

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

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Received: 8 March 2016 / Revised: 26 July 2016 / Accepted: 28 July 2016 / Published online: 9 August 2016
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Abstract Intraspecific geographic variation in morphology is common in animals along geographic or climatic clines. Local ecological factors are likely to act simultaneously at smaller spatial scales, but have hardly been contrasted with wide-ranging predictors. We tested here whether the morphological variation of Dupont's Larks (*Chersophilus duponti*) responded to ecological parameters at two different spatial scales. First, we investigated the effects of geographic and climatic gradients over its breeding range. Second, we focussed at a smaller spatial scale on a fragmented population and tested additionally several fine-grained ecological factors related to key components in the species' habitat. Contrary to Bergmann's rule, wing length and cranium size decreased with rainfall and increased with aridity and maximum temperature at the large scale, so birds tend to be larger at lower latitudes. At the same time, wing and tarsus length increased at high elevations where minimum temperatures are lower, providing some support to Bergmann's rule. At the small spatial scale we failed to detect any relationship between body size and positional or climatic variables, nor did food availability, intra- and inter-specific competition and predation pressure produce

any significant effect on morphology. Nevertheless, cranium size and wing length differed between habitats as measured by soil and vegetation types, and wing length decreased with patch size. This later result could be explained in the context of strong habitat fragmentation if larger individuals have a higher propensity of dispersing or a higher probability of surviving dispersal events. Our study indicates that several geographic and environmental sources may occur simultaneously at different spatial scales. Further, even at the same scale, intraspecific morphological variation may show contrasting patterns for climatic, latitudinal, and elevational gradients that make their interpretation difficult in the context of ecogeographical rules. The effects elicited by aridity, habitat loss, and fragmentation on body size should be considered in future studies of global change, as they may have serious consequences for the distribution, abundance, and ultimately the persistence of birds in arid environments.

Keywords Bergmann's rule · Body size · Dupont's Lark · Aridity · Patch size

Zusammenfassung

Merkmalsunterschiede der spezialisierten Dupontlerche *Chersophilus duponti*: geografische Gradienten vs. lokale ökologische Faktoren

Bei Tieren kommen intraspezifische Merkmalsunterschiede entlang von geografischen oder klimatischen Gradienten häufig vor. Lokale ökologische Faktoren, die gleichzeitig auf kleiner räumlicher Ebene wirken dürften, wurden bisher aber kaum mit großräumlichen Faktoren verglichen. Wir untersuchten hier den Zusammenhang zwischen Merkmalsunterschieden der Dupontlerche (*Chersophilus*

Communicated by J. T. Lifjeld.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-016-1383-x) contains supplementary material, which is available to authorized users.

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duponti) und ökologischen Faktoren auf zwei unterschiedlichen räumlichen Ebenen. Erstens analysierten wir die Effekte von geografischen und klimatischen Gradienten in ihrem gesamten Verbreitungsgebiet. Zweitens testeten wir zusätzlich verschiedene lokale ökologische Faktoren mit Bezug zu den Schlüsselfaktoren in ihrem Lebensraum auf kleiner räumlicher Ebene in einer fragmentierten Population. Auf großer räumlicher Ebene waren im Gegensatz zur Bergmannschen Regel die Flügellänge und Schädelgröße kleiner je höher die Niederschlagsmenge und grösser je höher die Werte für Trockenheit und maximale Temperatur. Die Dupontlerchen sind also tendenziell grösser in geringeren Breitengraden. Gleichzeitig verringerten sich Flügellänge und Tarsuslänge mit zunehmender Höhenlage, wo die minimalen Temperaturen tiefer sind, was die Bergmannsche Regel wiederum unterstützt. Auf kleiner räumlicher Ebene konnten wir keinen Zusammenhang zwischen Körpergröße und den räumlichen oder klimatischen Variablen finden, und weder Nahrungsverfügbarkeit, intra- und interspezifische Konkurrenz noch Prädationsdruck hatten einen signifikanten Effekt auf die untersuchten Merkmale. Schädelgröße und Flügellänge hingegen zeigten Unterschiede zwischen Lebensräumen, gemessen anhand Boden- und Vegetationstypen, und die Flügel waren länger je grösser die Fläche der Teilpopulationen. Dieses letzte Resultat könnte im Zusammenhang mit starker Habitatsfragmentierung erklärt werden: größere Individuen hätten demnach eine größere Tendenz, sich auszubreiten oder eine höhere Überlebenswahrscheinlichkeit während Dispersionsbewegungen. Unsere Studie zeigt, dass verschiedene geographische und umweltbedingte Einflüsse gleichzeitig auf verschiedenen räumlichen Ebenen wirken können. Zusätzlich können intraspezifische Merkmalsunterschiede sogar auf derselben räumlichen Ebene unterschiedliche Muster für Klima-, Breiten- und Höhengradienten zeigen. Dies erschwert ihre Interpretation in Bezug auf ökogeografische Regeln. Die hervorgerufenen Effekte durch Trockenheit, Verlust und Fragmentierung von Lebensraum sollten in zukünftigen Untersuchungen des globalen Wandels berücksichtigt werden, weil sie schwerwiegende Konsequenzen für die Verbreitung, Häufigkeit und letztlich das Fortdauern von Vögeln in ariden Umgebungen haben können.

