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Size and colour variation along a strong environmental gradient in Iberian bank voles (*Clethrionomys glareolus*)

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Abstract

This study investigates the influence of environmental gradients (temperature, rainfall, elevation, latitude, and longitude) in Iberian bank voles (*Clethrionomys glareolus*) from 56 localities in the northeastern Iberian Peninsula. We used a sample of 250 museum specimens to analyse body size (weight, body length), shape (relative size of appendices: ear, foot, and tail), and colour variation representing a broad range of habitats and climates. Using principal component analysis (PCA), and generalized linear and additive mixed models (GLMMs, GAMMs), we explored the relationship between morphometric and colour traits with sex and geographical and climatic variables. Our results revealed that body size and relative size of appendices were strongly correlated with elevation and temperature. Larger bank voles with shorter appendices were found at colder environments, supporting Bergmann's rule. However, body size and air temperature were spatially autocorrelated, both sharing an undetermined amount of spatial variance. But colour variation showed a different pattern, with dorsal and ventral colour primarily influenced by rainfall, longitude and latitude, rather than elevation or temperature, which aimed at a crypsis explanation to Gloger's rule. The relationship between body size and elevation could reflect selection for thermoregulation, while colour variation may be shaped by selection for crypsis in specific habitats. Males exhibited larger appendices relative to their body size compared to females. In the same vein, bank voles showed significant sexual dichromatism. These findings highlighted the complex interplay between the environmental factors shaping the morphology and colouration of Iberian bank voles, but future research need to be aimed at disentangling the sources of variation in body traits (i.e., genetic vs. environmental).

Keywords Small mammals · Ecogeographic rules · Body size · Fur colour · Iberian Peninsula · Environmental gradients

Introduction

The geographic and temporal diversity of body sizes among organisms is widely attributed to evolutionary processes and biological relationships that enable species to adapt to their specific environments (Yom-Tov and Geffen 2011). Phenotypic plasticity is crucial for how organisms respond to variation in their environment especially in the light of rapid environmental change (Villar and Naya 2018; Cui et al. 2020). Changes in body size and colouration– either spatially and temporally– are expected owing to various factors such as thermal influence and other environmental factors regulating the energy allocation to vital processes (Oli 1999; Lázaro et al. 2017; Caro and Mallarino 2020). The three most classical ecogeographical rules (mostly formulated in the XIX century) can be invoked to explain these differences. Bergmann's rule states that within a broadly distributed taxonomic clade, body size tends to be larger in colder climates and smaller in warmer climates (Meiri 2011). Allen's rule states that endothermic animals from colder climates tend to have shorter appendices than those from warmer climates (Ballinger and Nachman 2022). Gloger's rule states that animals living in warm and humid environments tend to have darker pigmentation than those living in cool and dry

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environments (Delhey 2019). On the one hand, Bergmann's and Allen's rules correlated the size of the body and the appendices, respectively, with environmental temperature in endothermic vertebrates, based on the changes in the surface-area-to-volume ratio which are presumed to affect heat conservation (Brown and Lomolino 1998). Animals tend to be larger and with small appendices in climates with low temperatures than in warm climates, following a latitudinal cline (Blackburn et al. 1999; Rodríguez et al. 2008; Meiri 2011; Ballinger and Nachman 2022; Valladares-Gómez et al. 2024). In spite of being formulated and described as an interspecific mechanism (Rodríguez et al. 2008; Watt et al. 2010), generalisations of the ecogeographical rules were confirmed in multiple species of birds and mammals (Meiri and Dayan 2003; Watt et al. 2010; Kryštufek et al. 2019). Similar effects can be stated along altitudinal gradients, and this also provides a ecogeographical basis for testing the effects of a thermal cline with elevation on morphological traits (Feijó et al. 2019; Stanchak and Santana 2019; Cui et al. 2020). In spite that phenotypic plasticity was invoked in shaping morphological traits along environmental clines, some authors pointed out that both adaptive phenotypic plasticity and genetic changes affect the patterns of clinal variation in small mammals (Ballinger and Nachman 2022). These authors highlighted that body appendices (ear and tail) are more prone to be shaped by environmental variability, whereas body size showed little plasticity. On the other hand and regarding colouration, Gloger's rule states that mammals should be darker in humid and cold environments in comparison with warm and drier areas (Delhey 2017, 2019). Indeed, dark colours will facilitate basking in cold environments and light colours will prevent overheating in hot environments (Brown and Lomolino 1998). But crypsis is one of the most stated reasons for the Gloger's rule because animals that match their colour with the environment will have more chance to avoid visually oriented predators (Brown and Lomolino 1998). Natural selection on cryptic colouration is prevalent in nature and camouflage is one of the strongest evolutionary forces driving colouration in mammals (Caro 2005). For example, many mammals in colder climates exhibit white winter coats, which provide effective camouflage in snowy environments, enhancing their ability to avoid predators and/or ambush prey (Atmeh et al. 2018).

Small mammals have been the subject of several studies about the environmental causes of changes in body size and colour, owing their small size, short life cycles, high breeding performance, and high energetic demands. Intraspecific tests of Bergmann's rule suggested that small mammals can be either less likely or, at least, not more likely than large mammals to conform to the rule (Stanchak and Santana 2019), especially in smaller species (Meiri and Dayan 2003). In the case of shrews, recent studies highlighted that they do not follow the ecogeographical rules (Stanchak and Santana 2019). In the same vein, several species of rodents did not match with expectations of body size variation following the ecogeographical rules (Meiri and Dayan 2003; Alhajeri and Steppan 2016). This means that there are very heterogeneous responses, suggesting the role for other factors on the patterns of body size variation observed, such as biotic interactions (e.g., primary productivity, predation: Yom-Tov and Geffen 2006; Feijó et al. 2019). Indeed, somatic characteristics such as body length, tail length, and especially weight, are variable and depend on other factors independent to the environment (e.g. Chitty effect: Oli 1999; Baláž 2010). In the case of shrews, seasonal and reversible reduction of size may improve the probability for survival during the winter (Dehnel effect: Lázaro et al. 2017). In the same way, coat colouration can change on a seasonal basis to match the environment (e.g., winter vs. summer coats: Zimova et al. 2018). On the contrary, other variables (e.g., hind-foot length) are persistent during life and are a fundamental as taxonomic characters (Baláž 2010). Nevertheless, pelage colouration (or pattern) and body size have been the main traits used to define subspecies in many mammal species during 19th and early 20th centuries (Mullen et al. 2009; Schiaffini 2020). However, despite being phenotypically distinct, some subspecies are considered to be the same genetic entity, and vice versa (Mullen et al. 2009). Hence, it is important to tease apart the particular variation that can be accounted by phenotypic plasticity (non-genetic) and the amount that can be accounted by the genotype (Brown and Lomolino 1998; Yom-Tov and Geffen 2011). Therefore, investigations analysing the effects of environment on body traits need to control for the genetic structure of the populations studied (Alhajeri and Steppan 2016; Feijó et al. 2019; Stanchak and Santana 2019). Unfortunately, disentangling the sources of variation in body traits is challenging because it requires experimental manipulation of small mammal populations to simultaneously analyse both genetic and environmental sources of morphological variation (Ballinger and Nachman 2022).

The bank vole *(Clethrionomys glareolus*, S., Kryštufek et al. 2020) is a common and widespread small rodent in temperate forests areas throughout the European continent. It is distributed throughout Europe, from the tundra of Norway to the south of Italy, with some isolated populations in Asia minor (Luque-Larena and Gosalbez 2007). As other small rodents, bank voles showed a decreasing size towards higher latitudes, thus, not following the Bergmann's rule (Ledevin et al. 2010). The variation of size and colour allowed describing thirty subspecies of bank vole in Europe, although the information about their status is questionable because of the lack of specific studies (MacDonald and

Barrett 2008). But different European clades were recently described on the basis of their genetic structure, highlighting the importance of the Mediterranean peninsulas as glacial refugia (Ledevin et al. 2010; Çolak et al. 2016; Kotlík et al. 2022). Based on these studies, the "Spanish clade" is a genetic entity considered to occupy the Iberian Peninsula, Andorra, and southern France.

