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## Higher and bigger: How riparian bats react to climate change

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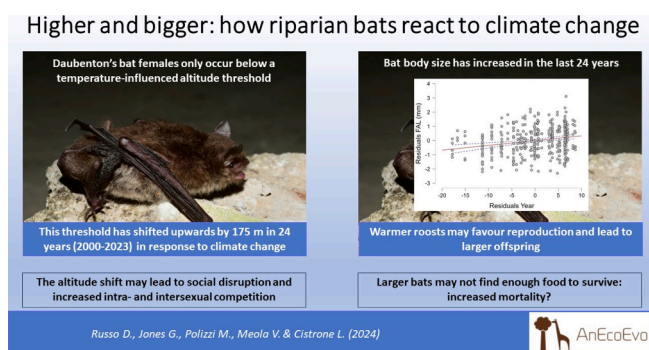
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### HIGHLIGHTS

- In 2000–23, Daubenton's bats reacted to climate change along an altitude gradient.
- Climate warmed, but habitat quality remained unchanged during this time.
- Females shifted their elevational limit upward by 175 m.
- Bats grew significantly larger, possibly due to more favourable roost temperatures.
- Future risks: Social disruption and higher mortality in larger bats.

### GRAPHICAL ABSTRACT



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### ABSTRACT

The altitudinal distribution of animals and changes in their body size are effective indicators of climate change. Bats are sensitive to climate change due to their dependence on temperature during critical life stages. However, long-term studies documenting responses over extended periods are rare. We present a 24-year investigation of *Myotis daubentonii*, a riparian bat known for altitudinal sexual segregation, along a river course in Central Italy. While males occupy the entire river course, females are confined to downstream warmer areas supporting successful reproduction due to improved foraging site productivity. In 2000, females were absent above 900 m a.s.l in our study area. We hypothesise that a) this altitude threshold is now higher, due to thermal gradient changes along the river course; and b) thermoregulatory costs for reproductive females have declined, leading to increased energy investment in offspring and subsequent generational growth in bat body size. Confirming our hypotheses, females exhibited a 175-m upward shift in altitude limit. Furthermore, we found a concurrent increase in body size (but not condition). Temperatures increased in the 24 years, likely allowing females to extend their range to higher elevations and favouring an increase in newborn body mass. Riparian vegetation remained unchanged, excluding habitat quality changes as the cause for the observed responses. The rapid female elevation rise might imply future disruption of established social structures, altering intra- and intersexual competition for roosts and food. Given the global decline in insect populations, larger bats might face future difficulties in finding food to sustain their body size, increasing mortality. However, the full impact of such changes on bat fitness

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remains unexplored and warrants further investigation, including other bat populations. This knowledge is crucial for informing conservation in the face of ongoing climate change and preserving the ecosystem services bats deliver in riparian ecosystems.

## 1. Introduction

Climate change is a pressing global issue that affects many important aspects of species dynamics including alterations in phenology, distribution, and body size (e.g., Brierley and Kingsford, 2009; Gilman et al., 2010; Peñuelas et al., 2013; Garcia et al., 2014; Scheffers et al., 2016).

The impact of climate change on organisms' distributions has been well-documented (e.g., Thomas, 2010), but the phenomenon is often complex and subtle and may vary intraspecifically, which is often neglected (Bennett et al., 2019; DeMarche et al., 2019). Fragmentation, resulting from human activities, has further hindered the capacity of many species to shift their range in response to climate change because a hostile landscape matrix such as agricultural or urban areas may be difficult or impossible to traverse to reach the next suitable habitat patch at higher latitudes or elevation (e.g., Hill et al., 2001; Travis, 2003; Opdam and Wascher, 2004; Hodgson et al., 2012; Littlefield et al., 2019).

Several species such as insects (Zhang et al., 2022), fishes (Comte et al., 2013), amphibians and reptiles (Burbrink et al., 1998), birds (Skagen et al., 1998), large mammals (Naiman and Rogers, 1997), and bats (Cortes and Gillam, 2020) may potentially provide valuable insights into how organisms respond to climate change in terms of spatial distribution along rivers and riparian vegetation. This is because they can exploit habitat connectivity, except when physically incapable of crossing barriers like dams, where these occur (Olden, 2016). Bats are considered particularly vulnerable to climate change due to their ecological and physiological traits (Frick et al., 2020; Festa et al., 2023). First, bats have a relatively large surface area in proportion to their body volume, which means they can lose or gain heat rapidly and dehydrate easily, for example when heatwaves occur (Sherwin et al., 2013; Korine et al., 2016; Adams and Hayes, 2021). Therefore, bats are more susceptible to temperature fluctuations and extreme weather events caused by climate change (Salinas-Ramos et al., 2023). Bats also depend on specific roosting sites, whose suitability strictly depends on a series of factors, including temperature and humidity, and different life stages often have different microclimatic requirements (Lewis, 1995; Boyles, 2007). Climate change may disrupt the availability and suitability of critical roosting sites, resulting in adverse effects on bat populations (Sherwin et al., 2013).

Bats often have specialized diets, and climate change can disrupt the availability and distribution of prey, for example by altering insect life cycles and phenology, leading to reduced foraging success and potential food shortages (Sherwin et al., 2013). Since bats typically have low reproductive rates, with most species giving birth to only one or two offspring per year, it is challenging for them to recover quickly from population declines caused by anthropogenic pressures (Jones et al., 2009), including factors related to climate change. On the other hand, bat dispersal away from thermally inhospitable areas may be hindered by poorly permeable habitat matrices, especially for species that avoid human-altered environments such as urban or agricultural areas (e.g., Kerth and Petit, 2005; Farneda et al., 2015; Meyer et al., 2016; Russo et al., 2023).

Due to these factors, bats face significant challenges in coping with the rapidly changing climate. It is essential to understand their vulnerabilities to develop effective conservation strategies and management plans to protect these ecologically important and diverse mammals. Despite such needs, there is a paucity of studies exploring the current effects of climate change on bats, and most research has employed modelling techniques to forecast future reactions, especially distributional changes. A recent review (Festa et al., 2023) showed that less than

half of the published studies present concrete evidence of how bats respond to climate change, and the most reported responses include range shifts in 57 % of species and changes in species diversity patterns in 26 % of cases. Few experimental studies (26 %) have been conducted, and only 11 % of the almost 400 studies illustrated climate-change-related alterations of bat phenotype or behaviour through field or laboratory experiments, or long-term field observations (Festa et al., 2023).

One aspect that remains controversial is how climate change influences the body size of bats. In general, a reduction in body size is expected to help dissipate more heat, and this has been proposed as a third universal response to anthropogenic temperature increases (Gardner et al., 2011). The extent and directions followed by an animal's size variation in response to climate change, as recorded so far, appear heterogeneous and sometimes contrasting. In bats, very little information is available. An increase in body size has been recorded in some cases over different time scales (Mundinger et al., 2021; Salinas-Ramos et al., 2021; Stapelfeldt et al., 2023), interpreted as a way to reduce evaporative water loss, according to the so-called "containment of dehydration" hypothesis, or as a consequence of reducing thermoregulatory costs at roosts and relying on greater food availability during reproduction, which would allow the mothers to invest more energy in foetal development and lactation (Mundinger et al., 2021). A very recent experiment (Mundinger et al., 2023a) has demonstrated that experimentally heated bat boxes lead to larger body sizes in both sexes of *M. bechsteinii*. This provides the most compelling evidence that climate change could result in larger individuals by promoting growth under warmer roosting conditions.

