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ARTICLE

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Body mass decline in a Mediterranean community of solitary bees supports the size shrinking effect of climatic warming

Carlos M. Herrera | **Alejandro Núñez** | **Javier Valverde** | **Conchita Alonso**

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, Spain

Correspondence
Carlos M. Herrera
Email: herrera@ebd.csic.es

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Abstract

The long-known, widely documented inverse relationship between body size and environmental temperature ("temperature-size rule") has recently led to predictions of body size decline following current climatic warming ("size shrinking effect"). For keystone pollinators such as wild bees, body shrinking in response to warming can have significant effects on pollination processes but there is still little direct evidence of the phenomenon because adequate tests require controlling for confounding factors linked to climate change (e.g., habitat change). This paper assesses the shrinking effect in a community of solitary bees from well-preserved habitats in the core of a large nature reserve experiencing climatic warming without disturbances or habitat changes. Long-term variation in mean body mass was evaluated using data from 1704 individual bees (137 species, 27 genera, 6 families) sampled over 1990–2023. Climate warmed at a fast rate during this period, annual mean of daily maximum temperature increasing 0.069°C/year on average during 2000–2020. Changes in bee body mass verified expectations from the size shrinking effect. The mean individual body mass of the community of solitary bees declined significantly, irrespective of whether the analysis referred to the full species sample or only to the subset of species that were sampled in both the old (1990–1997) and recent (2022–2023) periods. On average, body mass declined ~0.7%·year^{-1}, or an estimated average cumulative reduction of ~20 mg per individual bee from 1990 to 2023. Proportional size reduction was greatest among large-bodied species, ranging from around −0.6%·year^{-1} for the smallest species to −0.9%·year^{-1} for the largest ones. Declining rate was steeper for cavity-nesting than ground-nesting species. The pollination and mating systems of bee-pollinated plants in the study region are probably undergoing significant alterations as a consequence of supra-annual decline in bee body mass.

KEYWORDS
Baetic Mountain ranges, body mass, climate warming, maximum temperature, Mediterranean montane habitats, solitary bees, southern Spain

INTRODUCTION

Intra- and interspecific variation in individual body size is often predictably related to environmental temperature. Early recognition of such relationships led to the formulation of some classical ecological rules such as Bergmann's, Allen's, or the "temperature-size rule" (Atkinson, 1994; Ray, 1960). The temperature-size rule, a "widely documented and poorly understood pattern" (Klok & Harrison, 2013), predicts an inverse relationship across conspecific individuals between body size and the environmental temperature experienced during development (Atkinson, 1994; Forster & Hirst, 2012; Klok & Harrison, 2013). While the proximate and ultimate causes of the temperature-size rule are still far from being fully elucidated (Verberk et al., 2021; Walters & Hassall, 2006), it is a matter of fact that the rule has proven true in the majority of ectothermic organisms where it has been investigated (Atkinson, 1994; Klok & Harrison, 2013). Such a predictable relationship between body size and environmental temperature has recently acquired particular relevance in current ecological scenarios affected by climate warming, motivating predictions of reduced body size in response to rising temperatures ("size shrinking effect"; Ohlberger, 2013; Sheridan & Bickford, 2011; Verberk et al., 2021).

Given the many ecological and evolutionary consequences of body size (Bonner, 2006), its predicted decline due to climatic warming can trigger a complex cascade of effects whose details will depend on the ecological functionality of the organisms involved. In the case of keystone pollinators such as wild bees, body shrinking can alter crucial aspects of the pollination process such as foraging range, pollen load size and diversity, and pollen carryover, all of which depend on body size (Cullen et al., 2021; Földesi et al., 2021; Greenleaf et al., 2007). Limited evidence suggests that recent changes in bee sizes conform to expectations from the temperature-size rule, but studies conducted so far refer to few species, consider linear measurements as a proxy for body size rather than actual body mass, and/or the putative effects of temperature can be confounded with those of other factors correlated with climate change such as urbanization, land use changes, or habitat fragmentation (Barrett & Johnson, 2023; Garlin et al., 2022; Grab et al., 2019; Kelemen & Rehan, 2021; Oliveira et al., 2016; Suni & Dela Cruz, 2021). In this paper, we assess the size shrinking effect expected from the temperature-size rule by examining long-term changes in individual body mass in a diverse community of solitary bees sampled over three decades in Mediterranean habitats from a large protected area. Our study region is undergoing climatic warming but not disturbances or habitat changes that could confound the effects of the warming climate.

MATERIALS AND METHODS

As part of other studies (Herrera, 1995, 1997; Herrera et al., 2023; C. M. Herrera, unpublished data), a total of 1704 wild bees from 137 species, 27 genera, and six families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae; see Appendix S1: Table S1, for species and sample sizes) were hand-netted in the field during 1990–1997 ("old period" hereafter; $N = 473$ individuals, 47 species) and 2022–2023 ("recent period"; $N = 1231$ individuals, 130 species), in 55 localities from the core area of the Sierras de Cazorla, Segura y Las Villas Natural Park, a 2090 km^2 protected area in Jaén Province, southeastern Spain. A map of sampling locations is shown in Appendix S2: Figure S1. The sampled area is characterized by well-preserved habitats and outstanding biological diversity (Gómez Mercado, 2011; Médail & Diadema, 2009; Molina-Venegas et al., 2015). Our bee sampling sites were located at elevations between 740 and 1988 m, and did not undergo any obvious disturbance or habitat change over the 30-year period considered here which could have affected wild bee populations (e.g., wildfires, introduction of managed honeybee colonies, arrival or expansion of invasive plants). Total annual precipitation fluctuated widely over the study period but without a significant temporal trend (Herrera, 2019).

