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Research article

The effects of climate on bat morphology across space and time

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According to Bergmann's and Allen's rules, climate change may drive morphological shifts in species, affecting body size and appendage length. These rules predict that species in colder climates tend to be larger and have shorter appendages to improve thermoregulation. Bats are thought to be sensitive to climate and are therefore expected to respond to climatic changes across space and time. We conducted a phylogenetic meta-analysis on > 27 000 forearm length (FAL) and body mass (BM) measurements from 20 sedentary European bat species to examine body size patterns. We assessed the relationships between body size and environmental variables (winter and summer temperatures, and summer precipitation) across geographic locations, and also analysed temporal trends in body size. We found sex-specific morphological shifts in the body size of European bats in response to temperature and precipitation patterns across space, but no clear temporal changes due to high interspecific variability. Across Europe, male FAL decreased with increasing summer and winter temperatures, and BM increased with greater precipitation. In contrast, both FAL and BM of female bats increased with summer precipitation and decreased with winter temperatures. Our data can confirm Bergmann's rule for both males and females, while females' BM variations are also related to summer precipitation, suggesting a potential link to resource availability. Allen's rule is confirmed only in males in relation to summer temperature, while in females FAL and BM decrease proportionally with increasing temperature, maintaining a constant allometric relationship incompatible with Allen's rule. This study provides new insights into sex and species-dependent morphological changes in bat body size in response to temperature and precipitation patterns. It highlights how body size variation reflects adaptations to temperature and precipitation patterns, thus providing insights into potential species-level morphological responses to climate change across Europe.

Keywords: Allen's rule, Bergmann's rule, body size, Chiroptera, climate change, meta-analysis

Introduction

Global environmental change poses a significant threat to biodiversity, biological communities, and the ecosystem services they provide (Weiskopf et al. 2020). Changes in temperature regimes, patterns of rainfall and frequency and intensity of extreme weather have resulted in a range of responses from numerous species, from range shifts that track favourable climates to phenotypic and genetic adaptations to warming conditions over time (Cushman et al. 1993, Hoffmann and Sgró 2011, Weiskopf et al. 2020). Change in body size is the most common adaptive response to variations in temperature and precipitation (Sheridan and Bickford 2011, Jiang et al. 2019,

Mundinger and Scheuerlein 2021), as observed in numerous taxa, including mammals (Yom-Tov and Geffen 2006, Clements et al. 2018), birds (Cousins 1989, Yom-Tov and Geffen 2006, Tattersall et al. 2017), reptiles (Lindsey 1966, Olalla-Tárraga et al. 2006), amphibians (Lindsey 1966) and invertebrates (Sheridan and Bickford 2011).

In this context, Bergmann's rule (Bergmann 1848), and Allen's rule (Allen 1877) were postulated to explain patterns of morphological variation in endotherms within and across species in response to temperature gradients. Bergmann's rule predicts that colder regions are inhabited by larger-sized endothermic species as a result of the lower surface-to-volume ratio, allowing for a greater thermoregulatory

ability (Bergmann 1848, Shelomi and Zeuss 2017). In turn, Allen's rule posits that endothermic species inhabiting colder regions within their distribution range have reduced appendage length relative to body size (Allen 1877), thus mitigating thermoregulation costs due to the lower surface-to-volume ratio. Several studies have provided supporting evidence for a broad range of taxa (Bergmann's rule: Blackburn and Gaston 1996, Ashton 2002, Meiri and Dayan 2003, Symonds and Tattersall 2010, He et al. 2023, Henry et al. 2023; Allen's rule: Tilkens et al. 2007, Symonds and Tattersall 2010, Jiang et al. 2019, Alhajeri et al. 2020), and have shown how both mechanisms can operate simultaneously (Laiolo and Rolando 2001, Baldwin et al. 2023, Tabh and Nord 2023). Yet, multiple studies have highlighted deviations from Allen's (Stevenson 1986, Gutiérrez-Pinto et al. 2014, Probst et al. 2022) and Bergmann's rules (Geist 1987, Ashton et al. 2000, Mainwaring and Street 2021) in several taxa. The reasons for these discrepancies are not yet fully understood, but they may arise from methodological variations across studies (Salewski and Watt 2017), differences in sample sizes or geographic and/or thermal range coverage (Meiri et al. 2007, Henry et al. 2023), variation in natural history traits (Mainwaring and Street 2021), disequilibrium conditions (e.g. recent colonizations; Kirchman and Schneider 2014), and the interacting effect of additional drivers (e.g. predator–prey evolutionary dynamics; Korpimäki and Norrdahl 1989).

Beyond the study of biogeographic patterns, these rules hold interest in the context of climate change. An increasing number of studies on various taxa, including bats, have observed temporal trends in the body size and length of appendages of different organisms, potentially linked to a response to ongoing climate change (Bogdanowicz 1990, Yom-Tov 2003, Yom-Tov and Geffen 2011, Gardner et al. 2014, Salinas-Ramos et al. 2020a, Moroz et al. 2021). Bats are diverse, widespread mammals considered particularly sensitive to the effects of climate change due to their high surface-to-volume ratios, long lifespan, and low reproductive rates, which may limit their ability to evolve at a sufficient pace to cope with changing climatic conditions (Mundinger and Scheuerlein 2021, Festa et al. 2023). Most temperate zone bat species are heterotherms, i.e. they can adjust their body temperature according to environmental conditions. This ability allows bats to maintain plastic energetic requirements as their first-line defence against environmental challenges (Geiser and Turbill 2009). However, this does not exclude other important adaptations. Bats could adapt to altered temperature regimes through selection on their wing morphology to optimise their flight performance, foraging strategy, dispersal ability, thermoregulation, and evaporative water loss rates (Varzinczak 2020). Female bats form maternity colonies in spring and summer to cooperatively care for their young, a strategy that helps mitigate challenges posed by adverse environmental conditions (Kunz 1982).

Studies exploring changes in bat size in response to climate change have observed variations in this adaptive strategy, ranging from a decrease (Bogdanowicz 1990, Moroz et al. 2021, Mundinger and Scheuerlein 2021) to an increase (Jiang et al. 2019, Salinas-Ramos et al. 2020a, Russo et al. 2024a, 2024b) in body size. Yet, Bergmann's and Allen's rules in bats have rarely been examined explicitly at an intraspecific level (Rubalcaba et al. 2022). Examining whether bats conform to these ecological rules can provide a useful framework for predicting long-term climate-induced morphological changes, which can inform vulnerability assessments and guide effective conservation strategies, especially in areas with rapid environmental changes. Besides ambient temperature, changes in precipitation levels can also affect bat body size, with decreased rainfall and moisture levels corresponding with a smaller body size in some species (Burnett 1983, Bogdanowicz 1990, Yom-Tov and Geffen 2006). Indeed, increased rainfall, particularly in seasonal Mediterranean environments, can boost insect abundance, which in turn promotes larger bat body size (Anthony and Kunz 1977, Frick et al. 2010, Davy et al. 2022). Bats are important for providing valuable ecosystem services that benefit human well-being, such as pest suppression, seed dispersal, and pollination (Deutsch et al. 2018, Tuneu-Corral et al. 2023). In the context of climate change, it is essential to understand their life history traits as a function of environmental conditions to anticipate potential impacts on different species and the broader ecosystems they inhabit.