One of the challenges faced by studies addressing the responses of organisms to climate change is the difficulty in disentangling reactions to climate from those caused by other anthropogenic pressures, such as changes in land use, which may in turn influence resource availability, thus affecting distributional shifts or changes in body size (e.g., Yom-Tov, 2003; Greenfield et al., 2018). Understanding the complex interplay between climate change and other anthropogenic factors influencing species' distributions and behaviour is, therefore, crucial to identifying the true causes behind any observed trend.

Italy has undergone significant climate change over the past two centuries. Mean temperatures have exhibited an upward trend of 1 °C in the last century, while yearly precipitation has decreased by 5 % at the same time (Brunetti et al., 2006). These changes set the stage for potential reactions by animals, including bats. Our study focused on a population of Daubenton's bat (*Myotis daubentonii*) in central Italy, distributed along an elevational gradient (Russo, 2002; Nardone et al., 2015). The species is strictly associated with rivers, lakes, and ponds, where it uses its feet and tail membrane to "trawl" prey from the water surface (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Encarnação and Becker, 2020). Previous research has demonstrated that like other European populations (Senior et al., 2005; Encarnação and Becker, 2020), this population also exhibits intersexual segregation. Females are found only downstream, up to an elevational threshold that, in 2000–2001, was below 900 m a.s.l. (Russo, 2002), while males are spatially segregated into "downstream" and "upstream" groups with minimal overlap in their home ranges (Nardone et al., 2015). Downstream males form mixed-sex colonies at summer sites (Encarnação and Reiners, 2012), enabling them to exploit extra mating opportunities (Senior et al., 2005; Encarnação et al., 2007; Encarnação and Reiners, 2012). Noticeably, some form of sexual segregation persists even in lowland areas without an elevational gradient, where, however, even in these situations there are roosts where bats of both sexes can be found together (Linton and Macdonald, 2019).

Festa et al. (2023) emphasize the scarcity of studies documenting bat reactions to climate change, partly because of the short-term focus of research funding. We set out to help fill this gap, so we focused on a population of Daubenton's bats that has been studied for 24 years, enabling the collection of distributional and body mass data throughout major climate change. As a riparian habitat specialist, *M. daubentonii* makes an especially interesting case to explore distributional responses to climate change. Riparian habitats are important features for climate resilience because they span the climatic gradients (e.g., Krosby et al., 2018) as species undergo climate-induced range shifts in otherwise fragmented landscapes. Distributional shifts should occur promptly in habitat specialists such as *M. daubentonii* because of the high connectivity provided by the river systems they use.

Based on the available data and prior research, and bearing in mind that habitat changes may mimic or confuse genuine responses to climate change by wildlife, we first tested whether the climate has become warmer, or whether habitat quality (using, for *Myotis daubentonii*, riparian vegetation as a proxy) has changed in the 24 years as a confounding variable.

We then build on this assessment to present two additional hypotheses:

1. Females would change their altitudinal distribution and we predict that they will reach higher altitudes in response to a warming climate. Males are not considered here since their distribution shows no elevational thresholds (Nardone et al., 2015).
2. If climate has affected growth, bats would change their size over time and become larger in response to the warming temperatures (e.g., Mundinger et al., 2021, 2022, 2023a, 2023b).

## 2. Methods

### 2.1. Study area

We studied a mountain population of *M. daubentonii* located along a ca. 30-km stretch of the Sangro River within the Abruzzo, Lazio, and Molise National Park in Central Italy (41° 45' 46.8" N, 13° 58' 8.4" E). The area we investigated spans an elevational gradient varying between ca. 800–1100 m a.s.l. (Fig. 1). The river flow is mostly laminar with minimal turbulence, except in limited stretches. At ca. 950 m a.s.l., a

dam was built, creating an artificial lake known as the Barrea Lake. In 2000–1, this lake served as the geographical landmark between lowland and upland portions of Daubenton's bat population. The downstream portion consisted of reproductive females plus lowland males, while the upstream portion was made up of upland males only, whereas no females occurred (Russo, 2002; Nardone et al., 2015). Radiotracking work showed that the dam does not prevent bats from flying from downstream to upstream areas (Nardone et al., 2015). Along the majority of the river's course, well-established riparian vegetation thrives, mainly dominated by *Salix* spp.

### 2.2. Estimating the effects of climate change in the study area

To assess the potential impact of climate change on the study area for the 24 years considered, we obtained daily temperature data from the "Forca d'Acero" weather station, situated at an elevation of 1450 m a.s.l. and within 3.45 km of the Sangro River. The data corresponded to the "snow season," covering the months (typically, from December to April or May) associated with the first and last snow episodes, in our case, from December 1999 to May 2023. We obtained this information from the Carabinieri METEOMONT Service's website (<https://meteomont.carabinieri.it/>), dedicated to monitoring snowpack, assessing avalanche risk, and supporting related activities. Daily bulletins undergo quality control validation. Temperature data for the remaining months (provided by the Centro Funzionale e Ufficio Idrologia, Idrografico, Mareografico- Agenzia di Protezione Civile della Regione Abruzzo, or available at <http://www.regione.abruzzo.it/content/idrografico-mareografico>) were only accessible for a limited number of years out of the 24 under consideration. Consequently, we were only able to examine temperature fluctuations within a subset of these years at two specific sites: Barrea (corresponding to the lake altitude) for the years 2000–2008 and 2021–2022, and Montenero Val Cocchiara, located at approximately 800 m a.s.l., near the downstream female area, for the years 2016–2022.

### 2.3. Estimating changes in the amount of riparian vegetation

We delimited seven river stretches of varying sizes, referred to as "sites" (Fig. 1), each characterised by a homogeneous structure of riparian vegetation, where *M. daubentonii*'s foraging activity concentrates.