Netted bees were placed individually into sealed microcentrifuge tubes, kept in the dark in a portable refrigerator at 4–8°C, and brought to the laboratory within a few hours, where they were weighed to the nearest 0.1 mg always using the same Sartorius 1602MP8 analytical balance. The species sampled represented about one third of all species of bees occurring in the region (Ortiz-Sánchez et al., In press) and encompassed the whole range of body sizes (range of species means = 6–544 mg). Most bees weighed belonged to the genera *Andrena* (864 individuals, 40 species), *Anthophora* (167, 13), *Colletes* (139, 4), *Osmia* (112, 6), *Xylocopa*

(90, 3), and *Anthidium* (64, 2) (Appendix S1: Table S1). All bee species sampled were solitary, with the minor exception of a small proportion of data from primitively eusocial Halictids in the genera *Lasioglossum* and *Halictus* (15 individuals from five species; sociality data for Halictidae based on Appendix A of Gibbs et al., 2012). Each species was assigned to either ground-nesting ("soil excavators" sensu Danforth et al., 2019) or cavity-nesting (comprising "wood excavators," "renters" and "above-ground builders" types of Danforth et al., 2019) categories, using information from Michener (2000) and Danforth et al. (2019). Brood parasites (*Coelioxys*, *Epeolus*, *Melecta*, *Nomada*, *Thyreus*) were assigned to the same nesting class as their most frequent hosts. Body mass data of all individual bees included in this study, along with associated metadata (sex, nesting category, sampling date and site, and elevation and geographical coordinates of sampling site), are publicly available (Herrera, 2023).

Recent increase in environmental temperature has been well documented for the southeastern Iberian Peninsula (Fernández-Montes & Rodrigo, 2015; Gonzalez-Hidalgo et al., 2015). To corroborate this trend at the spatial and temporal scale of this study, daily maximum and minimum temperature data for 2000–2022 were gathered for 10 weather stations 15–60 km away from our bee sampling sites (Red de Información Agroclimática de Andalucía; https://www.juntadeandalucia.es/agriculturaypesca/ifapa/riaweb/web/; last accessed 23 October 2022). Relevant details and location map of weather stations are shown in Appendix S2: Figure S1, Table S1.

Data analysis

A similar analytical framework based on fitting linear mixed effects models to the data ("mixed models" hereafter; Bolker, 2015; Harrison et al., 2018) was adopted to test for supra-annual trends in both environmental temperature and body mass of solitary bees. In the case of temperatures, random intercepts models were fitted to daily maximum and daily minimum temperature data for every weather station. These models had year as the single fixed effect (treated as a continuous, numerical variable) and Julian date (=days since 1 January) as random effect. To circumvent the annual periodicity underlying weather data, Julian date was treated as an unordered random factor with 365 levels. Fixed-effect parameters obtained from these models provided estimates of the rate of change of annual means for daily maximum and daily minimum temperatures. For bee body mass, several random slopes–random intercepts models were fitted to individual mass data ($\log_{10}$ transformed), as detailed in the next paragraph. All these models had year of capture (centered and scaled to facilitate model convergence and interpretation of fixed effects; Harrison et al., 2018) as a fixed effect predictor, and bee species as random effect. Since sexual size dimorphism is frequent in solitary bees (Danforth et al., 2019), sex and its interaction with year of capture were included in each model as fixed-effect covariates. Preliminary analyses including Julian date and altitude of sampling site as additional fixed-effect covariates did not improve the fit of any model significantly. For simplicity, these two variables were omitted from the analyses reported here.

Most bee species were sampled on only one or a few years, which resulted in a sparse species × year data matrix (Appendix S1: Table S1). This was mainly a consequence of enhanced sampling effort in the recent period, but it could also conceal possible long-term change in bee community composition in response to climatic warming (e.g., increased representation of small-sized species and/or rarefaction of large-sized ones; Herrera, 2019; Herrera et al., 2023). Although linear mixed models are inherently robust to data sparseness (i.e., sparsely sampled levels of random effects, Bolker, 2015) and violation of distributional assumptions (Schielzeth et al., 2020), long-term changes in bee community composition could still bias our analyses because of changes in the sampling universe, and hence inference space, between the old and recent periods. To evaluate this possibility, mixed models were fitted to data sets that differed in temporal scope and bee species composition. The two main analyses considered the complete temporal scope of our study (1990–2023), but differed in the species composition of the sample. In one case, the model was fitted to all the data ($N = 1704$, 137 species), while in the other, only species that were sampled in both the old and recent periods were included ($N = 1385$, 40 species). Two additional, supplementary analyses were conducted which used data for all bee species but considered distinct temporal scopes: one was fitted to data from the old period (1990–1997; $N = 473$, 47 species) and the other to data from the recent one (2022–2023; $N = 1231$, 130 species).