Studies of changes in bat morphology to date mostly focused either on single species or on multiple species in a limited geographic context, often not showing a consistent pattern (Burnett 1983, Almeida et al. 2014). Studies over multiple species and across large geographic extents can shed light on the drivers and commonalities in species' responses to climate change. While ecogeographic rules usually pertain to spatial variation in traits, the study of species' morphological changes can also be approached from a temporal perspective. Intraspecific geographic patterns of trait variation may result from local adaptations (Gaston et al. 2008), highlighting a species' potential to adapt to environmental changes over time. Studies including both spatial and temporal scales of analysis are rare, yet they may reveal interesting patterns. Most studies of changes in bat morphology to date have focused on either spatial or temporal responses. For example, Alston et al. (2023) studied intraspecific variation in body size in 20 North American bat species, finding that they followed Bergmann's rule across space, whereby larger individuals occurred in cooler areas. However, as this study lacks longitudinal data (the temporal component), it is unknown how changes in temperature over the past few decades have affected variation in body size and therefore, whether bats are responding to climate change through morphological changes.

In this study, we test the applicability of Bergmann's and Allen's rules by analysing how bat morphology varies spatially and temporally across climatic gradients in Europe. We examine trends in body size, specifically forearm length (FAL) and body mass (BM), to determine if these rules act simultaneously and whether, due to the progressive increase

Table 1. Overview of the variables, analyses, expected results, and datasets used to test each of the five hypotheses in this study. The first column lists the five hypotheses. For each hypothesis, the second column specifies the environmental variables analysed (Tmax: maximum summer temperature, Tmin: minimum winter temperature, and SP: summer precipitation for spatial analysis; Year for temporal analysis). The third column indicates the analysis type (spatial or temporal) associated with each hypothesis. The 'Expected results' column outlines the expected correlations between the variables and forearm length (FAL) or body mass (BM), where '↑' indicates a positive correlation, '↓' a negative correlation. The final column specifies the dataset utilized for each analysis: the 'FAL dataset' includes all FAL measurements, while the 'Pairwise FAL–BM dataset' includes both BM and corresponding FAL values for the same individuals to observe FAL variation relative to BM.

Hypothesis	Variable	Analysis	Expected results	Dataset
1) Bergmann's rule	Tmax Tmin Year	Spatial Temporal	↓ FAL	• FAL dataset
2) Allen's rule	Tmax Tmin Year	Spatial Temporal	Positive allometric relationship of FAL to BM (Supporting information)	• Pairwise FAL–BM dataset
3) Precipitation	SP	Spatial	↑ FAL ↑ BM	• FAL dataset • Pairwise FAL–BM dataset
4) Body size influences adherence to Bergmann's rule	Tmax Year	Spatial Temporal	↓ FAL ↓ BM Depending on the species' body size	• FAL dataset • Pairwise FAL–BM dataset
5) Sex-specific responses in body size changes	Tmax Tmin SP	Spatial	↓ FAL ↓ BM Mainly in males	• FAL dataset • Pairwise FAL–BM dataset

in temperatures over the past 40 years in Europe, spatial and temporal trends align. Since small mammals seem to follow Bergmann's rule more closely (Porter et al. 1994, Steudel et al. 1994), though large mammals may also show strong conformity to it (Freckleton et al. 2003), we explore how bats' body size influences their adherence to Bergmann's rule.

We hypothesise that:

1. European bats follow Bergmann's rule; we predict a negative correlation between bat body size and temperature both across space and over time, as temperatures have increased across Europe.
2. European bats follow Allen's rule; we predict a positive relationship between forearm length and body mass driven by temperature, both across spatial gradients and over time (reflecting rising temperatures in recent decades). This correlation suggests that as temperatures increase, the relative size of appendages may increase more significantly or decrease less significantly than body mass, reflecting an adaptive response to warmer environments that enhances thermoregulation (Supporting information).
3. European bats' size depends on resource availability; we predict that bat body size will be larger in areas with higher levels of summer precipitation (used as a proxy for insect abundance).
4. Adherence to Bergmann's rule will depend on the species' average body size. We aim to clarify how bats' body size influences their adherence to Bergmann's rule.
5. Considering the clear sexual dimorphism in European bats, we hypothesise that morphological responses in the form of body size changes will be sex-specific. In particular, we predict that male bats are more sensitive to changes in temperature than females (Table 1).

Material and methods

Data

We collected > 64 000 adult body size records of 39 European bat species (covering 83% of the European bat community; Froidevaux et al. 2023) from bat researchers and conservation organisations from 18 countries across Europe and the Middle East (Israel), recorded between the years 1900 and 2023, as part of the European Cooperation in Science and Technology (COST) Action network on climate change and bats (ClimBats-CA18107; https://climbats.eu) (Supporting information). Forearm length (FAL) and body mass (BM) are the most commonly used body size measurements in bat studies (Jiang et al. 2019, Salinas-Ramos et al. 2020b, Wang et al. 2020, Yue et al. 2020). FAL correlates with body size (Thiagavel et al. 2017, Salinas-Ramos et al. 2020a, Mundinger and Scheuerlein 2021) as well as wing morphology (Thiagavel et al. 2017), whereby a longer forearm length relates to a larger body and longer wings. While BM is often used as a measure of body size (Almeida et al. 2014, Wang et al. 2020, Alston et al. 2023), it can fluctuate seasonally due to reproductive changes and preparation for hibernation, as well as daily with food intake (Neuweiler 2000, O'Mara et al. 2016, Kelling et al. 2024). Previous studies showed that migratory species conform less to ecogeographical rules than sedentary species (Mainwaring and Street 2021, Henry et al. 2023). For this reason, we excluded all migratory species (n = 13; Supporting Information) from the dataset (with migratory status defined based on Hutterer et al. 2005). We also checked the reliability of records by comparing them with the known species distribution and excluded six other species with dubious records, thus leaving a total of 20 bat species (Supporting information).

Finally, we combined data from different countries into a single dataset including the following variables: bat species, sex, spatial coordinates, forearm length (in mm), body mass (in g), sample size, country, and year.