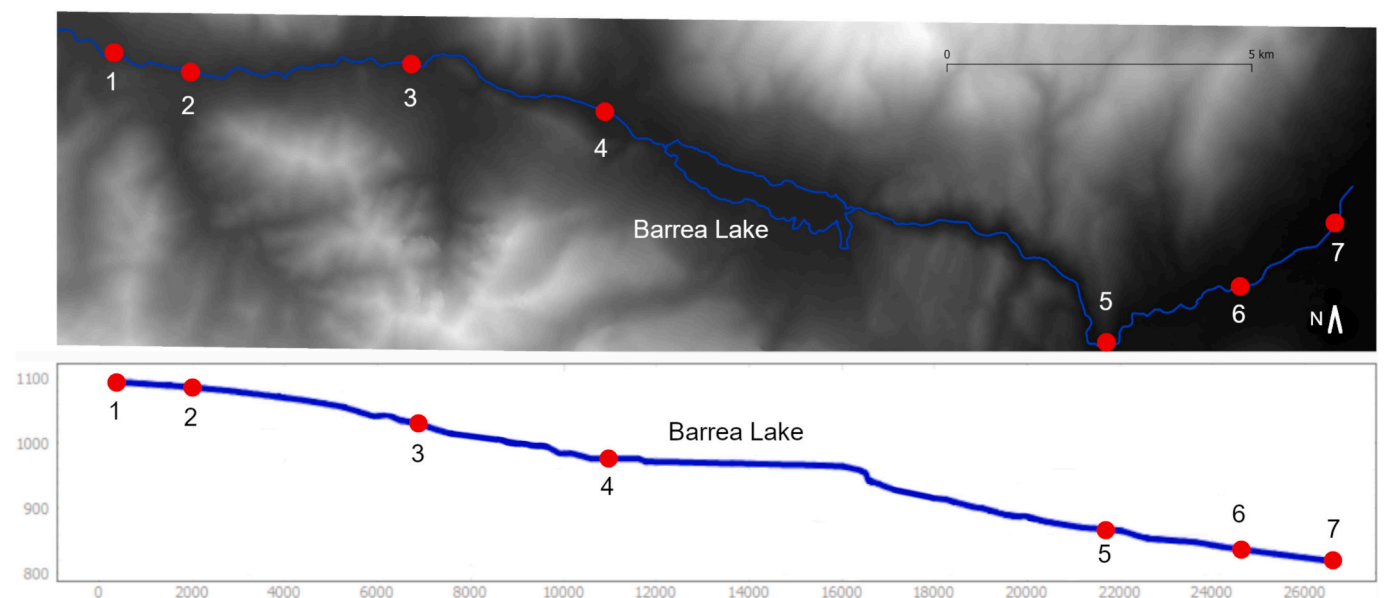


Fig. 1. Digital elevation model and altimetric profile of the stretch of the Sangro River (Italian Apennines, Central Italy) where the study of climate change effects on Daubenton's bats *Myotis daubentonii* took place. Sites are labelled with numbers 1–7).

These sites were identified based on radiotracking evidence (Nardone et al., 2015) and extensive bat detector surveys conducted since 2000 (D. Russo, pers. obs.). Sites were > 1.5 km apart from each other. The landscape structure of the Sangro River was digitized using QGIS software version 3.30 (distributed under the GNU General Public License). This was accomplished through ortho-photogrammetric interpretation of satellite images obtained from two sources: the WMS consultation service provided by the “National GeoPortal” (available at <http://www.pcn.minambiente.it/mattm/servizio-wms/>) and Google's freely accessible services (using Imagery @2023 CNES/Airbus and Maxar Technologies, along with Cartographic data @2023). The resulting information layer was then overlaid with a separate layer containing the above-mentioned seven sites. Around these sections, a buffer area extending 25 m on both sides of the river axis was defined. Within the buffer area, we quantified the extent of riparian vegetation present in the years 2000 and 2023, evaluating the surface area occupied by the ground projection of tree and shrub canopies, as detected during photo-interpretation.

#### 2.4. Sampling design and mistnetting

To assess shifts in the upper altitudinal limit of female *M. daubentonii*, we compared mistnetting data collected during two periods, primarily focused on the reproductive season (May to September): 2000–2001, and 2023 respectively. For analysis, the above-mentioned seven sites where foraging activity concentrates were further categorized according to three altitudinal zones relative to the above-mentioned lake: a downstream reach, or “low” zone (800–876 m a.s.l.) from the lake; and two upstream sections, respectively “intermediate” (975–1050 m a.s.l.) and “upper” (> 1050 m a.s.l.) zones. The intermediate zone was intentionally chosen to enhance the analysis resolution precisely at the boundary between downstream and upstream areas and observe any potential upward shift in the females' distributional upper limit.

In both periods, we mistnetted bats at 2–5 ( $3.7 \pm 0.95$ ) replicates per site (depending on the site size), employing an identical capture effort at each location between periods to ensure temporal comparability of data. Specifically, at each replicate, we set up one 6-m or 12-m net ca. 30 min after sunset, keeping it active for about 3 h. DR and LC collected data throughout the time minimizing observer-driven biases in data collection. For each captured bat, we measured body mass and forearm length (hereafter FAL) using a digital scale (with an accuracy to the nearest 0.1 g) and a calliper (with an accuracy to the nearest 0.1 mm). Sex was evaluated through the examination of genitalia (Racey 1988) while distinguishing juveniles from adults involved trans-illumination of wings and visual inspection. Juveniles exhibit cartilage epiphyseal plates in finger bones and more tapered finger joints (Anthony 1988). To determine the reproductive status of adult bats, we followed the methodology described by Racey (1988). Male bats were categorized as either reproductive (when enlarged testicles or swollen epididymides were noticed) or nonreproductive, while female bats were classified as pregnant, lactating, postlactating, or nonreproductive. Lactating bats were assessed by gently squeezing the mammal area and extruding milk to confirm their lactation status. In the year 2000, for some bats, we only recorded sex, age class, and reproductive condition without gathering any biometric data. Nevertheless, we still used this information to determine the relative number of females versus males.

To investigate variations in body size and body condition, we utilized multiple datasets and limited the analysis to adult individuals after removing pregnant females from the analysis. Besides the previously mentioned data collected in 2000 ( $n = 19$ ), 2001 ( $n = 74$ ) and 2023 ( $n = 164$ ), we incorporated body size and condition data measured from bats in capture sessions conducted for different research objectives in 2005 ( $n = 27$ ), 2007 ( $n = 16$ ), 2012, 2013 ( $n = 73$ ), and 2017 ( $n = 5$ ), for a total of 378 bats.

#### 2.5. Data analysis

To investigate the hypothesis regarding climate warming during the period under consideration, we first calculated the mean values of daily air temperatures for each month, then we averaged the values across the month and conducted univariate linear regression analysis. We employed the year of observation as the independent variable and the corresponding mean temperature of the “snow period” as the dependent variable. The validity of model assumptions was evaluated through Q-Q plots of standardised residuals, and model performance was compared with that of the null model by analysing the respective  $\text{adj}R^2$  values.

To compare the extent of riparian vegetation across the seven assessed sites for the years 2000 and 2023, we employed a Wilcoxon signed-rank test for paired measurements due to the departure of the dataset from the normal distribution.

To assess the impact of time and space on the relative number of females, we calculated the percentage of female *M. daubentonii* captured relative to the total number of bats caught for each of the replicates sampled at each site. We then used a General Linearized Mixed Model (GLMM) with a Gaussian family and an identity link. The dependent variable was the percentage of females in each replicate. Altitudinal Zone (Low, Intermediate, Upper), and Period (2000–2001 and 2023) served as fixed effects, while Site was considered a random factor. We evaluated the model's appropriateness by inspecting the residuals versus the fitted plot to detect signs of nonlinearity, unequal error variances, and outliers. Additionally, we visually examined a scatter plot (Q-Q plot) to assess potential deviations from normality and homoscedasticity. To assess the performance of the full model in comparison to the partial and null models, we employed the Akaike Information Criterion (AIC).

