

ARTICLE

Body size as a mediator of climatic effects: Insights from a long-term study of social Iberian magpies

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Abstract

The importance of considering body size in assessing evolutionary responses to climatic change is increasingly recognized, as body size correlates with morphological, physiological, and ecological traits that are climate-sensitive and influence fitness. However, the role of body size in mediating climatic effects in vertebrates remains poorly understood. Here, we examined structural body-size responses to natal and adult-experienced climate in a social bird and assessed whether body size mediates the direction of climatic effects. Using 26 years of data on cooperatively breeding Iberian magpies *Cyanopica cooki*, we found that adult males reared in late spring nests were smaller than those hatched earlier in the breeding season. This pattern was driven by smaller females, which reproduced later and produced smaller sons. Larger males born in hottest years had lower lifetime fledgling production, while larger males experiencing hotter springs as adults produced more fledglings over their lifetime. Additionally, larger males born in driest years or raised in nests with many brood mates had shorter lifespans. Despite a significant increase in temperature in the study area over 26 years, the average tarsus length of males has not changed, likely due to opposing effects of natal and adult climate on body size. Our findings illustrate how inherited body size mediates climatic effects at different life stages, with these effects acting in contrasting directions on fecundity, resulting in apparent trait stasis despite ongoing climate warming.

KEYWORDS

birds, body size, climatic warming, *Cyanopica cockii*, fitness, Iberian magpie, lifetime reproductive success, Mediterranean region

INTRODUCTION

Climate change, along with its associated extreme environmental episodes, gives rise to resource unpredictability, forcing organisms to confront conditions never experienced

before (Boyce et al., 2006; Parmesan et al., 2000). This phenomenon has attracted exponential research attention due to its profound impacts on human society and natural systems (Easterling et al., 2000; Hatfield & Prueger, 2015; McMichael et al., 2006; Parmesan & Yohe, 2003;

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Tylianakis et al., 2008). In animal populations, climatic events can affect individuals mainly via two primary pathways. First, they can affect the vital rates and fitness of adults encountering the climatic event, a phenomenon extensively documented across taxa such as fishes, birds, and mammals (e.g., Both et al., 2004; Dunn et al., 2010; Pankhurst & Munday, 2011; Porter et al., 2000; Radchuk et al., 2019). Second, extreme climatic events can influence juveniles born during such conditions, with natal environmental factors shaping growth, development, and demographic performance throughout life (reviewed in Lindström, 1999; Lummaa & Clutton-Brock, 2002; Metcalfe & Monaghan, 2001). Numerous studies on fish (Taborsky, 2006), reptiles (Baron et al., 2010; Le Galliard et al., 2010; Madsen & Shine, 2000; Marquis et al., 2008), birds (Avilés et al., 2022; Reid et al., 2003; Saino et al., 2018; Van de Pol et al., 2006), mammals (Albon et al., 1987; Descamps et al., 2008; Forchhammer et al., 2001; Hamel et al., 2009; Pigeon et al., 2017), and humans (Hayward et al., 2013) show that individuals developing in favorable habitats or during resource-abundant periods are larger, more fecund, and longer lived than those facing harsher natal environments.

In this context, a key question arises: do the fitness benefits gained by developing in favorable environments persist throughout life (the silver spoon effect sensu Grafen, 1988) or do these benefits depend on the environmental conditions individuals encounter during adulthood (Monaghan, 2008; Pigeon et al., 2019)? The “developmental constraint” or “silver spoon” hypothesis posits that poor conditions during early development constraint phenotype quality and future fitness, meaning that individuals developing in favorable conditions consistently outperform those reared under scarcity, regardless of the environmental conditions faced in adulthood (Monaghan, 2008). In contrast, the “environmental matching hypothesis” or so-called “predictive adaptive response” hypothesis (PAR) suggests that the benefits of favorable early-life conditions depend on the environmental conditions encountered in adulthood (Gluckman et al., 2005, 2008). Accordingly, early developmental conditions shape the phenotype in ways that enhance success when adult environmental conditions resemble those experienced during development.

Previous studies testing these hypotheses often overlooked the role of inherited variation in body size, which may modulate environmental effects. Although body size is a plastic trait influenced by early-life environmental conditions, it is also heritable (e.g., Merila, 1997) and correlates with morphological, physiological, and ecological traits that mediate evolutionary responses to climate change (Shipley et al., 2022; van Gils et al., 2016; Zimova et al., 2023). In fishes, birds, and mammals, thermal and energetic models reveal that the optimal body

size for maximizing growth and reproduction shifts with changing climatic conditions and diet quality (Lindmark et al., 2018; Mitchell et al., 2018; Porter et al., 2000). For instance, genetic lines of smaller individuals may tolerate low food availability better than larger ones, as smaller individuals require less energy for efficient growth (Price & Grant, 1984). In adulthood, body size differences may affect thermal tolerance and resilience to extreme thermal events (Di Santo & Lobel, 2017). Within the framework of Bergmann’s Biogeographic Rule, larger individuals are more common in colder regions, while smaller individuals dominate in warmer regions (Bergmann, 1847; Mayr, 1956). The metabolic basis of Bergmann’s rule suggests that larger individuals retain body heat more efficiently due to their greater volume to surface ratio making them more susceptible to hyperthermia under extreme heat events (Bergmann, 1847). Here we propose that inherited variation in body size predisposes individuals to different climatic effects during early-life and adulthood. We termed this possibility the “Size-Dependent Sensitivity to Climate” hypothesis.