All statistical analyses were carried out using the R environment (R Core Team, 2022). Mixed models were fitted with the lmer function in the lme4 package (Bates et al., 2015). Model fit adequacy was assessed using the check_model function in the performance package (Lüdecke et al., 2021). In the analyses of weather data, confidence intervals of fixed-effect parameters were obtained by bootstrapping (function bootstrap_model from the parameters package; Lüdecke et al., 2020), and p values for tests of the same hypothesis for multiple weather stations were corrected using the Benjamini-Hochberg procedure (p.adjust function, stats package). Statistical significance of fixed effects was assessed using Wald χ^2 tests (Anova function, car package; Fox & Weisberg, 2019). The function ggpredict from the ggeffects package (Lüdecke, 2018) was used to compute marginal effects of year on mean temperature and mean bee body mass. Random slopes from the mixed model fitted to all bee mass data, which reflected the variation among levels of the random effect (bee species) in the effect of the predictor (year) on the response variable (body mass), were obtained using the coef function. These species-specific declining rates were then related to interspecific variation in body mass and nesting habit.

RESULTS

The study area underwent significant warming over the period 2000–2022. This trend was mainly due to a steep increase in yearly means of daily maximum temperatures, which took place consistently at all weather stations (Figure 1). All mixed models fitted to daily maximum temperature data yielded statistically significant, positive temperature/year relationships, with model-estimated slopes averaging +0.069°C/year and ranging between +0.042 and +0.12°C/year depending on the station (see Appendix S2: Table S1, for parameter estimates and confidence intervals). Increases in mean daily minimum temperature also took place, but were less marked (Figure 1). Statistically significant relationships between daily minimum temperature and year occurred in only six weather stations, and in these cases, the estimated slopes averaged +0.036°C/year and ranged between +0.012 and +0.088°C/year (Appendix S2: Table S1).

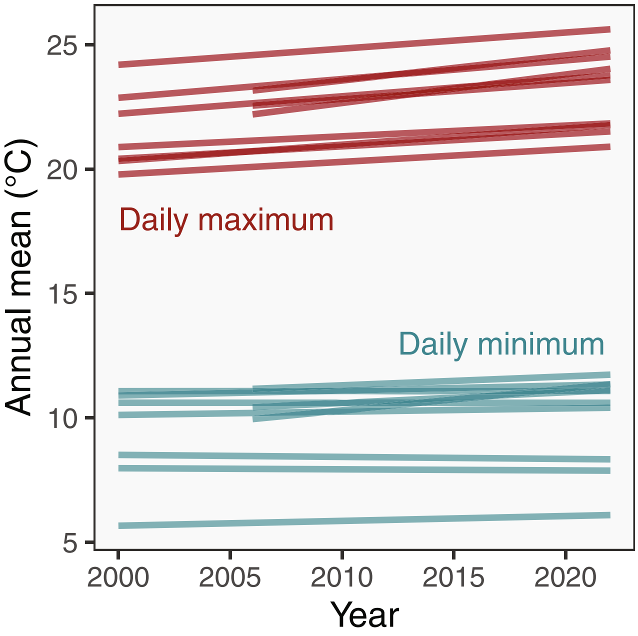

FIGURE 1 Linear trends in annual means for daily maximum and daily minimum temperatures for 10 weather stations near and around the bee sampling sites (see Appendix S2: Figure S1 for a map). Each line is the prediction obtained from the linear mixed model fitted to daily temperature data for one station, with year as the single fixed effect and Julian date (unordered, qualitative factor) as random effect. A summary of analytical results is given in Appendix S2: Table S1.

Mean individual body mass of the community of solitary bees declined significantly over the 1990–2023 sampling period, irrespective of whether the analysis referred to all species or only to those that were sampled in both the old and recent period (Table 1). The two main analyses revealed a negative effect of year on body mass after statistically accounting for significant sexual size dimorphism and allowing for interspecific variation in intercepts and slopes of the body mass/year relationship (Table 1). The two models yielded remarkably similar parameter estimates, and fitted well the ($\log_{10}$ transformed) individual body mass data and model assumptions (Appendix S3: Figures S1 and S2). The two supplementary analyses, fitting separate mixed models on data from the old and recent sampling periods, also revealed statistically significant trends of declining body mass within each period (Table 1). Results for the sex × year interaction effect were inconsistent among models, being statistically nonsignificant when the data encompassed the whole study period and significant in each of the two within-period analyses (Table 1). Only the main effect of year on body mass estimated from the two models fitted to data from the 1990 to 2023 period will be considered hereafter.

Because of the transformations applied to year and mass, the estimated slopes of the body mass/year relationship over the 1990–2023 period for the whole data set and for the subset of species sampled in both periods (−0.0386 and −0.0378, respectively, Table 1) denote changes in $\log_{10}$(mass) per year standard deviation unit and reflect multiplicative rather than additive changes. Back-transforming these slopes to the original scales of measurement yielded average body mass declines of 0.681%·year^{-1} and 0.666%·year^{-1}, for all the data and for species sampled in the two periods, respectively, or an estimated average cumulative reduction of ~20 mg per individual bee from 1990 to 2023 (Figure 2). Within-species decline in mean body mass for every species × sex combinations which was sampled in both the old and recent periods are depicted in Figure 3.