Body condition was estimated by calculating the Scaled Mass Index, SMI, as described by Peig and Green (2009). For each bat “*i*”, the formula  $\text{SMI}_i = \text{body mass (g)} \times (\text{FAL}_{\text{mean}}/\text{FAL}_i)^{\text{bSMA}}$  was applied. Here,  $\text{FAL}_{\text{mean}}$  represents the arithmetic mean of FAL (Forearm Length) for all individuals caught and bSMA, the scaling exponent of the power function, is determined by computing the regression coefficient ‘bSMA’ from the linearized power equation  $\ln(\text{body mass}) = \ln(a) + b \ln(\text{FAL})$ . We achieved this computation by fitting a Standardised Major Axis Regression (SMA) line to the ln-transformed data, whose slope corresponds to bSMA, following the methodology outlined in Peig and Green (2009).

*Myotis daubentonii* is sexually dimorphic, with females larger than males (Encarnação and Becker, 2020). To investigate the effects of years of observation and altitude on body size (FAL and body mass) and body condition (estimated from the corresponding SMI values) while considering the influence of sex and month of capture, we conducted Multiple Linear Regression with Categorical Predictors using Dummy Coding. Year and elevation (in m) were treated as continuous variables, and sex and month of capture were treated as categorical factors. We included the month of capture in our analysis based on findings from Nardone et al. (2015), who focused on males from the same population. Their research indicated that this factor, especially in June, influenced SMI. Downstream males exhibited a decline in body condition later in the summer, aligning their SMI values more closely with those of upstream males. The tenability of model assumptions was assessed through Q-Q plots of standardised residuals, and model performance was compared with that of the null model by comparing the respective  $\text{adj}R^2$  values.

Significance was set at  $P < 0.05$  for all tests. The statistical analyses were performed using JASP 0.17.0.2.1 (JASP Team, 2023) for all tests except for standardised major axis regression, which was conducted using the ‘smatr’ package (version 3.4–8) in R (R Development Core Team, 2022).

### 3. Results

#### 3.1. The climate has changed, but riparian vegetation has not

From December 1999 to May 2023, the monthly mean air temperature during the snow period exhibited a noticeable upward trend (Fig. 2). In 1999–2000, it was recorded at  $0.9\text{ }^{\circ}\text{C} \pm 3.8\text{ }^{\circ}\text{C}$ , whereas in 2023, it escalated to  $4.6\text{ }^{\circ}\text{C} \pm 2.6\text{ }^{\circ}\text{C}$ , resulting in a significant linear regression model (adjusted  $R^2 = 0.260$ ,  $F_{(1,22)} = 9.07$ ,  $P = 0.006$ ). Similarly, the mean temperatures calculated between May and September increased significantly both in Montenero Val Cocchiara (adjusted  $R^2 = 0.656$ ,  $F_{(1,5)} = 12.44$ ,  $P = 0.02$ ; Fig. S1) and Barrea (adjusted  $R^2 = 0.314$ ,  $F_{(1,9)} = 5.59$ ,  $P = 0.04$ ; Fig. S2). In all cases, null models had an  $R^2 = 0.0$  and were not a suitable fit for the data, further supporting the relevance of the regression analyses.

We also found that riparian vegetation has not changed in the 24 years considered, except in one site at low altitude, in the area occupied by females already in 2000, where an increase was noticed (Fig. 3). The Wilcoxon signed-rank test revealed that there was no significant difference in riparian vegetation between the years 2000 and 2023 across the evaluated sites (Wilcoxon statistic = 12.000,  $z = -0.338$ ,  $p = 0.813$ ).

#### 3.2. Upstream movement of females and shifting of the sexual segregation elevational threshold

In the year 2000, the highest altitude where female *M. daubentonii* were captured was downstream of the Barrea Lake, situated at an altitude of 875 m a.s.l. However, in July 2023, a remarkable shift in their distribution was observed. Reproductive adult females and volant juveniles were now spotted in the intermediate zone, ranging between 975 and 1050 m a.s.l. (Fig. 4). This upward movement of the sexual segregation threshold amounted to 175 m over 24 years.

The GLMM analysis indicated that the elevational zone and period significantly influenced the percentage of females captured at each site,

without a significant interaction between the two factors (Table 1). Over the 24 years under consideration, the mean percentage of females exhibited a significant increase, and females appeared in the intermediate elevational zone (Fig. 4). A Tukey's post-hoc test further revealed significant differences ( $P < 0.001$ ) between the low and intermediate zones, as well as between the low and high zones. However, no significant difference was observed between the intermediate and high zones. This lack of significance could be attributed to the higher variance in the intermediate zone, despite the occasional presence of females (absent in the high zone) in certain replicates. The model, fitted using restricted maximum likelihood, achieved an AIC = 199.005, vs. an AIC = 255.194 of the null model. AIC values for all models are illustrated in the Supplementary Material (Table S1).

#### 3.3. Body size increases over time

SMI was calculated using a mean population FAL of 37.13 mm ( $n = 378$ ), and  $b_{\text{SMA}}$  was estimated to be 3.066. In the FAL model (adj $R^2 = 0.215$ ,  $F_{(8, 369)} = 13.494$ ,  $P < 0.001$ ), there was a significant difference between sexes, with males being smaller than females, and a significant positive influence of “year,” with forearms becoming progressively longer over the 24 years considered, whereas “altitude” and “month” played no role (Table 2; Fig. 5). In both sexes, the mean FAL increased by 0.8 mm.

Significant effects were also detected for the “body mass” model (adj $R^2 = 0.207$ ,  $F_{(8, 369)} = 13.281$ ,  $P < 0.001$ ), indicating an increase in body masses over time, with females exhibiting larger values than males and larger sizes observed at lower altitudes (Fig. 5). However, the ponderal increase was mostly restricted to males (+0.4 g), while females showed practically no change. Besides, in this model “month” also has significant effects, with positive effects detected for June and September (Table 2). Finally, the SMI model explained little of the overall sample variance (adj $R^2 = 0.036$ ,  $F_{(8, 369)} = 2.773$ ,  $P = 0.005$ ), but significant effects were detected for “altitude,” with bats at lower elevations