Analysis

We assessed support for Allen's and Bergmann's rules, as well as the resource availability hypothesis, by evaluating whether the 95% confidence intervals of species-level standardised correlation coefficients between FAL or BM and temperature or time (years) excluded zero and matched expectations (i.e. positive slopes for Allen's rule and negative slopes for Bergmann's). To test Bergmann's rule, we used the full dataset of > 27 000 FAL measurements across 20 species and tested whether FAL correlates positively or negatively with temperature (spatial analysis) or with years (temporal analysis) (Supporting information). To test Allen's rule, we generated a subset dataset including only pairwise FAL and BM measurements for the same individual (Pairwise FAL–BM dataset, ca 18 500 pairwise measurements). In this way we could investigate how temperature (spatial analysis) or years (temporal analysis) affect the allometric relationship between appendage size (FAL) and body size (BM) (Santoro and Calzada 2022). Given the hypotheses of our study, we conducted a spatial and temporal analysis separately and performed separate analyses for the two sexes only for spatial patterns, due to insufficient sample sizes in the temporal data. In the spatial analysis, besides verifying the generalizability of Allen's and Bergmann's rules to European bats, we tested whether bat body size also depends on precipitation. We tested this hypothesis by including both the FAL dataset and the pairwise FAL–BM dataset to provide a broader perspective on how different aspects of body size (FAL and BM) may vary with precipitation. In the spatial analysis we considered three environmental variables: 1) the mean daily maximum ambient temperature of the warmest month (Tmax, variable BIO5 from Chelsa; Karger et al. 2017), used to account for heat dissipation; 2) the mean daily minimum ambient temperature of the coldest month (Tmin, variable BIO6 from Chelsa; Karger et al. 2017), to account for heat conservation; and 3) the mean monthly precipitation amount of the warmest quarter (summer precipitation, variable BIO18 from Chelsa; Karger et al. 2017), used as a proxy for resource availability. In the temporal analysis, we assessed how bat body size changes across different years for each species and location to evaluate the validity of Bergmann's and Allen's rules over time. Here we used years (time) as a proxy for increasing temperatures, given the recorded rise in temperatures across all locations over the past few decades (IPCC 2022).

For both spatial and temporal analyses, we grouped the data by cells into a 10 × 10 km grid and extracted the centroid coordinates to reduce the influence of environmental variability across different geographic locations. We then filtered the data. For the temporal analysis, we only retained species that were measured over a period of at least 20 years in the same grid cell. For the spatial analysis we retained records

obtained from 2010 onwards, to avoid the effect of time and the increase in temperatures in Europe over the past few decades. Since we aim to examine the consistency of trends in body size across multiple species in relation to environmental gradients across Europe and over time, we focus on species with sufficient coverage in terms of the number of individuals per cell and the number of cells. To ensure adequate sample size and environmental variation, we limited the analysis to species sampled in more than five cells (spatial analysis) or years per cell (temporal analysis), resulting in a total of 19 species in the spatial analysis (14 843 body size measurements) and 12 species in the temporal analysis (4926 body size records) (Fig. 1). We calculated the weighted average of FAL (wFAL) and BM (wBM) in each cell (spatial analysis) and in each cell and year (temporal analysis) based on the sample size for each species. Since we did not expect the relationship between body size measurements and environmental variables (in the spatial analysis) or time (in the temporal analysis) to be linear, we used Spearman's rank correlation coefficients to analyse the relationships for each species across cells or years (Santini et al. 2019, Henry et al. 2023). To account for the unequal sample sizes across cells, we weighted the correlations using the $\log_{10}$-transformed count of individuals within each cell, adding 1 to prevent the weight from becoming zero when $n = 1$ (Henry et al. 2023). Correlation coefficients were converted into Fisher's z-scores with the formula $\dfrac{\log\left(\dfrac{(1+r)}{(1-r)}\right)}{2}$, using the corresponding sample size to determine the effect size for each species. We also calculated the sampling variances using the formula $Vz = \dfrac{1}{n-3}$, ensuring that species with larger sample sizes (number of cells or years) were given more weight in the analysis (Borenstein et al. 2021).

We conducted a phylogenetic meta-analysis to test the consistency of the correlation between species body size (FAL and BM) and the environmental variables (Tmax, Tmin, SP, and Year) across multiple species (Hillebrand and Azovsky 2001, Weber et al. 2017, Henry et al. 2023 for similar methodological approaches). We used z-scores and variances to weight each correlation based on its statistical strength and controlled for pseudoreplication at the species level and their phylogenetic relatedness (Supporting information) by including both phylogeny and species name as random effects (Hadfield and Nakagawa 2010). The species name accounts for similarities among individuals resulting from shared ecology, while phylogeny accounts for the evolutionary history shared among species (Cinar et al. 2022). We modelled phylogenetic similarity as a variance–covariance matrix, using synthetic phylogenetic trees obtained from the Open Tree of Life (Hinchliff et al. 2015). We pruned phylogenetic trees for our species list, dealt with single polytomies via randomisation, and estimated branch lengths using the Grafen method (Grafen 1989). Additionally, we analysed
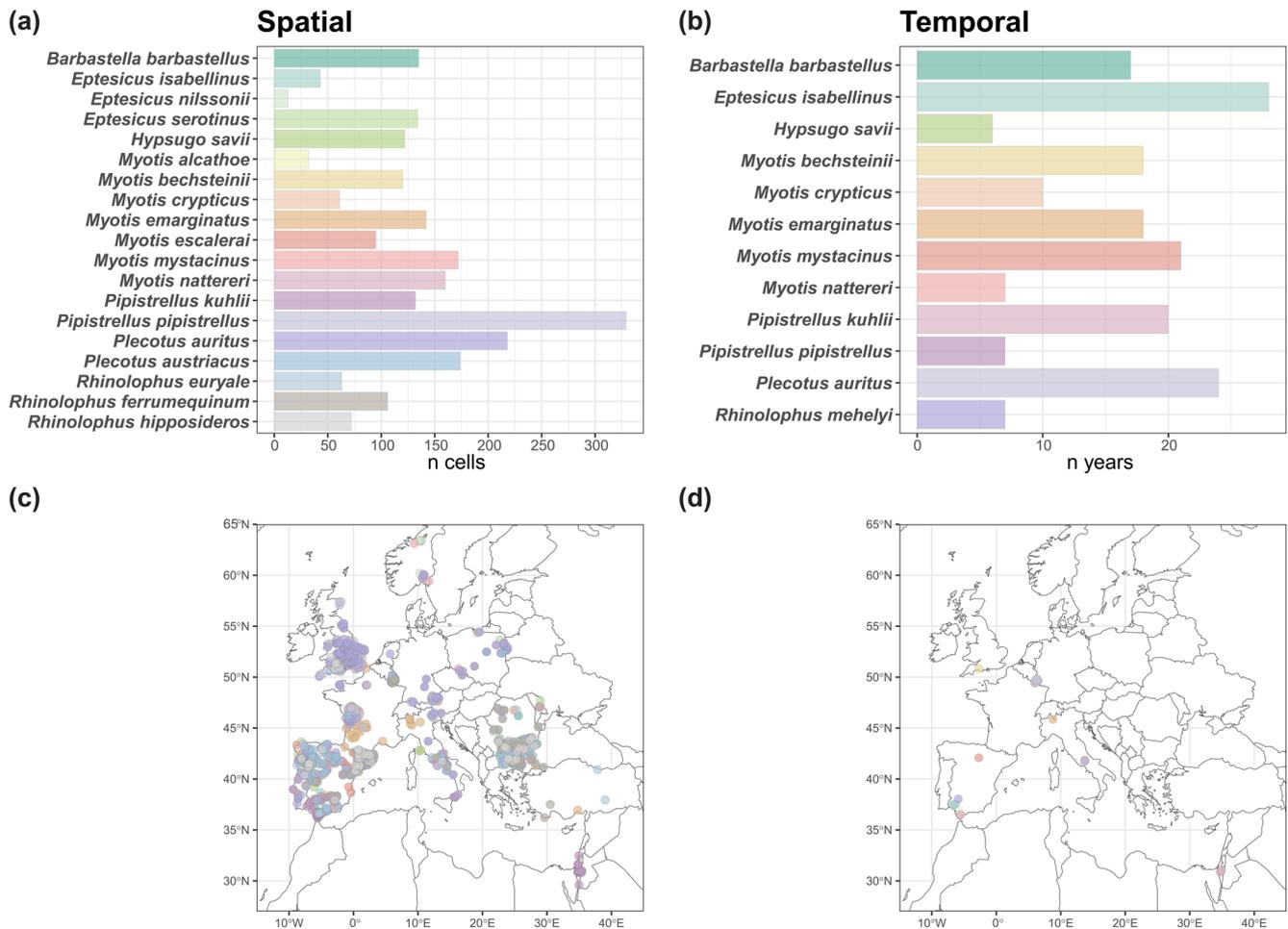
Figure 1. Distribution of the populations of bat species used in the (a) spatial and (b) temporal analysis. Each colour represents a different species. The bar-plots illustrate how many 10 × 10 km cells (spatial analysis) or years (temporal analysis) each species is sampled in. The maps display the geographical distribution of the bat species considered in both (c) spatial (n = 19 species) and (d) temporal analysis (n = 12 species), respectively.

