10.2307/2533097

584 Price TD, Hooper DM, Buchanan CD, et al (2014) Niche filling slows the
585 diversification of Himalayan songbirds. *Nature* 509:222–225.

586 Promislow DEL, Harvey PH (1990) Living fast and dying young: A comparative
587 analysis of life-history variation among mammals. *J Zool* 220:417–437. doi:
588 10.1111/j.1469-7998.1990.tb04316.x

589 Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. *Trends Ecol Evol*
590 17:462–468. doi: 10.1016/S0169-5347(02)02578-8

591 Sæther B-E (1989) Survival Rates in Relation to Body Weight in European Birds. *Ornis*
592 *Scand* (Scandinavian J Ornithol 20:13–21. doi: 10.2307/3676702

593 Sandercock BK, Jaramillo A (2002) Annual survival rates of wintering sparrows:
594 assessing demographic consequences of migration. *Auk* 119:149–165. doi:
595 10.1642/0004-8038(2002)119[0149:ASROWS]2.0.CO;2

596 Sandercock BK, Martin K, Hannon SJ (2005) Demographic consequences of age-
597 structure in extreme environments: population models for arctic and alpine

598 ptarmigan. *Oecologia* 146:13–24. doi: 10.1007/s00442-005-0174-5

599 Santoro S, Green AJ, Figuerola J (2013) Environmental instability as a motor for
600 dispersal: a case study from a growing population of glossy ibis. *PLoS One*
601 8:e82983. doi: 10.1371/journal.pone.0082983

602 Sears MW, Angilletta MJ (2003) Life-history variation in the sagebrush lizard:
603 phenotypic plasticity or local adaptation? *Ecology* 84:1624–1634. doi:
604 10.1890/0012-9658(2003)084[1624:LVITSL]2.0.CO;2

605 Sibly RM, Brown JH (2007) Effects of body size and lifestyle on evolution of mammal
606 life histories. *Proc Natl Acad Sci* 104:17707–17712. doi:
607 10.1073/pnas.0707725104

608 Stearns SC (1992) *The evolution of life histories* (Vol. 249). Oxford University Press,
609 UK

610 Stearns CS (2000) Life history evolution: successes, limitations, and prospects.
611 *Naturwissenschaften* 87:476–486. doi: 10.1007/s001140050763

612 Tavecchia G, Pradel R, Boy V, et al (2001) Sex- and age-related variation in survival
613 and cost of first reproduction in greater flamingos. *Ecology* 82:165–174. doi:
614 10.1890/0012-9658(2001)082[0165:SAARVI]2.0.CO;2

615 Tavecchia G, Pradel R, Lebreton J-D, et al (2002) Sex-biased survival and breeding
616 dispersal probability in a patchy population of the Rock Sparrow *Petronia*
617 *petronia*. *Ibis (Lond 1859)* 144:E79–E87. doi: 10.1046/j.1474-919X.2002.00059.x

618 Tavecchia G, Pradel R, Genovart M, Oro D (2007) Density-dependent parameters and
619 demographic equilibrium in open populations. *Oikos* 116:1481–1492. doi:
620 10.1111/j.0030-1299.2007.15791.x

621 Vellend M, Lajoie G, Bourret A, et al (2014) Drawing ecological inferences from
622 coincident patterns of population- and community-level biodiversity. *Mol Ecol*
623 23:2890–2901. doi: 10.1111/mec.12756

624 Versteegh MA, Schwabl I, Jaquier S, Tieleman BI (2012) Do immunological, endocrine
625 and metabolic traits fall on a single Pace-of-Life axis? Covariation and constraints
626 among physiological systems. *J Evol Biol* 25:1864–1876. doi: 10.1111/j.1420-
627 9101.2012.02574.x

628 White GC, Burnham KP (1999) Program MARK: survival estimation from populations
629 of marked animals. *Bird Study* 46:S120–S139. doi: 10.1080/00063659909477239

