

1 **Article**

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4 **Morphological variation in the specialist Dupont's lark *Chersophilus duponti*:**
5 **geographical clines vs. local ecological determinants**

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24

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36 **Abstract**

37 Intraspecific geographic variation in morphology is common in animals along
38 geographic or climatic clines. Local ecological factors are likely to act simultaneously at
39 smaller spatial scales, but have hardly been contrasted with wide-ranging predictors. We
40 tested here whether the morphological variation of Dupont's larks (*Chersophilus*
41 *duponti*) responded to ecological parameters at two different spatial scales. First, we
42 investigated the effects of geographic and climatic gradients over its breeding range.
43 Second, we focussed at a smaller spatial scale on a fragmented population and tested
44 additionally several fine-grained ecological factors related to key components in the
45 species' habitat. Contrary to Bergmann's rule, wing length and cranium size decreased
46 with rainfall and increased with aridity and maximum temperature at the large scale, so
47 birds tend to be larger at lower latitudes. At the same time, wing and tarsus length
48 increased at high elevations where minimum temperatures are lower, providing some
49 support to Bergmann's rule. At the small spatial scale we failed to detect any
50 relationship between body size and positional or climatic variables, and food
51 availability, intra- and inter-specific competition and predation pressure neither
52 produced any significant effect on morphology. Nevertheless, cranium size and wing
53 length differed between habitats as measured by soil and vegetation types, and wing
54 length decreased with patch size. This later result could be explained in a context of
55 strong habitat fragmentation if larger individuals have a higher propensity of dispersing
56 or a higher probability of surviving dispersal events. Our study indicates that several
57 geographic and environmental sources may occur simultaneously at different spatial
58 scales. Further, even at the same scale, intraspecific morphological variation may show
59 contrasting patterns for climatic, latitudinal and elevational gradients that make it
60 difficult their interpretation in a context of ecogeographical rules. The effects elicited by

61 aridity, habitat loss and fragmentation on body size should be considered in future
62 studies of global change, as they may have serious consequences for the distribution,
63 abundance, and ultimately the persistence of birds in arid environments.

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80 **Introduction**

81 Intraspecific geographic variation in species attributes such as morphology, coloration
82 or life-history has been a central issue in ecology and evolutionary biology, with special
83 consideration to the association among phenotypic variation, climate and speciation
84 (Mayr 1963; Futuyma 1998). Within-species variation in morphology is common along
85 latitudinal gradients (Blackburn et al. 1999), which is usually interpreted in the
86 framework of Bergmann's rule given that climate is correlated with latitude (Ashton
87 2002; Meiri and Dayan 2003; Meiri et al. 2007). Bergmann's rule, the tendency of
88 animals to have larger bodies in cooler areas, originally referred to interspecific
89 comparisons, has frequently been applied at the intraspecific level (Mayr 1956; James
90 1970). It is among the best known biogeographical generalizations, despite an ongoing
91 debate on its definition, validity and underlying mechanisms (Blackburn et al. 1999,
92 Watt et al. 2009, Olalla-Tárraga 2011). The interpretation of the correlation between
93 morphology and positional or environmental variables is difficult because these factors
94 often covary, and other climatic and ecological factors are also key predictors of
95 morphological traits (Yom-Tov and Geffen 2006).

96 Furthermore, different forces are likely to act on within-species variation in
97 morphology at different spatial scales. For example, recent evidence have challenged
98 the interpretation of temporal declines in mean body size as adaptive responses to
99 increased temperatures in the context of global change, indicating that they merely
100 result from phenotypic plasticity and not from genetic microevolutionary changes,
101 claiming for the assessment of alternative environmental factors (Teplitsky et al. 2008;
102 Husby et al. 2011). Nevertheless, only a few studies have contrasted wide-ranging
103 positional or environmental clines with detailed local ecological factors, which could
104 account for morphological changes at a smaller spatial scale (habitat loss and

105 fragmentation: Lomolino and Perault 2007; competition and hybridisation: Guillaumet
106 et al. 2008; urbanisation: Evans et al. 2009). In this paper, we used a small steppe-
107 specialist passerine, the Dupont's lark (*Chersophilus duponti*), for investigating whether
108 intraspecific morphological variation correlates to ecological parameters at large and
109 small spatial scale. Several attributes makes this species especially suitable for such
110 study (see below for details).

111 We first investigated whether morphological characters related to body size
112 showed variation along a climatic and geographic gradient over its breeding range in
113 Spain and North Africa (Figure 1). In a second step, we zoomed in on a geographically
114 and topographically well separated and confined region of Spain where Dupont's lark
115 distribution is spatially structured due to habitat loss and fragmentation. As intraspecific
116 morphological patterns can be highly contingent to the species' biology (Meiri et al.
117 2005), we tested at this spatial scale additionally the effects of the several candidate
118 factors, which were hypothesized to modulate Dupont's lark morphology. For this
119 purpose, we pooled the morphological characters into four different groups according to
120 their functionality: (i) body size, (ii) feeding performance, (iii) flight ability and (iv)
121 locomotion. Testable predictions and underlying hypotheses at this spatial scale are:

122 1. *Food availability*: Food limitation should generate selection against large
123 individuals (MacArthur and Wilson 1967). Given that Dupont's lark is predominantly
124 an insectivorous species (Cramp 1988), morphological variation in body size and
125 feeding performance characters should be related to ground-dwelling arthropod
126 abundance, biomass and species richness.

127 2. *Intraspecific and interspecific competition*: Great overlap in resource use
128 within and between species should intensify the strength of competition (Emerson and
129 Arnold 1989), with the potential of producing shifts in morphological measures. We

130 expected variation in body size and feeding performance traits to be related to the
131 densities and species richness of a set of steppe passerines potentially competing with
132 Dupont's lark for the same resources.

133 3. *Predation pressure*: Larger values of characters related to flight ability in
134 birds have been reported to stem from increased vulnerability to aerial predators (Smith
135 et al. 1997). We tested whether the abundance of aerial predators is correlated to flight-
136 related morphological traits.

137 4. *Habitat characteristics*: Environmental conditions at a local scale have been
138 suggested to affect lark physiology (Fairhurst et al. 2013), so they are likely to have
139 some effects on morphology. Vegetation's species composition summarizes this
140 environmental information since it is closely related to soil characteristics, microslope,
141 water availability and nutrients (e.g. Peñuelas et al. 1999). Moreover, plant species
142 composition may reflect the abundance of keystone predators and the availability and/or
143 quality of food resources (Sánchez-Zapata and Calvo 1999; Buchanan et al. 2006; Ho et
144 al. 2010). Even though these predictions were partially tested directly (see above), we
145 additionally investigated the relationship between Dupont's lark morphology and
146 vegetation communities.