In the Iberian Peninsula, the bank vole is evenly distributed throughout the north, from the Catalan Pyrenees to the Cantabrian system. The Spanish common name is *"topillo rojo"* referring to the shiny red colour that adult individuals show on its back (Gosálbez 1987). This colour gradually degrades on the sides from a dark grey to an almost pale white ventral colouration. This pattern varies between the different subspecies, although there is scarce information about that topic (Gosálbez 1987). In Spain, three subspecies were described regarding morphometry and colouration: *C.g. vasconiae* (Miller, 1900) in the Pyrenees, *C.g. bernisi* (Rey 1972) in the Iberic system, and *C.g. glareolus* (Schreber, 1780) in the Cantabric system (Blanco 1998; Luque-Larena and Gosalbez 2007; Sanz and Turón 2017). Mostly, it is considered that there are changes of body size along longitude, that is, a small increase in size from the centre (Cantabria and the Basque Country) to the ends (Galicia and the Pyrenees) of the Spanish range. Furthermore, there is also a latitudinal increase in size, being *C.g. bernisi* (Rey 1972) the smallest subspecies in Spain (Ventura et al. 1993). Nevertheless, it presents few differences with *C.g. vasconiae* and its recognition in the field is mostly based on the geographic isolation (Luque-Larena and Gosalbez 2007); Ventura et al. 1993). Additionally, the isolation of the Pyrenean subspecies *C.g. vasconiae* and the French populations of *C.g. glareolus* remains unclear. Nonetheless, there is a lack of detailed genetic studies of the bank vole in the Iberian Peninsula (i.e., within the genetic clade, Kotlík et al. 2022), and whether the geographic distance and isolation between populations could be translated to different subspecies is undetermined. Studies in Italy emphasised the strong variability of the genetic structure within clades of the bank vole populations (*sensu* Kotlík et al. 2022), identifying different genetic entities that could be related to subspecies formerly described (Chiocchio et al. 2019).

Owing to previous studies, the taxonomy and morphometry of Iberian bank voles showed geographical variability following spatial patterns that changed with latitude and longitude (Rey 1972; Ventura et al. 1993). Going further, in this study we analysed whether the variability in morphological traits was associated to different climatic and geographic predictors. We measured external traits related to overall size (e.g., body length) and size of appendices, as well as fur colour (quantifying colour using image analysis) of bank voles in the NE of the Iberian Peninsula to ascertain whether this species followed the ecogeographical rules.

Materials and methods

Study area and sampling locations

We analysed body size and colouration of 250 *Clethrionomys glareolus* that were captured during live trapping sessions conducted between 1983 and 2010 in 56 localities from Catalonia, Andorra, Navarre, and the Basque country (Fig. 1). The sample covered different habitats (coniferous, deciduous, and sclerophyllous forests, scrubland, grassland, scree) along a strong elevation (180–2280 m.a.s.l.) and climatic gradient. Due to their geographical location, we can find three different climates in the area: the Atlantic, the Mediterranean, and the mountain climate.

The Atlantic climate corresponds to the Basque Country and Navarre. This climate is characterised by high and uniform precipitation through the year with little summer drought (Barrio-Anta et al. 2020). We sampled 13 localities, and the annual mean temperature was 9.7 ± 1.1ºC (8.5–13.4 ºC), the mean annual precipitation was 1672.8 ± 93.1 mm (1526–2100 mm), with a mean elevation of 715 ± 154 m (180–962 m.a.s.l.). The mountain climate was mostly found in the Pyrenees, a high mountain range that is influenced by the Atlantic Ocean and by the Mediterranean Sea. In this area we sampled 18 localities and the mean temperature was 5.7 ± 1.2ºC (3.4–9.5 ºC) and the mean precipitation 1024.1 ± 79.6 mm (825–1150 mm), with a mean elevation of 1527 ± 549 m (1050–2280 m.a.s.l.)(Amblar-Francés et al. 2020). The Mediterranean climate is defined by mild winters and hot and dry summers, with periods of severe drought (Lionello et al. 2006). In this area we sampled 25 localities, with a mean temperature of 9.4 ± 1.7ºC (5.6–13.6 ºC), a mean precipitation of 896.1 ± 60.1 mm (726–978 mm), and the mean elevation of the localities sampled was 872 ± 346 m (400–1450 m.a.s.l.).

Data analysis

250 bank voles found dead after capture were prepared by the same two people (the main curator–A.A., and an investigator– I.T.) using the same processing technique (Arrizabalaga and Uribe 1988) and stored as Museum vouchers in the collection of the Natural Sciences Museum of Granollers (Barcelona, Spain). Museum collections can be valuable resources for zoological research (Davis et al. 2013), and provided those specimens are properly stored and conserved, this material can be used for population studies (i.e., taxonomy, systematics, biogeography, etc.) (Sandoval

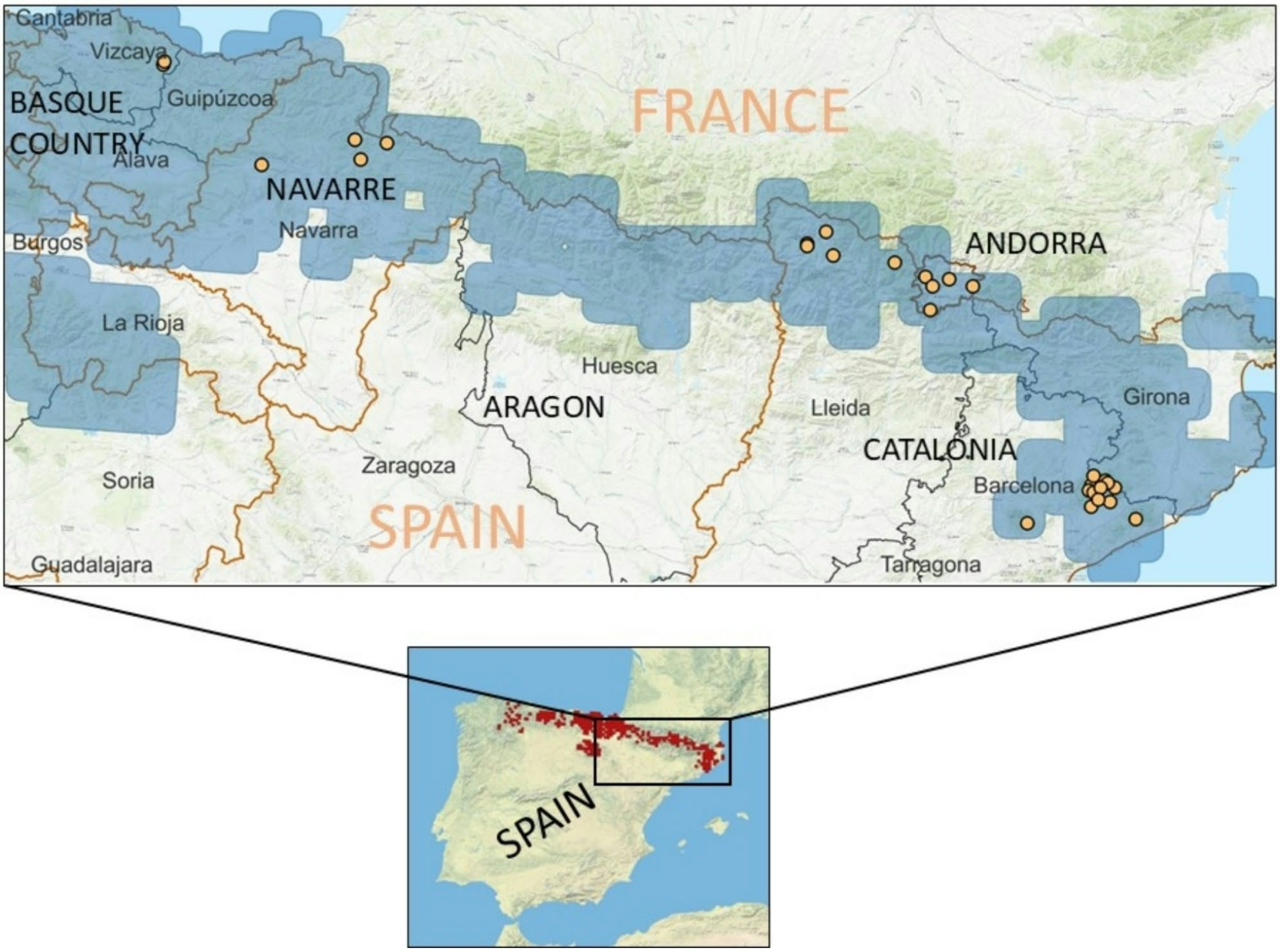


Fig. 1 Distribution of the localities (orange dots) where bank voles were sampled in the NE of the Iberian Peninsula. The blue shape indicates the known distribution of bank voles after a 5-km buffer around the 10 × 10 UTM grids of the Mammal Spanish Atlas (Palomo et al., 2007). In the small figure, the known distribution (red) of the bank vole in Spain

Salinas et al. 2018). One of the forms of conservation of small mammals is the flat skin, due to the easy way for storing and conservation (Arrizabalaga and Uribe 1988; Díaz et al. 1998). However, skins are subject to temporal changes regarding colour and other conservation issues, and fur colour can be modified due to chemical or structural degradation of pigments (Sandoval Salinas et al. 2018).