630 Wiersma P, Muñoz-Garcia A, Walker A, Williams JB (2007) Tropical birds have a slow
631 pace of life. *Proc Natl Acad Sci* 104:9340–9345. doi: 10.1073/pnas.0702212104

632 Wilson S, Martin K (2011) Life-history and demographic variation in an alpine
633 specialist at the latitudinal extremes of the range. *Popul Ecol* 53:459–471. doi:
634 10.1007/s10144-011-0261-x

635 Zammuto RM, Millar JS (1985) Environmental Predictability, Variability, and
636 *Spermophilus columbianus* Life History over an Elevational Gradient. *Ecology*
637 66:1784–1794. doi: 10.2307/2937374

638

639 Electronic Supplementary Materials (Appendix 1, Appendix 2, Appendix 3, Appendix
640 4, Appendix 5).

641

642 **Table 1.** List of models testing for the effect of average elevation in the Cantabrian
643 Mountains, average elevation in Europe, body mass and migratory status on average
644 adult survival. Models are ranked according to their plausibility, as indicated by AICc:
645 Akaike's Information Criterion corrected for small sample size; Δ AICc: difference of
646 AICc values between the model in question and the best model (lowest AICc); AICc
647 weights: weights of evidence in favour of a model being the actual Kullback-Leibler
648 best model; K: number of parameters. The best models are highlighted in bold.

| Cantabrian elevation | | | | | | |
|-----------------------------|---------------------|---------------|--------------------------------|--------------|-------------------|----------|
| | Model | AICc | ΔAICc | AICcw | Likelihood | K |
| 1 | elev + bm | -14.54 | 0 | 0.57 | 13.85 | 5 |
| 2 | bm | -12.74 | 1.80 | 0.23 | 11.37 | 4 |
| 3 | elev + bm + elev*bm | -11.82 | 2.72 | 0.15 | 14.24 | 6 |
| 4 | ms + bm | -9.58 | 4.96 | 0.05 | 11.37 | 5 |
| European elevation | | | | | | |
| 1 | elev + bm | -14.70 | 0 | 0.61 | 13.93 | 5 |
| 2 | bm | -12.74 | 1.96 | 0.23 | 11.37 | 4 |
| 3 | elev + bm + elev*bm | -11.41 | 3.30 | 0.12 | 14.04 | 6 |
| 4 | ms + bm | -9.58 | 5.12 | 0.05 | 11.37 | 5 |

Model notation: elev = elevation, bm = body mass; ms = migration status. Number of species = 25.

649 **Table 2.** Parameter estimates and statistics of PGLS regressions testing for the effect of
650 elevation (in the Cantabrian Mountains or in Europe) and body mass of species on their
651 average adult survival. For each predictor, parameter estimate, its standard error (SE), t
652 and p-values are shown. The λ parameters express the influence of phylogeny on the
653 relationship.

| Predictor | Estimate | SE | t | P | λ |
|----------------------|-----------------|-----------|----------|----------|-----------------------------|
| Intercept | 0.60 | 0.05 | 11.10 | 0 | |
| Cantabrian elevation | 0.05 | 0.02 | 2.37 | 0.03 | 0.70 |
| Body mass | -0.06 | 0.03 | 2.05 | 0.05 | |
| Intercept | 0.58 | 0.05 | 12.20 | 0 | |
| European elevation | 0.06 | 0.03 | 2.23 | 0.04 | 0.49 |
| Body mass | -0.02 | 0.03 | 0.94 | 0.36 | |

Number of species = 25

654 **Table 3.** Models of local annual adult survival in (a) the Water pipit and (b) Northern wheatear in the Cantabrian Mountains. Models are listed
655 following the order of building. AICc: Akaike's Information Criterion corrected for small sample size; Δ AICc: difference of AICc values
656 between the model in question and the best model (lowest AICc); AICc weights: weights of evidence in favour of a model as being the actual
657 Kullback-Leibler best model; K: number of parameters. When the models estimating both S* and S as a function of an environmental predictor,
658 the symbol “+” between two parameters means that the slope of the effect of elevation on survival was considered identical between newly
659 marked individuals and already marked individuals, the lack of symbol “+” means that different slopes were specified for S* and S. The apex “2”
660 means that we tested for quadratic effects. The plausible models are highlighted in bold.