Introduction

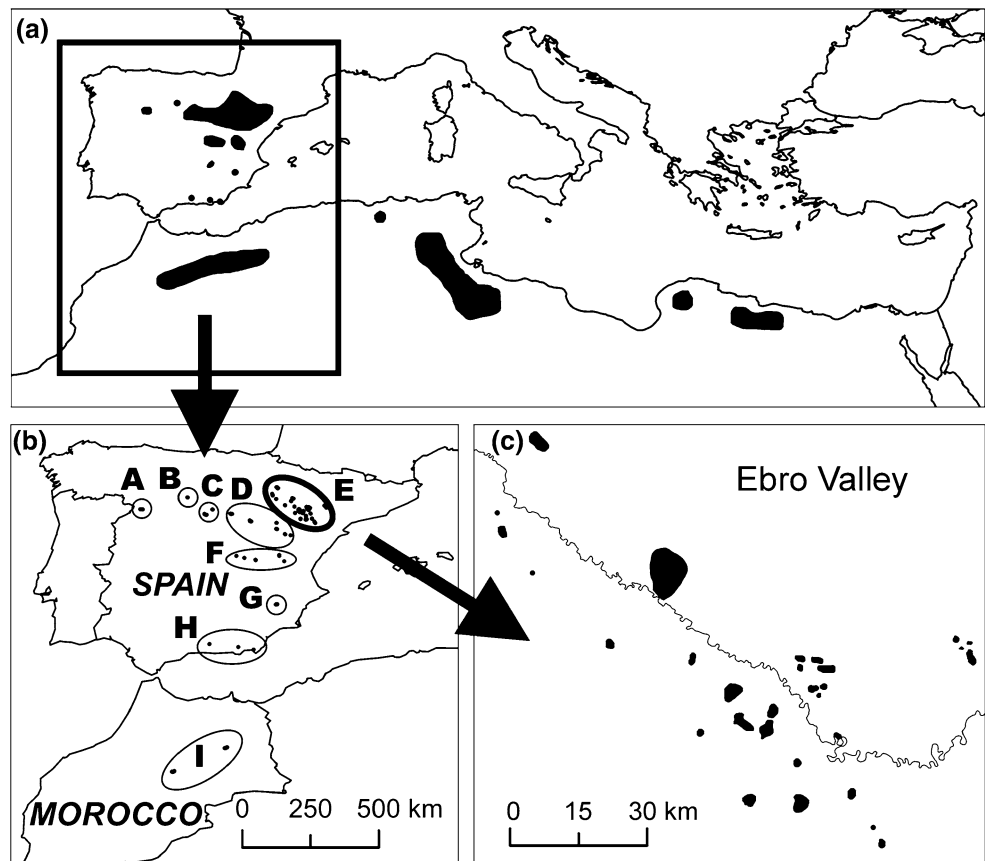
Intraspecific geographic variation in species attributes such as morphology, coloration, or life-history has been a central issue in ecology and evolutionary biology, with special consideration to the association among phenotypic variation, climate, and speciation (Mayr 1963; Futuyma 1998).

Within-species variation in morphology is common along latitudinal gradients (Blackburn et al. 1999), which is usually interpreted in the framework of Bergmann's rule given that climate is correlated with latitude (Ashton 2002; Meiri and Dayan 2003; Meiri et al. 2007). Bergmann's rule, the tendency of animals to have larger bodies in cooler areas, originally referred to interspecific comparisons, has frequently been applied at the intraspecific level (Mayr 1956; James 1970). It is among the best known biogeographical generalizations, despite an ongoing debate on its definition, validity, and underlying mechanisms (Blackburn et al. 1999; Watt et al. 2010; Olalla-Tárraga 2011). The interpretation of the correlation between morphology and positional or environmental variables is difficult because these factors often covary, and other climatic and ecological factors are also key predictors of morphological traits (Yom-Tov and Geffen 2006).

Furthermore, different forces are likely to act on within-species variation in morphology at different spatial scales. For example, recent evidence has challenged the interpretation of temporal declines in mean body size as adaptive responses to increased temperatures in the context of global change, indicating that they merely result from phenotypic plasticity and not from genetic microevolutionary changes, claiming for the assessment of alternative environmental factors (Teplitsky et al. 2008; Husby et al. 2011). Nevertheless, only a few studies have contrasted wide-ranging positional or environmental clines with detailed local ecological factors, which could account for morphological changes at a smaller spatial scale (habitat loss and fragmentation: Lomolino and Perault 2007; competition and hybridisation: Guillaumet et al. 2008; urbanisation: Evans et al. 2009). In this paper, we used a small steppe-specialist passerine, the Dupont's Lark (*Chersophilus duponti*), to investigate whether intraspecific morphological variation correlates with ecological parameters at large and small spatial scale. Several attributes make this species especially suitable for such study (see below for details).