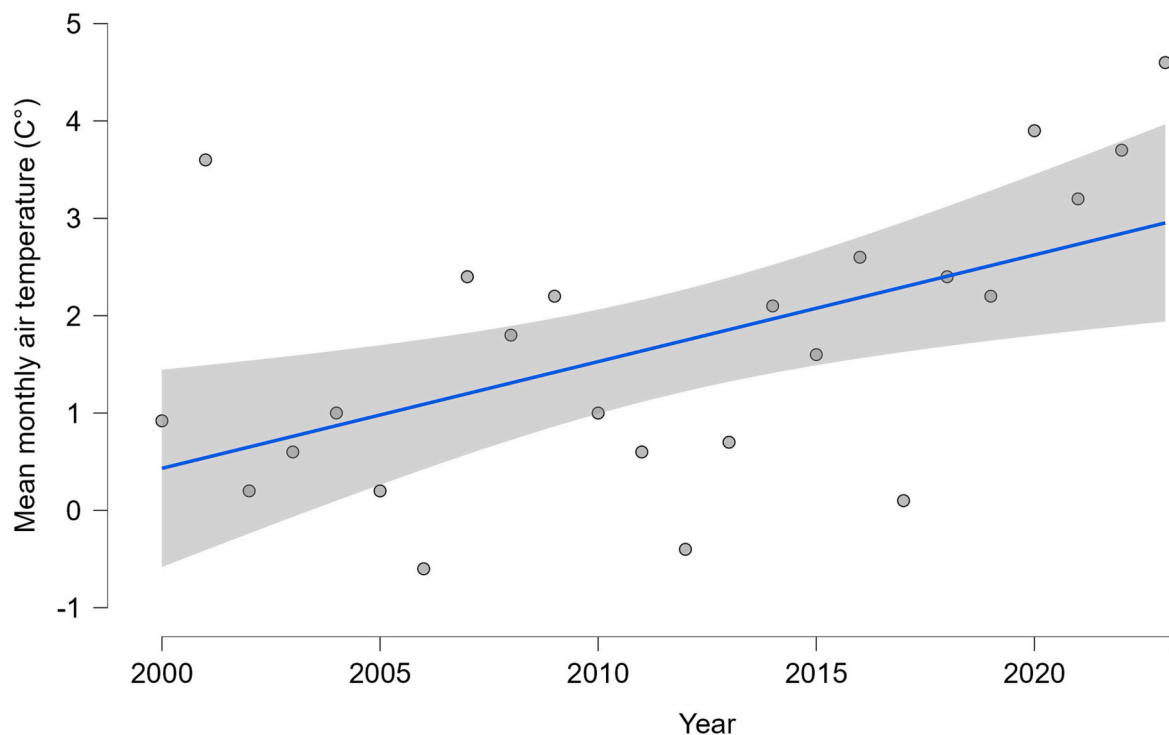
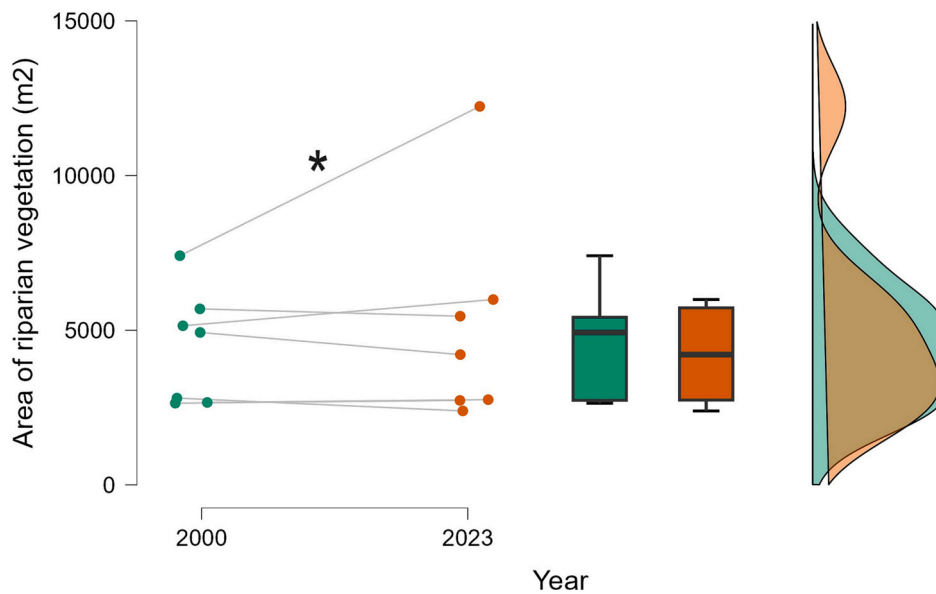
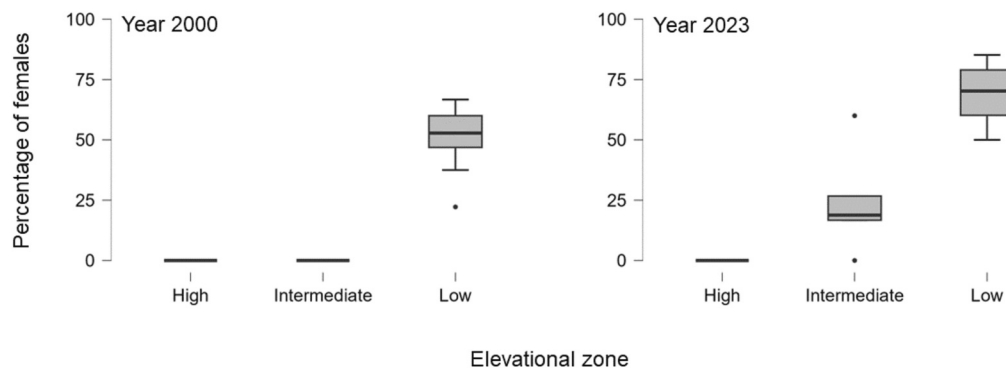


Fig. 2. Linear Regression Analysis of Monthly Mean Daily Air Temperature during the “Snow Season” over 24 years (Winter 1999–2000 to Winter/Spring 2023) at the Abruzzo Lazio and Molise National Park, Central Italy (“Forca d’Acero” Weather Station). The “Snow Season” includes all months between those featuring the first and last snow episodes of each year. The mean daily temperatures were calculated for each month, obtaining yearly averages, and generating the regression model. Data sourced from the METEOMONT service website.



**Fig. 3.** Assessment of changes in riparian vegetation along the Sangro River in Central Italy (2000–2023) at 7 focal sites for foraging *Myotis daubentonii*. Photo interpretation was employed, and the figure displays sites with coloured dots, accompanied by box plots indicating data distributions. Connections between 2000 and 2023 measurements are shown with lines. Box plots highlight key statistics: bold black line (median), hinges (25th and 75th quantiles), and whiskers (1.5 times interquartile range). Density estimation uses a Gaussian kernel with bandwidth determined by the ‘nrd0’ method (Silverman, 1986). The asterisk denotes the trend observed at the only site, situated at a low altitude, where a change was detected.



**Fig. 4.** Box and Whisker Plots depicting the distribution of female *Myotis daubentonii* mistnetted at 26 replicate plots within 7 sites, spanning three elevational zones (low = 800–876 m a.s.l., intermediate = 975–1050 m a.s.l., high >1050 m a.s.l.) along the Sangro River in the Abruzzo, Lazio, and Molise National Park (central Italy) during the years 2000–2001 and 2023.

**Table 1**

ANOVA summary table for GLMM analysis with fixed effects of the period (2000–1 vs. 2023) and elevational zone (low = 800–876 m a.s.l., intermediate = 975–1050 m a.s.l., high >1050 m a.s.l.) on the percentage of female *Myotis daubentonii* over the total number of individuals captured at each replicate plot ( $n = 26$ ) along the Sangro River (Central Italy), with site ( $n = 7$ ) as the random effect.

Effect	df	Chi-square value	p-value
Elevational zone	2	19.595	<0.001
Period	1	5.021	0.025
Elevational zone x period	2	2.644	0.267

exhibiting a better body condition (Fig. 5), and positive effects were also shown for June and September, whereas SMI did not increase over the years (Table 2). For all dependent variables, the corresponding null models had an  $\text{adj}R^2 = 0.00$ .