To avoid increasing intra-population colour/size variability on our population estimates, we decided to use only the data from adult voles (Rey 1972), a standardised approach for comparison between populations (Yom-Tov and Geffen 2011; Kryštufek et al. 2019). We selected the individuals weighing 20 or more grams (81% of specimens considered adults and 5% of subadults from the whole sample of 370 individuals, Prévot-Julliard et al. 1999)(Huerta-Schliemann et al. 2025).

We used 250 individuals for the study of biometry and colouration sampled within the continuous distribution range of the species (Fig. 1). The specimens were collected in 56 localities from Catalonia, Andorra, Basque Country and Navarra, which are considered from the same genetic population (Spanish clade, Kotlík et al. 2022). To describe climatic data of the localities, the Climatic Atlas of Spain (http://agroclimap.aemet.es/) and Andorra (http://www.acda.ad/) have been used. The mean values of precipitation and temperature were obtained for a period of twenty-nine years (1971–2000 in Spain, and 1981–2010 in Andorra). We also obtained the mean elevation and the mean geographic coordinates (Latitude and Longitude) for the sampling sites. Other relevant predictors, such as potential evapotranspiration, were not used due to its strong positive correlation with temperature (Rodríguez et al. 2008). This research relied solely on existing museum specimens and did not involve any additional animal sacrifices.

Biometry and colouration

To describe the biometry of the specimens we used standard body measures (Arrizabalaga and Uribe 1988); Gosálbez 1987), taken in millimetres, and the weight (g) was measured using a dynamometer. Tail length (*TL*): From the vertex of the angle formed by the proximal ventral base of the tail and the posterior part of the anal prominent, to the apex of the tail. The remaining hair doesn't count. Head and body length (*HBL*): From the tip of the snout to the vertex defined in the TL measure. Ear length (*EL*): Maximum length from the lower notch until the distal marge of the ear. Posterior foot length (*FL*): From the distal end of the longest finger, without the nail, to the end of the heel.

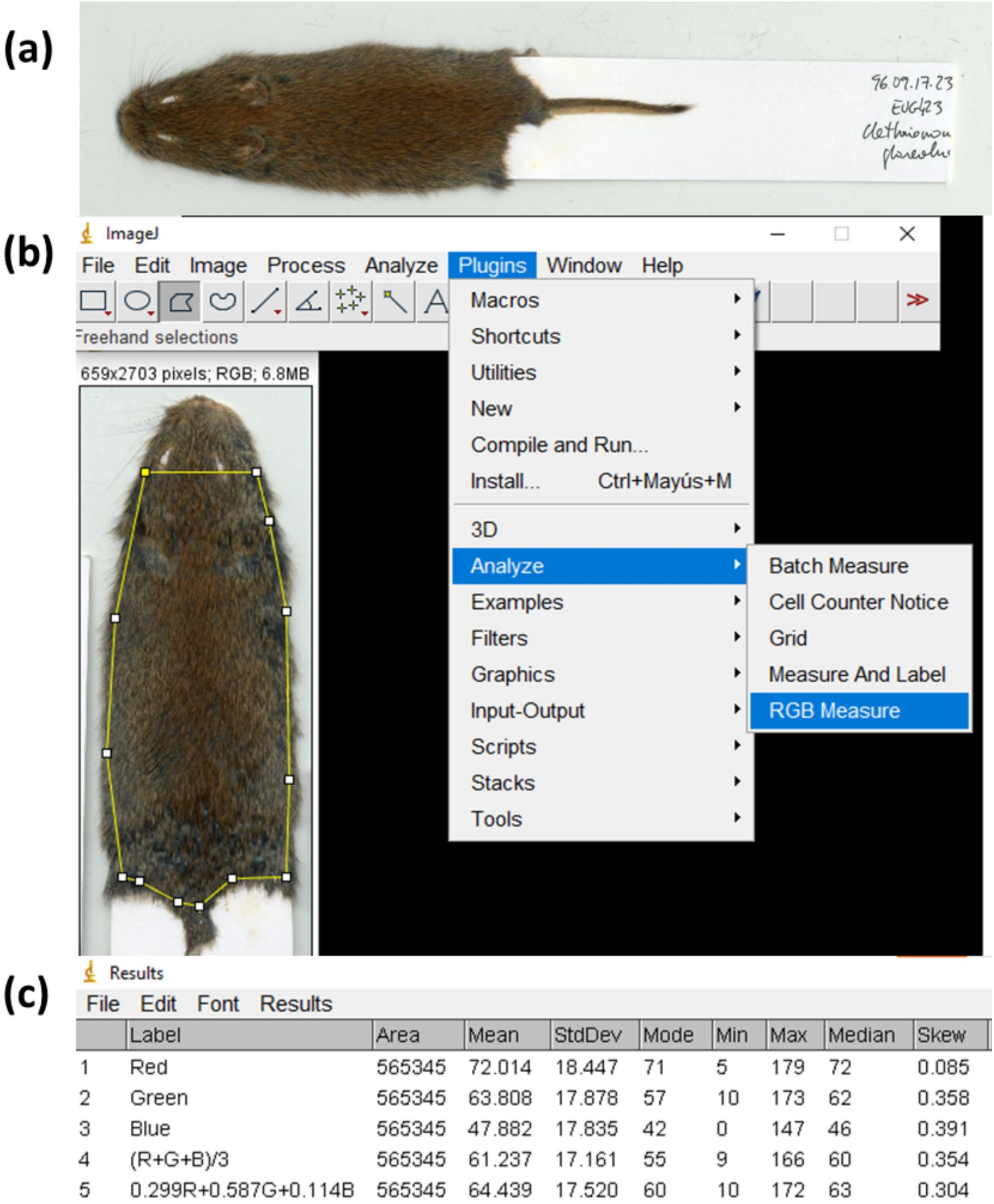
Colour is difficult to quantify because it depends on the light incidence on the hair. Photographs with a digital camera (Davis et al. 2013; Boratyński et al. 2014; Stanchak and Santana 2019) were discarded owing to the difficulties of light standardization (i.e., environmental light, camera options such as ISO, f-stops, program; focusing targets, etc.). Hence, the flat skins were scanned by a GT 1500 EPSON to have more control over illumination variables (Fig. 2). The first step was to calibrate the scanner with the ICC profiles to ensure colour reliability. Nevertheless, all the samples were measured with the same machine and conditions, therefore the skins are comparable for all the samples in this period. After scanning the skins, ImageJ software (https://imagej.net/ij/) was used for colour estimation. Red, green and blue profiles (following the RGB code) were obtained, and the combination of the three of them as an average RGB profile (R + G + B/3) measured the brightness or intensity of colour of the pelage (Boratyński et al. 2014; Stanchak and Santana 2019). To correctly measure the colours, the area of the dorsal and ventral images was framed (Boratyński et al. 2014) while trying to maximise the area without including damaged zones (Fig. 2).

Statistical analysis

We adhered to the comprehensive statistical protocol detailed by Zuur and Ieno (2016) to ensure rigorous execution of all analytical stages. First, we explored the distribution of variables. Biometric and colour are continuous variables, thus following a Gaussian distribution. This was confirmed for colour variables but was not achieved for most of biometric variables, even after transformation (appendix). Regarding predictors, only temperature and elevation were normally distributed. Two principal component analysis (PCA) were performed to reduce dimensions in the two sets of biometric (five variables) and climatic-geographic (five variables) variables, and to analyse their patterns of covariation. These new variables can be interpreted as gradients with biological and ecological meaning and were used as response and predictors, respectively, in further analyses (Dytham 2011). Regarding morphometric data, the first extracted component summarizes isometric size alone, and the second component contrasts allometric patterns of covariation among characters, representing variation in shape (Somers 1986). For colour, we used the two original variables summarising the pelage brightness for dorsal and ventral views, that is, the mean of the three RGB colours (Stanchak and Santana 2019). All variables were previously scaled to zero mean and unit standard deviation (Riera and Oliva 2023). For PCA plots we used the *factoextra* package (Kassambara and Mundt 2020), and for the correlation matrices the package *corrplot* (Wei and Sim 2017).