We first investigated whether morphological characters related to body size showed variation along a climatic and geographic gradient over its breeding range in Spain and North Africa (Fig. 1). In a second step, we zoomed in on a geographically and topographically well-separated and confined region of Spain where Dupont's Lark distribution is spatially structured due to habitat loss and fragmentation. As intraspecific morphological patterns can be highly contingent on the species' biology (Meiri et al. 2005), we additionally tested at this spatial scale the effects of several candidate factors, which were hypothesized to modulate Dupont's Lark morphology. For this purpose, we pooled the morphological characters into four different groups according to their functionality: (1) body size, (2) feeding performance, (3) flight ability, and (4) locomotion.

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



Testable predictions and underlying hypotheses at this spatial scale are:

1. *Food availability* Food limitation should generate selection against large individuals (MacArthur and Wilson 1967). Given that Dupont's Lark is predominantly an insectivorous species (Cramp 1988), morphological variation in body size, and feeding performance characters should be related to ground-dwelling arthropod abundance, biomass, and species richness.
2. *Intraspecific and interspecific competition* Great overlap in resource use within and between species should intensify the strength of competition (Emerson and Arnold 1989), with the potential of producing shifts in morphological measures. We expected variation in body size and feeding performance traits to be related to the densities and species richness of a set of steppe passerines potentially competing with Dupont's Lark for the same resources.
3. *Predation pressure* Larger values of characters related to flight ability in birds have been reported to stem from increased vulnerability to aerial predators (Smith et al. 1997). We tested whether the abundance of aerial predators is correlated to flight-related morphological traits.
4. *Habitat characteristics* Environmental conditions at a local scale have been suggested to affect lark physiology (Fairhurst et al. 2013), so they are likely to have some effects on morphology. Vegetation's species composition summarizes this environmental information since it is closely related to soil characteristics, microslope, water availability, and nutrients (e.g. Peñuelas et al. 1999). Moreover, plant species composition may reflect the abundance of keystone predators and the availability and/or quality of food resources (Sánchez-Zapata and Calvo 1999; Buchanan et al. 2006; Ho et al. 2010). Even though these predictions were partially tested directly (see above), we additionally investigated the relationship between Dupont's Lark morphology and vegetation communities.
5. *Patch size and isolation* As in most species, hampered dispersal seems to be a key factor in Dupont's Larks distribution and determines patterns of song and call diversity, genetic structure, and diversity (Laiolo and Tella 2005, 2007; Méndez et al. 2011, 2014). If large individuals are more likely to succeed in immigrating to island patches, mean body size of Dupont's Larks, particularly regarding morphological traits facilitating flight performance, should decrease with patch area and connectivity.

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

Methods

Species information and morphological data

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

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

To avoid potential biases due to personal skill in measuring bird morphometrics, all investigators involved

standardised their measurement. A drop of blood was extracted for molecular sexing (see details in Vögeli et al. 2007). All birds were released at the site of capture, and captures were carried out under approval of all competing wildlife agencies. As the Dupont's Lark shows a pronounced sexual dimorphism (Vögeli et al. 2007) and males constituted over 80 % of all captured birds, we only used adult males in this study ($n = 450$). For analysis at the large spatial scale, we used all the captures carried out at 50 localities (hereafter "subpopulations") in Spain and Morocco (A: Zamora, B: Palencia, C: Segovia, D: Iberian Mountains, E: Ebro Valley, F: Cuenca, G: Murcia, H: Andalusia, I: Morocco, see Fig. 1b). The ecogeographical region's categorization was based on Laiolo and Tella (2006). To analyse fine-grained ecological factors at the smaller spatial scale, we used individuals captured at 29 localities in the Ebro Valley ($n = 286$), the second most important breeding population of Dupont's Lark in Spain despite hosting 450–500 male territories only (Fig. 1c).

Geographic and climatic variables

Coordinates and elevation of each individual's capture point were recorded with a GPS. We obtained mean maximum temperature of the hottest month (T_{\max}), mean minimum temperature of the coldest month (T_{\min}), and annual precipitation (P) for all capture points from the digital climatic atlas of the Iberian Peninsula (Ninyerola et al. 2005) for Spain and from an online database (Rivas-Martínez and Rivas-Saenz 1996–2016) for Morocco. We also calculated Emberger's (1955) index of aridity, Q , calculated as $Q = 2000P/(T_{\max}^2 - T_{\min}^2)$. Values of Emberger's index were logarithmically transformed for statistical analyses because Q increases nonlinearly in more mesic habitats (Tieleman et al. 2003). The resulting variable refers to $-\ln Q$, which is positively correlated with actual aridity and negatively correlated with primary productivity in arid and semi-arid areas (Emberger 1955). Although we have data on climatic factors, we also included positional variables in our analyses because they often are used in studies of body size variation at large spatial scales (Ashton 2002).