147 5. *Patch size and isolation*: As in most species, hampered dispersal seems to be a
148 key factor in Dupont's larks distribution and determines patterns of song and call
149 diversity, genetic structure and diversity (Laiolo and Tella 2005, 2007; Méndez et al.
150 2011; Méndez et al. 2014). If large individuals are more likely to succeed in
151 immigrating to island patches, mean body size of Dupont's larks, particularly regarding
152 morphological traits facilitating flight performance, should decrease with patch area and
153 connectivity.

154 Finally, we tried to integrate all this information to show that a species'
155 morphology can be explained by factors acting simultaneously at different spatial scales
156

157 **Methods**

158 **Species information and morphological data**

159 Dupont's lark is a threatened songbird restricted to natural and flat steppe areas of Spain
160 and North Africa (Cramp 1988; Figure 1a). The Spanish population has recently been
161 estimated to be as low as around 2000 breeding pairs (Tella et al. 2005; Suárez et al.
162 2010), whereas the knowledge about the species' populations in North Africa is still
163 scarce (García et al. 2008a). Even within this relatively confined area, positional and
164 environmental characteristics vary considerably (Electronic Supplementary Material
165 Table S1). Virtually across all its distribution range, the species' habitat has been
166 reduced to a series of fragments of variable size and isolation. These steppe remnants
167 may resemble islands (e.g. small size, barriers of hostile habitat hampering dispersal),
168 and habitat loss and fragmentation have been sufficient to extirpate the species from
169 many areas (Tella et al. 2005). The Dupont's lark is extremely habitat selective (Vögeli
170 et al. 2010), and breeding individuals show high site fidelity (Vögeli et al. 2008).
171 Acoustic and physical capture-mark-recapture methods hardly detected movements
172 between subpopulations only separated by few kilometres. Nine out of 333 acoustically
173 marked male birds were known to be immigrants in seven subpopulations, whereas
174 none of the 312 individuals banded with colour rings was re-sighted outside its home
175 subpopulation (Laiolo 2008; Vögeli et al. 2008). To sum up, the high isolation among
176 occupied habitat remnants and the species' low dispersal attitude, which is promoting
177 genetic drift as the main driving force of evolution (Méndez et al. 2011), constitute a

178 scenario that could favour the appearance of local morphological variation at fine-
179 grained spatial scale.

180 For the present study we used data of Dupont's larks captured from 2002 to
181 2008 with clap nets baited with meal worms (see Vögeli et al. 2007 for further trapping
182 details). Wing length (maximum wing chord) and tail length were measured with a ruler
183 to the nearest 0.5 mm. Tarsus length, hind claw length, cranium size (tip of the bill to
184 posterior pole of head), and three different bill variables (tip of the bill to skull, tip of
185 the bill to distal edge of nostrils, and bill depth) were measured with a digital calliper to
186 the nearest 0.01 mm.

187 To avoid potential biases due to personal skill in measuring bird morphometrics,
188 all investigators involved standardised their measurement. A drop of blood was
189 extracted for molecular sexing (see details in Vögeli et al. 2007). All birds were released
190 at the site of capture, and captures were carried out under approval of all competing
191 wildlife agencies. As the Dupont's lark shows a pronounced sexual dimorphism (Vögeli
192 et al. 2007) and males constituted over 80% of all captured birds, we only used adult
193 males in this study (n = 450). For the analysis at the large spatial scale, we used all the
194 captures carried out at fifty localities (hereafter "subpopulations") in Spain and
195 Morocco (A: Zamora, B: Palencia, C: Segovia, D: Iberian Mountains, E: Ebro Valley,
196 F: Cuenca, G: Murcia, H: Andalusia, I: Morocco, see Figure 1.b). The ecogeographical
197 region's categorization was based on Laiolo and Tella (2006). For the analyses of fine-
198 grained ecological factors at the smaller spatial scale we used individuals captured at
199 twenty-nine localities in the Ebro Valley (n = 286), the second most important breeding
200 population of Dupont's lark in Spain despite hosting 450-500 male territories only
201 (Figure 1c).

202

203 **Geographic and climatic variables**

204 Coordinates and elevation of each individual's capture point were recorded with a GPS.
205 We obtained mean maximum temperature of the hottest month (T_{\max}), mean minimum
206 temperature of the coldest month (T_{\min}) and annual precipitation (P) for all capture
207 points from the digital climatic atlas of the Iberian Peninsula (Ninyerola et al. 2005) for
208 Spain, and from an online database (Rivas-Martínez 2008) for Morocco. We also
209 calculated Emberger's (1955) index of aridity, Q, calculated as $Q = 2000P/(T_{\max}^2 -$
210 $T_{\min}^2)$. Values of Emberger's index were logarithmically transformed for statistical
211 analyses because Q increases nonlinearly in more mesic habitats (Tieleman et al. 2003).
212 The resulting variable refers to $-\ln Q$, being positively correlated with actual aridity,
213 and negatively correlated with primary productivity in arid and semi-arid areas
214 (Emberger 1955). Although we have data on climatic factors, we also included
215 positional variables in our analyses because they often are used in studies of body size
216 variation at large spatial scales (Ashton 2002).
217 Since the strait of Gibraltar is an effective barrier to gene flow between Moroccan and
218 Spanish populations of Dupont's larks (García et al. 2008b, Méndez et al. 2011),
219 analyses at this scale were also performed after excluding the Moroccan populations.

220

221 **Fine-grained ecological variables in the Ebro Valley**

222 During the breeding seasons (April-May) of 2005 and 2006, we established 89 linear
223 transects in 25 different subpopulations within the Ebro Valley where we captured
224 Dupont's larks. The number of transects carried out per subpopulation was
225 approximately proportional to its size (Tellería et al. 2008). These transects had a
226 maximum length of 500 m and were spaced more than 200 m apart if several transects
227 were carried out in the same subpopulation. Within the sampled subpopulations, which

228 could consist of various fragmented patches of adequate habitat for Dupont's lark, the
229 length of transects was adjusted to the patch size if the maximum length (500 m) could
230 not be reached (mean = 413 m, range 120-500 m). Along these transects, we established
231 five equidistantly separated sampling points where the botanical composition, soil type
232 and arthropod availability variables were recorded. Densities of other passerines were
233 estimated from censuses performed within the same transect line (see below).

234

235 **Food availability**

236 Arthropod sampling was carried out in May and early June of 2005 and 2006. We chose
237 pitfall traps as they are one of the least selective methods for ground-dwelling
238 invertebrates (Ausden 1996). Five pitfall traps (opening diameter 6 cm, height 8 cm,
239 filled with 70 percent ethyl alcohol) were randomly installed in each transect, but
240 separated by at least 25 m from each other because ground invertebrates are strongly
241 influenced by microclimatic conditions and vegetation structure within a few metres
242 (Antvogel and Bonn 2001). After three days, we emptied the traps, filtered and washed
243 the contents, which were stored in 70% ethyl alcohol until its identification. After
244 discarding the traps with evident signs of disturbance or manipulation (mostly by
245 rabbits or sheep), 596 traps remained for examination. All specimens were identified to
246 species when possible or otherwise to morphospecies and labelled as recognizable
247 taxonomic units (RTUs) (Oliver and Beattie 1993). This method avoids the use of fine-
248 scaled formal taxonomy at the species level, and is considered adequate for the
249 detection of differences among assemblages (Oliver and Beattie 1993). All
250 identification and classification work was carried out by the same investigator (M.V.) to
251 minimize observer bias. For each transect the number of RTUs and a biomass index
252 (weighing the RTU abundance against its respective mean body length) was computed

253 as the mean of the values obtained at each sampling point. Furthermore, the arthropod
254 diversity of each transect was calculated using the Shannon information index (Shannon
255 and Weaver 1949).