the relationship between the Fisher's z-scores (derived from Spearman correlations between temperature or year and body size records) of FAL and BM to explore the allometry between FAL and BM in response to temperature, so as to determine whether Bergmann's and Allen's rules act simultaneously.

To assess how species' size influences adherence to Bergmann's rule, we conducted a phylogenetic meta-regression analysis using Fisher's z-scores and the mean body size of each species (i.e. species-level forearm length and body mass; see the Supporting information). This analysis examined how morphological variations in relation to temperature and time differ across species of varying body sizes.

Our results are presented by back-transforming Fisher's z-scores into Spearman's r for ease of interpretation, which summarises the overall intraspecific patterns detected across species. We also report confidence intervals and exact p-values, and we use the language of evidence to present our results rather than depending on a fixed p-value threshold to

determine statistical significance. We categorize our findings into the following levels of evidence: no ($p > 0.1$), weak ($0.05 < p < 0.1$), moderate ($0.01 < p < 0.05$), strong ($0.001 < p < 0.01$), and very strong ($p < 0.001$) evidence for each finding (Amrhein et al. 2019, Muff et al. 2022).

The data collection and analysis were completed using R ver. 4.3.2 and RStudio ver. 2023.12.1+402 (RStudio Team 2023, www.r-project.org). For data processing we used R packages 'stringr' (Wickham 2023) and 'dplyr' (Wickham et al. 2023). For raster operations we used 'raster' (Hijmans 2023), 'sp' (Pebesma and Bivand 2005, Bivand et al. 2013) and 'rgdal' (Bivand et al. 2013) R packages. Lastly, we used the package 'metafor' for the meta-analysis, meta-regressions, and z-score transformations (Viechtbauer 2010), 'ape' for estimating branch lengths and resolving polytomies (Paradis and Schliep 2019), 'rotl' for building the phylogenies for our species by searching the open tree taxonomy (Michonneau et al. 2016, Rees and Cranston 2017) and retrieving the phylogenetic relationships from the open tree of life (Hinchliff et al. 2015),

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and 'ggplot2' (Wickham 2016) and 'ggpubr' (Kassambara 2023) for creating figures.

Results

The dataset used for the spatial analysis (Fig. 1a, c) included 14 843 body size measurements from a total of 19 species distributed across 920 distinct cells and 17 countries. The species with the highest number of observations were *Pipistrellus pipistrellus* and *Plecotus auritus*, distributed in 329 and 218 cells, respectively. In the temporal analysis (Fig. 1b, d) the dataset included a total of 4926 measurements from 12 distinct species distributed in 18 cells that were sampled between 1905 and 2022. *Eptesicus isabellinus* had the highest number of records, with 28 between 1983 and 2013.

Spatial trends in body size

In the phylogenetic meta-analysis based on Spearman's correlations (Fig. 2, Supporting information), for females (Fig. 2a–c), we found no effect of maximum temperature on body size (FAL, pairwiseFAL and pairwiseBM), but a strong negative effect of minimum temperature, with FAL and BM decreasing with increasing minimum temperature (FAL: $r_{\text{size-Tmin}} = -0.167$ (95CI: -0.266 to -0.069), $p < 0.001$; pairwiseFAL: $r_{\text{size-Tmin}} = -0.206$ (95CI: -0.313 to -0.099), $p < 0.001$; pairwiseBM: $r_{\text{size-Tmin}} = -0.194$ (95CI: -0.291 to -0.098), $p < 0.001$) and a positive effect of summer precipitation (FAL: $r_{\text{size-SP}} = 0.123$ (95CI: 0.024–0.219), $p = 0.015$; pairwiseFAL: $r_{\text{size-SP}} = 0.185$ (95CI: 0.008–0.351), $p = 0.041$; pairwiseBM: $r_{\text{size-SP}} = 0.126$ (95CI: 0.058–0.192), $p < 0.001$). For males (Fig. 2d–f), FAL and
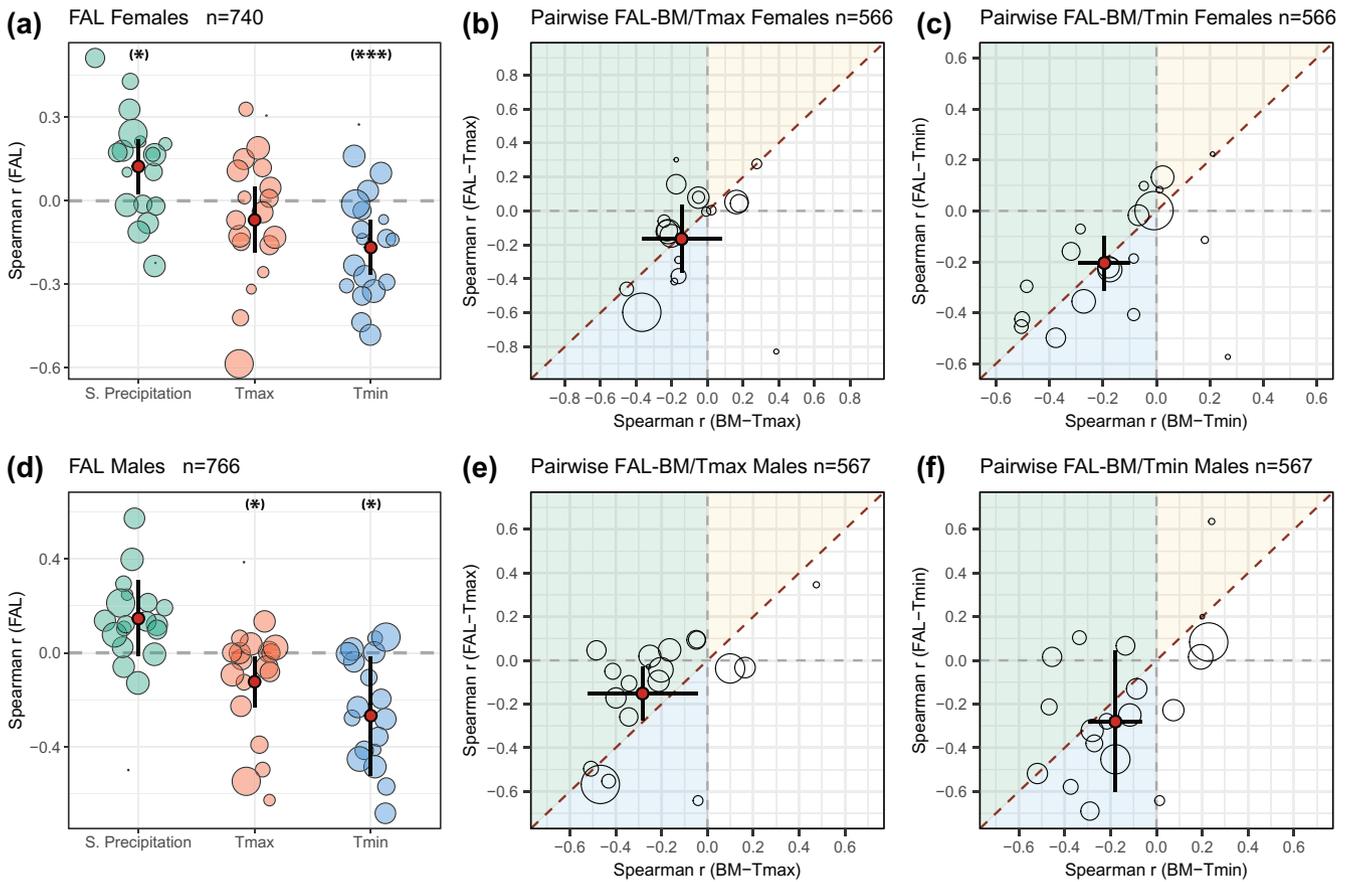