Here we use long-term field data (1995–2021) on male Iberian magpies *Cyanopica cooki* to examine how natal and adult environmental conditions interact with body size to influence fitness. Data collection took place in southwestern Iberia (Extremadura), a Mediterranean ecosystem experiencing unprecedented warming over the past three decades (Acero et al., 2018). In a first step, we analyze the relationships between early-life environmental conditions and adult body size. In Iberian magpies, a cooperatively breeding species, the presence of helpers at the nest increases offspring provisioning rate and breeding success of breeders (Canario et al., 2004; Valencia et al., 2003), suggesting that helper presence reflects a high-quality natal social environment. Iberian magpies inhabit the Mediterranean region (Madge & de Juana, 2020), characterized by high climatic variability, including very high temperatures and low rainfall late in the breeding season. Low rainfall correlates with reduced productivity in insectivorous birds, likely due to its negative impact on insect abundance (García & Arroyo, 2001). Additionally, higher temperatures associate with reduced egg hatchability (García & Arroyo, 2001) and poorer offspring condition, including smaller body size (Salaberría et al., 2014). We predict that: (1) Poorer natal environmental conditions (i.e., absence of helpers, low rainfall, high temperature, or late breeding) associate with smaller body sizes. Smaller body sizes at the end of the breeding season may also result if larger parents bred earlier than smaller ones, given that body size is an inheritable trait. This would predict (2) that adult body size in sons correlates positively with parental body size, and (3) that breeding

phenology correlates with parental body size, with larger parents breeding earlier.

In a second stage, we investigate how the interplay between early-life and adult environmental effects is mediated by body size, considering three hypothetical scenarios summarized in Figure 1. In the “silver spoon” scenario, we expect that: (4) Individuals experiencing favorable early-life conditions achieve greater fitness (i.e., higher lifetime reproductive success [LRS] and longevity) than those experiencing poor early-life conditions, regardless of adult environmental conditions or body size (Figure 1). However, fitness gains from favorable adult environmental conditions may vary based on early-life environmental conditions, leading to a significant interaction between natal and adult environmental factors. In the “environmental matching” scenario, fitness peaks when early-life and adult environmental conditions align. This predicts: (5) A significant interaction between natal and adult environmental conditions, with the highest fitness observed when both conditions match (Figure 1). Finally, the “size-dependent sensitivity” scenario hypothesizes that body size mediates environmental effects on fitness, predicting: (6) A significant interaction between adult environmental conditions and body size, independent of natal environmental effects (Figure 1).

Finally, we will analyze changes in the body size of male Iberian magpies over the 26-year study. During this time, environmental temperature at our study site in southwestern Spain has significantly increased (see results). Based on the widely documented pattern in endotherms—including

birds—which links warming with body size reduction (e.g., Gardner et al., 2009, 2011; Jirinec et al., 2021; Sheridan & Bickford, 2011; Weeks et al., 2020), we expect a similar decrease in body size. However, if individuals with different body sizes exhibit contrasting sensitivities to natal and reproductive environments, we would instead expect no significant change in body size over time.

MATERIALS AND METHODS

Study site and system

Iberian magpies are small colonial corvids (~70 g) endemic to the Mediterranean open woodlands of the Iberian Peninsula (Madge & de Juana, 2020). They exhibit a flexible, cooperative breeding system (Valencia et al., 2003). The species is socially monogamous, with pairs often mating assortatively based on body size and condition (Avilés et al., 2008). Individuals can live for up to 15 years, although the average lifespan in our study area is 2.00 ± 1.40 years, with an annual adult survival rate of approximately 50% (de la Cruz et al., 2022). Males are slightly larger (de la Cruz & Valencia, 2016) and exhibit more vividly blue plumage than females (Avilés et al., 2008). The breeding season extends from early April to late May, with females laying 4–9 eggs (average \pm SD: 6.58 ± 0.89 eggs) in a single clutch. Some pairs may re-nest if their initial clutch fails (de la Cruz et al., 1990). Incubation lasts ~15–16 days followed by a ~14- to 16-day nesting period