Autocorrelation describes the dependence between observations based on their proximity in time or space (Diniz-Filho et al. 2003). It's a common characteristic of ecological data, where nearby values tend to be more similar than distant ones, and non-independence of observations can undermine the validity of statistical tests (Legendre 1993). We analysed the presence of spatial autocorrelation in body size (PCs on biometric variables) and fur colour (RGB/3 for either dorsal or ventral views) using the *DHARMa* package (Hartig 2022). Also, we explored spatial autocorrelation in air temperature. Spatial autocorrelation analysis only considers independent spatial coordinates for each observation, and the presence of different individuals in each locality forced the use of the mean values of the response variables, reducing the effective sample ($n = 49$). In case of spatial structure of the residuals of the response variables (positive or negative autocorrelation), we analysed spatial patterns using a bidimensional spline (including Longitude and Latitude) as a predictor using GAM (Generalized Additive Models) for temperature, and GAMM (Generalized Additive Mixed Models) for body size and colour (*mgcv* package), including fixed (sex) and random effects (locality, year). To account for the spatial dependency of observations (i.e., individuals), the locality was included as a random effect. The year was introduced as a random effect in order to control for pigment degradation of the flat skins with age (Sandoval Salinas et al. 2018) and body size reduction with time (Yom-Tov and Geffen 2011; Kryštufek et al. 2019). Model fitting was assessed by the explained variance (adjusted r^2) and the residual analyses provided by the *DHARMa* package.

In the case of absence of spatial autocorrelation in the residuals of the response variables, we used conventional Generalized Linear Mixed models (Bolker et al. 2009). GLMMs were performed with the same response variables (with Gaussian error distributions) and the two PCAs extracted from the geo-climatic data as predictors, either in linear or quadratic forms (to test hump-shaped patterns), and



	Label	Area	Mean	StdDev	Mode	Min	Max	Median	Skew
1	Red	565345	72.014	18.447	71	5	179	72	0.085
2	Green	565345	63.808	17.878	57	10	173	62	0.358
3	Blue	565345	47.882	17.835	42	0	147	46	0.391
4	(R+G+B)/3	565345	61.237	17.161	55	9	166	60	0.354
5	0.299R+0.587G+0.114B	565345	64.439	17.520	60	10	172	63	0.304

Fig. 2 Steps for the flat skin colour processing: **(a)** Flat skin of *Clethrionomys glareolus*, **(b)** Selection of the area and plugin to analyse the skin on ImageJ software, and **(c)** output of the software showing the area sampled (in pixels) and the descriptive statistics of the RGB colours

using the same fixed and random effects than in GAMMs. To fit the models we used the *lmer* function in the *lme4* R package (Bates et al. 2015). We also calculated pseudo-R^2 values by means of the R function *r.squaredGLMM* and the delta method for variance estimation (Nakagawa and Schielzeth 2013). All analyses and figures were performed under the R and RStudio environments (R Core Team 2023; R Studio Team 2020).

Results

The PCA performed with the five geo-climatic variables obtained two components extracting most of the variation of the original variables (93.3% of variation, Fig. 3a). The first component (CLIMA1, 57.1%) was related to precipitation and latitude, and inversely related to longitude. The second component (CLIMA2, 35.4%) was positively associated with temperature and inversely related to elevation. Analysis of temperature residuals revealed a strong positive spatial autocorrelation (Moran's I = 0.51, $p < 0.0001$), indicating a clustered spatial pattern where locations with similar temperatures tended to be in close proximity. A Generalized Additive Model (GAM) incorporating a bidimensional

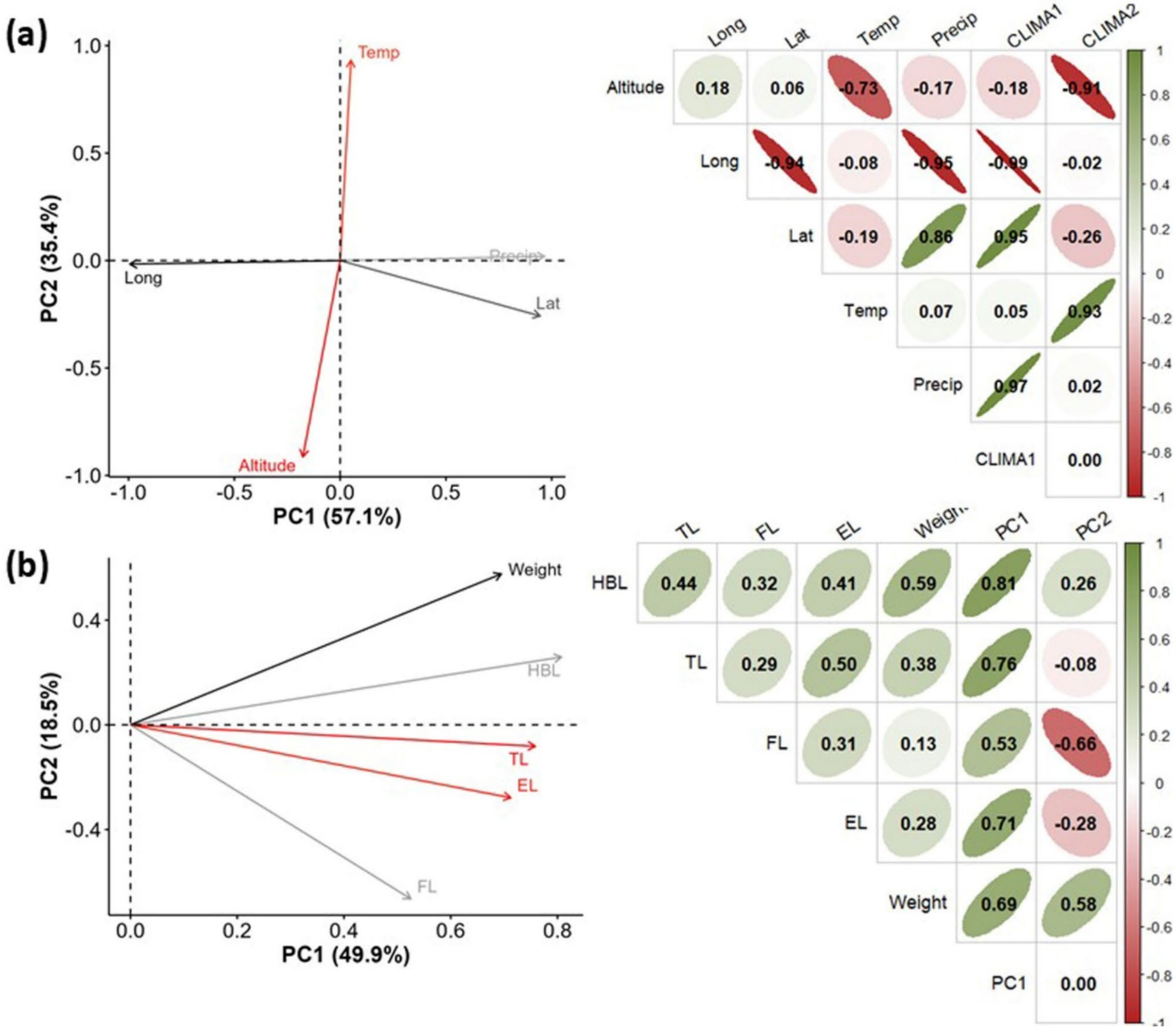


Fig. 3 Results of the Principal Component Analysis (PCA) performed on **(a)** the five geographic and climatic variables and **(b)** the five morphological variables. The figure displays the factor loadings of each variable on the first two extracted components, as well as the variance explained by each component. On the right, a Pearson correlation matrix is presented, showing the coefficient of correlation between the original variables and the two extracted components in both the geographic-climatic (CLIMA) and the morphometric matrices (PC)

spline of longitude and latitude demonstrated a substantial effect of spatial location on mean temperature ($F = 24.18$, $p < 0.0001$, r^2 (adj.) $= 95.1\%$, $n = 49$), effectively capturing the spatial structure of temperature within the study area (appendix). Despite being distant, both the Mediterranean and Atlantic areas showed similar mean annual temperatures and were situated at similar elevations but showed contrasting patterns in cumulative precipitation (Fig. 4). Therefore, temperature was inversely associated to elevation, and precipitation positively related to latitude and negatively to longitude (Fig. 3a).