#### 4. Discussion

Most research investigating the impact of climate change on bats primarily relies on predictive models, and only a limited number of studies provide observations on bat responses spanning longer periods, so studies covering >10 years are rare and especially needed (Festa et al., 2023). Our study on *Myotis daubentonii*, covering 24 years, stands as the first to report a dual response to climate change. This entails an upward shift in the upper altitude threshold reached by female bats and a gradual increase in body size over time.

By analysing air temperatures and habitat productivity measurements (quantifying the extent of riparian vegetation), we were able to establish that noteworthy changes have occurred in our study area. Specifically, it became evident that while climate conditions have undergone significant transformations, the availability and quality of habitats have remained relatively stable. The temperature records from the snow season in the same area, gathered by the Carabinieri’s METEOMONT Service, along with the limited datasets for the months spanning from May to September, unequivocally demonstrate a consistent upward trend in temperatures during both winter and summer. This

**Table 2**

Coefficients of Multiple Linear Regression with Categorical Predictors using Dummy Coding were generated for forearm length (FAL, in mm), body mass (g), and Scaled Mass Index (SMI) in a population of *Myotis daubentonii* along the Sangro River at the Abruzzo Lazio and Molise National Park (Central Italy). The population spans across an elevational gradient. The predictors employed include “year” (2000–2023), “altitude” (m above sea level, covering an elevational range of 820–1093 m a.s.l.), “sex”, and “month of observation”. “April” and “female” were used for dummy coding and are not shown. \*The coefficients are standardised for continuous predictors only (year and altitude).

		Coefficients*	Standard error	t	P
<b>FAL (mm)</b>					
H <sub>0</sub>	Intercept	37.134	0.055	675.867	< 0.001
H <sub>1</sub>	Intercept	−30.296	15.262	−1.985	0.048
	Year	0.294	0.008	4.429	< 0.001
	Altitude (m a.s.l.)	0.002	6.633 × 10 <sup>−4</sup>	0.033	0.974
	Sex (male)	−0.721	0.142	−5.070	< 0.001
	May	−0.112	0.417	−0.269	0.788
	June	0.020	0.386	0.051	0.959
	July	0.007	0.389	0.019	0.985
	August	−0.171	0.395	−0.433	0.665
	September	−0.433	0.539	−0.803	0.423
<b>Body mass (g)</b>					
H <sub>0</sub>	Intercept	7.168	0.033	218.576	< 0.001
H <sub>1</sub>	Intercept	−22.481	9.125	−2.464	0.014
	Year	0.222	0.005	3.335	< 0.001
	Altitude (m a.s.l.)	−0.166	3.966 × 10 <sup>−4</sup>	−2.902	0.004
	Sex (male)	−0.357	0.085	−4.197	< 0.001
	May	0.194	0.249	0.249	0.437
	June	0.609	0.231	0.231	0.009
	July	0.437	0.233	0.233	0.061
	August	0.274	0.236	0.236	0.248
	September	0.679	0.322	0.322	0.036
<b>SMI</b>					
H <sub>0</sub>	Intercept	7.179	0.036	200.564	< 0.001
H <sub>1</sub>	Intercept	17.283	10.979	1.574	0.116
	Year	−0.063	0.005	−0.855	0.393
	Altitude (m a.s.l.)	−0.163	4.772 × 10 <sup>−4</sup>	−2.571	0.011
	Sex (male)	0.084	0.102	0.818	0.414
	May	0.268	0.300	0.895	0.371
	June	0.629	0.278	2.266	0.024
	July	0.461	0.280	1.644	0.101
	August	0.398	0.284	1.400	0.162
	September	0.992	0.388	2.556	0.011

robustly corroborates the presence of a climate warming pattern. Therefore, we conclude that the bats' observed reactions can be attributed to shifts in climate conditions, rather than alterations in habitat factors.

#### 4.1. Upstream movement of females and shifting of the sexual segregation elevational threshold

The elevation effect we recorded confirms our hypothesis, and, to the best of our knowledge, has not been documented in any other bat species. Notably, the presence of lactating and postlactating females at the beginning of August in the intermediate zone suggests that these individuals may not be merely moving from lower elevations. Instead, it hints at the possibility of the establishment of new reproductive roosts at the higher altitudes mentioned earlier.

Furthermore, the upstream shift might not be exclusive to females; it could potentially involve a portion of the male population as well by shifting the upper distributional limit of mixed-sex colonies. Male *Myotis daubentonii* exhibit strong intrasexual separation: downstream males share both roosting and foraging habitats with females and for this reason, they increase their reproductive success (Senior et al., 2005; Encarnação, 2012; Encarnação and Reiners, 2012). High-altitude males exhibit no interaction with the remaining males, being confined to

upstream roosting and foraging areas, which are comparatively less productive than their downstream counterparts (Nardone et al., 2015).

The observed process is unlikely to be confined solely to our Italian case study. Similar patterns are expected for other populations of *M. daubentonii* situated along elevational gradients in various European regions. The threshold's altitude value follows a north-to-south gradient, from northern England (54°N) at 0–150 m a.s.l. (Senior et al., 2005), to Germany (50°N), ranging from 175 to 260 m a.s.l. (Encarnação et al., 2007), and Switzerland (47°N) at 450–550 m a.s.l. (Leuzinger and Brossard, 1994). Notably, these thresholds tend to shift to lower altitudes with increasing latitudes, suggesting their relationship with environmental temperatures.

A question arises concerning why female *M. daubentonii* are shifting upwards. One potential explanation is provided by resource availability: since global productivity tends to be higher at elevated temperatures (Chu et al., 2016), and females require highly efficient feeding strategies to manage pregnancy and lactation (Kurta et al., 1989, 1990), regions that have become thermally more favourable may also yield greater foraging success. Although we did not quantify food availability throughout the 24 years under consideration, it is worth noting that, at least in terms of spatial distribution, sites at lower altitudes tend to be more productive than those at higher elevations in our study areas, as previously established by assessing the biomass of insect groups potentially preyed upon by *M. daubentonii* (Nardone et al., 2015). Moreover, differences in body mass and condition have been observed between individuals at high and low elevations, respectively (Nardone et al., 2015; this study), reflecting a higher food availability downstream.

An alternative explanation relies on the innate tendency of females, including humans, to seek warm spots, as postulated by Magory Cohen et al. (2021), who proposed the existence of a widespread differential sex-related thermal preference (DSTP). In their analysis, Magory Cohen et al. (2021) found that elevation was not a significant explanatory variable supporting a general pattern of sexual segregation in bats, even when temperature was excluded from the models. They also suggested that elevation does not act as a proxy for productivity in the general picture they drew based on 13 bird and 18 bat case studies. The adaptive value of females' thermal preferences might, among other potential factors, reside in the tendency to select warmer reproductive habitats (for bats, especially roosting sites) to reduce thermoregulatory costs and increase the energetic investment in offspring development and nursing. This would make sense for our case since the uprise in elevational threshold was accompanied by the appearance of reproductive females and juveniles at higher altitudes, indicative of the establishment of new reproductive sites.