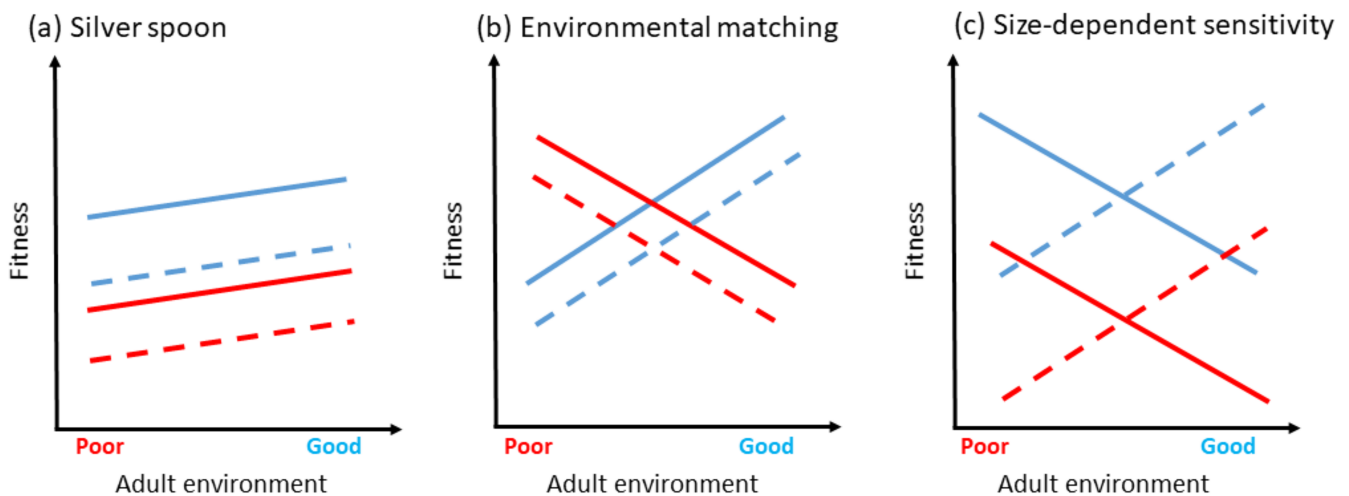


FIGURE 1 Schematic representation of models predicting fitness consequences of adult environmental conditions in relation to natal environmental conditions and body size. Red and blue lines represent cohorts born in poor and good environmental conditions, respectively. The solid and dashed lines indicate large and small individuals within such cohorts, respectively. (a) “Silver spoon” model, where fitness is greater when natal environmental conditions are favorable, improves with the improvement of adult environmental conditions, and is higher for larger individuals. (b) “Environmental matching” model where fitness is greater when natal and adult environmental conditions match and is greater for larger individuals. (c) “Size-dependent sensitivity” model where the effect of adult environmental conditions changes with differences in inherited body size irrespective of the effect of natal environmental conditions.

(Madge & de Juana, 2020). Nest predation is the main cause of reproductive failure, affecting over 50% of reproductive attempts annually (average \pm SD: 55.0% \pm 18.4% of breeding attempts, $N = 1756$ breeding attempts from 1992 to 2021; Appendix S1: Table S1). Approximately half of successful breeding attempts in our colony involve helpers (Valencia et al., 2003). Helpers are categorized into two types: “First-option helpers,” typically yearling males assisting their parents, and “second-option helpers,” males whose own clutch has failed and who redirect their parental effort to a neighbor nest (de la Cruz et al., 2019).

The study was conducted at Finca Valdesequera, a 200-ha open holm oak *Quercus ilex* woodland near Badajoz, Extremadura, Spain (39°03' N, 6°48' W), situated near the center of the species' distribution (Madge & de Juana, 2020). Colonies in this area range from 30 to 50 ha, comprising \sim 20 breeding pairs nesting in loose groups (2–5 nests/ha; de la Cruz et al., 2022). The region experiences a Mediterranean climate, characterized by cold, rainy winters and hot, extremely dry summers. As the breeding season progresses, conditions markedly deteriorate due to the decline in food resources (de la Cruz et al., 2022). Climatic data, including maximum temperature and accumulated rainfall on a daily basis for the study period, were collected from the Talavera airport weather station, \sim 20 km from the study site.

Data collection

From 1995 to 2021, we surveyed 1–3 colonies annually within the study area to search for nests. Over the study period, we located and monitored 1756 Iberian magpie nests (mean \pm SD: 65.0 \pm 20.0 nests/year; see Appendix S1: Table S1). During the early reproduction phase (last week of March and April), nest searches were conducted every third day, changing to weekly searches (May and early June) once the majority of the nests were identified to detect possible replacement clutches. Since 1992, an intensive capture and marking program has been implemented in the population, allowing for the identification of approximately 87% of individuals each year (see details in Valencia, de la Cruz, et al., 2006). Each fledgling was marked with a unique combination of metal and colored plastic rings ($N = 1660$ fledglings ringed during the period 1995–2021; Appendix S1: Table S1).

Additionally, adult birds remaining or recruited in the study area were routinely captured using baited cage traps deployed from September to July for marking and measuring (see details in de la Cruz et al., 2022). At capture, tarsus length was measured with a digital caliper (to the nearest 0.01 mm), and weight was recorded with a Pesola balance (precision \pm 0.5 g). Tarsus measurements

used to estimate body size in our study correspond to those taken upon recapture, when males join the reproductive contingent and have reached adulthood.

In Iberian magpies, all females disperse from their natal territories (no females were recruited over 26 years from 1660 ringed fledglings; de la Cruz, unpublished data), and helpers are predominantly males (Valencia et al., 2003). Thus, the individuals analyzed in this study were metal-ringed male fledglings (15–18 days after hatching) raised in the population and subsequently recruited as adults.

All nests were either directly observed through telescope or video recorded from hides for at least 1 h every other day to identify breeder and helper individuals. The sex of breeders was determined by behavior, as only females incubate eggs and brood chicks in this species (de la Cruz & Valencia, 2016). Helpers rarely contribute during egg incubation, but males observed repeatedly feeding an incubating female were identified as the breeding male. Birds occasionally seen at the nest during incubation or present only during the brooding phase were classified as helpers (de la Cruz et al., 2022).