Figure 2. (a), (d): Correlation coefficients between forearm length (FAL dataset) and the environmental factors considered, representing ecological hypotheses of body size variation in relation to resource availability (S. Precipitation: summer precipitation), heat dissipation (Tmax: maximum temperatures of the warmest month) and heat conservation (Tmin: minimum temperatures of the coldest month) for 19 European bat species. (b), (c), (e), (f): Relationship between the correlation coefficients of forearm length and body mass (Pairwise FAL–BM dataset) related with Tmax (b), (e) and Tmin (c), (f) to test their allometry. Points in the yellow panel represent species adhering to Allen's rule, those in the blue panel follow Bergmann's rule, and points in the green panel represent species that align with both Allen's and Bergmann's rules. (a)–(f): Size of the points indicates the weight of the correlation coefficient in the random-effect intercept-only phylogenetic meta-analysis, with the weight being the inverse of the sampling variance plus the between-species variance. Red points represent the mean effect size estimates for the three environmental variables from the phylogenetic meta-analysis. Solid lines represent 95% CI. The level of evidence is indicated by the following symbols: (***) very strong evidence for $p < 0.001$; (**) strong evidence for $p < 0.01$; (*) moderate evidence for $p < 0.05$; (.) weak evidence for $p < 0.1$; and no symbol, denoting no evidence, for $p \geq 0.1$. FAL: forearm length (mm), BM: body mass (g), n: number of population-level (10 × 10 km grid cell) average size measurements.
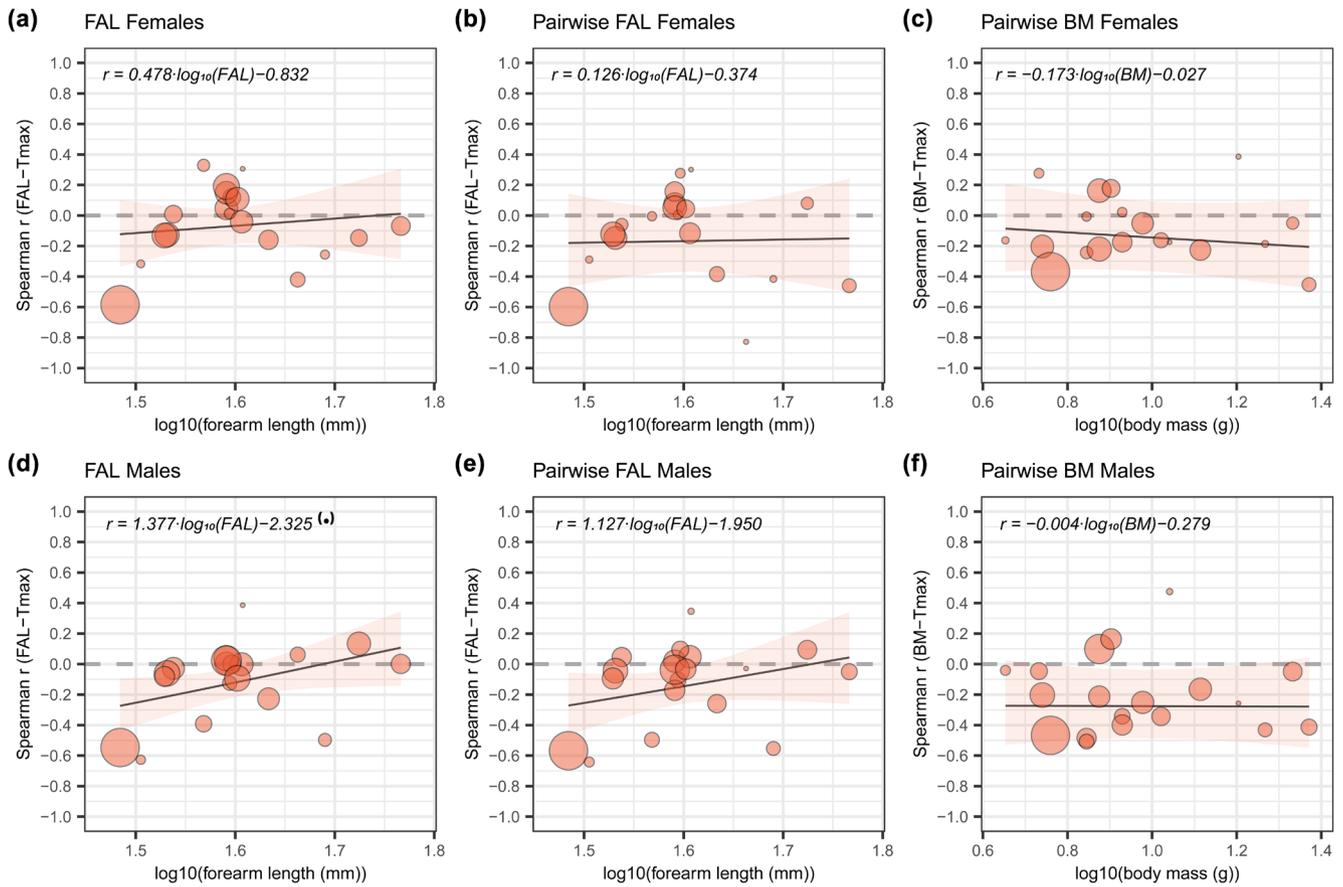
Figure 3. Results of meta-regression models testing variations in correlation coefficients of FAL–Tmax (a), (b), (d), (e) and BM–Tmax (c), (f) across species with different body sizes, using mean species-level FAL and BM as a proxy for size. Shaded areas indicate 95% CI. Size of the points indicates the weight of the correlation coefficient in the phylogenetic meta-regressions, with the weight being the inverse of the sampling variance plus the between-species variance. The level of evidence is indicated by the following symbols: (***) very strong evidence for $p < 0.001$; (**) strong evidence for $p < 0.01$; (*) moderate evidence for $p < 0.05$; (.) weak evidence for $p < 0.1$; and no symbol, denoting no evidence, for $p \geq 0.1$. FAL: forearm length (mm), BM: body mass (g).