#### 4.2. Body size increases over time

In agreement with our second hypothesis, we found that Daubenton's bats tended to increase body size over more than two decades: the significant positive influence of “year” on forearm length shows an ongoing trend of increasing forearm size over the 24 years considered. Our multivariate regression model explained approximately 21.5 % of the variability in FAL, which is consistent with or greater than temporal body size changes observed in other bat species across different studies (Mundinger et al., 2021, 2023b; Stapelfeldt et al., 2023; Salinas-Ramos et al., 2021). The size increase is comparable to that observed in *M. bechsteinii* (Mundinger et al., 2023b) over a very similar period.

Such findings are in line with research conducted on museum specimens of *Rhinolophus ferrumequinum* collected in Italy over a century and a half (Salinas-Ramos et al., 2021), and the clear evidence from a long-term study monitoring individual females of *Myotis bechsteinii* over 25 years (Mundinger et al., 2021). We posit that the most persuasive explanation for the pattern we observed aligns with such cases, suggesting that under warmer conditions, larger body sizes may result from reduced thermoregulatory costs at roosts, as also elegantly shown by



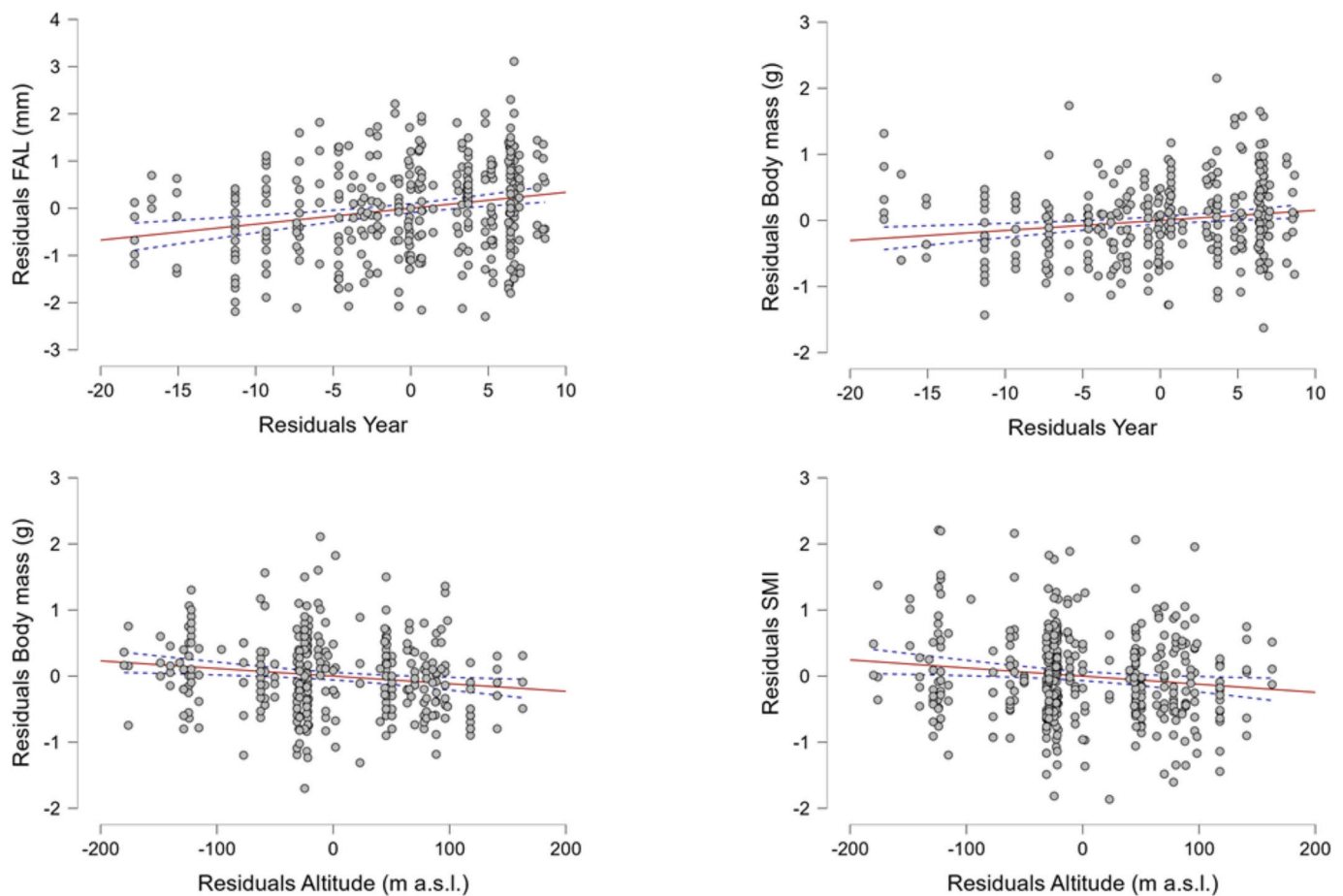


Fig. 5. Partial Regression Plots from a Multiple Linear Regression with Categorical Predictors using Dummy Coding drawn for forearm length (FAL, in mm), body mass (g), and Scaled Mass Index (SMI) in a population of *Myotis daubentonii* along the Sangro River at the Abruzzo Lazio and Molise National Park (Central Italy). The population spans across an elevational gradient. Only significant relationships between the dependent variables and year or altitude are depicted.

experimental manipulation of bat box microclimate (Mundinger et al., 2023a), and improved food availability during reproduction. This enables nursing females to allocate more resources to the size of their offspring (Mundinger et al., 2021). Higher temperatures may advance births and accelerate juvenile growth, which may increase juvenile survival in bats (Ransome, 1989; Hoying and Kunz, 1998; Frick et al., 2010; Mundinger et al., 2023b). Based on a 43-year (1970–2012) dataset of births recorded at a *M. daubentonii* colony, Lučan et al. (2013) found that the timing of reproduction was strongly influenced by the mean April temperature, with higher temperatures leading to the earlier appearance of neonates. Notably, there is experimental support for the impact of warming temperatures on bat growth. The use of thermostatically controlled electrical tubular heaters (incubators) placed in *Rhinolophus ferrumequinum* nursery roosts led to enhanced juvenile growth compared to unheated sites (Ransome and Hutson, 2000), in line with experiments done on *M. bechsteini* (Mundinger et al., 2023a). Although we have no elements to assess whether phenotypic plasticity plays a dominant role rather than heritability in such an increase, this may be the case as suggested for *Myotis bechsteini*, for which in hot summers, the heritability and genetic variance for body size were lower (Mundinger et al., 2023b).

We were unable to factor in the influence of social thermoregulation linked to colony size, a critical factor that significantly impacts energy conservation and prevents daytime torpor in reproductive females (Russo et al., 2017). These effects, which have been underscored in other species (Mundinger et al., 2021; Stapelfeldt et al., 2023), could potentially provide valuable insights. In contrast to our comprehensive understanding of the thermal behaviour of male *M. daubentonii* in the study

area (Nardone et al., 2015), we did not measure the thermoregulation of female individuals within the downstream colonies of the study area. However, males in those colonies do not use daytime torpor, unlike upstream males in bachelor colonies (Nardone et al., 2015). Downstream colonies consist of 15–20 bats encompassing both sexes (Russo, 2002). This is likely because downstream males cluster together with females, which maintain normothermic states. It is plausible that in these males, the abundance of food characterizing low-elevation foraging sites largely compensates for the lost energetic gain of not using torpor.