Fitness outcome of males

Nests were inspected every 5 days, with intervals reduced to 2–3 days during egg-laying and hatching periods. For each nest, laying date, clutch size, and number of fledglings were recorded. The number of fledglings per nest was used as a measure of male reproductive success, while LRS was calculated as the sum of fledglings produced across all breeding attempts during a male's lifetime. The last recorded breeding year of each male was used to estimate their age at last reproduction, serving as a reliable proxy for lifespan. Male Iberian magpies live an average of 3.21 years (see below). Therefore, males born during the final years of study might not have completed their lifespan, potentially leading to underestimated LRS and lifespan. To mitigate this bias, analyses of LRS and lifespan included only males born before 2017.

Selection of climatic time windows

To identify the climatic windows most influencing reproduction in Iberian magpies, the annual average laying date was selected as a key variable due to its inverse relationship with clutch size and fledging success (de la Cruz et al., 1990). Using the function `slidingwin` from the `climwin` R package (Bailey & van de Pol, 2016), we identified the most influential climatic window for laying date based on daily climate data and annual average laying

date from 1992 to 2020 and using corrected Akaike information criterion (AIC_c). We evaluated the effect of accumulated rainfall and maximum temperature using absolute climate windows anchored to March 25, the earliest recorded laying date in our dataset. As we lacked prior knowledge of when climate signals might occur, all possible windows over the preceding year were tested separately for temperature and rainfall. The five best-fitting windows for temperature and precipitation had similar model weights (see Appendix S1: Table S2). Therefore, we used the medwin function in the climwin package to calculate median window size and model averaged parameter estimates (Bailey & van de Pol, 2016). Median climatic windows for temperature and rainfall were then used to assess whether these variables, in either natal or breeding years, interacted with body size to influence lifespan and fecundity in male Iberian magpies.

Statistical analyses

All statistical analyses were conducted using SAS v.9.4 software (SAS Institute, Cary, NC, USA). Continuous variables were z-standardized for improved interpretability (Schielzeth, 2010). Temporal trends in annual temperature and rainfall were examined using two linear regression models, with year as a continuous predictor (general linear model [GLM] procedure in SAS).

To evaluate the effects of natal environmental conditions on adult male body size, a GLM procedure in SAS was used with tarsus length as the response variable and natal laying date, temperature, rainfall, helper presence (binary), and brood size as predictors. Helper presence was included due to its positive association with provisioning rate (Canario et al., 2004) and offspring immune response (Valencia, Solis, et al., 2006). Furthermore, brood size is likely related to the level of sibling competition during development or parental qualities, and it may influence offspring phenotype (e.g., Saino et al., 1997). A second GLM included parental tarsus lengths and laying date as predictors to assess whether seasonal declines in offspring size were linked to early reproduction by larger parents.

Structural equation modeling (SEM) was used to analyze the direct and indirect effects of parental body size on offspring body size. Specifically, we tested whether parental body size had a direct effect on male body size and/or an indirect effect mediated by laying date. For this purpose, a structural equation model comprising two linear models was fitted (Figure 2) using the *piecewiseSEM* R package (Lefcheck, 2016; Lefcheck et al., 2016). A linear mixed model (LMM) was first fitted with male tarsus length as the response variable and father tarsus length, mother tarsus length, and natal laying date as explanatory

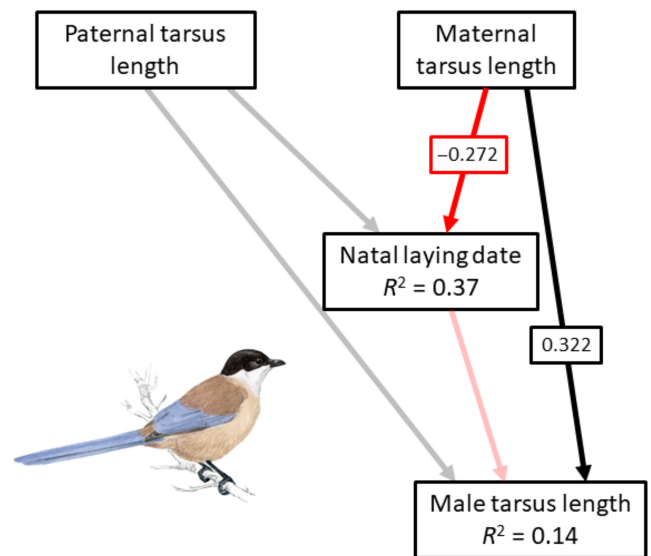


FIGURE 2 Structural equation model derived from the hypothesis of body size differences in phenology exploring the relationships among male tarsus length, laying date of natal nest, and parental tarsus lengths. Arrows represent unidirectional relationships among variables. Black arrows denote positive relationships, and red arrows denote negatives ones. Arrows for non-significant paths ($p \geq 0.05$) are semi-transparent. R^2 s values for component models are given in the boxes of response variables. Model fit using piecewise structural equation modeling (SEM) included the natal year as a random term. Illustration credit for the Iberian magpie picture: Juan Varela.

variables. Natal year was included as a random intercept. A second LMM linked natal laying date (response variable) and parental tarsus lengths (explanatory variables), again including natal year as a random intercept. Direct and indirect relationships were also tested outside the SEM framework to extract specific effects.