Bee species differed in annual rates of body mass decline, as shown graphically in Figure 3 and analytically by the significant difference between mixed models with and without random slopes, both for the models fitted to

TABLE 1 Results of linear mixed models fitted to body mass data for individual bees sampled over 1990–2023.

Analysis and data set	Fixed effect	Parameter estimate [SE]	χ^2	*p*-value
Main analyses (all study period, 1990–2023)				
All data ($N = 1704$, 137 species)	Year	−0.0385 [0.0056]	47.2	6.3e-12
	Sex (male)	−0.3015 [0.0059]	2614.3	<2.2e-16
	Year × sex (male)	0.0116 [0.0060]	3.7	0.055
Species sampled in old and recent periods ($N = 1385$, 40 species)	Year	−0.0377 [0.0056]	48.6	3.2e-12
	Sex (male)	−0.3091 [0.0062]	2480.7	<2.2e-16
	Year × sex (male)	0.0077 [0.0061]	1.6	0.21
Supplementary analyses (within periods)				
Old period, 1990–1997, all species ($N = 473$, 47 species)	Year	−0.0208 [0.1627]	5.3	0.021
	Sex (male)	−1.4564 [0.2281]	795.3	<2.2e-16
	Year × sex (male)	−0.7305 [0.1472]	24.6	6.9e-07
Recent period, 2022–2023, all species ($N = 1231$, 130 species)	Year	−0.0302 [0.1177]	3.9	0.049
	Sex (male)	0.0376 [0.1122]	1658.9	<2.2e-16
	Year × sex (male)	−0.5094 [0.1746]	8.5	0.0035

Note: Model parameters are expressed in the transformed scales (body mass $\log_{10}$ transformed, years scaled to mean = 0 and standard deviation = 1).

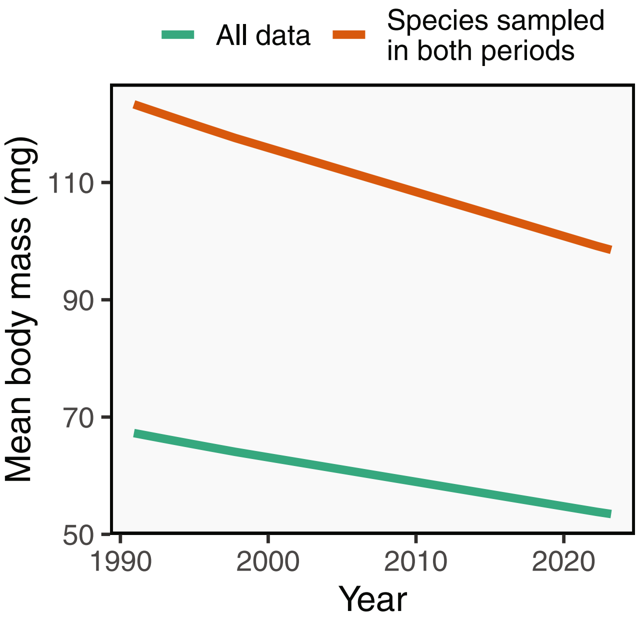

FIGURE 2 Mean estimated marginal effect of year on bee body mass, as predicted from random slopes–random intercepts mixed models with body mass as response variable, year, sex, and their interaction as fixed effects, and bee species as random effect (Table 1). Separate analyses were done on the whole sample (green) and on the subset of species which were sampled on both the old (1990–1997) and recent (2022–2023) periods (red). The original analyses were conducted on transformed variables, and the mean marginal effects shown here are the back-transforms to the original measurement scales.

all data ($\chi^2 = 23.3$, df = 2, $p = 8.8\text{e-}06$; likelihood ratio test) and only to data from species sampled in the two periods ($\chi^2 = 23.3$, df = 2, $p = 8.8\text{e-}06$; likelihood ratio test). For all data, species-specific estimated slopes ranged between −0.078 and + 0.007 $\log_{10}$(mass)/year standard deviation, and were negative in 136 out of the 137 instances (99.3%). Body mass was a significant predictor of interspecific variation in declining slope for the whole set of species ($F_{1,135} = 28.9$, $p = 3.2\text{e-}07$), but not for the subset of species sampled in both periods ($F_{1,38} = 3.6$, $p = 0.065$). In the first case, the heavier a bee species, the steeper the declining rate of body mass over the study period (Figure 4). Back-transforming the values plotted in Figure 4 to the original measurement scales, species-specific proportional declining rates ranged from around −0.6%·year^{-1} for the smallest species to −0.9%·year^{-1} for the largest ones. The relationship between species-specific declining slope and nesting habit (ground vs. cavity-nesting) was not statistically significant in the whole data set ($F_{1,135} = 2.7$, $p = 0.10$), but it was in the subset of species sampled in both periods ($F_{1,38} = 8.5$, $p = 0.006$). In this latter data set, average declining rate was steeper for cavity-nesting than ground-nesting species (mean ± SE = −0.0524 ± 0.0046 and −0.0374 ± 0.0023, respectively).