The role of productivity at foraging sites is also undeniably significant, warranting thorough consideration. Bats, being long-lived income breeders, manage the energetic demands of reproduction by consuming larger quantities of food. Thus, they are highly reliant on the availability of food at their foraging sites (Henry et al., 2002; Stapelfeldt et al., 2023). This principle holds not only for bats in general but also for the specific case of *Myotis daubentonii*: in this species, the likelihood of pregnancy and lactation is heavily contingent (>50 %) on the extent of available foraging time, and these probabilities escalate with improving foraging conditions (Culina et al., 2019).

Alston et al. (2023) analysed 20 North American bat species and found that most of them experienced increased body mass in years with higher net primary productivity, underscoring the critical importance of resource availability. It is plausible that the combined effect of warmer roosts and greater food availability results in surplus energy that can be invested by maternal bats in their offspring, leading to the development of larger bats.

The patterns exhibited by body mass over time closely parallel those

of FAL. However, these patterns are predominantly associated with males. This is likely because various confounding factors may come into play in females, such as undiagnosed early pregnancy or fat depletion due to the energetic costs of reproduction. However, no temporal effect on SMI was detected, suggesting that productivity over time did not change sufficiently to increase body condition in adult foragers, but only – directly or indirectly – body size. Other anticipated variations in body size (FAL and body mass) pertain to the larger values observed in females compared to males, confirming sexual dimorphism in *M. daubentonii* (Encarnação and Becker, 2020). Additionally, greater body mass and SMI values were observed at lower elevations, a phenomenon previously documented for males (Nardone et al., 2015), which indicates the higher productivity associated with low-altitude environments.

Regarding the influence of the month, heavier bats with a higher SMI were detected in both June and September. The June increase, already established for adult males in the same area (Nardone et al., 2015), may reflect fat storage occurring during the late spring's productivity peak. This peak was recorded between April and May in males of the same species in Germany (Encarnação et al., 2007). The subsequent increase in September also parallels the pattern observed in adult males in Germany (Encarnação et al., 2007) and is likely a result of fat accumulation by males during the warm months, as well as increased fat storage in post-reproductive females preparing for hibernation.

#### 4.3. Implications for social structure, survival, and reproductive success

The consequences of the observed effects of climate change on between-sex distribution and body size are unknown, but based on current knowledge, some hypotheses are possible. Despite the uncertainty surrounding the adaptive value and selective pressures governing this male segregation, it is speculated that intrasexual or intersexual agonistic interactions are responsible (Nardone et al., 2015). However, the detection of any altitude shift in males remains elusive without marked individuals, a scenario applicable to the bat population under our study. Conversely, the notable 175-m rise observed in females is conspicuous, even more so considering its swift occurrence over a mere two decades. Given the likelihood that altitudinal segregation between sexes in *M. daubentonii* populations holds functional significance and can be attributed to social factors, we propose that the elevation shift observed in females may carry implications for ecological, social, and reproductive dynamics, such as disruptions in social structures and alterations in both intra- and intersexual competition patterns.

In regions where altitudinal gradients are absent, lowland *Myotis daubentonii* populations express sexual segregation differently. Here, roosts are dominated by either adult males or adult females, coexisting within the same areas albeit at varying distances from water sources (Linton and Macdonald, 2019). Over the considered timeframe, in our study area female bats elevated their upper limit by 7.3 m per year. The process has been especially fast since the river acted as a corridor, and the only dam present does not stop bats from moving upstream, as radiotracking has shown (Nardone et al., 2015). Notably, the species is already relatively scarce above the Sangro River at altitudes exceeding 1200 m a.s.l., likely due to limited river flow. Consequently, altitude appears to impose an upper limit on *M. daubentonii*'s habitat suitability. Should females persist in their expansion at the current rate, they would potentially colonise the entire river course in approximately two decades.

This scenario raises questions about the potential adverse impacts on population structure. Might spatial segregation come to resemble the downhill pattern described by Linton and Macdonald (2019)? Anticipating outcomes is challenging, particularly since the next two decades are likely to witness further shifts in habitat productivity, alterations in water availability, and changes in roost availability – all of which could crucially influence the reshuffling of spatial population structures and alter intra- and intersexual competition over roosts and food. While the

rarefaction and eventual extinction of montane wildlife caused by climate-change-driven habitat loss are well-known effects, the cryptic social and ecological impacts on intersexual dynamics, as discussed here, could potentially raise a so-far neglected issue in conservation biology under climate change.

Foreseeing whether the body size effect of temperature observed in *Myotis daubentonii* extends to other populations of the same species is complex. In the case of Natterer's bats (*Myotis nattereri*) studied in Germany, high mean summer temperatures were correlated with larger body sizes in only one northern population but not in another population located to the south (Stapelheldt et al., 2023). Additionally, the absence of body size effects in the southern population contrasts with the size increase observed in sympatric *Myotis bechsteinii* over two decades (Mundinger et al., 2021, 2022), indicating potential species-specific responses. Notably, higher temperatures in nursery roosts at lower altitudes may lead to increased mortality rates due to acute dehydration and heat shock (Salinas-Ramos et al., 2023). Climate change may also affect bat reproduction adversely via reduced precipitations and associated reduction in food availability in critical times for breeding females (Amorim et al., 2015). It is also worth noting that the limited available information makes it challenging to predict whether *Myotis daubentonii* in our population would alter their life expectancy in response to the attained larger body size. For instance, in female *M. bechsteinii*, survival rates decrease as they grow larger (Mundinger et al., 2021, 2022), whereas the opposite trend was found in *M. nattereri* (Stapelheldt et al., 2023).

We found that SMI did not increase during the 24 years under consideration. While increased temperatures may have a positive effect on insect availability to bats (Taylor, 1963), insect populations are globally declining (Seibold et al., 2019), most likely due to land use changes and pesticide spread. In our study area, food availability might have increased over time and helped bats to keep their SMI constant despite their larger body size. However, a future decline in insect populations cannot be ruled out, as already recorded in other protected areas (Hallmann et al., 2017). A scenario of increasing temperatures and larger bats over time, not accompanied by an increase in food availability, could lead to insufficient trophic resources to sustain the *M. daubentonii* populations and increased mortality, as postulated for *M. bechsteinii* (Mundinger et al., 2023b).

In conclusion, our 24-year study of *Myotis daubentonii* along an altitudinal gradient has revealed significant shifts in their behaviour and physical traits, yet the implications for the overall fitness of the population remain largely unexplored and warrant further investigation comprising other bat populations along similar altitudinal clines. This knowledge is crucial for informing effective conservation strategies in the face of ongoing climate change and preserving the ecosystem services these bats deliver in riparian ecosystems.

#### CRediT authorship contribution statement

**Danilo Russo:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. **Gareth Jones:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Marta Polizzi:** Formal analysis, Investigation, Writing – review & editing. **Vincenzo Meola:** Formal analysis, Investigation, Writing – review & editing. **Luca Cistrone:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Danilo Russo reports financial support was provided by National Park of Abruzzo Lazio e Molise. Vincenzo Meola and Luca Cistrone report

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## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169733>.

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