Morphometric variability

In the PCA performed with the five morphometric variables, the first two components explained 68.4% of the variance (PC1 = 49.9%; PC2 = 18.4%, Fig. 3b). The first component (PC1) was associated with body size in general, since all five variables showed positive loadings on it. As predicted, the first component was attributed to isometric size alone, while the second component (PC2) corresponded to body shape (allometric patterns), with overall size (weight and body length) being negatively correlated to the length of the three appendices (foot, ear and tail length).

All three appendices showed a negative allometry because their size increased with decreasing body size (HBL and weight). Allometry was revealed after obtaining the beta coefficients of the linear regression of the appendices on body size (HBL), and all were <1 ($\beta = 0.21$–0.61, all $p < 0.001$) (Suppl. Figure 1).

Spatial autocorrelation analyses revealed positive autocorrelation in PC1-size (Moran's $I = 0.14$, $p = 0.03$), and negative autocorrelation in PC2-size (Moran's $I = -0.19$, $p = 0.01$, appendix). These results indicated that overall body size exhibited spatial clustering, with individuals of similar size tending to be in close proximity. Generalized Additive Mixed Models (GAMMs) incorporating a bidimensional spline to account for spatial autocorrelation demonstrated a good fit to body size PC1 (Table 1, *DHARMa* residual tests, appendix). In contrast, the model exhibited a comparatively weaker negative fit to temperature, suggesting that the spline effectively captured the spatial variation of overall body size within the study area. Relative size of appendices (PC2) was barely associated with the bidimensional spline and exhibited a lower positive association with temperature. Therefore, overall size (PC1) decreased with temperature and relative size of appendices (PC2) increased with temperature (Fig. 5).

The size-PC1 showed a significant hump-shaped pattern along the gradient represented by the geo-climatic PC1. That is, size increased towards the middle values of the gradient and were lower at both extremes (Table 1; Fig. 6a), showing significant differences between the three populations (Fig. 6b). There were no sexual differences in overall size. The size-PC2 (relative size of the appendices) showed a valley-shaped pattern along the gradient represented by the geo-climatic PC1 (Table 1; Fig. 6c). But the comparison of the three populations studied highlighted that the two northern-western populations (Pyrenees and Atlantic) were similar (Fig. 6d). Interestingly, there was a significant effect

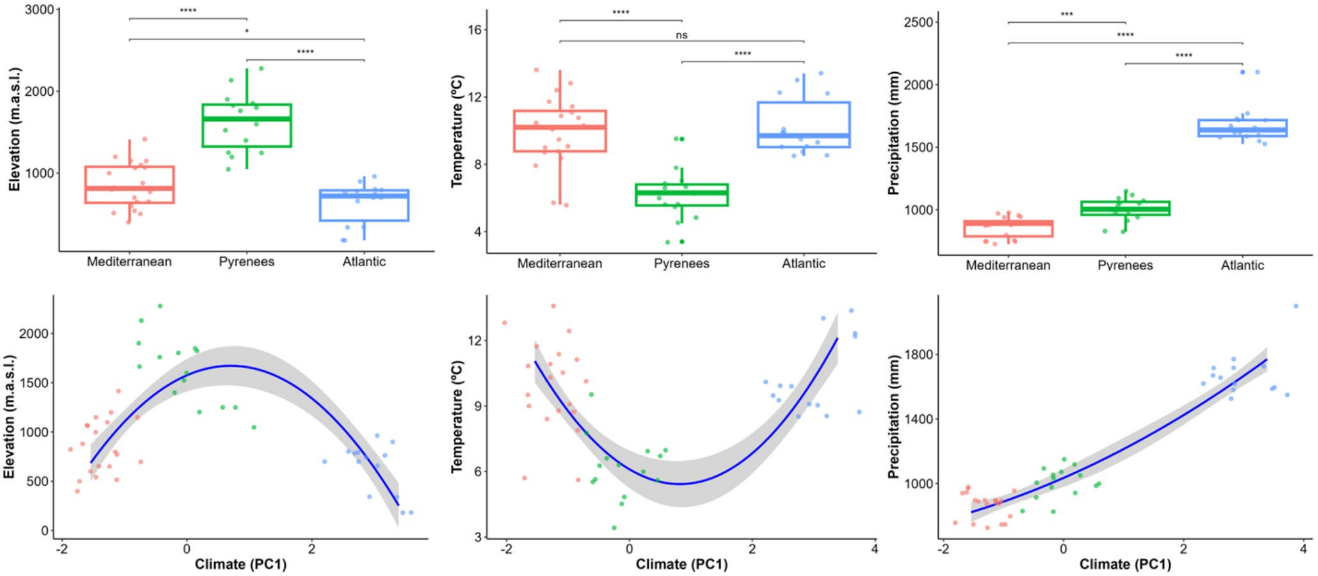


Fig. 4 Boxplots showing differences in elevation, annual mean temperature, and annual precipitation of the bank vole sampling locations between the three study areas, and patterns along the environmental gradient represented by the first geo-climatic principal component (CLIMA1, Fig. 3). Pairwise statistical differences between the three areas were tested after a post-hoc Bonferroni correction. Smoothed lines were fitted by a polynomial function of degree two to test for non-linear relationships (hump-shaped or valley-shaped). Significance codes: '****' 0.0001; '***' 0.001; '**' 0.01; ns = non-significant

Table 1 Estimated coefficients±se of four GAMMs showing the effects of the temperature-elevation gradient (Climate_2), sex, year, and the geographical space (bidimensional spline), on the size (PC1 and PC2) of bank voles. Site was included as a random effect. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Response	Predictor	Estimate	SE
PC1 (size)	(Intercept)	–33.72	58.47
	Climate_2	–0.51***	0.10
	Sex (Male)	-0.08	0.17
	Year	0.01	0.02
	R^2 (adj,)	0.19	
PC1 (size)	(Intercept)	-0.02	0.08
	Spline (Long-Lat)	F=30.24***	
	R^2 (adj,)	0.34	
PC2 (shape)	(Intercept)	30.37	34.20
	Climate_2	0.15*	0.05
	Sex (Male)	-0.22*	0.11
	Year	–0.02	0.01
	R^2 (adj,)	0.07	
PC2 (shape)	(Intercept)	0.02	0.05
	Spline (Long-Lat)	F=10.18***	
	R^2 (adj,)	0.07	

of sex on the size-PC2, males showing larger appendices related to body size than females.

Colour variability

The analyses of spatial autocorrelation of dorsal and ventral fur colour did not yield significant patterns, both tests showing almost identical results (RGB_Dorsal and Ventral: Moran's I = −0.09, p=0.63, both). The statistical mixed models (GLMMs) with the mean RGB dorsal and ventral colour as response and the two geo-climate predictors showed a positive linear association with the PC1 and a negative linear association with the PC2 (Table 2; Fig. 7a, c). This means that colour was mostly affected by longitude, latitude, and precipitation (and barely affected by elevation or temperature), but it did not show a clear geographic spatial structure. But the colour comparison of the three populations studied highlighted that the two western-northern populations (Pyrenees and Atlantic) were similar (Fig. 7b, d). Among the dorsal colours, the red was the one with largest variation along the geo-climatic PC1 (adj. r^2=0.54, p<0.001), followed by the green (adj. r^2=0.19, p<0.001), but the blue colour did not change along the gradient (adj. r^2=0.0, p=0.87). Among the ventral colours, the red was the one with largest variation along the geo-climatic PC1 (adj. r^2=0.47, p<0.001), followed by the green (adj. r^2=0.40, p<0.001), and the blue colour (adj. r^2=0.15, p<0.001; Suppl. Figure 2). Individuals living in the eastern and southernmost warm area (Barcelona province) showed lower values of red and high values of blue, and individuals living in the western and humid area (Navarre) showed higher values of red and green, and lower values of blue (Fig. 8). This means that the eastern and southern individuals were darker, either for dorsal and ventral views, and western individuals showed lighter colours. These variations were mostly caused by the red colour, the only showing significant differences between the three populations in dorsal and ventral views (Suppl. Figure 2). The males showed higher pelage brightness than females, but only for the ventral view (Table 2). But a MANOVA with the eight colour variables (4 dorsal and 4 ventral) and sex as the classification factor