Since the strait of Gibraltar is an effective barrier to gene flow between Moroccan and Spanish populations of Dupont's Larks (García et al. 2008b; Méndez et al. 2011), analyses at this scale were also performed after excluding the Moroccan populations.

Fine-grained ecological variables in the Ebro Valley

During the breeding seasons (April–May) of 2005 and 2006, we established 89 linear transects in 25 different subpopulations within the Ebro Valley where we captured

Dupont's Larks. The number of transects carried out per subpopulation was approximately proportional to its size (Tellería et al. 2008). These transects had a maximum length of 500 m and were spaced more than 200 m apart if several transects were carried out in the same subpopulation. Within the sampled subpopulations, which could consist of various fragmented patches of adequate habitat for Dupont's Lark, the length of transects was adjusted to the patch size if the maximum length (500 m) could not be reached (mean = 413 m, range 120–500 m). Along these transects, we established five equidistantly separated sampling points where the botanical composition, soil type, and arthropod availability variables were recorded. Densities of other passerines were estimated from censuses performed within the same transect line (see below).

Food availability

Arthropod sampling was carried out in May and early June of 2005 and 2006. We chose pitfall traps as they are one of the least selective methods for ground-dwelling invertebrates (Ausden 1996). Five pitfall traps (opening diameter 6 cm, height 8 cm, filled with 70 % ethyl alcohol) were randomly installed in each transect, but separated by at least 25 m from each other because ground invertebrates are strongly influenced by microclimatic conditions and vegetation structure within a few metres (Antvogel and Bonn 2001). After 3 days, we emptied the traps, filtered and washed the contents, which were stored in 70 % ethyl alcohol until its identification. After discarding the traps with evident signs of disturbance or manipulation (mostly by rabbits or sheep), 596 traps remained for examination. All specimens were identified to species when possible or otherwise to morphospecies and labelled as recognizable taxonomic units (RTUs) (Oliver and Beattie 1993). This method avoids the use of fine-scaled formal taxonomy at the species level, and is considered adequate for the detection of differences among assemblages (Oliver and Beattie 1993). All identification and classification work was carried out by the same investigator (M.V.) to minimize observer bias. For each transect the number of RTUs and a biomass index (weighing the RTU abundance against its respective mean body length) was computed as the mean of the values obtained at each sampling point. Furthermore, the arthropod diversity of each transect was calculated using the Shannon information index (Shannon and Weaver 1949).

Bird densities and species diversity

We carried out line-transects recording all birds detected by sight or sound inside and outside 50-m-wide belts on either side (Carrete et al. 2009). We then evaluated the occurrence and density of the following steppe passerine

species, which coexist and potentially compete in the breeding season with the Dupont's Lark for habitat and food (Cramp 1988): Lesser Short-Toed Lark (*Calandrella rufescens*), Greater Short-Toed Lark (*Calandrella brachydactyla*), Thekla Lark (*Galerida theklae*), Crested Lark (*Galerida cristata*), Calandra Lark (*Melanocorypha calandra*), Eurasian skylark (*Alauda arvensis*), Black-Eared Wheatear (*Oenanthe hispanica*), Spectacled Warbler (*Sylvia conspicillata*), and Tawny Pipit (*Anthus campestris*). Censuses were performed from 1 h after dawn until noon, avoiding the central hours of the day, as well as rainy and windy days. Determining Dupont's Lark density by line-transects is not valid due to its elusive behaviour and the difficulty of evaluating the distance to singing individuals (Tella et al. 2005). Hence, for this species we used the mean distance of the nearest singing neighbours in each occupied patch as a proxy for Dupont's Lark density (see Laiolo and Tella 2008). For each subpopulation, we calculated both the total density of steppe passerines and the correspondent species diversity, measured by the Shannon information index (Shannon and Weaver 1949).

Predator abundance

During field work, we recorded all observations of possible aerial predators. These data were collected from the beginning of spring 2004 until the end of spring 2007. We calculated a relative abundance index for passerine hunting predators exclusively by dividing the observations ($n = 659$) by the time spent in the respective subpopulation, which totaled 3506 h. The following species were considered: European Marsh Harrier (*Circus aeruginosus*), Hen Harrier (*Circus cyaneus*), Montagu's Harrier (*Circus pygargus*), Sparrowhawk (*Accipiter nisus*), Merlin (*Falco columbarius*), Lesser Kestrel (*Falco naumanni*), Common Kestrel (*Falco tinnunculus*), Eurasian Hobby (*Falco subbuteo*), Peregrine Falcon (*Falco peregrinus*), Booted Eagle (*Hieraetus pennatus*), and Southern Grey Shrike (*Lanius meridionalis*).