256

257 **Bird densities and species diversity**

258 We carried out line-transects recording all birds detected by sight or sound inside and
259 outside 50 m-wide belts on either side (Carrete et al. 2009). We then evaluated the
260 occurrence and density of the following steppe passerine species which coexist and
261 potentially compete in the breeding season with the Dupont's lark for habitat and food
262 (Cramp 1988): Lesser short-toed lark (*Calandrella rufescens*), Greater short-toed lark
263 (*Calandrella brachydactyla*), Thekla lark (*Galerida theklae*), Crested lark (*Galerida*
264 *cristata*), Calandra lark (*Melanocorypha calandra*), Eurasian skylark (*Alauda arvensis*),
265 Black-eared wheatear (*Oenanthe hispanica*), Spectacled warbler (*Sylvia conspicillata*)
266 and Tawny pipit (*Anthus campestris*). Censuses were performed from one hour after
267 dawn until noon, avoiding the central hours of the day, as well as rainy and windy days.
268 Determining Dupont's lark density by line-transects is not valid due to its elusive
269 behaviour and the difficulty of evaluating the distance to singing individuals (Tella et al.
270 2005). Hence, for this species we used the mean distance of the nearest singing
271 neighbours in each occupied patch as a proxy for Dupont's lark density (see Laiolo and
272 Tella 2008). For each subpopulation, we calculated both the total density of steppe
273 passerines and the correspondent species diversity, measured by the Shannon
274 information index (Shannon and Weaver 1949).

275

276 **Predator abundance**

277 During field work, we recorded all observations of possible aerial predators. These data
278 were collected from the beginning of spring 2004 until the end of spring 2007. We
279 calculated a relative abundance index for passerine hunting predators exclusively by
280 dividing the observations ($n = 659$) by the time spent in the respective subpopulation,
281 which totalised 3506 hours. The following species were considered: European marsh
282 harrier (*Circus aeruginosus*), Hen harrier (*Circus cyaneus*), Montagu's harrier (*Circus*
283 *pygargus*), Sparrowhawk (*Accipiter nisus*), Merlin (*Falco columbarius*), Lesser kestrel
284 (*Falco naumanni*), Common kestrel (*Falco tinnunculus*), Eurasian hobby (*Falco*
285 *subbuteo*), Peregrine falcon (*Falco peregrinus*), Booted eagle (*Hieraetus pennatus*) and
286 Southern grey shrike (*Lanius meridionalis*).

287

288 **Habitat characteristics**

289 Based on direct recording of the predominant species in circular plots of 25 m radius
290 around each sampling point, we determined the vegetation communities in each
291 subpopulation (six classes, after Braun-Blanquet and de Bolós 1957; Table 1).

292

293 **Patch size and isolation**

294 We calculated the area for each subpopulation (i.e. the size of the patch of natural
295 steppe vegetation occupied by Dupont's lark) in the Ebro Valley and log-transformed
296 them for statistical analyses. We determined the isolation index $I_i = - \sum \exp(-d_{ij}) N_j$,
297 where d_{ij} is Euclidean distance between patches i and j , and N_j is the population size of
298 patch j , including only occupied patches by Dupont's lark in the Ebro Valley (Hanski et
299 al. 1994). These descriptors were obtained from aerial orthophotographs of the study
300 area and from previous research (Tella et al. 2005; Vögeli et al. 2010).

301

302 **Statistical analyses**

303 *Morphological variables*

304 First, we carried out a principal component analysis (PCA) on the matrix of all
305 measured morphological traits to obtain new uncorrelated variables summarizing
306 variation in morphology. Nevertheless, the three principal components with eigenvalues
307 > 1 accumulated less than 70% of the morphological variation. Moreover, they could
308 hardly be related to a functional significance as it is usually done with principal
309 components (see Guillaumet et al. 2008). In turn, we built a matrix of Pearson
310 correlation coefficients to explore collinearity between the measured morphological
311 characters. Morphological traits with high correlations ($r \geq 0.5$) were grouped together
312 according to the functional significance of the respective characters, and we retained the
313 variables with most relevant biological meaning as response variables for the
314 subsequent analyses (Green 1979, Table 2). It is worth noting that wing length is
315 generally considered a good indicator of avian body size, and thus is the most frequently
316 used variable for assessing within-species body size variation in birds (Ashton 2002).
317 Furthermore, other skeletal measurements like tarsus length have been also used to
318 characterise body size (Zink and Remsen 1986; Yom-Tov 2001).

319 Dupont's larks undergo a unique and complete moult in July/August and their
320 feather size is constantly reduced until the next moulting cycle due to the exposure to
321 wear (Van Balen 1967). Hence, we corrected for this possibly confounding effect by
322 adding the season (spring/autumn) as a fixed term in the statistical models when
323 analysing wing length. The rest of the measured morphological characters analysed did
324 not show any significant patterns of temporal variation.

325

326 *Geographic variables and spatial autocorrelation*

327 We explored collinearity among climatic and positional predictor variables by means of
328 Spearman correlation coefficients, which showed that both predictor groups frequently
329 covary (Results not shown). Two principal component analyses with varimax rotation
330 were successful at reducing variable redundancy at both spatial scales (see Electronic
331 Supplementary Material Table S2), so factor scores were used in subsequent analyses.

332 Before modelling the different effects on the respective morphometric variables,
333 we tested the null models of each trait, i.e. models that lack predictor variables, for
334 spatial autocorrelation at both spatial scales. Spatial autocorrelation may invalidate
335 systematically the assumption of independent errors, thus distorting classical statistical
336 tests and giving misleading correlation coefficients, regression slopes and associated
337 significance tests (Lennon 2000; Legendre et al. 2002). First, we assumed independent
338 errors and implemented null intercept-only linear models (LMs). Second, we built null
339 spatial correlation models that fitted six alternative spatial covariance matrices
340 (exponential, spherical, Gaussian, linear, log linear, power) to the data and used the best
341 matrix to adjust test statistics, thus taking spatial autocorrelation into account (Littell et
342 al. 2006). Third, we implemented as an alternative approach null linear mixed models
343 (LMM) in which the subpopulation structure was fitted as a random term to take in
344 account spatial autocorrelation. For these later analyses at large spatial scale we entered
345 region identity and subpopulation identity within region as random factors, whereas
346 subpopulation identity exclusively was entered as random factor when analysing the
347 data at small spatial scale within the Ebro Valley (see Electronic Supplementary
348 Material Table S1 for details on subpopulation and region identity). The spatial
349 correlation models fitted best with a spherical spatial covariance structure and revealed
350 spatial autocorrelation in all morphometric variables, except for tarsus, being more
351 pronounced at the large (all $P < 0.0001$) than at the small spatial scale (all $P < 0.05$). We