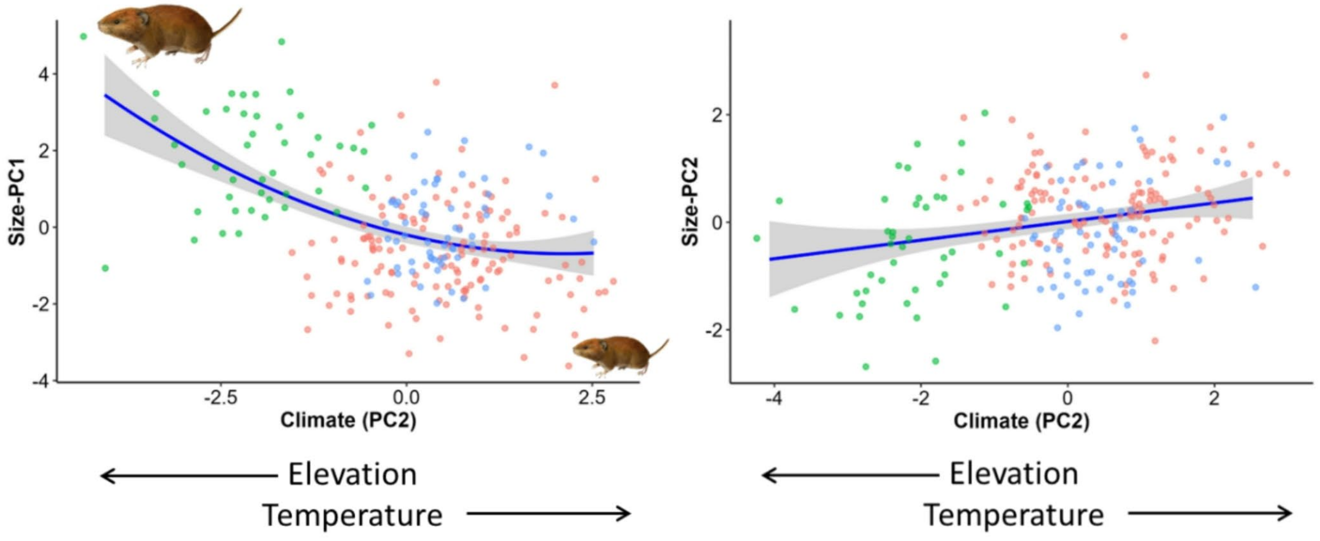


Fig. 5 Changes in overall body size (size-PC1) and relative size of appendices (size-PC2) of the bank vole along the elevation-temperature gradient represented by climate PC2 (Fig. 3). The direction of the arrows indicates increase of the predictor variables. Smoothed lines along the environmental gradient were fitted by a polynomial function of degree two to test for non-linear relationships (hump-shaped or valley-shaped). Dot colours as in Fig. 4

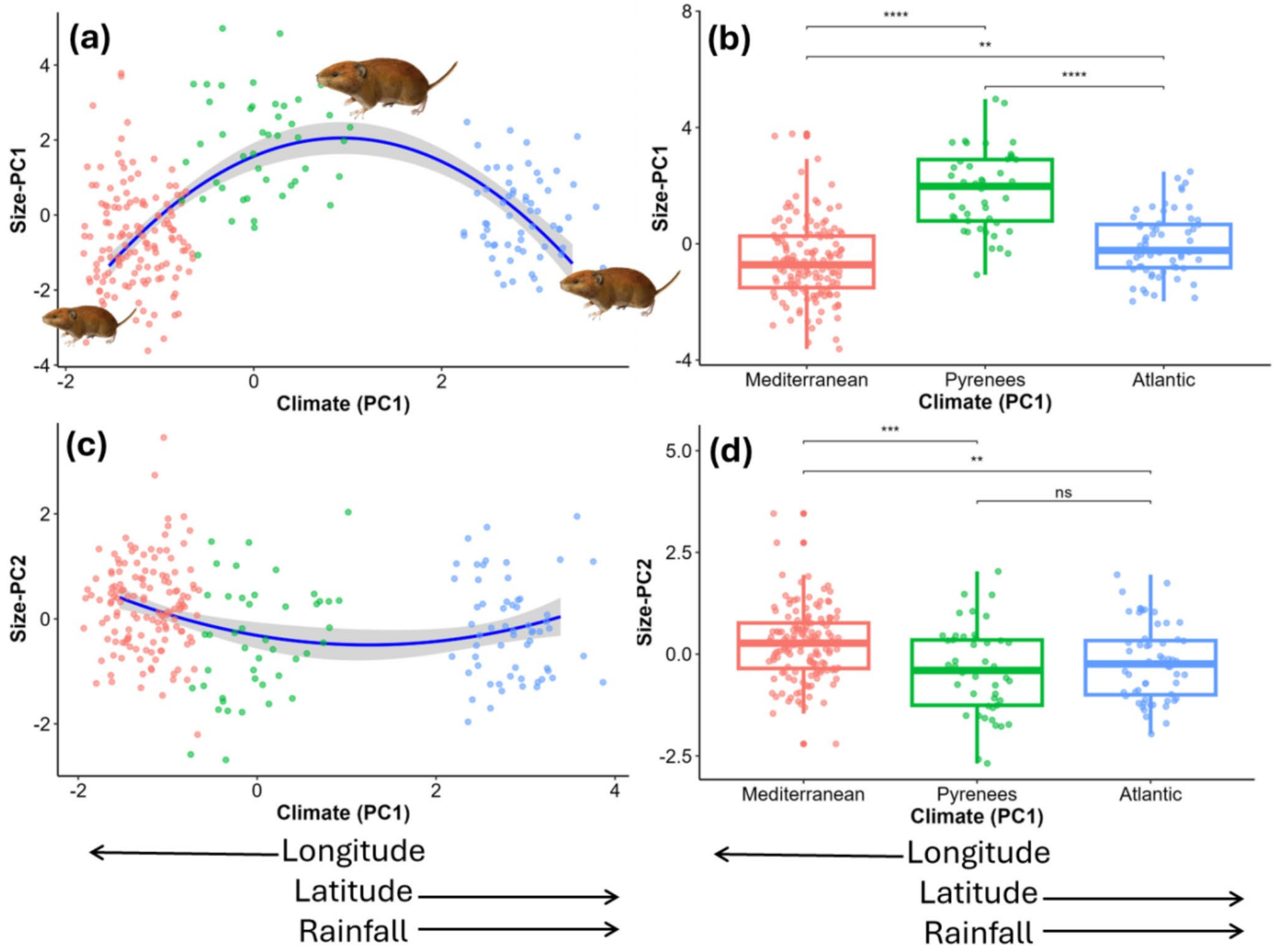


Fig. 6 Changes in overall body size (size-PC1) and relative shape of the appendices (size-PC2) of the bank vole along the environmental gradient represented by the first geo-climatic principal component (PC CLIMA1, Fig. 3). **(a, c)** Smoothed lines along the environmental gradient, and **(b, d)** pairwise statistical differences between the three areas after a post-hoc Bonferroni correction. The direction of the arrows indicates increase of the predictor variables. Lines were fitted by a polynomial function of degree two to test for non-linear relationships (hump-shaped or valley-shaped). Significance codes: '****' 0.0001; '***' 0.001; '**' 0.01; ns = non-significant

confirmed that males showed higher significant values for all but the blue dorsal colour ($F_{1, 128} = 2.41$, $p = 0.01$, Suppl. Figure 3).

Regarding colour variability of the flat skins with age, for the dorsal view the red colour decreased, and the blue colour increased (but both showing marginally significant results, $r^2 = 0.02$, $p = 0.05$), whereas the green colour remained unchanged with time. Interestingly, for the ventral view red and blue colours decreased (but both showing marginally significant results, $r^2 = 0.02$, $p < 0.07$), whereas the green colour remained unchanged with time (Suppl. Figure 4).