DISCUSSION

The climate of our study area warmed significantly during the past few decades, as shown by increasing mean daily maximum and, to a lesser extent, minimum temperatures, thus confirming the general trend for the southeastern Iberian Peninsula (see references in the *Introduction* section) at the reduced spatial scale of our

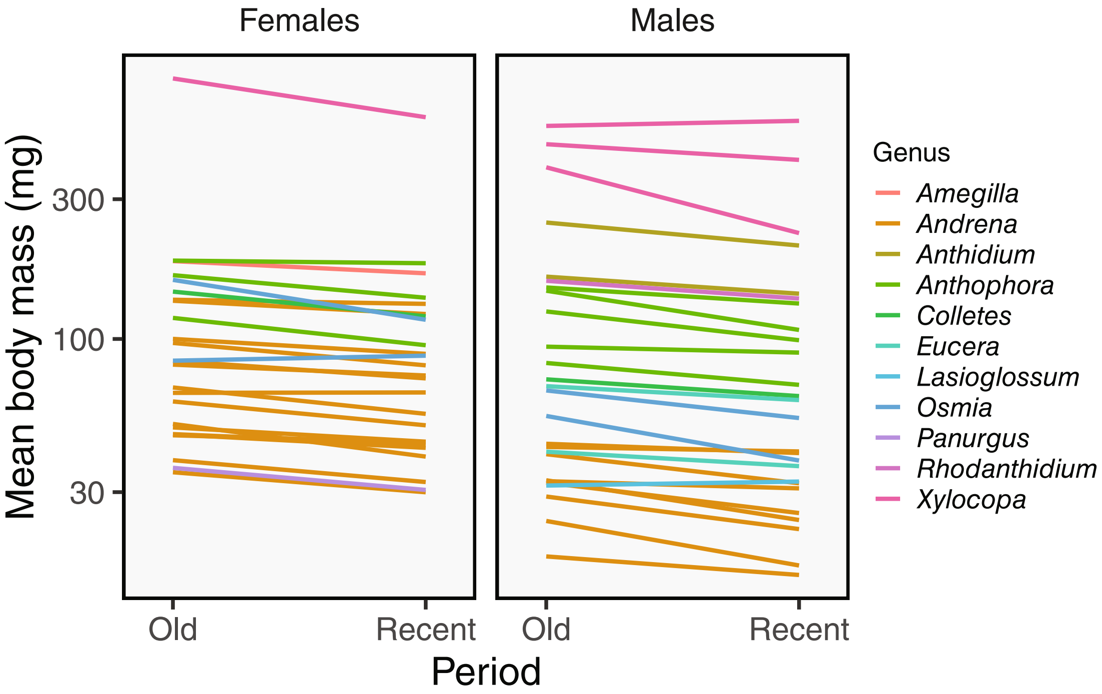

FIGURE 3 Within-species paired comparisons of mean body mass for all sex × species combinations ($N = 51$, involving 37 species in 11 genera) that were sampled in both the old (1990–1997) and recent (2022–2023) periods. Each line connects the old and recent averages for the same species.

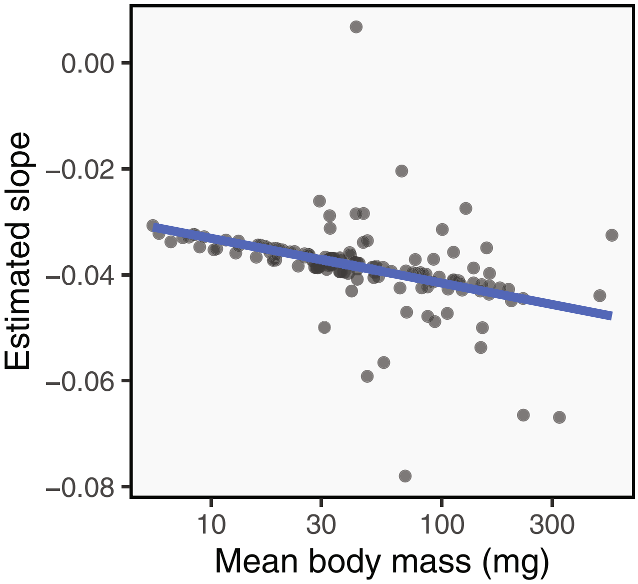

FIGURE 4 Inverse relationship between the slopes of $\log_{10}$(body mass)/year relationships estimated from the mixed model fitted to all the data (Table 1) and the mean body mass of individual bee species ($N = 137$). Line is the least-squares regression.

study. In agreement with expectations from the size shrinking effect, the warming climatic trend was concomitant with a decline in the mean individual body mass of the regional community of solitary bees over the whole study period (1990–2023), irrespective of whether the whole data set or only the subset of species sampled in both periods were considered. The declining trend was even discernible within each of the old and recent periods, despite the decreased statistical power to detect trends due to reduction in sample sizes and, particularly, temporal ranges, which in the recent period consisted of just 2 years. Most remarkably, the four $\log_{10}$(mass)/year fixed-effect estimates fell within a narrow interval, irrespective of temporal span and species composition of the data set (from −0.021 to −0.038, Table 1). Taken together, these findings allow to confidently rule out the possibility that the observed trend in body size reduction is a spurious effect of heterogeneous sampling and possible long-term changes in bee community composition. We thus conclude that long-term reduction in mean community-level bee body mass was chiefly or exclusively a consequence of the pervasive reduction in body size experienced by individual bee species.