352 consequently built three candidate models according to the three modelling approaches
353 (independent errors, spherical covariance matrix and random subpopulation structure),
354 for each of the five morphological traits at both spatial scales. Then we identified the
355 most parsimonious null models for each morphometric variable (10 comparisons, 5 for
356 each spatial scale) based on their differences in AIC_c (Littell et al. 2006, see also
357 below). At both spatial scales, the null linear mixed models with the random
358 subpopulation structure fitted the data better (difference in $AIC_c > 4$ in eight of the
359 comparisons) or equally (difference in $AIC_c < 2$ in the remaining two comparisons) for
360 all five morphological traits when compared to either LMs with independence of errors
361 or spatial correlation models. Hence, we decided to continue the analyses with LMMs
362 acknowledging spatial autocorrelation with the subpopulation structure as random
363 factors accordingly to the tested spatial level.

364 For each spatial scale and morphological trait, we constructed an a priori set of
365 candidate models that only included biologically meaningful explanatory variables
366 besides the random terms. Within this candidate set, an only-intercept null model (fitted
367 with the appropriate random subpopulation structure) was always included. Competing
368 models were ranked using Akaike information criterion corrected for small sample size
369 (AIC_c , see Burnham and Anderson 2002), and models within 2 AIC_c points ($\Delta AIC_c <$
370 2) were considered as statistically equivalent. A pervasive problem with information
371 theoretic approaches, intrinsically linked to the way in which extra parameters are
372 penalized, is that variables with poor explanatory power added to an otherwise good
373 model can result in a wrongly competitive model. These pretending or uninformative
374 parameters do not truly contribute to a better fit and should not be considered (Burnham
375 and Anderson 2002:131, Anderson 2008:65, Arnold 2010). Top-ranked models with
376 uninformative parameters were identified and discarded by examining changes in

377 maximized log-likelihood as well as the standard errors and 85% confidence intervals of
378 parameter estimates (Anderson 2008, Arnold 2010). In addition, the relative effect size
379 of each correlate was calculated using its cumulative Akaike weight across all models
380 where it occurred, and model averaging was employed to deal with model selection
381 uncertainty (Burnham and Anderson 2002). Models were constructed via maximum
382 likelihood techniques using PROC MIXED in SAS 9.3 (SAS Institute, Cary NC) and
383 library lme4 (Bates et al. 2015) in R 3.1.3 (R Core Team 2015). AICc tables, model
384 averaging and post-hoc comparisons were performed with the R libraries AICcmodavg
385 (Mazerolle 2015), lsmeans (Lenth 2015) and multcomp (Hothorn et al. 2008).

386

387 **Results**

388 **Morphological variation at the large spatial scale**

389 After discarding models with uninformative parameters, model selection procedures
390 suggested that variation in wing length, tarsus length and cranium size (the
391 morphological characters related to body size) exhibited different patterns depending on
392 the climatic and positional variables (Electronic Supplementary Material Table S3). Our
393 data indicate that both wing length and cranium size increased with the first principal
394 component of the PCA (Table 3), with the largest birds occurring on average at arid
395 localities with low rainfall and high maximum temperatures during the hottest month,
396 which tend to be situated at low latitudes (see Figure 2 for the relationship with aridity,
397 the variable with the highest factor loading in the first PCA component). In addition,
398 wing length and tarsus length showed a negative relationship with the second principal
399 component (Electronic Supplementary Material Table S3), although for wing length the
400 effect seemed to be weaker than that described for the first component (Evidence ratio:
401 1.45, see Table 3). In this way, birds had on average larger wings and longer tarsus in

402 elevated populations with low minimum temperatures during the coldest month, which
403 tend to be located at low latitudes and longitudes.

404 After excluding the Moroccan populations, results remained qualitatively similar
405 (Electronic Supplementary Material Table S5). Only bill depth showed a distinctive
406 defined cline very similar to that of wing length when only Spanish populations were
407 analysed, with thicker bills in both the most arid and driest, and in the most elevated and
408 coldest localities.

409

410 **Morphological variation at the small spatial scale**

411 *1. Geographic and climatic variables*

412 In opposition to the large spatial scale, we did not detect any variation in any of the
413 measured morphometric traits of Dupont's larks in the Ebro Valley in relation to either
414 positional or climatic variables (Table 4, Electronic Supplementary Material Table S4).

415

416 *2. Ecological variables*

417 Despite an extensive sampling effort for testing the potential effects of food availability,
418 intra- and inter-specific competition and avian predation pressure on morphology, none
419 of these fine-grained ecological characters appeared to have an effect on the measured
420 morphological variables (Table 4, Electronic Supplementary Material Table S4).

421 Models including an effect of soil types on wing and hind claw lengths,
422 however, were supported by data (Electronic Supplementary Material Table S4). These
423 models indicated that birds from populations characterized by harder soils had shorter
424 wings and claws than birds inhabiting softer substrates (Table 4). The vegetation types
425 also had an effect on cranium size (Electronic Supplementary Material Table S4). Effect
426 sizes examination and post-hoc pair-wise comparisons revealed that the main difference

427 was between the populations characterized by the vegetation association *Lygeeto-*
428 *Stipetum lagascae* holding a low plant species diversity (vegetation community 2) and
429 those with vegetation dominated by *Rosmarinus officinalis* with large interspersed areas
430 of bare gypsum soil (vegetation community 5) (Table 4).

431 Regarding patch size and isolation, a negative trend between wing length and
432 patch size was supported by data (Electronic Supplementary Material Table S4, Table 4,
433 Figure 3). The isolation of the different populations, however, did not evidence any
434 remarkable effect on the tested characters (Electronic Supplementary Material Table
435 S4).

436

437 **Discussion**

438 **Morphological variation at the large spatial scale**

439 Intraspecific morphological variation along geographical clines has usually been
440 assessed by examining a species' conformity with Bergmann's rule, which is assumed
441 to be a valid ecological generalization for birds (Ashton 2002, Meiri and Dayan 2003).
442 It has mostly been shown as a positive correlation between body size and latitude
443 explained by thermal trends (Mayr 1956). Regarding lark species, both support and non-
444 conformity to Bergmann's rule have been reported (Niles 1973; Yom-Tov 2001;
445 Guillaumet et al. 2008). Sedentary species such as Dupont's lark are expected to be
446 more affected by natural selection linked to climatic factors and are thus more likely to
447 follow Bergmann's rule than migratory species that evade the extreme winter
448 temperatures by relocating (Meiri and Dayan 2003). Indeed, we found some evidence
449 supporting Bergmann's rule in Dupont's larks, but our findings mostly contradict its
450 original conception whether it is seen as a latitudinal or a temperature clinal pattern.