BM decrease with increasing maximum temperature, with a moderate negative effect of maximum temperature on body size (FAL: $r_{\text{size-Tmax}} = -0.122$ (95CI: -0.226 to -0.016), $p = 0.025$; pairwiseFAL: $r_{\text{size-Tmax}} = -0.152$ (95CI: -0.268 to -0.031), $p = 0.014$; pairwiseBM: $r_{\text{size-Tmax}} = -0.277$ (95CI: -0.482 to -0.043), $p = 0.021$) and a respectively moderate, weak and strong effect of minimum temperature on FAL, pairwise FAL and pairwise BM (Fig. 2d–f). We did not find a clear relationship between FAL and summer precipitation, whereas the relationship between BM and summer precipitation was clearly positive (pairwiseBM: $r_{\text{size-SP}} = 0.212$ (95CI: 0.108–0.312), $p < 0.001$). The relationship between the z-scores of FAL-T and BM-T (Fig. 2b, c, e, f) showed that both Tmax and Tmin cause a constant allometric difference in females (Fig. 2b–c), indicating that FAL and BM decrease proportionally when temperatures increase. In males, Tmax causes a positive allometric difference of FAL to BM, reflecting the simultaneous action of both Bergmann's and Allen's rules (Fig. 2e), while Tmin causes a constant allometric difference, incompatible with Allen's

rule but in line with Bergmann's rule (Fig. 2f, Supporting information).

The meta-regression analysis (Fig. 3, Supporting information) revealed a weak positive relationship between the correlation coefficients (of FAL with Tmax) and the species-level mean body size, but only in males (slope = 1.377 (95% CI: -0.004 to 2.758), $p = 0.051$, Fig. 3d). This finding indicates that smaller species have more negative correlation coefficients than larger species. In the pairwise FAL–BM database (Fig. 3b, c, e, f), for both sexes there was no evidence of changes in correlation coefficients across the range of species' mean body sizes.

Temporal trends in body size

There was no significant relationship between bat body size (FAL, pairwise FAL, pairwise BM) and time (year), i.e. body size in bats did not show a clear trend of increase or decrease over the past few decades with increasing ambient temperatures. Specifically, our analyses revealed the following results:
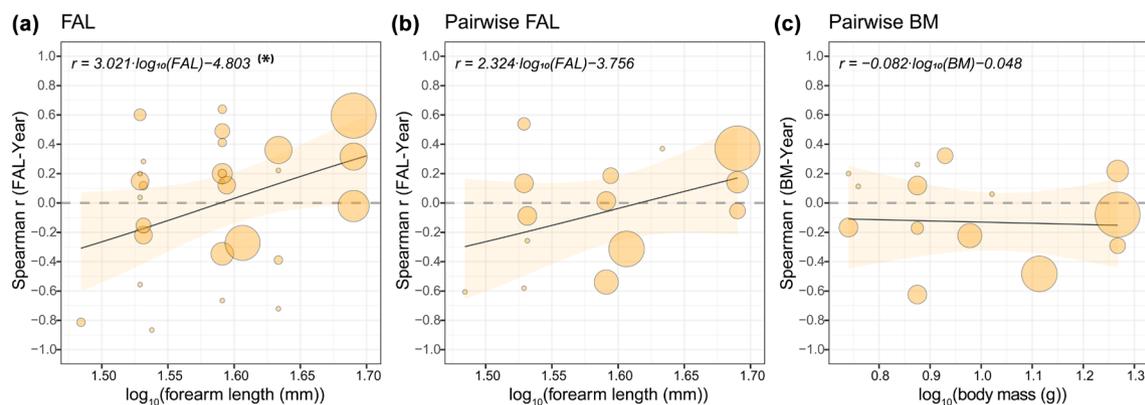
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Figure 4. Results of meta-regression models testing variations in Spearman's r between FAL–Year (a), (b) and BM–Year (c) across species with different body sizes, using mean species-level forearm length and body mass as a proxy for size. Shaded areas indicate 95% CI. Size of the points indicates the weight of the correlation coefficient in the phylogenetic meta-regressions, with the weight being the inverse of the sampling variance plus the between-species variance. The level of evidence is indicated by the following symbols: (***) very strong evidence for $p < 0.001$; (**) strong evidence for $p < 0.01$; (*) moderate evidence for $p < 0.05$; (.) weak evidence for $p < 0.1$; and no symbol, denoting no evidence, for $p \geq 0.1$. FAL: forearm length (mm), BM: body mass (g).

FAL: $r_{\text{size-Year}} = 0.009$ (95CI: −0.193 to 0.211), p = 0.928; pairwise FAL: $r_{\text{size-Year}} = -0.041$ (95CI: −0.277 to 0.194), p = 0.731; pairwise BM: $r_{\text{size-Year}} = -0.133$ (95CI: −0.329 to 0.062), p = 0.182 (Supporting information).

In the meta-regression analysis (Fig. 4, Supporting information), the correlation coefficients between FAL and time showed a moderate positive relationship with species-level mean body size (slope = 3.021 (95CI: −0.094 to 5.949), p = 0.043; Fig. 4a), consistent with the results of the spatial analyses . In the Pairwise database (Fig. 4b–c) we found no evidence of a relationship between the correlation coefficients and the species' mean body sizes.

Discussion

We performed a phylogenetic meta-analysis to assess the relationship between bat body size and climatic conditions across geographic locations and to examine temporal changes in the body size of European bat species. Moreover, we investigated whether these size-climate and size-time correlations varied among species with different body sizes. The results reveal sex-specific morphological shifts in the body size of European bats in response to temperature and rainfall patterns, but no clear changes over time. Across Europe, the forearm length of males tended to decrease with higher summer and winter temperatures, and only body mass tended to increase with greater rainfall. In contrast, the body size of female bats was not affected by summer temperature, but both forearm length and body mass increased with higher levels of summer precipitation and decreased with higher winter temperatures. Thus, based on our data, we can confirm Bergmann's rule for both males and females, while females' body size variations are also linked to rainfall-driven resource availability. The allometric relationship between FAL and BM showed evidence supporting Allen's rule only in males in relation to summer temperature.