Bees for this study were sampled in a well-preserved, protected area located ≥10 km away from urbanized or agricultural land; hence, observed body size reduction can be parsimoniously attributed to the effects of climate warming. These results also provide unique evidence to date of size shrinking in a diverse wild bee community based on body mass data rather than size metrics based on linear measurements of body parts, which are poor predictors of intraspecific variation in body mass (Kendall et al., 2019) and can produce biased results because of heterogeneous responses of body parts to temperature (Klok & Harrison, 2013; Ray, 1960). Adding robustness to our results is the treatment of the different bee species as levels of a random effect. Mixed models allow to make inferences that apply to different populations of effects, or "inference spaces" (Schabenberger & Pierce, 2002). In the context of this study, the whole regional community of solitary bees represents the "broad inference space" and our conclusions refer specifically to that space, not just the set of species sampled. This means that model parameter estimates for fixed effects refer to temporal changes in mean individual body mass for the solitary bee community as a whole, not just the 137 species sampled (see Herrera, 2019, for further discussion on the value of treating species as random effect levels when investigating community-level trends).

As it often happens with natural patterns conforming to the temperature-size rule (Klok & Harrison, 2013; Verberk et al., 2021), the possible mechanism(s) responsible for the decline in body mass of solitary bees documented in this paper can only be tentatively suggested. The fact that estimated slopes for individual species were consistently negative suggests that the ultimate cause of size reduction was universal enough as to affect similarly to all species. Experimental studies under controlled conditions have documented inverse effects on body size of the temperature experienced during larval growth for some genera or species of bees included in this study (e.g., *Osmia bicornis*, *Lasioglossum*; Kamm, 1974; Kierat et al., 2017; Radmacher & Strohm, 2010). These findings are in line with the size-temperature rule, and point to the ubiquitous direct effects of rising temperatures as the principal cause of body shrinking of solitary bees in our study region. This interpretation is supported by our finding that, for species sampled in both periods, species-specific declining slopes were steeper on average for species nesting in above-ground cavities than for those nesting underground, since developing larvae in underground nests are expected to be better buffered against rising ambient temperatures than those in above-ground cavities owing to the insulatory properties of soil (Antoine & Forrest, 2021). In addition to its direct effect on larval development, however, long-term increase in ambient temperature may also have indirect effects on adult body size through effects on food supply. Climate warming can reduce the floral food resources available to bees (Moss & Evans, 2022; Takkis et al., 2015), and impairment in quantity and quality of larval food provisions will also have a negative effect on adult body sizes (Chole et al., 2019). In Mediterranean-climate areas, supra-annual variation in rainfall can influence primary production and availability of floral resources, which could eventually translate into variations in bee body size. The influence of this effect on the patterns revealed by this study, if any, is probably negligible, because (1) no significant supra-annual trend in total annual rainfall is currently taking place in the study region, and (2) there is a significant trend towards proportionally more rainfall falling in January–June (Herrera, 2019; C. M. Herrera, unpublished data), which includes the period of year when precipitation is most influential on primary production in Mediterranean ecosystems (Bartsch et al., 2020).

Larger bee species experienced the largest proportional reductions in body mass (see Oliveira et al., 2016, for similar patterns). Regardless of the factors accounting for this differential response, which cannot be addressed with the data available, size-dependent reduction in bee body size has two important implications. First, the close relationship linking body size and fecundity in insects (Honek, 1993) suggests that per-capita fecundity of the largest species of solitary bees may have declined significantly in our study region over the past few decades. This effect could account for the recent rarefaction of some large-sized species (e.g., *Andrena assimilis*, *A. thoracica*, *Xylocopa cantabrita*; C. M. Herrera, unpublished data). And second, larger species tend to forage over wider areas, perform more and more effective pollinations, and deposit larger and more diverse pollen loads with greater carryover (Cullen et al., 2021; Földesi et al., 2021; Greenleaf et al., 2007; Herrera, 1987). The fact that larger bees experience the steepest declines in body mass thus suggests that the pollination and mating systems of many bee-pollinated plants of our study region may currently be undergoing significant changes and, possibly, also some shift in selective regime. These effects are predicted to occur most frequently among plants with large flowers with restrictive corollas that are predominantly or exclusively pollinated by large bees (e.g., *Antirhinum*, *Digitalis*, *Helleborus*, *Linaria*; Herrera, 2020).

AUTHOR CONTRIBUTIONS

Carlos M. Herrera conceptualized the study, analyzed the data and led writing. Alejandro Núñez identified bee specimens. Conchita Alonso provided financial support and project management. All authors participated in field and laboratory work, contributed to interpretation of results, edited and revised manuscript drafts, and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and metadata (Herrera, 2023) are available in Figshare: https://doi.org/10.6084/m9.figshare.22736696.

ORCID

Carlos M. Herrera https://orcid.org/0000-0003-2452-3888
Alejandro Núñez https://orcid.org/0000-0002-4937-0534
Javier Valverde https://orcid.org/0000-0001-8807-567X
Conchita Alonso https://orcid.org/0000-0002-7418-3204

REFERENCES

Antoine, C. M., and J. R. K. Forrest. 2021. "Nesting Habitat of Ground-Nesting Bees: A Review." *Ecological Entomology* 46: 143–59.

Atkinson, D. 1994. "Temperature and Organism Size–A Biological Law for Ectotherms?" *Advances in Ecological Research* 25: 1–58.