451 Climate is usually correlated with latitude and altitude and may therefore shape
452 selection pressures on body size, either directly, e.g. by heat dissipation (James 1970) or
453 fasting endurance (Boyce 1979), or indirectly by affecting food availability, competition
454 and predation pressure (McNab 1971). The use of latitude and elevation as
455 environmental predictors in biogeographical studies has been severely criticised when
456 disposing on direct environmental variables such as temperature and precipitation
457 (Hawkins and Diniz-Filho 2004). Both wing length and cranium size showed a gradient
458 which increased towards higher aridity, which tend to characterize populations of lower
459 latitudes. Aridity is an important characteristic of many Dupont's lark populations; larks
460 have their evolutionary origin in Africa and occupy mostly open and semi-arid or arid
461 regions, showing interspecific clines in physiological adaptations to cope with aridity
462 (Tieleman et al. 2003) and appropriate behaviours to avoid overheating and excessive
463 water loss (De Juana et al. 2004). Indeed, trade-offs between foraging efficiency and
464 heat-dissipation behaviours have been described in such arid ecosystems (du Plessis et
465 al. 2012). Under these circumstances, a larger body size of Dupont's lark could be
466 favoured in arid environments with growing incidence of seasonal food shortages and
467 heat waves because it permits the accumulation of more body reserves and facilitates
468 heat loss by evaporation (James 1970; Ashton 2002). Accordingly, increases in body
469 size with temperature have been said to be mediated through size-dependent mortality in
470 another semi-arid passerine (Gardner et al. 2014). As aridity and primary productivity
471 are negatively correlated (Emberger 1955), the gradient in Dupont's lark body size is
472 contrary to the hypothesis that body size of individuals is positively correlated with
473 productivity and eventually with food availability, especially in semi-arid or arid
474 environments (Rosenzweig 1968).

475 Additionally, the tendency for wing and tarsus length to increase at cooler,
476 elevated areas was also supported by data in accord of Bergmann's rule (Ashton 2002).
477 This pattern has been found in other larks (Guillaumet et al. 2008, Camfield et al. 2010),
478 and seemingly conflicts with the trend we found with the aridity component. However,
479 what arid and cold areas have in common is a marked seasonality which implies strong
480 temporal variations in food availability (Guillaumet et al. 2008). Larger sizes favour
481 fasting endurance, which may be advantageous in seasonal environments (Ashton
482 2002), and could confer physiological advantages in both cooler and drier conditions
483 (James 1970). Moreover, contrasting patterns for latitudinal and elevational gradients
484 have been documented elsewhere, likely as a result of differences in the steepness of
485 environmental gradients (Gouveia et al. 2013) and in the way organisms are affected by
486 ecological pressures along elevational and latitudinal axes (Gutiérrez-Pinto et al. 2014).

487 Finally, parallel mechanisms including other natural selection pressures,
488 phenotypic plasticity, genetic drift or barriers to gene flow, could contribute to explain
489 body size variation. Body size variation in Dupont's lark could have arisen nowadays
490 by the effect of genetic drift and the absence of gene flow due to fragmentation
491 (Méndez et al. 2011; Méndez et al. 2014) or in the past by barriers to gene flow between
492 geographical areas (García et al. 2008b). In effect, functional diversification has been
493 said to be facilitated when geographic isolation act in concert with differential
494 ecological pressures (e.g. Benham and Witt 2016). Although genetic drift is an
495 important force of evolution, being more intense in small and isolated populations, the
496 genetic signal of a well-connected historical population still remains in Dupont's lark
497 (Méndez et al. 2011). In this sense, genetic drift may have occurred in localities as
498 Tariego, which holds five unusually large individuals (see Electronic Supplementary
499 Material Table S1), but clinal patterns in body size would not be expected to result from

500 this mechanism due to its stochastic nature. Interspecific competition with other steppe
501 passerines has also been suggested as a possible reason favouring character
502 displacement and increased body size for Dupont's lark and larks from the genus
503 *Galerida* in Morocco (Guillaumet et al. 2006; García et al. 2008b). Alternatively,
504 phenotypic plasticity could also produce larger body size in birds in some environments
505 (James 1983; Teplitsky et al. 2008).

506

507

508 **Local patterns in morphological variation**

509 An exhaustive sampling of environmental variables within the Ebro Valley (Figure 1.c)
510 allowed us to test for numerous possible effects of ecotypic differentiation in
511 morphology at a small spatial scale. However, we failed to detect any relationship
512 between body size and positional or climatic variables, probably due to low variation of
513 most of these predictors at this scale. Additionally, neither food availability, nor intra-
514 and interspecific competition, nor predator pressure seemed to influence the studied
515 morphological characters of Dupont's lark within the Ebro Valley. Dupont's lark is
516 reported to feed on a large range of ground-dwelling arthropods (Cramp 1988).
517 Nonetheless, several studies have shown that certain arthropod groups are preferably
518 selected by passerines for both adult and nestling diets (Buchanan et al. 2006). These
519 subtle preferences may have remained undetected by our general approach of arthropod
520 availability sampling. Despite covering over 10,000 km², the composition of both the
521 steppe passerine community and its aerial predators does not change substantially
522 within the Ebro Valley. Although we also accounted for density effects, comparison at
523 large spatial scale might shed more light on possible effects of interspecific competition,
524 as species composition changes noticeably throughout the sampled range in Spain and

525 Morocco. Parallel to this outcome, we could not confirm the hypothesis that larger
526 values of wing length are a consequence of increased vulnerability to aerial predators
527 (Smith et al. 1997).

528 Differences in claw length with soil characteristics are likely due to a greater
529 abrasion in harder substrates. Similarly, the variation in cranium size may be best
530 interpreted with the contrasted soil characteristics of the concerned vegetation
531 communities. A very stony surface is a frequent feature of the vegetation community 2,
532 mostly due to a shallow profile depth. In contrast, the vegetation dominated by
533 *Rosmarinus officinalis* with large interspersed areas of bare ground is characterised by
534 loose gypsum soil, which is easy to penetrate. As a consequence, bill abrasion may
535 underlie the differences in cranium size due to Dupont's lark behaviour: it feeds almost
536 exclusively on arthropods that are picked from the ground surface or burrowed a few
537 centimetres under the surface (Cramp 1988). Alternatively, larger craniums could reflect
538 local feeding adaptations or phenotypic plasticity to prey on underground invertebrates
539 in soils in which it is easier to scratch around or to dig a hole. More intriguing is the
540 relationship between wing size and soil type, but one plausible explanation is that flight
541 feathers may be increasingly subject to wear in more stony and hard substrates.