(a) Water pipit

| | Model | AICc | Δ AICc | AICcw | Likelihood | K | Deviance |
|---|-------------------------------|-------------|---------------------------------|--------------|-------------------|----------|-----------------|
| 1 | S* (site) S (site) p (.) | 497,28 | 15,52 | 0,00 | 0,00 | 17 | 461,66 |
| 2 | S*(x+y+x*y) S (x+y+x*y) p (.) | 485,66 | 3,90 | 0,03 | 0,14 | 6 | 473,44 |
| 3 | S*(rain) S (rain) p (.) | 486,32 | 4,56 | 0,02 | 0,10 | 5 | 476,17 |
| 4 | S*(rain) + S (rain) p (.) | 485,56 | 3,81 | 0,03 | 0,15 | 4 | 477,46 |
| 5 | S*(rain) S (.) p (.) | 486,86 | 5,10 | 0,01 | 0,08 | 4 | 478,76 |
| 6 | S*(.) S (rain) p (.) | 484,72 | 2,96 | 0,04 | 0,23 | 4 | 476,61 |
| 7 | S*(shrub) S (shrub) p (.) | 487,93 | 6,18 | 0,01 | 0,05 | 5 | 477,78 |
| 8 | S*(shrub) + S (shrub) p (.) | 487,65 | 5,90 | 0,01 | 0,05 | 4 | 479,55 |

| | | | | | | | |
|-----------|--|---------------|-------------|-------------|-------------|----------|---------------|
| 9 | S*(shrub) S(.) p(.) | 487,89 | 6,13 | 0,01 | 0,05 | 4 | 479,79 |
| 10 | S*(.) S(shrub) p(.) | 485,94 | 4,19 | 0,02 | 0,12 | 4 | 477,84 |
| 11 | S*(rock) S(rock) p(.) | 489,54 | 7,79 | 0,00 | 0,02 | 5 | 479,39 |
| 12 | S*(rock) + S(rock) p(.) | 487,70 | 5,94 | 0,01 | 0,05 | 4 | 479,59 |
| 13 | S*(rock) S(.) p(.) | 487,62 | 5,87 | 0,01 | 0,05 | 4 | 479,52 |
| 14 | S*(.) S(rock) p(.) | 487,88 | 6,13 | 0,01 | 0,05 | 4 | 479,78 |
| 15 | S*(elev) S(elev) p(.) | 483,79 | 2,03 | 0,07 | 0,36 | 5 | 473,63 |
| 16 | S*(elev) + S(elev) p(.) | 481,76 | 0,00 | 0,19 | 1,00 | 4 | 473,66 |
| 17 | S*(elev) S(.) p(.) | 482,71 | 0,96 | 0,12 | 0,62 | 4 | 474,61 |
| 18 | S*(.) S(elev) p(.) | 485,65 | 3,89 | 0,03 | 0,14 | 4 | 477,55 |
| 19 | S*(elev ²) S(elev ²) p(.) | 487,46 | 5,70 | 0,01 | 0,06 | 7 | 473,17 |
| 20 | S*(elev²) + S(elev²) p(.) | 483,69 | 1,94 | 0,07 | 0,38 | 5 | 473,54 |
| 21 | S*(elev ²) S(.) p(.) | 484,52 | 2,76 | 0,05 | 0,25 | 5 | 474,36 |
| 22 | S*(.) S(elev ²) p(.) | 487,55 | 5,79 | 0,01 | 0,06 | 5 | 477,40 |
| 23 | S*(elev²) + S(elev²) p(shrub) | 482,47 | 0,71 | 0,13 | 0,70 | 5 | 472,31 |
| 24 | S*(elev) S(.) p(shrub) | 483,41 | 1,65 | 0,08 | 0,44 | 5 | 473,25 |
| 25 | S*(.) S(.) p(.) | 485,85 | 4,10 | 0,02 | 0,13 | 3 | 479,79 |