Discussion

In this study we analysed the changes in morphology and colouration in Iberian bank voles along a strong environmental gradient in the NE of the Iberian Peninsula. The results confirmed that variation in size, shape (relative size of the appendices), and colour within the same genetic clade of Iberian bank voles was related to abiotic environmental variability. The use of Principal Component Analysis (PCA) on morphometric variables allowed the obtention of two independent factors (PCs), one correlated to overall size and other to shape (Somers 1986), and both showed association to the environmental predictors. Remarkably, our results showed linear associations of size and shape with a PC summarising temperature and elevation (both inversely related), suggesting that temperature was a causal factor. Individuals living in cold areas were large in overall

Table 2 Estimated coefficients ± se of two GLMMs showing the effects of sex, year, and the first two components of the PCA with the five geo-climatic variables (Climate_1, Climate_2) on the two variables representing colour intensity (RGB/3) for the dorsal and ventral views of the flat skins of the bank vole. The random effect was the site, and marginal (i.e., fixed effects) and conditional (i.e., whole model effects) variance was also shown. The year was changed from random to fixed effect due to problems with model fitting (see appendix). Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Response	Predictor	Estimate	SE
RGB/3 DORSAL	(Intercept)	78.57·	46.22
	Sex (Male)	0.22	0.15
	Climate_1	0.29***	0.05
	Climate_2	–0.05	0.06
	Year	–0.04·	0.02
	R^2 marginal	0.29	
	R^2 conditional	0.31	
RGB/3 VENTRAL	(Intercept)	142.42**	45.66
	Sex (Male)	0.27*	0.13
	Climate_1	0.33***	0.06
	Climate_2	–0.15*	0.07
	Year	–0.07**	0.02
	R^2 marginal	0.42	
	R^2 conditional	0.55	

size, but they showed proportionately shorter appendices (ears, feet, and tail). Non-linear associations with a PC summarising latitude, rainfall and longitude, indicated that larger voles with smaller appendices (related to body size) were found in colder, higher areas, while smaller voles with larger appendices were found in warmer, lower areas. Since size of individuals increased and relative size of the appendices decreased along elevation, bank voles living in NE Iberian peninsula followed the expected patterns predicted by ecogeographical rules for endotherms (i.e., Bergmann and Allen), tending to be larger and with smaller appendices in cold climates to reduce heat dissipation (Brown and Lomolino 1998). In spite of the reduced latitudinal gradient studied, our results agreed with an increase in size from southern (Mediterranean) to northern (Pyrenees) populations previously documented in Iberian bank voles (e.g., cranial variation: Ventura et al. 1993). This aligns with the strong biotic boundaries described in the area regarding the biogeography of small mammal communities (Sans-Fuentes and Ventura 2000), and with the significant role of abiotic factors on the population dynamics of the bank vole, a species with northern requirements (Huerta-Schliemann et al. 2025). However, several authors suggested that small rodents did not follow the ecogeographical rules, and this was mainly related to the influence of other environmental parameters that covary with temperature (Yom-Tov and Geffen 2006; Alhajeri and Steppan 2016; Alhajeri et al. 2020). Indeed, the bank vole displays strong body size variability over its geographical range (Yoccoz and Mesnager 1998) and, as most rodents, it shows a decreasing size towards higher latitudes in Europe, thus, not following the Bergmann's rule (Ledevin et al. 2010). Some explanations invoked to the pattern are that high-latitude (or high-elevation) environments are characterized by low primary production and food scarcity, especially during winter (Yom-Tov and Geffen 2006), and they may favour smaller body sizes as an adaptation to reduce overall energy requirements. In the study area, temperature showed a strong spatial structure being determined by elevation, and precipitation by a longitudinal gradient (Cuadrat et al. 2024). Since bank vole size and environmental variables exhibited congruent spatial patterns, it was difficult to tease apart the influence of temperature once its spatial patterning was statistically removed (e.g., using partial constrained ordination analyses: Borcard et al. 1992).

Regarding size, another generalised pattern among the *Clethrionomys* genus is the reversed sexual size dimorphism, males being generally smaller than females. Some studies documented sexual differences in bank voles' size in anatomical traits, such as the pelvis (Matysiak et al. 2017) and cranial traits (Csanády and Mosansky 2021). But studies of the Iberian populations highlighted the lack of remarkable sexual size dimorphism in bank voles (Ventura et al. 1993). This generally agreed with our results concerning overall size (lack of sexual differences), but did not agree with the results regarding the relative size of the appendices (PC2). In this vein, our results indicated a small increase of appendices related to body size in males, but this increase was mostly detected in the foot length (Fig. S5). In spite that somatic characteristics such as body length, tail length, and especially weight, are variable and depend on environmental factors (Adamczewska-Andrzejewska and Nabagło 1977), the foot length is persistent during life and is considered as a fundamental taxonomic character (Baláž 2010).

On the contrary, dorsal and ventral colour did not change along elevation but showed a linear trend along the east-west longitudinal gradient. Therefore, our results suggested that colour variability was barely related to temperature (or elevation) and strongly related to longitude and rainfall. Mammal colouration is primarily determined by the deposition of the two types of melanin pigments, red-to-pink phaeomelanin, and black-to-brown eumelanin (Boratyński et al. 2014; Delhey 2019). Eumelanin increases with humidity, while phaeomelanin dominates in dry, warm regions and decline rapidly in cold conditions. Hence, the observed colour pattern in bank voles was in contradiction with Gloger's rule (Delhey 2019), because reddish-brighter individuals were found in extremely wet areas. However, it has been described that colouration has three main reasons: regulation of physiological processes, communication, and concealment (predator-prey interactions, Caro 2005). Pelage colouration can play an important role in physiological regulation, and dark colours will facilitate basking in cold environments and light colours will prevent overheating in hot environments (Brown and Lomolino 1998). Furthermore, darker colours

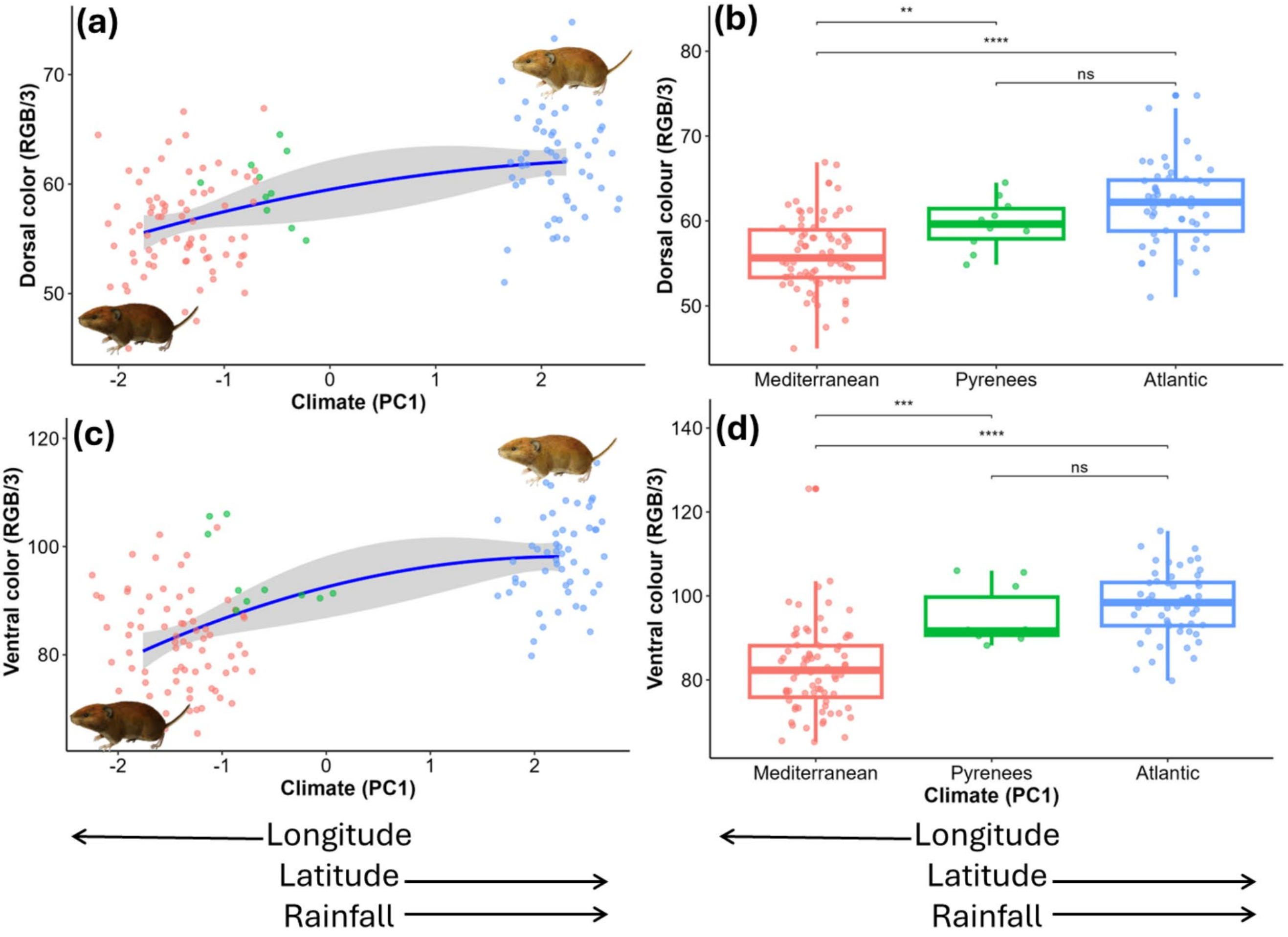


Fig. 7 Changes in dorsal and ventral colour (mean values for RGB profiles) of the bank vole along the environmental gradient represented by the first geo-climatic principal component (Climate PC1). **(a, c)** Smoothed lines along the environmental gradient, and **(b, d)** pairwise statistical differences between the three studied populations after a post-hoc Bonferroni correction. The direction of the arrows indicates increase of the variables, and bank vole pictures showed darker-lighter populations. Lines were fitted by a polynomial function of degree two to test for non-linear relationships (hump-shaped or valley-shaped). Significance codes: '****' 0.0001; '***' 0.001; '**' 0.01; ns = non-significant