Habitat characteristics

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

Patch size and isolation

We calculated the area for each subpopulation (i.e. the size of the patch of natural steppe vegetation occupied by Dupont's Lark) in the Ebro Valley and log-transformed

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

	Class	Order	Association	Type
1	Thero-Brachypodieta	Rosmarinetalia	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	Helianthemetum squamati	Dominance of <i>Helianthemum squamatum</i> , high species diversity
4	Ononido-Rosmarianetea	Gypsophilion	Helianthemetum squamati	Presence/dominance of <i>Artemisia herba alba</i> , low species diversity
5	Ononido-Rosmarianetea	Gypsophilion	Helianthemetum squamati	Dominance of <i>Rosmarinus officinalis</i> , low species diversity
6	Salicornietea	Limonietalia	Suadetum brevifoliae	

them for statistical analyses. We determined the isolation index $I_i = -\sum \exp(-d_{ij}) N_j$, where d_{ij} is Euclidean distance between patches i and j , and N_j is the population size of patch j , including only occupied patches by Dupont's Lark in the Ebro Valley (Hanski et al. 1994). These descriptors were obtained from aerial orthophotographs of the study area and from previous research (Tella et al. 2005; Vögeli et al. 2010).

Statistical analyses

Morphological variables

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

length have been also used to characterise body size (Zink and Remsen 1986; Yom-Tov 2001).

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

Geographic variables and spatial autocorrelation

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

Before modelling the different effects on the respective morphometric variables, we tested the null models of each trait, i.e. models that lack predictor variables, for spatial autocorrelation at both spatial scales. Spatial autocorrelation may invalidate systematically the assumption of independent errors, thus distorting classical statistical tests and giving misleading correlation coefficients, regression slopes, and associated significance tests (Lennon 2000; Legendre et al. 2002). First, we assumed independent errors and implemented null intercept-only linear models (LMs). Second, we built null spatial correlation models that

Table 2 Morphological characters classified by their functionality

Functional significance	Main character	Covarying characters	<i>r</i>
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	–	–

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)

fitted six alternative spatial covariance matrices (exponential, spherical, Gaussian, linear, log linear, power) to the data and used the best matrix to adjust test statistics, thus taking spatial autocorrelation into account (Littell et al. 2006). Third, we implemented as an alternative approach null linear mixed models (LMM) in which the subpopulation structure was fitted as a random term to take into account spatial autocorrelation. For these later analyses at large spatial scale we entered region identity and subpopulation identity within region as random factors, whereas subpopulation identity exclusively was entered as a random factor when analysing the data at small spatial scale within the Ebro Valley (see Electronic Supplementary Material Table S1 for details on subpopulation and region identity). The spatial correlation models fitted best with a spherical spatial covariance structure and revealed spatial autocorrelation in all morphometric variables, except for the tarsus, which was more pronounced at the large (all $P < 0.0001$) than at the small spatial scale (all $P < 0.05$). We consequently built three candidate models according to the three modelling approaches (independent errors, spherical covariance matrix, and random subpopulation structure), for each of the five morphological traits at both spatial scales. Then we identified the most parsimonious null models for each morphometric variable (ten comparisons, five for each spatial scale) based on their differences in AIC_c (Littell et al. 2006, see also below). At both spatial scales, the null linear mixed models with the random subpopulation structure fitted the data better (difference in $AIC_c > 4$ in eight of the comparisons) or equally (difference in $AIC_c < 2$ in the remaining two comparisons) for all five morphological traits when compared to either LMs with independence of errors or spatial correlation models. Hence, we decided to continue the analyses with LMMs acknowledging spatial autocorrelation with the subpopulation structure as random factors accordingly to the tested spatial level.

For each spatial scale and morphological trait, we constructed an a priori set of candidate models that only included biologically meaningful explanatory variables in addition to the random terms. Within this candidate set, an

intercept-only null model (fitted with the appropriate random subpopulation structure) was always included. Competing models were ranked using Akaike information criterion corrected for small sample size (AIC_c , see Burnham and Anderson 2002), and models within two AIC_c points ($\Delta AIC_c < 2$) were considered statistically equivalent. A pervasive problem with information theoretic approaches, intrinsically linked to the way in which extra parameters are penalized, is that variables with poor explanatory power added to an otherwise good model can result in a wrongly competitive model. These pretending or uninformative parameters do not truly contribute to a better fit and should not be considered (Burnham and Anderson 2002:131; Anderson 2008:65; Arnold 2010). Top-ranked models with uninformative parameters were identified and discarded by examining changes in maximized log-likelihood as well as the standard errors and 85 % confidence intervals of parameter estimates (Anderson 2008; Arnold 2010). In addition, the relative effect size of each correlate was calculated using its cumulative Akaike weight across all models where it occurred, and model averaging was employed to deal with model selection uncertainty (Burnham and Anderson 2002). Models were constructed via maximum likelihood techniques using PROC MIXED in SAS 9.3 (SAS Institute, Cary, NC, USA) and library lme4 (Bates et al. 2015) in R 3.1.3 (R Core Team 2015). AIC_c tables, model averaging and post hoc comparisons were performed with the R libraries AICcmodavg (Mazerolle 2015), lsmeans (Lenth 2015) and multcomp (Hothorn et al. 2008).