542 When analysing for effects related to patch size and isolation at the Ebro Valley,
543 we found a negative relationship between wing length and patch size. Fragmentation
544 and loss of habitat have drastically diminished the extent of Dupont's lark in recent
545 decades in the Ebro Valley and extinctions of local populations are ongoing even today
546 (Tella et al. 2005; Laiolo et al. 2008). As a consequence of shrunk population sizes
547 and created barriers to individual movement, the cultural transmission of Dupont's lark
548 has been disrupted and gene flow is reduced (Laiolo and Tella 2005, 2006, 2007;
549 Méndez et al. 2014). Studies accounting explicitly for the effect of fragmentation and

550 habitat loss on intraspecific morphological variation are rare (see Lomolino and Perault
551 2007). Nevertheless, intraspecific morphological shifts have received much attention
552 especially in evolutionary studies (e.g. Mayr 1963) or those related with island rule
553 (Meiri et al. 2005), and their findings may help interpret our results. Small habitat
554 patches in our study system are usually fragmented and show the highest lark densities
555 as a consequence of limited connectivity and crowding effects (Laiolo and Tella 2006;
556 Vögeli et al. 2010; Méndez et al. 2014). In this context, individuals may suffer
557 unusually strong intraspecific competition and limited food availability, circumstances
558 under which a large body size would be favoured (Ashton 2002; Robinson-Wolrath and
559 Owens 2003). Although direct tests for these hypotheses were unsupported (see above),
560 we cannot rule out that multiple social and ecological factors were synergistically
561 affecting habitat quality in complex ways in small patches. The increased wing length
562 could also be a consequence of need for greater aerodynamic efficiency (Smith et al.
563 1997) or just be a phenotypic trait correlated to dispersal propensity. Capture-recapture
564 studies of Dupont's lark during four years in the Ebro Valley revealed limited dispersal
565 behaviour in the species (Laiolo and Tella 2008; Vögeli et al. 2008). Hence, the few
566 successful dispersal events between subpopulations could account for large individuals
567 whose contribution to the increase of the mean wing length would be perceived to a
568 greater extent in populations with only a few individuals than in larger subpopulations.
569 Tella et al. (2005) showed that extinction of Dupont's lark populations occurred more
570 often in small (<100 ha) habitat patches. Moreover, Méndez et al. (2014) showed that
571 small populations (<16 males or 300 ha) are prone to suffer genetic erosion. The
572 individual advantages of a larger body size for fitness may thus be accentuated in small
573 remnant habitat patches, even though the survival of Dupont's larks did not seem to be
574 affected by the patch size (Laiolo et al. 2008).

575

576 **Conclusions**

577 Our study indicates that morphological variation may have several geographic,
578 environmental sources occurring simultaneously at different spatial scales. At a large
579 scale, we found contrasting patterns for geographical and climatic gradients, which
580 revealed the species and context dependent nature of morphological variation in birds.
581 Furthermore, the significant differences in wing length among the subpopulations in the
582 Ebro Valley were associated with habitat loss and fragmentation. This pattern must have
583 arisen rapidly since these anthropogenic changes occurred in large part during the last
584 few decades. Since differences in body size, other morphological traits and genetics of
585 Dupont's lark have also been found among populations of Spain and Morocco (García
586 et al. 2008b; Méndez et al. 2011), further disentangling of ecotypic differentiation
587 should include genetic analyses to test whether evolutionary changes in species genetics
588 or merely reaction norms across latitudinal or climatic gradients are behind the
589 described patterns. Models of global climate change predict that mean temperature will
590 increase and hot-weather episodes will be more frequent in arid environments (Meehl
591 and Tebaldi 2004). Further, future anthropogenic changes will likely result in smaller
592 and more isolated habitat patches. In these scenarios, our findings point out that global
593 change could affect variations in body size in the future, and therefore metabolism and
594 fitness, with far-reaching consequences for the persistence of populations.

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Table 1. Classification of vegetation communities in the Ebro Valley (after Braun-Blanquet and de Bolós 1957).

	Class	Order	Association	Type
1	Thero-Brachypodieta	Rosmarineta	Rosmarineto-Linetum suffruticosi	no dominant species, high species diversity
1	Thero-Brachypodieta	Lygeo-Stipetalia	Lygeeto-Stipetum lagascae	no dominant species, high species diversity
2	Thero-Brachypodieta	Lygeo-Stipetalia	Lygeeto-Stipetum lagascae	shallow profile depth, low species diversity
2	Thero-Brachypodieta	Lygeo-Stipetalia	Lygeeto-Stipetum lagascae	presence/dominance of <i>Artemisia herba-alba</i> , low species diversity
3	Ononido-Rosmarianetea	Gypsophilion	Helianthemum squamati	dominance of <i>Helianthemum squamatum</i> , high species diversity
4	Ononido-Rosmarianetea	Gypsophilion	Helianthemum squamati	presence/dominance of <i>Artemisia-herba alba</i> , low species diversity
5	Ononido-Rosmarianetea	Gypsophilion	Helianthemum squamati	dominance of <i>Rosmarinus officinalis</i> , low species diversity
6	Salicornietea	Limonietalia	Suadetum brevifoliae	

Table 2. Morphological characters classified by their functionality. The main characters were used as response variables in this study. The r-values are the coefficients according to Pearson correlation (n = 450) and statistically significant ($P < 0.01$). Bill length refers either to the measurement from the tip of the bill to the skull (BC) or from the tip of the bill to the distal edge of nostrils (BN).

Functional significance	Main character	Covarying characters	r
Body size, flight ability	Wing length	Tail length	≥ 0.5
Body size, feeding performance	Cranium size	Bill length (BC and BN)	≥ 0.5
Feeding performance	Bill depth	-	-
Body size, locomotion	Tarsus	-	-
Locomotion	Hind claw length	-	-

Table 3. Climatic, positional and ecological correlates of morphological traits in Dupont's larks at the whole breeding range according to the top-ranked mixed-effects models (see model selection in Electronic Supplementary Material Table S3). F1 and F2 are the loading scores of the principal component analyses performed to eliminate redundancy of positional and climatic variables (Electronic Supplementary Material Table S2). High scores of F1 indicate arid localities with high temperatures and low rainfall, situated mainly at low latitudes. High scores of F2 correspond to low altitudes, high minimum temperatures, and high longitudes and latitudes. Parameter estimates, unconditional standard errors (SE) and 85% confidence intervals (85% CI) were obtained directly from model output when a single model was selected, or by means of model averaging when several top-ranked models were statistically equivalent to include model selection uncertainty. The cumulative weight column shows the sum of the Akaike weights across all models where the variable of interest occurs. Uninformative parameters are denoted in the explanatory variable column with a *.