Given the relatively low number of recruited males compared to the number of potential natal and adult environmental factors considered, we sequentially analyzed the mediating role of body size. First, we tested whether body size mediated natal environmental effects. Then, we assessed whether body size mediated adult environmental effects. Finally, we evaluated the interaction between the two, focusing only on significant natal environmental effects in combination with reproductive factors or, conversely, significant adult environmental effects in combination with natal factors.

Analyses of LRS incorporated data across the entire lifespan of individuals. Many Iberian magpie males bred only once (40 males), or served as helpers without producing fledglings (24 males). To address this, we used three Zero-inflated Poisson regression models (GENMOD procedure in SAS). Model 1 included natal environmental variables (laying date, natal temperature, natal rainfall, helper

presence and natal brood size), tarsus length (as proxy of body size), and all the possible interaction terms between body size and natal environmental variables. Model 2 included adult environmental variables (adult temperature and rainfall), tarsus length, and all the possible interactions between body size and adult environmental variables. Model 3 examined interactions between adult temperature, natal temperature, and tarsus length, including all possible interaction terms. All models controlled for sampling effort by including the number of breeding attempts per male as a covariate. To analyze lifespan, we used three Negative binomial regression models (GENMOD procedure in SAS) with the same predictors as the LRS models. The extent of over-dispersion in the LRS models (Appendix S1: Tables S5–S7) and in the lifespan models (Appendix S1: Tables S8–S10) was evaluated using the ratio of the Pearson χ^2 statistic to its df ($n - p$). No evidence of over-dispersion was found (Payne et al., 2018).

To evaluate the potential directional changes in tarsus length over the study period, we fitted two general linear mixed models (GLMMs) using the GLMMIX procedure in SAS with an identity link function. The first model analyzed 151 males captured in the colony during the year of birth, before recruitment as breeders or helpers. The dependent variable was individual tarsus length, with year (as a linear term) and natal laying date included as predictors. Since males may continue to grow after leaving the nest, the date of capture (i.e., when tarsus length was measured) was added as an additional linear predictor. To account for potential random fluctuations in body size between years, year was included as a random intercept. The second GLMM focused on males recruited into the population in subsequent seasons, reflecting their final adult body size. Its structure mirrored the first GLMM but excluded the capture date as a predictor, as body size was already considered final at recruitment.

Standard model validation graphs (Zuur, 2009) confirmed that the assumptions of homogeneity of variance and normality of residuals were fulfilled.

RESULTS

Temporal trends in climate and selection of climatic time windows

Spring temperatures in the colony have increased at a rate of $0.04^\circ\text{C}/\text{year}$ over the past three decades ($R^2 = 0.16$, $F_{1,27} = 5.05$, $p = 0.03$; Appendix S1: Figure S3), while annual rainfall showed no significant trend during the same period ($R^2 = 0.05$, $F_{1,27} = 1.60$, $p = 0.21$; Appendix S1: Figure S3).

The top five best time windows for temperature and rainfall showed similar model weights (Appendix S1: Table S2). Temperature exhibited a strongly negative relationship with laying date ($\beta = -2.87$ to 2.72 days/ $^\circ\text{C}$) while rainfall showed a strongly positive relationship ($\beta = 2.72$ – 3.00 days/mm; Appendix S1: Table S2). Model averaging indicated that the average laying date of Iberian magpies advances by 2.78 days for every 1°C increase in mean temperature between February 6 and March 25. Conversely, it is delayed by 2.72 days for every 1 mm increase in rainfall between March 3 and March 25 (Appendix S1: Table S2).

Natal environmental conditions and body size in Iberian magpies

The tarsus length of males born in the colony averaged $35.7 \text{ mm} \pm 0.71$ and was significantly influenced by the laying date of the natal nest: males raised in late nests had relatively smaller tarsi compared to those raised in earlier nests (GLM: $\beta = -0.32$, 95% CI $[-0.58, -0.06]$, $F_{1,81} = 5.96$, $p = 0.02$; Appendix S1: Table S3, Figure S2). Tarsus length was not significantly influenced by variation in natal climatic or social environment (Appendix S1: Table S3).

A second GLM including paternal and maternal tarsus length and laying date as predictors of male tarsus length reveals that maternal tarsus length was the only significant predictor of tarsus length in males (Appendix S1: Table S4). Males born from females with longer tarsi had longer tarsi themselves (GLM: $\beta = 0.37$, 95% CI $[0.08, 0.66]$, $F_{1,59} = 6.58$, $p = 0.01$; Appendix S1: Table S4, Figure S2). Additionally, maternal tarsi (LMM: laying date effect; $\beta = -0.28$, 95% CI $[-0.53, -0.03]$, $F_{1,71.92} = 5.07$, $p = 0.02$), but not paternal ones (LMM: laying date effect; $\beta = 0.04$, 95% CI $[-0.19, -0.27]$, $F_{1,75.71} = 0.10$, $p = 0.75$), are significantly smaller in late nests (Appendix S1: Figure S2). SEM further showed that maternal body size negatively affects natal laying date and positively influences male body size (Figure 2). In our population, smaller female Iberian magpies breed later and produce smaller males (Figure 2).