Results

Morphological variation at the large spatial scale

After discarding models with uninformative parameters, model selection procedures suggested that variation in wing length, tarsus length, and cranium size (the morphological characters related to body size) exhibited different patterns depending on the climatic and positional variables

(Electronic Supplementary Material Table S3). Our data indicate that both wing length and cranium size increased with the first principal component of the PCA (Table 3), with the largest birds occurring on average at arid localities with low rainfall and high maximum temperatures during the hottest month, which tend to be situated at low latitudes (see Fig. 2 for the relationship with aridity, the variable with the highest factor loading in the first PCA component). In addition, wing length and tarsus length showed a negative relationship with the second principal component (Electronic Supplementary Material Table S3), although for wing length the effect seemed to be weaker than that described for the first component (Evidence ratio: 1.45, see Table 3). In this way, birds had on average larger wings and longer tarsus in elevated populations with low minimum temperatures during the coldest month, which tend to be located at low latitudes and longitudes.

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

Morphological variation at the small spatial scale

Geographic and climatic variables

In opposition to the large spatial scale, we did not detect any variation in any of the measured morphometric traits of

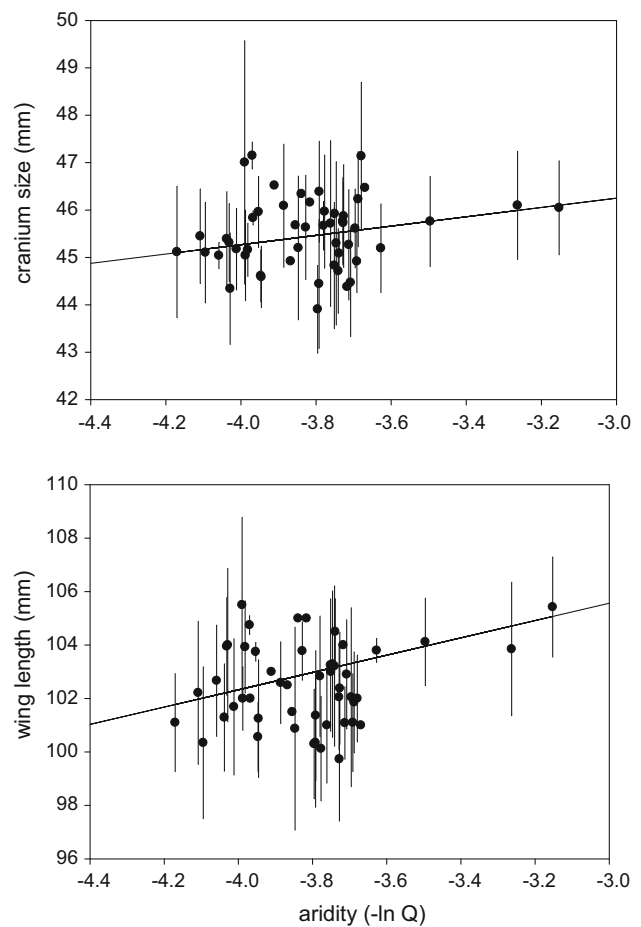


Fig. 2 Cranium size and wing length variation (mean value \pm 1 standard deviation) in Dupont's Lark in relation to aridity within its distribution in Spain and Morocco

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)

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
Cranium	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

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

Dupont’s Larks in the Ebro Valley in relation to either positional or climatic variables (Table 4, Electronic Supplementary Material Table S4).

Ecological variables

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

Models including an effect of soil types on wing and hind claw lengths, however, were supported by data (Electronic Supplementary Material Table S4). These models indicated that birds from populations characterized

by harder soils had shorter wings and claws than birds inhabiting softer substrates (Table 4). The vegetation types also had an effect on cranium size (Electronic Supplementary Material Table S4). Effect sizes examination and post hoc pair-wise comparisons revealed that the main difference was between the populations characterized by the vegetation association *Lygeeto-Stipetum lagascae* holding a low plant species diversity (vegetation community 2) and those with vegetation dominated by *Rosmarinus officinalis* with large interspersed areas of bare gypsum soil (vegetation community 5) (Table 4).