Sexual dimorphism in changes in body size in response to temperature

Following Bergmann's rule, males of our studied bat species have larger body sizes in locations with cold winter temperatures, and exhibit smaller body sizes in areas with warmer summer temperatures. These thermoregulatory adaptations facilitate heat conservation and dissipation, respectively (Riek and Geiser 2013). This trend remained when using both forearm length and body mass as a proxy of body size. In females, body sizes (FAL and BM) are larger in locations with cold winter temperatures, but there is no relationship with summer temperatures, indicating a sex-specific adaptation towards heat conservation, rather than dissipation. This discrepancy underscores the complexity of sexual dimorphism and highlights the diverse physiological and behavioural responses of bats to environmental variables. Previous research has documented sexual dimorphism in body size across various insectivorous bat species, with females often being slightly larger than males (Myers 1978, Williams and Findley 1979, Lisón et al. 2014, Hurtado et al. 2015, Vannatta and Carver 2022, Russo et al. 2024a). Males and females are faced with distinct ecological and reproductive challenges (Altringham 1996, Ortega et al. 2008, Alviz and Pérez-Torres 2020), with body size playing a critical role in influencing reproductive rates (Storz et al. 2001, Voigt et al. 2005). Moreover, female maternity colonies tend to be located in higher-quality habitats at lower elevations than male roosts (Barclay 1991, Linton and MacDonald 2019), thus further decreasing the importance of body size for thermoregulation during summer in female bats.

The challenges posed by climatic conditions may be more pronounced for females than males due to higher energy investment and constraints during the reproductive season (Ruedas et al. 1994, Cryan et al. 2000, Adams 2010). Female bats experience higher energy demands during pregnancy and lactation (Angell et al. 2013, Pfeiffer and Mayer 2013),

and therefore may benefit from maintaining a larger body size. Larger females can store more fat, access a greater array of prey, and experience reduced energy costs associated with reproduction (Williams and Findley 1979). Additionally, the formation of maternity colonies during spring and summer, where they cooperatively care for their young through shared roosting and protection (Williams and Brittingham 1997, Dekeukeleire and Janssen 2014, Ružinská and Kaňuch 2021), is used as a strategy to mitigate the challenges posed by adverse external conditions such as low temperatures and humidity (Kunz 1982). These colonies create microenvironments that can alleviate the costs for reproductive females, contributing to maintaining homeothermy and energy-efficient pregnancy and lactation (Williams and Findley 1979). In contrast, males tend to roost alone or in small groups in summer (Kunz 1982), rendering them more vulnerable to changes in summer temperatures. This disparity in roosting strategies during the summer and the use of behavioural strategies of social thermoregulation may also explain the lack of support for Allen's rule in female bats. Despite this, due to reproduction constraints, females are more likely to be negatively affected by climate change than males due to thermoregulation challenges. This is especially true if temperature increases to the point where bats must elevate their metabolic rates and energy consumption to dissipate heat. This issue will be particularly pronounced in the warmer parts of species' ranges, such as southern Europe, where females lack the thermoregulatory advantages of males' smaller body sizes. However, if increases in temperature in the spring decrease the cost of maintaining homeothermy, the impact on females might be less severe.

Increase in size in response to increased precipitation and associated greater resource availability

Both males (for body mass only) and females (for both forearm length and body mass) show an increase in body size with increasing summer precipitation. As previous studies have linked summer precipitation with increased insect abundance, the primary food source for European bats (Nurul-Ain et al. 2017, Liu et al. 2020, Tsantalidou et al. 2023), this increase in body size may be related to resource availability. Although many environmental factors contribute to body size, food availability plays a crucial role in changes in body size for many species (Ashton 2004, Meiri et al. 2004, Yom-Tov and Geffen 2011), particularly during the growth period (Henry and Ulijaszek 1996, Arnett and Gotelli 1999, Lindström 1999). Several studies have confirmed that increases in mammalian body size can be attributed to greater food availability (Yom-Tov 2003, Yom-Tov and Yom-Tov 2005, Raia and Meiri 2006, Eastman et al. 2012, Henry et al. 2023). Our findings indicate a stronger correlation between body size and precipitation in females than in males. This suggests that females may be more responsive to changes in resource availability, particularly in areas with higher food abundance. Indeed, females reach maximum

food consumption levels in July, coinciding with a peak in young preweaning development (Kunz 1974). A greater food intake allows females to sustain milk production levels during this critical period. Hence, the availability of additional resources can be advantageous for female bats during high energy-demanding periods such as pregnancy and lactation. By using these additional resources, females can better support their reproductive efforts and ensure the successful development and care of their offspring.

Comparison between body mass and forearm length trends in response to temperature and summer precipitation

Both BM and FAL exhibited similar trends in response to environmental variables, increasing with precipitation and decreasing with high temperatures, suggesting general adherence to Bergmann's rule. In males, BM decreased more than FAL in response to summer temperature, reflecting the simultaneous action of both Bergmann's and Allen's rules. However, it is important to acknowledge the reliability of body mass records in bats. While FAL remains stable once individuals have reached adult size, body mass fluctuates dramatically both seasonally and daily in response to reproductive condition and food consumption (Neuweiler 2000, O'Mara et al. 2016, Kelling et al. 2024). This variability in body mass underscores the limitations of using it as a proxy for bats' body size. Including variables such as wing surface area and head-body length in future studies could provide a more comprehensive understanding of how bat morphology responds to environmental changes and clarify whether Allen's rule applies to European bats. In addition, it is important to take into account that changes in size and appendage length can have important consequences for bats' flight abilities, so there may be ecomorphological constraints countering the patterns expected based on ecogeographical rules.

Additionally, communities might be in a disequilibrium state, lagging behind optimal adaptation to current conditions (Hoffmann and Sgró 2011) because they are still adapted to local conditions experienced before recent rapid climatic changes. This could be especially true for long-lived and slow reproducing species like bats, where adaptation to environmental changes can be slow. For instance, Salinas-Ramos et al. (2020a) found no changes in the body and skull size of lesser horseshoe bats *Rhinolophus hipposideros* in Italy over a period of 147 years, suggesting that these bats have not fully adapted to the local environmental conditions. However, they did observe an increase in body size from south to north, consistent with Bergmann's rule.

Temporal trends in bats body size

We did not find any clear trend in body size (either forearm length or body mass) over time (1905–2022), despite temperature increases in Europe over the past few decades. Other studies that used time as a proxy for climate warming have found species-level responses, but these were observed

at much smaller geographic scales than the one considered in the present study. In such cases, bats exhibited an increase in body size over time, rather than a reduction. For instance, a clear increase of body size over time with warming climate was found for Bechstein's bats *Myotis bechsteinii* in Germany (Mundinger and Scheuerlein 2021, Mundinger et al. 2023a, 2023b). This was best explained, and experimentally demonstrated, as a phenotypically plastic response to warmer nursery roosts, where reproductive females can save energy otherwise spent on thermoregulation and invest it in newborn biomass (Mundinger et al. 2023a, 2023b). In Italy, Daubenton's bats *Myotis daubentonii* also showed similar trends on both local (Russo et al. 2024b) and national (Russo et al. 2024a) scales.