Trait	Explanatory variable	Estimate	SE	85% CI	Cumulative weight
Wing	F1	0.69	0.15	0.47,0.92	1
	season (2)	1.66	0.25	1.3,2.2	1
	F2	-0.35	0.16	-0.58,- 0.12	0.69
Tarsus	F2	-0.1	0.04	-0.15,- 0.04	0.79
	F1*	-0.03	0.04	-0.08,0.02	0.34
Craneum	F1	0.20	0.09	0.07,0.32	0.79
Bill depth	F2*	-0.03	0.06	-0.14,0.06	0.30
Claw length	F1*	-0.22	0.16	-0.45,0	0.49
	F2*	0.17	0.51	-0.17,0.51	0.31

Table 4. Climatic, positional and ecological correlates of morphological traits in Dupont's larks at the Evro valley according to the top-ranked mixed-effects models (see model selection in Electronic Supplementary Material Table S4). F1' and F2' are the loading scores of the principal component analyses performed to eliminate redundancy of positional and climatic variables (Electronic Supplementary Material Table S2). High scores of F1' correspond to populations with high rainfall, low aridity and temperature, and located at elevated places. High scores of F2' indicate primarily populations located at high longitudes and low latitudes with strong thermal contrast. Parameter estimates, unconditional standard errors (SE) and 85% confidence intervals (85% CI) were obtained directly from model output when a single model was selected, or by means of model averaging when several top-ranked models were statistically equivalent to include model selection uncertainty. The cumulative weight column shows the sum of the Akaike weights across all models where the variable of interest occurs. Uninformative parameters are denoted in the explanatory variable column with a *.

Trait	Explanatory variable	Estimate	SE	85% CI	Cumulative weight
Wing	season (2)	1.6	0.33	1.13,2.08	1
	soil (2)	0.6	0.69	-0.4,1.6	0.55
	soil (3)	-0.78	0.5	-1.5,-0.06	
	patch size	-0.78	0.52	-1.53,-0.03	0.52
Tarsus	patch size*	-0.13	0.11	-0.28,0.02	0.24
	connectivity*	29.91	24.7	-5.65,65.46	0.29
	predation pressure*	0.49	0.53	-0.28,1.25	0.19
	heterospecific density*	0.02	0.04	-0.03,0.07	0.11
Craneum	vegetation type (2)	-0.80	0.42	-1.4,-0.2	0.88
	vegetation type (3)	-0.85	0.35	-1.36,-0.34	
	vegetation type (4)	-0.82	0.59	-1.67,0.03	
	vegetation type (5)	1.15	0.43	0.53,1.77	
	vegetation type (6)	-0.58	0.45	-1.23, 0.07	
	biomass invertebrates*	0.00	0.03	-0.04,0.03	0.39
	patch size*	0.29	0.27	-0.11,0.68	0.30
Bill depth	heterospecific density*	-0.06	0.08	-0.17,0.05	0.10
	heterospecific density*	-0.04	0.03	-0.07,0	0.45
	F2'*	-0.13	0.1	-0.27,0.01	0.40
Claw length	soil (2)	0.72	0.41	0.14,1.31	0.30
	soil (3)	0.63	0.4	0.05,1.21	

F2'*	0.16	0.25	-0.2,0.51	0.14
biomass invertebrates*	0.01	0.03	-0.04,0.06	0.22
F1'*	0.05	0.12	-0.12,0.23	0.13

FIGURE CAPTIONS

Figure 1. (a) World distribution of Dupont's Lark (after Del Hoyo et al. 2004). (b) Sampled regions in Spain and Morocco (see text for explanation of the abbreviations). (c) Sampled populations in the Ebro Valley.

Figure 2. Cranium size and wing length variation (mean value \pm 1 standard deviation) in Dupont's lark in relation to aridity within its distribution in Spain and Morocco.

Figure 3. Relationship between Dupont's lark wing length (mean value \pm 1 standard deviation) and patch size of the corresponding subpopulation (log transformed) in the Ebro Valley.

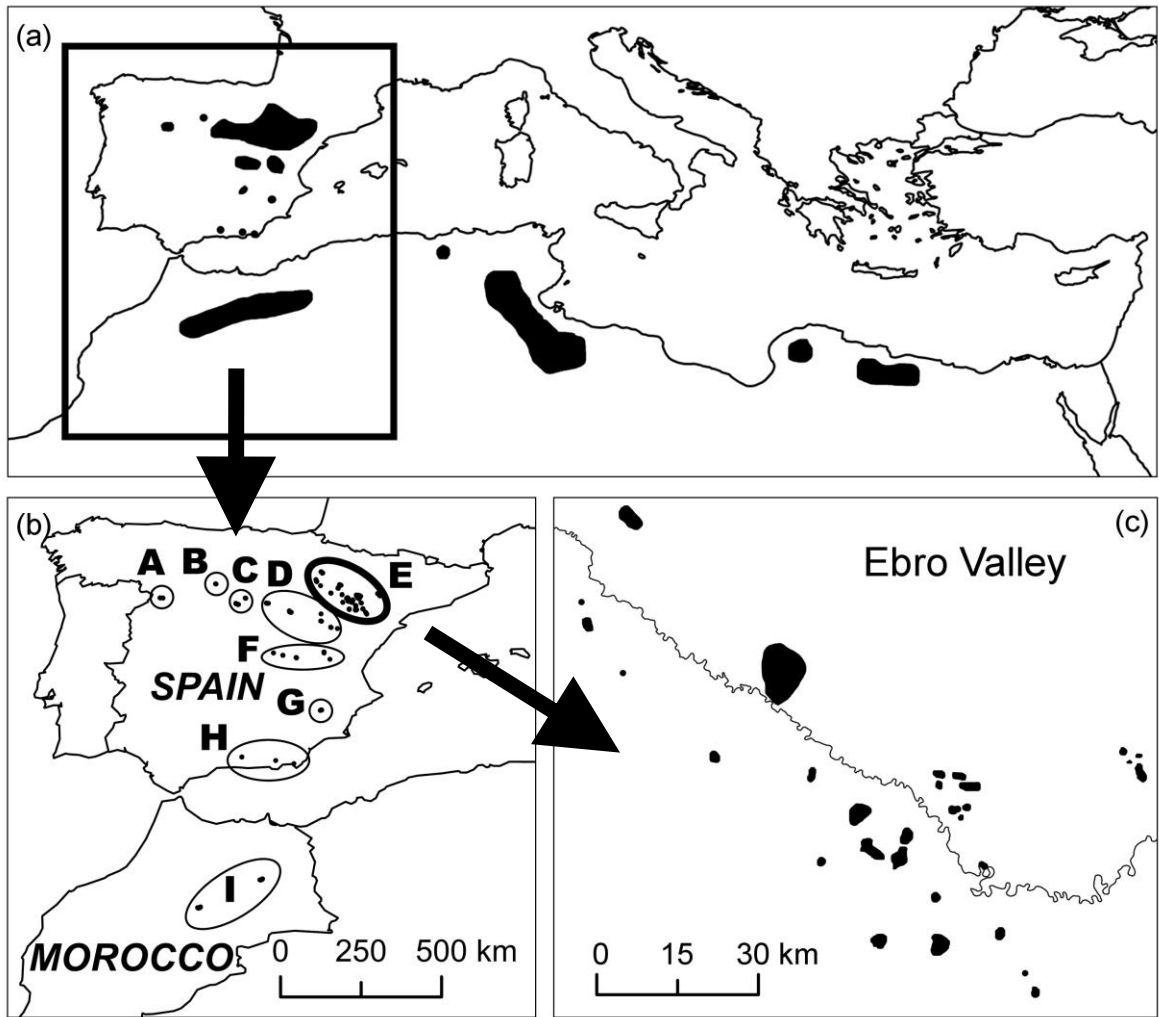


Figure 1.