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

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)

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	
Tarsus	Patch size	−0.78	0.52	−1.53, −0.03	0.52
	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
Cranium	Heterospecific density*	0.02	0.04	−0.03, 0.07	0.11
	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
Bill depth	Patch size*	0.29	0.27	−0.11, 0.68	0.30
	Heterospecific density*	−0.06	0.08	−0.17, 0.05	0.10
	Heterospecific density*	−0.04	0.03	−0.07, 0	0.45
Claw length	F2’*	−0.13	0.1	−0.27, 0.01	0.40
	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

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 higher elevations. 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

Discussion

Morphological variation at the large spatial scale

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

Climate is usually correlated with latitude and altitude and may, therefore, shape selection pressures on body size, either directly, e.g. by heat dissipation (James 1970) or fasting endurance (Boyce 1979), or indirectly by affecting food availability, competition, and predation pressure (McNab 1971). The use of latitude and elevation as environmental predictors in biogeographical studies has been severely criticised when disposing on direct environmental variables such as temperature and precipitation (Hawkins and Diniz-Filho 2004). Both wing length and cranium size showed a gradient, which increased towards higher aridity, and tends to characterize populations of lower latitudes.

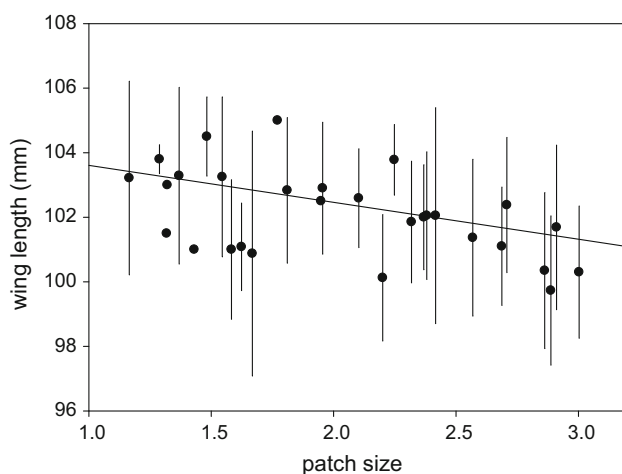


Fig. 3 Relationship between Dupont's Lark wing length (mean value \pm 1 standard deviation) and patch size of the corresponding subpopulation (log transformed) in the Ebro Valley

Aridity is an important characteristic of many Dupont's Lark populations; larks have their evolutionary origin in Africa and occupy mostly open and semi-arid or arid regions, showing interspecific clines in physiological adaptations to cope with aridity (Tieleman et al. 2003) and appropriate behaviours to avoid overheating and excessive water loss (De Juana et al. 2004). Indeed, trade-offs between foraging efficiency and heat-dissipation behaviours have been described in such arid ecosystems (du Plessis et al. 2012). Under these circumstances, a larger body size of Dupont's Lark could be favoured in arid environments with growing incidence of seasonal food shortages and heat waves because it permits the accumulation of more body reserves and facilitates heat loss by evaporation (James 1970; Ashton 2002). Accordingly, increases in body size with temperature have been said to be mediated through size-dependent mortality in another semi-arid passerine (Gardner et al. 2014). As aridity and primary productivity are negatively correlated (Emberger 1955), the gradient in Dupont's Lark body size is contrary to the hypothesis that body size of individuals is positively correlated with productivity and eventually with food availability, especially in semi-arid or arid environments (Rosenzweig 1968).

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

Finally, parallel mechanisms including other natural selection pressures, phenotypic plasticity, genetic drift or barriers to gene flow, could contribute to explain body size variation. Body size variation in Dupont's Lark could have arisen nowadays by the effect of genetic drift and the absence of gene flow due to fragmentation (Méndez et al. 2011, 2014) or in the past by barriers to gene flow between geographical areas (García et al. 2008b). In effect, functional diversification has been said to be facilitated when geographic isolation act in concert with differential

ecological pressures (e.g. Benham and Witt 2016). Although genetic drift is an important force of evolution, being more intense in small and isolated populations, the genetic signal of a well-connected historical population still remains in Dupont's Lark (Méndez et al. 2011). In this sense, genetic drift may have occurred in localities as Tariego, which holds five unusually large individuals (see Electronic Supplementary Material Table S1), but clinal patterns in body size would not be expected to result from this mechanism due to its stochastic nature. Interspecific competition with other steppe passerines has also been suggested as a possible reason favouring character displacement and increased body size for Dupont's Lark and larks from the genus *Galerida* in Morocco (Guillaumet et al. 2006; García et al. 2008b). Alternatively, phenotypic plasticity could also produce larger body size in birds in some environments (James 1983; Teplitsky et al. 2008).