661 **Model notation:** S*= survival for newly marked, S= adult survival, p = probability of re-encounter, (.) = the model assumes that the parameter is
662 fixed through the time. Effects: site (factorial variable), x = longitude, y = latitude, x*y = product between longitude and latitude, elev = elevation
663 (continuous variable) rain = annual rainfall (continuous variable), shrub = shrub cover (continuous variable), rock = rock cover (continuous variable).

(b) Northern wheatear

| | Model | AICc | Δ AICc | AICcw | Likelihood | K | Deviance |
|----------|----------------------------|---------------|---------------|--------------|-------------------|----------|-----------------|
| 1 | S(site) p(.) | 388,13 | 7,80 | 0,01 | 0,02 | 10 | 367,40 |
| 2 | S(x+y+x*y) p(.) | 384,61 | 4,28 | 0,03 | 0,12 | 5 | 374,41 |
| 3 | S(rain) p(.) | 382,28 | 1,95 | 0,10 | 0,38 | 3 | 376,20 |
| 4 | S(shrub) p(.) | 382,12 | 1,79 | 0,11 | 0,41 | 3 | 376,04 |
| 5 | S(rock) p(.) | 381,97 | 1,64 | 0,11 | 0,44 | 3 | 375,89 |
| 6 | S(elev) p(.) | 382,35 | 2,02 | 0,09 | 0,37 | 3 | 376,27 |
| 7 | S(elev ²) p(.) | 383,65 | 3,32 | 0,05 | 0,19 | 4 | 375,52 |
| 8 | S(.) p(.) | 380,33 | 0,00 | 0,26 | 1,00 | 2 | 376,29 |
| 9 | S(.) p(elev) | 382,12 | 1,78 | 0,11 | 0,41 | 3 | 376,04 |
| 10 | S(rain) p(elev) | 383,91 | 3,58 | 0,04 | 0,17 | 4 | 375,78 |
| 11 | S(shrub) p(elev) | 383,83 | 3,49 | 0,05 | 0,17 | 4 | 375,69 |
| 12 | S(rock) p(elev) | 383,60 | 3,27 | 0,05 | 0,19 | 4 | 375,47 |

664 **Model notation:** S= adult survival, p = probability of re-encounter, (.) = the model assumes that the parameter is fixed through the time. Effects: site
665 (factorial variable), x = longitude, y = latitude, x*y = product between longitude and latitude, elev = elevation (continuous variable), rain = annual
666 rainfall (continuous variable), shrub = shrub cover (continuous variable), rock = rock cover (continuous variable).

Figure captions

667 **Fig 1** Relationship between adult survival and both (a) Cantabrian and (b) European
668 elevations. The dashed lines represent the 95% confidence intervals on either side of the
669 solid trend line. Circles show survival values of each species. The letter codes indicate
670 the name of the species for each survival value (Aa: *Alauda arvensis*; As: *Anthus*
671 *spinoletta*; At: *Anthus trivialis*; Cca: *Carduelis cannabina*; Ccx: *Corvus corax*; Cc:
672 *Corvus corone*; Ec: *Emberiza cia*; Ect: *Emberiza citrinella*; Eh: *Emberiza hortulana*;
673 Lc: *Lanius Collurio*; La: *Lullula arborea*; Ls: *Luscinia svecica*; Mc: *Miliaria calandra*;
674 Ma: *Motacilla alba*; Moc: *Motacilla cinerea*; Oo: *Oenanthe oenanthe*; Ppt: *Petronia*
675 *petronia*; Po: *Phoenicurus ochruros*; Pc: *Prunella collaris*; Pm: *Prunella modularis*; Pg:
676 *Pyrrhocolax graculus*; Pp: *Pyrrhocolax pyrrhocolax*; Sr: *Saxicola rubetra*; St: *Saxicola*
677 *torquata*; Sc: *Sylvia communis*).