Natal and adult environmental conditions, body size, and LRS

On average, male Iberian magpies produced 3.44 (range 0–33) fledglings over their lifetime, with an average of 1.93 breeding attempts (range 1–9) (Appendix S1: Figure S1). Notably, 48.5% of males failed to produce any fledglings (Appendix S1: Figure S1). The number of fledglings produced by a male depended on the interaction between its body size and natal temperature

(Zero-inflated Poisson model: $\chi^2_1 = 4.95$, $p = 0.03$; Appendix S1: Table S5, Figure S3). Males born in the hottest years exhibited a decline in LRS with increasing body size, from 4.86 ± 0.64 (SE) fledglings in smaller males to 2.13 ± 0.51 (SE) fledglings in larger males ($F_{1,16} = 4.58$, $p = 0.04$; Figure 3). In contrast, there was no significant relationship between LRS and tarsus length for males born in the coldest

years ($F_{1,14} = 0.004$, $p = 0.95$), when the smaller and larger males produced 2.54 ± 0.92 and 2.02 ± 0.52 fledglings, respectively (Figure 3).

Independent of natal temperature, LRS was also influenced by the interaction between body size and adult temperature (Zero-inflated Poisson model: $\chi^2_1 = 6.17$, $p = 0.01$; Appendix S1: Table S6; Figure 4). In colder

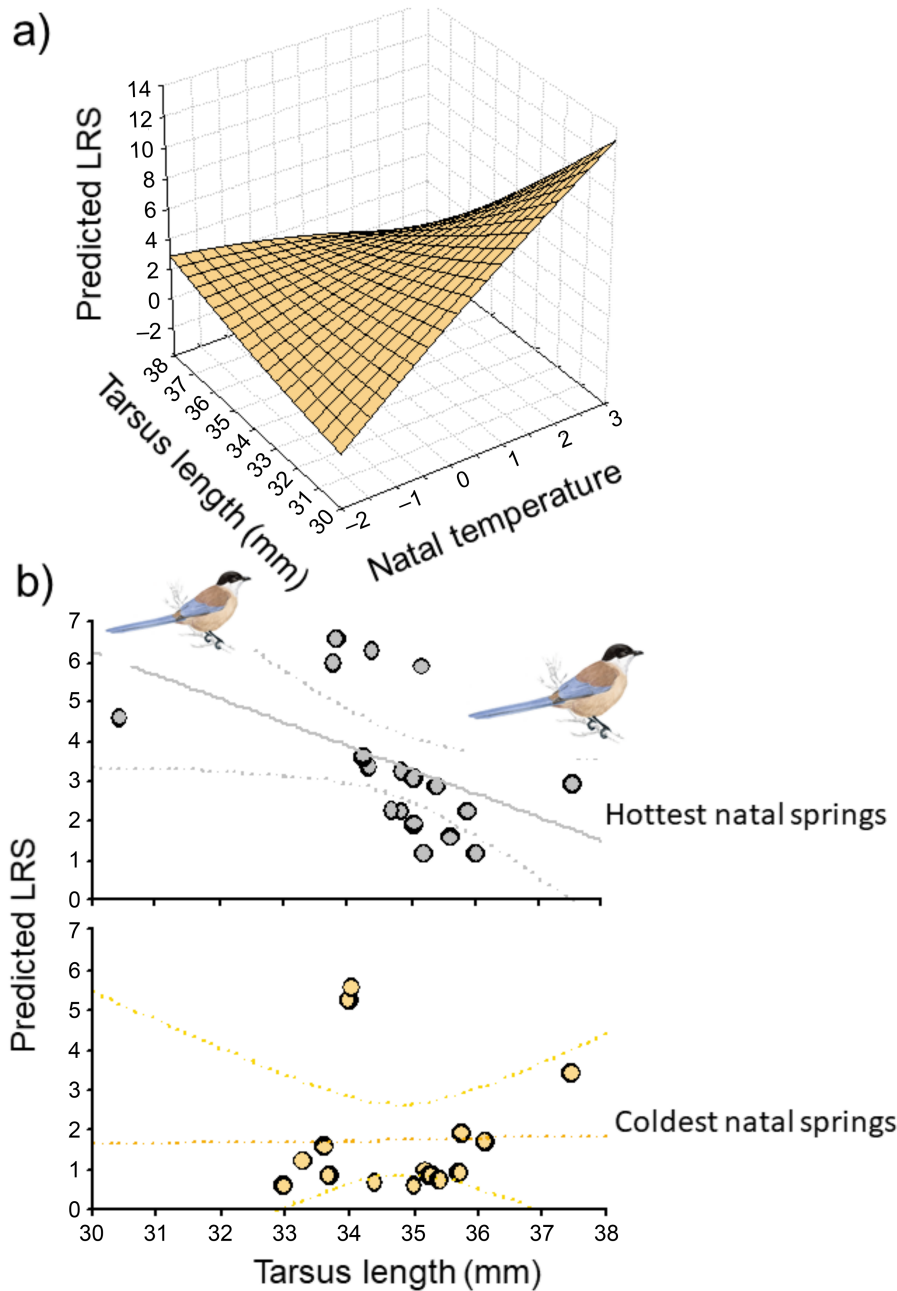


FIGURE 3 Lifetime reproductive success (LRS) depends on natal climatic conditions and body size in the Iberian magpie. (a), Relationship between the total number of produced fledglings per male and tarsus length in interaction with natal temperature. The predicted surface from a Zero-inflated Poisson model is presented. (b) Detailed effects of body size on LRS. Shown are the predicted values of LRS in relation to tarsus length, regression lines (continuous lines reflect significant associations), and 95% CI for hottest (i.e., above the third quantile of natal temperature [gray dots, $N = 18$ males]) and coldest (i.e., below the first quantile of natal temperature [orange dots, $N = 16$ males]) springs. Illustration credit for the Iberian magpie picture: Juan Varela.