Barrett, M., and M. G. Johnson. 2023. "*Centris pallida* (Hymenoptera: Apidae) Male Body Size Decreases across Five Decades." *Ecological Entomology* 48: 154–63.

Bartsch, S., A. I. Stegehuis, C. Boissard, J. Lathière, J. Y. Peterschmitt, I. M. Reiter, T. Gauquelin, et al. 2020. "Impact of Precipitation, Air Temperature and Abiotic Emissions on Gross Primary Production in Mediterranean Ecosystems in Europe." *European Journal of Forest Research* 139: 111–26.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Bolker, B. M. 2015. "Linear and Generalized Linear Mixed Models." In *Ecological Statistics: Contemporary Theory and Application*, edited by G. A. Fox, S. Negrete-Yankelevich, and V. J. Sosa, 309–33. Oxford: Oxford University Press.

Bonner, J. T. 2006. *Why Size Matters: From Bacteria to Blue Whales*. Princeton: Princeton University Press.

Chole, H., S. H. Woodard, and G. Bloch. 2019. "Body Size Variation in Bees: Regulation, Mechanisms, and Relationship to Social Organization." *Current Opinion in Insect Science* 35: 77–87.

Cullen, N., J. Xia, N. Wei, R. Kaczorowski, G. Arceo-Gomez, E. O'Neill, R. Hayes, and T. L. Ashman. 2021. "Diversity and Composition of Pollen Loads Carried by Pollinators Are Primarily Driven by Insect Traits, Not Floral Community Characteristics." *Oecologia* 196: 131–43.

Danforth, B. N., R. L. Minckley, and J. L. Neff. 2019. *The Solitary Bees*. Princeton: Princeton University Press.

Fernández-Montes, S., and F. S. Rodrigo. 2015. "Trends in Surface Air Temperatures, Precipitation and Combined Indices in the Southeastern Iberian Peninsula (1970–2007)." *Climate Research* 63: 43–60.

Földesi, R., B. G. Howlett, I. Grass, and P. Batáry. 2021. "Larger Pollinators Deposit More Pollen on Stigmas across Multiple Plant Species—A Meta-Analysis." *Journal of Applied Ecology* 58: 699–707.

Forster, J., and A. G. Hirst. 2012. "The Temperature-Size Rule Emerges from Ontogenetic Differences between Growth and Development Rates." *Functional Ecology* 26: 483–92.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*, Third ed. Thousand Oaks: Sage Publishing.

Garlin, J., P. Theodorou, E. Kathe, J. J. G. Quezada-Euán, R. J. Paxton, and A. Soro. 2022. "Anthropogenic Effects on the Body Size of Two Neotropical Orchid Bees." *BMC Ecology and Evolution* 22: 1–13.

Gibbs, J., S. G. Brady, K. Kanda, and B. N. Danforth. 2012. "Phylogeny of Halictine Bees Supports a Shared Origin of Eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae)." *Molecular Phylogenetics and Evolution* 65: 926–39.

Gómez Mercado, F. 2011. "Vegetación y Flora de la Sierra de Cazorla." *Guineana* 17: 1–481.

Gonzalez-Hidalgo, J. C., D. Peña-Angulo, M. Brunetti, and N. Cortesi. 2015. "MOTEDAS: A New Monthly Temperature Database for Mainland Spain and the Trend in Temperature (1951–2010)." *International Journal of Climatology* 35: 4444–63.

Grab, H., J. Brokaw, E. Anderson, L. Gedlinske, J. Gibbs, J. Wilson, G. Loeb, R. Isaacs, and K. Poveda. 2019. "Habitat Enhancements Rescue Bee Body Size from the Negative Effects of Landscape Simplification." *Journal of Applied Ecology* 56: 2144–54.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. "Bee Foraging Ranges and their Relationship to Body Size." *Oecologia* 153: 589–96.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. "A Brief Introduction to Mixed Effects Modelling and Multi-Model Inference in Ecology." *PeerJ* 6: e4794.

Herrera, C. M. 1987. "Components of Pollinator "Quality": Comparative Analysis of a Diverse Insect Assemblage." *Oikos* 50: 79–90.

Herrera, C. M. 1995. "Floral Biology, Microclimate, and Pollination by Ectothermic Bees in an Early-Blooming Herb." *Ecology* 76: 218–28.

Herrera, C. M. 1997. "Thermal Biology and Foraging Responses of Insect Pollinators to the Forest Floor Irradiance Mosaic." *Oikos* 78: 601–11.

Herrera, C. M. 2019. "Complex Long-Term Dynamics of Pollinator Abundance in Undisturbed Mediterranean Montane Habitats over Two Decades." *Ecological Monographs* 89: e01338.

Herrera, C. M. 2020. "Flower Traits, Habitat, and Phylogeny as Predictors of Pollinator Service: A Plant Community Perspective." *Ecological Monographs* 90: e01402.

Herrera, C. M. 2023. "Live Body Mass of Solitary Bees in the Sierra de Cazorla Region (Jaén Province, Spain) Over The Period 1990–2023." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.22736696.

Herrera, C. M., A. Núñez, L. O. Aguado, and C. Alonso. 2023. "Seasonality of Pollinators in Mediterranean Montane Habitats: Cool-Blooded Bees for Early-Blooming Plants." *Ecological Monographs* 93: e1570.