678 **Fig 2** Water pipit annual adult survival (i.e. annual survival probability of already
679 marked animals, S) (a) and proportion of transients (estimated as $1-(S^*/S)$, where S^* is
680 the survival probability estimated over the first year after marking) (b) in the Cantabrian
681 Mountains. The continuous line indicates the elevational trend of adult survival (S) (a)
682 and proportion of transients (b), the dotted lines indicate the respective 95% confidence
683 intervals, estimated in the top ranking model (model 16 in Table 3a, AICc weight =
684 0.19). The points (a) and the squares (b) represent the average survival of residents and
685 the proportion of transients in each sampling site, respectively. These average values are
686 estimated in the model considered the geographical position of each site (model 2 in
687 Table 3a). The bars represent the standard errors.

Fig. 1

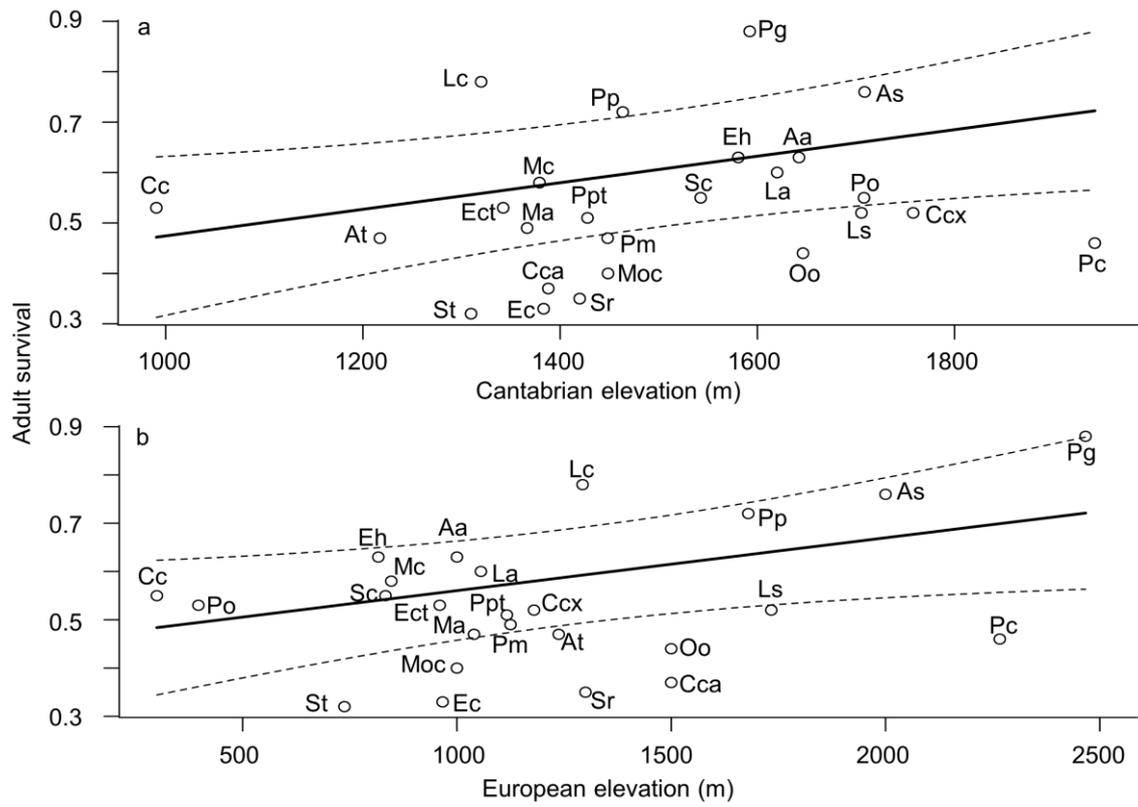


Fig. 2