However, temporal trends are not consistent across species. For instance, in Italy, only three out of 15 species investigated showed an increase in body size over the last three decades (Russo et al. 2024a). Among rhinolophids, greater *Rhinolophus ferrumequinum*, but not lesser *Rhinolophus hipposideros*, horseshoe bats showed an increase in forearm length over a century and a half (Salinas-Ramos et al. 2020a, 2021). The sensitivity of such responses to geographic scale is so strong that an increase in body size recorded in Natterer's bat *Myotis nattereri* in Germany was only found in a northern population, whereas a southern population exposed to a warmer climate did not show this pattern (Stapelfeldt et al. 2023). Therefore, our findings exemplify the difficulty of identifying at a continental scale a common trend in a process highly sensitive to geographic scale and is most likely dependent on the life history of the species considered, including the type of maternity roost selected and the sensitivity of its microclimate to changes in external temperatures.

Influence of species average body size on bats' adherence to Bergmann's rule

In both the spatial and temporal analysis, only small-sized and medium-sized species showed adherence to Bergmann's rule, with large-sized species showing no significant change in size with increasing temperatures. This pattern had support only for males in the spatial analysis. Steudel et al. (1994) found that larger mammals (up to 10 kg) typically respond to temperature changes by adjusting their fur density rather than their body size. Our dataset could not test whether these dynamics apply to bat species across their body mass range (4.5–23.5 g), which is considerably smaller than the species included in Steudel et al.'s (1994) simulation study. This would require further investigation. It is also important to note that the two bat species with the largest body sizes included in the temporal analysis, *Eptesicus isabellinus* and *Rhinolophus mehelyi*, are both restricted to southern Europe. Previous local-scale studies showed that body size shifts with increasing temperatures are only apparent in northern populations compared to southern populations of Natterer's bats (Stapelfeldt et al. 2023). Hence, since the larger species are confined to warmer southern regions, it may be difficult to

disentangle the effect of larger body size from geographic location in our study. Indeed, further investigation with more comprehensive data spanning different regions would yield a more comprehensive understanding of how the size of bats influences their response to climate change.

Conclusions

We investigated how bats' body size (forearm length and body mass) changes in response to environmental factors, such as summer and winter temperatures, and summer rainfall. Our findings revealed similar trends between forearm length and body mass in bats in response to environmental changes. Bats conformed to Bergmann's rule by exhibiting smaller body sizes in warmer local climates (only winter temperatures for females), likely due to thermoregulatory adaptations. Only males conformed to Allen's rule, specifically in relation to summer temperature, exhibiting a positive allometric relationship between the body mass and the forearm length. Females also increased in size with higher precipitation, suggesting the critical role of resource availability driven by rainfall. We further found that smaller and medium-sized species exhibit greater responsiveness to temperature changes compared to larger species, suggesting that body size plays a significant role in how species adapt to climatic variations. These sex-specific and species-specific responses emphasise the complexity of bats' morphological adaptations and their ecological and evolutionary strategies. Our study provides novel insights into sex-specific morphological shifts in body size in response to temperature and rainfall patterns, emphasizing how these adaptations reflect varying ecological pressures. While we were not able to identify overall temporal trends in response to climate change, our spatial trends indicate a decrease in female bat sizes in areas predicted to experience increased aridity under climate change, such as the Mediterranean region. Impacts of these changes on bat survival and reproductive success should be monitored. By finding that smaller and medium-sized bat species are more likely to adhere to Bergmann's rule and showing a positive correlation with precipitation, with these patterns differing between sexes, we enhance our understanding of the mechanisms driving bat species' adaptations to environmental changes across geographical distributions and based on sex. These findings not only advance our understanding of eco-geographical patterns but also underscore the importance of targeted conservation strategies, as they indicate that resilience to climate changes may significantly differ based on body size and sex, necessitating targeted efforts for the most vulnerable species and populations.

Author contributions

Laura Paltrinieri: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Orly Razgour**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Luca Santini**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Danilo Russo**: Conceptualization (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Joxerra Aihartza**: Resources (equal). **Ostaizka Aizpurua**: Resources (equal); Writing – original draft (supporting). **Francisco Amorim**: Resources (equal). **Leonardo Ancillotto**: Resources (equal); Writing – original draft (supporting). **Konrad Bidziński**: Resources (equal). **Rasit Bilgin**: Resources (equal). **Philip Briggs**: Resources (equal). **Lisette Cantù-Salazar**: Resources (equal). **Mateusz Ciechanowski**: Resources (equal); Writing – original draft (supporting). **Luca Cistrone**: Resources (equal). **Dina K. N. Dechmann**: Resources (equal); Writing – original draft (supporting). **Katrine Eldegard**: Resources (equal); Writing – original draft (supporting). **Mari Aas Fjelldal**: Resources (equal); Writing – original draft (supporting). **Jérémy Froidevaux**: Resources (equal); (equal); Writing – original draft (supporting). **Joanna Furmankiewicz**: Resources (equal); Writing – original draft (supporting). **Inacio Garin**: Resources (equal). **Luke Hamel**: Resources (equal). **Carlos Ibanez**: Resources (equal). **Martyna Jankowska-Jarek**: Resources (equal). **Javier Juste**: Resources (equal); Writing – original draft (supporting). **Carmi Korine**: Resources (equal). **Grzegorz Lesiński**: Resources (equal). **Maxime Leuchtmann**: Resources (equal). **Adriano Martinoli**: Resources (equal). **Maria Mas**: Resources (equal). **Fiona Mathews**: Resources (equal). **Reed April McKay**: Resources (equal). **Thijs Molenaar**: Resources (equal). **Colin Morris**: Resources (equal). **Victoria Nistreanu**: Resources (equal). **Kevin J. Olival**: Resources (equal). **Andrea Pereswiet-Soltan**: Resources (equal). **Áron Péter**: Resources (equal). **Kendra Phelps**: Resources (equal). **Dominique Pontier**: Resources (equal). **Lucy Pope**: Resources (equal); Writing – original draft (supporting). **Hugo Rebelo**: Resources (equal). **Damiano G. Preatoni**: Resources (equal). **Xavier Puig-Monserat**: Resources (equal). **Niamh Roche**: Resources (equal). **Ireneusz Ruczyński**: Resources (equal). **Attila D. Sándor**: Resources (equal); Writing – original draft (supporting). **Rune Sørås**: Resources (equal); Writing – original draft (supporting). **Martina Spada**: Resources (equal). **Nia Toshkova**: Resources (equal); Writing – original draft (supporting). **Jeroen van der Kooij**: Resources (equal); Writing – original draft (supporting). **Christian C. Voigt**: Resources (equal); Writing – original draft (supporting). **Zuzanna Wikar**: Resources (equal). **Aneta Zapart**: Resources (equal). **Marcin Zegarek**: Resources (equal). **Ana Benítez-López**: Conceptualization (lead); Formal analysis (equal); Investigation (equal); Methodology (lead); Software (equal); Supervision (lead); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Zenodo Repository: https://doi.org/10.5281/zenodo.15074859 (Paltrinieri et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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