Honek, A. 1993. "Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship." *Oikos* 66: 483–92.

Kamm, D. R. 1974. "Effects of Temperature, Day Length, and Number of Adults on the Sizes of Cells and Offspring in a Primitively Social Bee (Hymenoptera: Halictidae)." *Journal of the Kansas Entomological Society* 47: 8–18.

Kelemen, E. P., and S. M. Rehan. 2021. "Opposing Pressures of Climate and Land-Use Change on a Native Bee." *Global Change Biology* 27: 1017–26.

Kendall, L. K., R. Rader, V. Gagic, D. P. Cariveau, M. Albrecht, K. C. R. Baldock, B. M. Freitas, et al. 2019. "Pollinator Size and its Consequences: Robust Estimates of Body Size in Pollinating Insects." *Ecology and Evolution* 9: 1702–14.

Kierat, J., H. Szentgyörgyi, M. Czarnoleski, and M. Woyciechowski. 2017. "The Thermal Environment of the Nest Affects Body and Cell Size in the Solitary Red Mason Bee (*Osmia bicornis* L.)." *Journal of Thermal Biology* 68: 39–44.

Klok, C. J., and J. F. Harrison. 2013. "The Temperature Size Rule in Arthropods: Independent of Macro-Environmental Variables but Size Dependent." *Integrative and Comparative Biology* 53: 557–70.

Lüdecke, D. 2018. "Ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." *Journal of Open Source Software* 3: 772.

Lüdecke, D., M. S. Ben-Shachar, I. Patil, and D. Makowski. 2020. "Extracting, Computing and Exploring the Parameters of Statistical Models Using R." *Journal of Open Source Software* 5: 2445.

Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. "Performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6: 3139.

Médail, F., and K. Diadema. 2009. "Glacial Refugia Influence Plant Diversity Patterns in the Mediterranean Basin." *Journal of Biogeography* 36: 1333–45.

Michener, C. D. 2000. *The Bees of the World*. London: John Hopkins University Press.

Molina-Venegas, R., A. Aparicio, J. A. Slingsby, S. Lavergne, and J. Arroyo. 2015. "Investigating the Evolutionary Assembly of a Mediterranean Biodiversity Hotspot: Deep Phylogenetic Signal in the Distribution of Eudicots across Elevational Belts." *Journal of Biogeography* 42: 507–18.

Moss, E. D., and D. M. Evans. 2022. "Experimental Climate Warming Reduces Floral Resources and Alters Insect Visitation and Wildflower Seed Set in a Cereal Agro-Ecosystem." *Frontiers in Plant Science* 13: 826205.

Ohlberger, J. 2013. "Climate Warming and Ectotherm Body Size–From Individual Physiology to Community Ecology." *Functional Ecology* 27: 991–1001.

Oliveira, M. O., B. M. Freitas, J. Scheper, and D. Kleijn. 2016. "Size and Sex-Dependent Shrinkage of Dutch Bees during One-and-a-Half Centuries of Land-Use Change." *PLoS One* 11: e0148983.

Ortiz-Sánchez, F. J., J. Valverde, A. Núñez Carbajal, C. Alonso, and C. M. Herrera. In press. "Las Abejas (Hymenoptera, Apoidea) de la Sierra de Cazorla (España)." Monografías de la Sociedad Entomológica Aragonesa.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Radmacher, S., and E. Strohm. 2010. "Factors Affecting Offspring Body Size in the Solitary Bee *Osmia bicornis* (Hymenoptera, Megachilidae)." *Apidologie* 41: 169–77.

Ray, C. 1960. "The Application of Bergmann's and Allen's Rules to the Poikilotherms." *Journal of Morphology* 106: 85–108.

Schabenberger, O., and F. J. Pierce. 2002. *Contemporary Statistical Models for the Plant and Soil Sciences*. Boca Raton: CRC Press.

Schielzeth, H., N. J. Dingemanse, S. Nakagawa, D. F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N. A. Dochtermann, L. Z. Garamszegi, and Y. G. Araya-Ajoy. 2020. "Robustness of Linear Mixed-Effects Models to Violations of Distributional Assumptions." *Methods in Ecology and Evolution* 11: 1141–52.

Sheridan, J. A., and D. Bickford. 2011. "Shrinking Body Size as an Ecological Response to Climate Change." *Nature Climate Change* 1: 401–6.

Suni, S. S., and K. Dela Cruz. 2021. "Climate-Associated Shifts in Color and Body Size for a Tropical Bee Pollinator." *Apidologie* 52: 933–45.

Takkis, K., T. Tscheulin, P. Tsalkatis, and T. Petanidou. 2015. "Climate Change Reduces Nectar Secretion in Two Common Mediterranean Plants." *AoB Plants* 7: plv111.

Verberk, W. C. E. P., D. Atkinson, K. N. Hoefnagel, A. G. Hirst, C. R. Horne, and H. Siepel. 2021. "Shrinking Body Sizes in Response to Warming: Explanations for the Temperature–Size Rule with Special Emphasis on the Role of Oxygen." *Biological Reviews* 96: 247–68.

Walters, R. J., and M. Hassall. 2006. "The Temperature-Size Rule in Ectotherms: May a General Explanation Exist after all?" *American Naturalist* 167: 510–23.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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