springs, LRS declined with increasing body size, from 3.40 ± 0.56 (SE) fledglings in smaller males to 2.00 ± 0.44 (SE) in larger males ($F_{1,16} = 9.30$, $p = 0.007$; Figure 4).

Conversely, in warmer springs larger males achieved higher LRS (5.77 ± 0.64 SE) compared to smaller males (1.18 ± 0.45 SE; $F_{1,18} = 66.20$, $p < 0.001$; Figure 4).

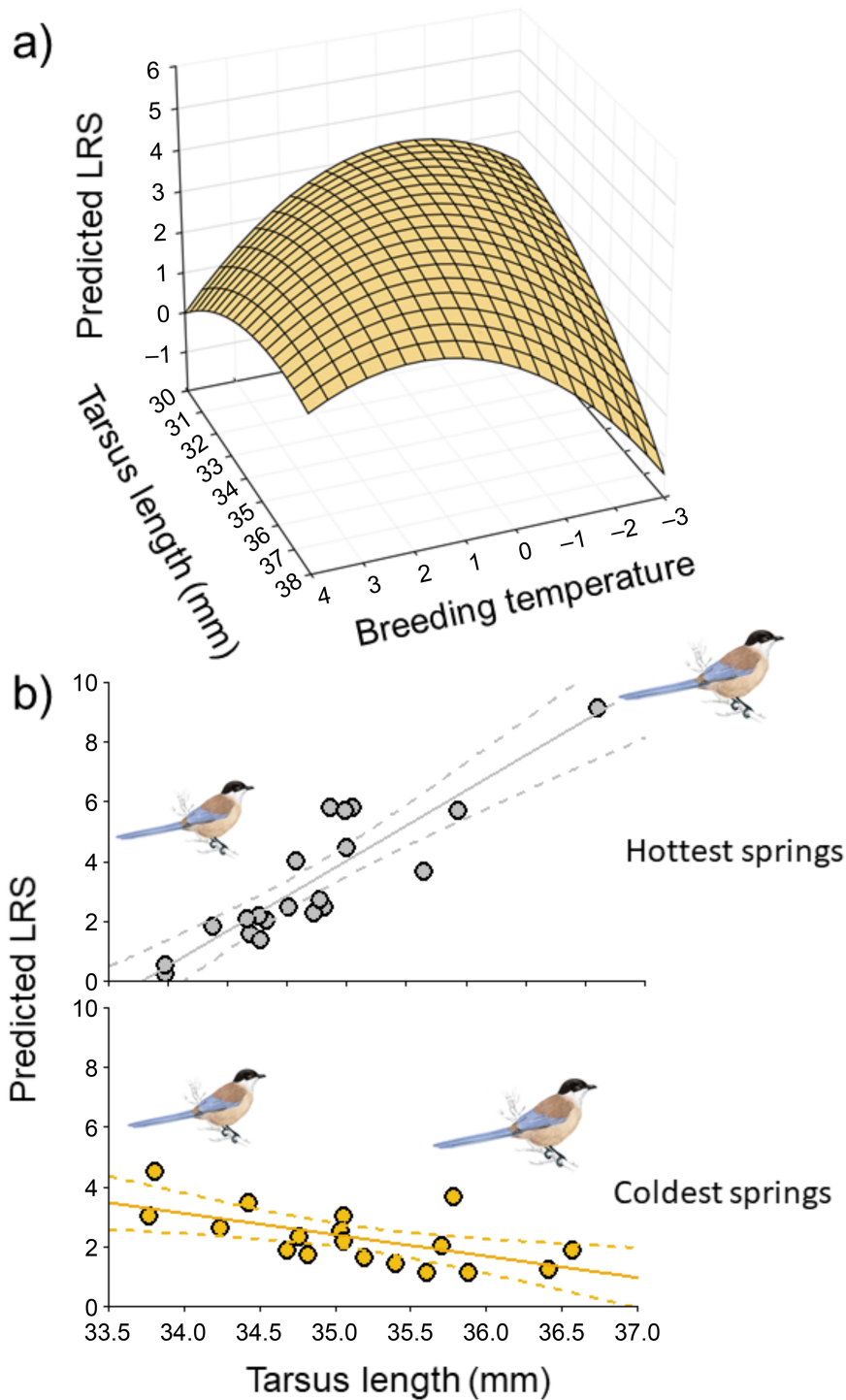


FIGURE 4 Lifetime reproductive success (LRS) depends on adult climatic conditions and body size in the Iberian magpie. (a) Relationship between total number of produced fledglings per male and tarsus length in interaction with adult temperature. The predicted surface from a Zero-inflated Poisson model is presented. (b) Detailed effects of body size on LRS. Shown are the predicted values of LRS in relation to tarsus length, regression lines (continuous lines reflect significant associations) and 95% CI, for hottest (i.e., above the third quantile of natal temperature [gray dots, $N = 18$ males]) and coldest (i.e., below the first quantile of natal temperature [orange dots, $N = 20$ males]) springs. Illustration credit for the Iberian magpie picture: Juan Varela.