can be resistant to parasite/bacterial infection in warm and humid climates (Stanchak and Santana 2019), following a consistent latitudinal pattern (Caro and Mallarino 2020). Our results did not support the first main reason (climate-related colouration), but stressed sexual differences in colouration, being males brighter (higher mean RGB values) than females (Suppl. Figure 3). Whether these differences could be related to sexual communication remains intriguing, but the existence of sexual dichromatism for signalling is unreliable in nocturnal rodents which are mostly oriented by olfactory cues rather than visual ones (Howell and Caro 2024). But camouflage is the most commonly cited mechanism underlying Gloger's rule (Delhey 2019), fur colour playing a relevant role to avoid detection in small mammal prey, with hair colour evolving to resemble the environment (cryptic patterns) by natural selection as a response to predation (Caro and Mallarino 2020). Bank voles, as many other woodland rodents, are the target of several aerial and terrestrial forest predators, such as Tawny owls and Common genets (Zmihorski et al. 2011; Torre et al. 2018), and some authors pointed out selective predation on that species (Torre et al. 2003). The most contrasting fur colour patterns were observed at the most distant areas (Navarre and Barcelona, Suppl. Figure 2) both showing similar elevation and temperatures, but under contrasting rainfall conditions that affected the vegetal communities. We hypothesised that western-northern bank vole populations living in deciduous forests showed brighter light orange back colours to mimic the environment. These forests are leafless in autumn-winter, and the forest floor is covered by a large amount of dead orange leaves almost the whole year (Jacob et al. 2010). On the other hand, eastern-southern populations mostly living in sclerophyllous evergreen forests showed darker back colours to mimic a shady floor. Darker animals

Fig. 8 Dorsal and ventral RGB colours of a female bank vole captured in **(a)** a holm-oak evergreen sclerophyllous forest in the Mediterranean area (Barcelona) and **(b)** a beech deciduous forest in the Atlantic area (Navarre), both captured in 1996. RGB colour patterns of the flat skins of both individuals were obtained using the software RGB Colour Mixer: https://csunplugged.jp. Right pictures, idealised fur colour patterns (darker-Mediterranean and lighter-Atlantic) contrasting against the forest floor to give support to the "concealment hypothesis". Forest backgrounds (holm oak and beech) were generated by Microsoft Bing image creator

would be better camouflaged under dense vegetation which blocks light resulting in shaded environments with dark backgrounds (Delhey 2019). The importance of this concealment with background colours has been demonstrated for many species of small mammals (Belk and Smith 1996; Hoekstra and Nachman 2003; Hoekstra et al. 2004; Mullen et al. 2009). But more specific studies directly addressing the relationship between fur colour and the vegetation composition and structure of the environment are needed to properly test the concealment hypothesis. Furthermore, we are aware that other environmental factors affect fur colour, in particular, older specimens of museum collections tend to be redder than more recent individuals due to eumelanin pigment degradation (Davis et al. 2013; Sandoval Salinas et al. 2018). Despite the short period analysed (25 years: 1983–2008), our results agreed with previous findings, with older specimens looking reddish (high red and less blue in dorsal views), and specimens recently collected showing the opposite. But according to RGB colour patterns with time, melanin degradation was different for the dorsal and ventral views of the flat skins (Suppl. Figure 4). Therefore, it is reasonable to question how accurately museum specimens represent the actual colours of living animals (Sandoval-Salinas et al. 2018), and it is necessary to control fur colour age-related differences in statistical models (i.e., including year as a random/fixed effect).

Some authors suggested that morphological differences in rodent populations were caused by phenotypic variation resulting from interactions with the environment, but without producing changes in the genotype (Mullen et al. 2009). Studies performed during the last century uncovered that the morphometry and colouration of Iberian bank voles showed variability following latitudinal and longitudinal gradients (Rey 1972; Ventura et al. 1993). Indeed, conspicuous differences in body size and colour of some populations allowed the description of three subspecies of Iberian bank voles

(Rey 1972), but their validity remains uncertain due to the lack of detailed genetic studies. Nonetheless, recent investigations confirmed that Iberian populations of bank voles are considered to belong to the same genetic clade (Spanish clade: Ledevin et al. 2010; Kotlík et al. 2022). However, giving the reliance of these genetic studies on mitochondrial DNA methods, the phylogeographic results to infer genetic homogeneity of these populations can be questioned (Chiocchio et al. 2019). Indeed, Mullen et al. (2009) detected genetically divergent subspecies with similar phenotype, and genetically similar subspecies with divergent phenotypes. Thus, the observed variations in body size and colour among the Iberian populations studied could be caused by phenotypic plasticity, by genetic differences, or both. This suggests that evolutionary processes and biological adaptations have enabled the species to respond to their specific environments (Yom-Tov and Geffen 2011). Factors like temperature and other environmental conditions influence the allocation of energy, leading to spatial fluctuations in body size and colouration (Oli 1999; Lázaro et al. 2017; Caro and Mallarino 2020). However, some authors pointed out that genetic changes underlie major patterns of clinal variation in small mammals, likely facilitating the expansion into new environments (Ballinger and Nachman 2022). That is, adaptative evolution involves changes in the genetic makeup of a population over generations due to natural selection. By studying the adaptive responses of bank voles, we can gain valuable insights into their biology, conservation, and how they might fare in a changing world.

Conclusions

- Bank voles in the northeastern Iberian Peninsula exhibit patterns consistent with Bergmann's and Allen's Rules. Individuals at higher elevations, where temperatures are colder, tend to be larger in size and have smaller relative appendix sizes, likely adaptations to reduce heat loss (Brown and Lomolino 1998). However, body size and air temperature were spatially autocorrelated, both sharing an undetermined amount of spatial variance.
- Bank voles in the northeastern Iberian Peninsula did not conform to Gloger's rule, at least owing to its modern definition (i.e., gradients of humidity: Delhey 2019). But fur colour has several causes regarding the deposition of melanin, and we hypothesised crypsis as a possible reason in the studied populations. More specific studies relating colour with habitat features are needed to confirm this hypothesis.
- Our findings do not distinguish phenotypic plasticity from local adaptation by natural selection. While correlations between traits and environmental variables are consistent with plasticity, they are equally consistent with adaptive genetic differentiation. Some polygenic traits, such as body size, length, and colouration, may evolve under selection even in genetically similar populations.
- We assumed genetic homogeneity based on the phylogenetic clade membership (i.e. Spanish clade, Kotlík et al. 2022), but this does not preclude the existence of nuclear genetic variation among the studied populations. Future research incorporating genetic markers or genomic data is necessary to test for population structure and its potential role in shaping phenotypic traits.

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Author contributions Conceptualization: Ignasi Torre and Lídia Freixas; Methodology: Laura Jou, Antoni Arrizabalaga, Lídia Freixas, Ignasi Torre; Formal analysis and investigation: Laura Jou, Ignasi Torre; Writing - original draft preparation: Laura Jou, Ignasi Torre; Writing - review and editing: Ignasi Torre; Data curation: Antoni Arrizabalaga; Supervision: Antoni Arrizabalaga.

Data availability The material used in this article is deposited in the collection of the Natural Sciences Museum of Granollers (Barcelona, Spain). The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article. No funding was received to assist with the preparation of this manuscript.

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