Local patterns in morphological variation

An exhaustive sampling of environmental variables within the Ebro Valley (Fig. 1c) allowed us to test for numerous possible effects of ecotypic differentiation in morphology at a small spatial scale. However, we failed to detect any relationship between body size and positional or climatic variables, probably due to low variation of most of these predictors at this scale. Additionally, neither food availability, nor intra- and interspecific competition or predator pressure seemed to influence the studied morphological characters of Dupont's Lark within the Ebro Valley. Dupont's Lark is reported to feed on a large range of ground-dwelling arthropods (Cramp 1988). Nonetheless, several studies have shown that certain arthropod groups are preferably selected by passerines for both adult and nestling diets (Buchanan et al. 2006). These subtle preferences may have remained undetected by our general approach of arthropod availability sampling. Despite covering over 10,000 km², the composition of both the steppe passerine community and its aerial predators does not change substantially within the Ebro Valley. Although we also accounted for density effects, comparison at large spatial scale might shed more light on possible effects of interspecific competition, as species composition changes noticeably throughout the sampled range in Spain and Morocco. Parallel to this outcome, we could not confirm the hypothesis that larger values of wing length are a consequence of increased vulnerability to aerial predators (Smith et al. 1997).

Differences in claw length with soil characteristics are likely due to a greater abrasion in harder substrates. Similarly, the variation in cranium size may be best interpreted with the contrasted soil characteristics of the concerned vegetation communities. A very stony surface is a frequent

feature of the vegetation community 2, mostly due to a shallow profile depth. In contrast, the vegetation dominated by *Rosmarinus officinalis* with large interspersed areas of bare ground is characterised by loose gypsum soil, which is easy to penetrate. As a consequence, bill abrasion may underlie the differences in cranium size due to Dupont's Lark behaviour: it feeds almost exclusively on arthropods that are picked from the ground surface or burrowed a few centimetres under the surface (Cramp 1988). Alternatively, larger craniums could reflect local feeding adaptations or phenotypic plasticity to prey on underground invertebrates in soils in which it is easier to scratch around or to dig a hole. More intriguing is the relationship between wing size and soil type, but one plausible explanation is that flight feathers may be increasingly subject to wear in more stony and hard substrates.

When analysing for effects related to patch size and isolation at the Ebro Valley, we found a negative relationship between wing length and patch size. Fragmentation and loss of habitat have drastically diminished the extent of Dupont's Lark in recent decades in the Ebro Valley and extinctions of local populations are ongoing even today (Tella et al. 2005; Laiolo et al. 2008). As a consequence of shrinking population sizes and creating barriers to individual movement, the cultural transmission of Dupont's Lark has been disrupted and gene flow is reduced (Laiolo and Tella 2005, 2006, 2007; Méndez et al. 2014). Studies accounting explicitly for the effect of fragmentation and habitat loss on intraspecific morphological variation are rare (see Lomolino and Perault 2007). Nevertheless, intraspecific morphological shifts have received much attention especially in evolutionary studies (e.g. Mayr 1963) or those related to island rule (Meiri et al. 2005), and these findings may help interpret our results. Small habitat patches in our study system are usually fragmented and show the highest lark densities as a consequence of limited connectivity and crowding effects (Laiolo and Tella 2006; Vögeli et al. 2010; Méndez et al. 2014). In this context, individuals may suffer unusually strong intraspecific competition and limited food availability, circumstances under which a large body size would be favoured (Ashton 2002; Robinson-Wolrath and Owens 2003). Although direct tests for these hypotheses were unsupported (see above), we cannot rule out that multiple social and ecological factors were synergistically affecting habitat quality in complex ways in small patches. The increased wing length could also be a consequence of a need for greater aerodynamic efficiency (Smith et al. 1997) or just be a phenotypic trait correlated to dispersal propensity. Capture–recapture studies of Dupont's Lark during 4 years in the Ebro Valley revealed limited dispersal behaviour in the species (Laiolo and Tella 2008; Vögeli et al. 2008). Hence, the few successful dispersal

events between subpopulations could account for large individuals whose contribution to the increase of the mean wing length would be perceived to a greater extent in populations with only a few individuals than in larger subpopulations. Tella et al. (2005) showed that extinction of Dupont's Lark populations occurred more often in small (<100 ha) habitat patches. Moreover, Méndez et al. (2014) showed that small populations (<16 males or 300 ha) are prone to suffer genetic erosion. The individual advantages of a larger body size for fitness may thus be accentuated in small remnant habitat patches, even though the survival of Dupont's Larks did not seem to be affected by the patch size (Laiolo et al. 2008).

Conclusions

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

Acknowledgments We are indebted to numerous people helping during fieldwork, especially P. Laiolo, M.A. Carrero, and I. Afán. M.V. was supported by an I3P pre-doctoral fellowship from the Spanish Research Council (CSIC), D.S. by an I3P post-doctoral contract from the CSIC during fieldwork, M.M. by a grant from Telefónica Móviles S.A. and all four authors by an Excellence Project of the Junta de Andalucía to J.L.T. The fieldwork in Morocco was supported by the commission for travel grants of the Swiss Academy of Natural Sciences SCNAT+(Grant to M.V.). We also thank M. Carrete and F. Pacios for assistance with data analyses, J.V. López-

Bao for fruitful discussion of the results, and S. Young for greatly improving the English usage.

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