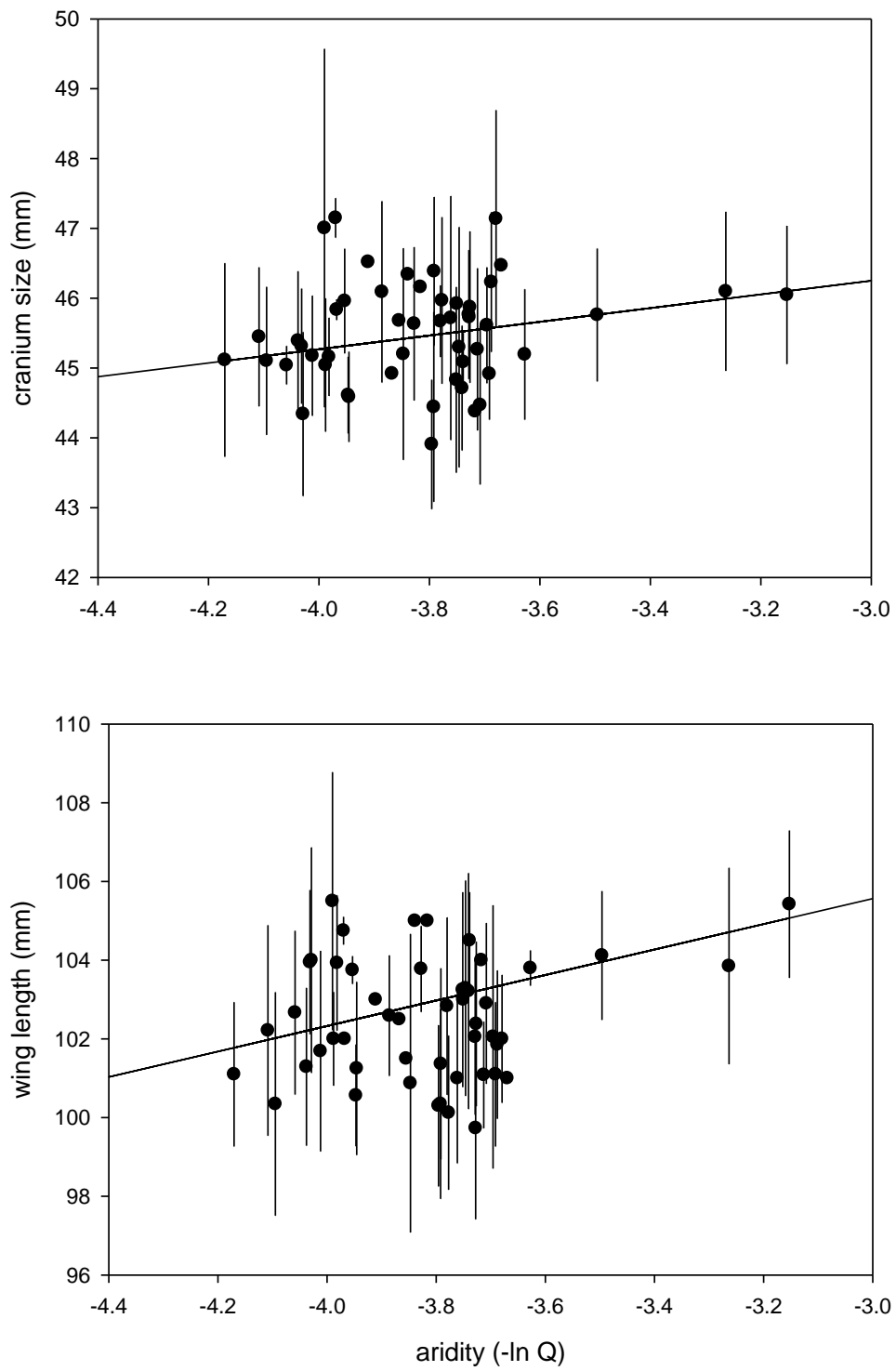


Figure 2.

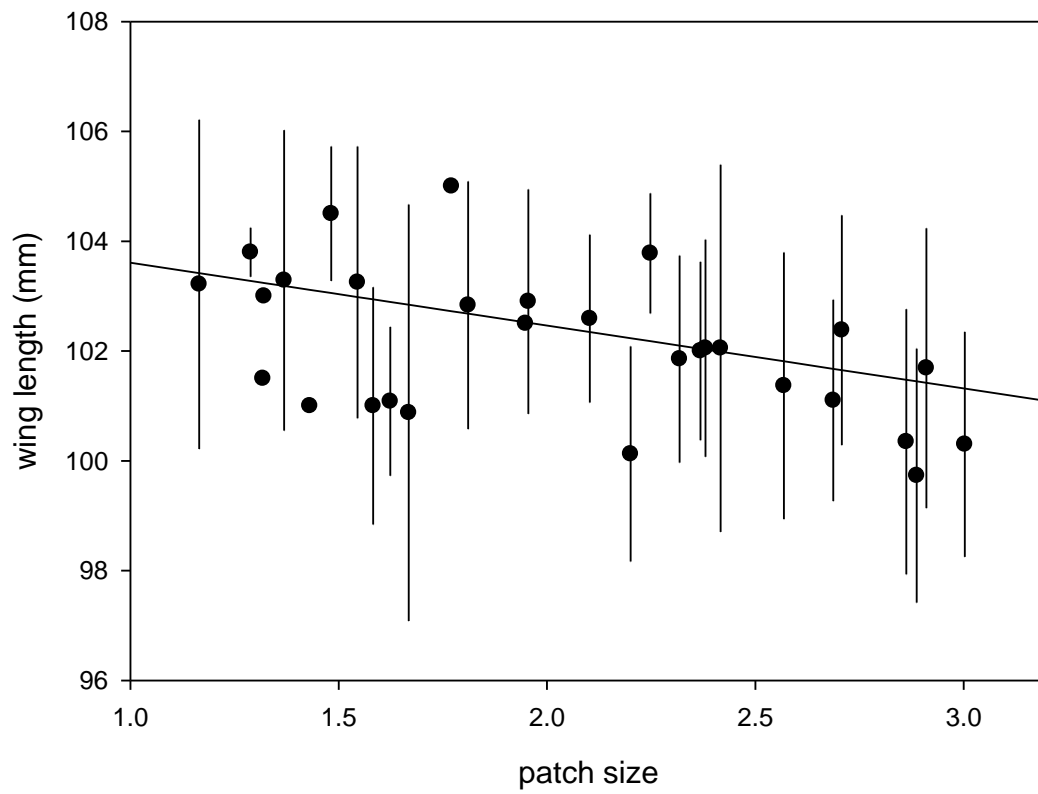


Figure 3.