There was not a significant interaction between natal temperature, adult temperature, and body size on LRS (Appendix S1: Table S7).

Natal and adult environmental conditions, body size, and lifespan

Male Iberian magpies lived on average 3.21 years (range 1–13; Appendix S1: Figure S1). Lifespan was significantly influenced by the interaction between body size and natal temperature (Negative binomial GLMM: $\chi^2_1 = 6.93$, $p = 0.01$; Appendix S1: Table S8; Figure 5). Males born in the driest springs exhibited a decline in lifespan with increasing body size, from 4.18 ± 0.59 (SE) years in smaller males to 2.29 ± 0.29 (SE) years in larger males ($F_{1,24} = 54.96$, $p < 0.001$; Figure 5). In contrast, no significant relationship was found between lifespan and the tarsus length for males born in the wettest springs ($F_{1,24} = 0.13$, $p = 0.71$). During these years, smaller males lived 3.24 ± 0.41 years, while larger males lived 3.04 ± 0.41 years (Figure 5).

Lifespan was also significantly influenced by the interaction between body size and brood size in the year of birth ($\chi^2_1 = 4.07$, $p = 0.04$; Appendix S1: Table S8; Figure 5). Males raised in nests with larger broods showed a lifespan decline with increasing body size, from 3.37 ± 0.48 (SE) in smaller males to 2.71 ± 0.24 (SE) in larger males ($F_{1,39} = 7.11$, $p = 0.01$; Figure 5). A similar trend, although not statistically significant, was observed for males raised in nests with fewer siblings ($F_{1,20} = 3.69$, $p = 0.07$), where smaller and larger males lived for 2.50 ± 0.42 and 4.03 ± 0.46 years, respectively (Figure 5).

Adult environmental conditions did not significantly interact with body size to affect lifespan (Appendix S1: Table S9). Furthermore, the reported effects of natal conditions were not modified by adult environmental conditions (Appendix S1: Table S10).

Temporal trends in body size

The tarsus length of male Iberian magpies that fledged or were recruited into the population showed no significant temporal change over the study period after correcting for natal laying date and capture date (Appendix S1: Table S11 and Figure S3).

DISCUSSION

In this study, we examined the intricate interplay between body size, climatic conditions, and fecundity in Iberian magpies, shedding light on the mechanisms that

shape the fitness outcomes in populations experiencing significant warming at their breeding grounds. Our findings provide compelling evidence supporting the hypothesis that body size is a critical mediator of climate impacts on fecundity in this species, a concept we termed “Size-dependent sensitivity.” We found that the adult body size of male Iberian magpies is not significantly influenced by early-life environmental conditions in a Mediterranean population that has experienced substantial warming over the last three decades. However, male body size was positively associated with maternal, but not paternal, body size, and was generally smaller in males reared in late spring nests, which are predominantly held by smaller females (Figure 2). In endothermic organisms such as birds, population-level patterns of adult body size variation reflect both genetic variation (Merila, 1997) and environmentally induced plasticity in growth rates during early development (e.g., Lepage et al., 1998; Ross et al., 2018). Our results suggest that adult body size in Iberian magpies is more strongly influenced by genetic factors than by proximate environmental conditions during development, even under rising temperatures. These findings align with experimental studies demonstrating minimal effect of developmental conditions on adult body size in passerines (Dawson et al., 2005; Schmidt et al., 2012), and strong correlations between offspring size and that of their genetic parents (Schmidt et al., 2012; Smith & Dhondt, 1980). However, genetic studies would be necessary to determine whether the lack of a relationship between the tarsus of males and the paternal tarsus can be explained by the occurrence of extra-pair copulations in the species.

In cooperatively breeding birds, the natal social environment can vary widely: while some offspring are reared by a single breeding pair, others are reared cooperatively by parents and helpers (Stacey & Koenig, 1990). Such variability likely has profound short- and long-term effects on offspring fitness due to differences in food provisioning between helped and non-helped broods. For instance, a long-term study of the Florida Scrub-Jay *Aphelocoma coerulescens* revealed complex effects of natal group size on fitness, contingent on territory quality (Mumme et al., 2015). Similarly, in the rifleman *Acanthisitta chloris*, the presence of adult helpers did not influence nestling mass or body condition but was associated with a long-term increase in the survival of closely related offspring (Preston et al., 2016). In our study, we found no evidence that the presence of helpers at the natal nest influenced males’ LRS or lifespan.

The absence of a direct effect of the natal conditions on adult body size does not preclude the possibility that a suboptimal natal environment could have affected growth strategies, physiology, or metabolism, with long-term fitness consequences (Dawson et al., 2005; Schmidt et al., 2012).

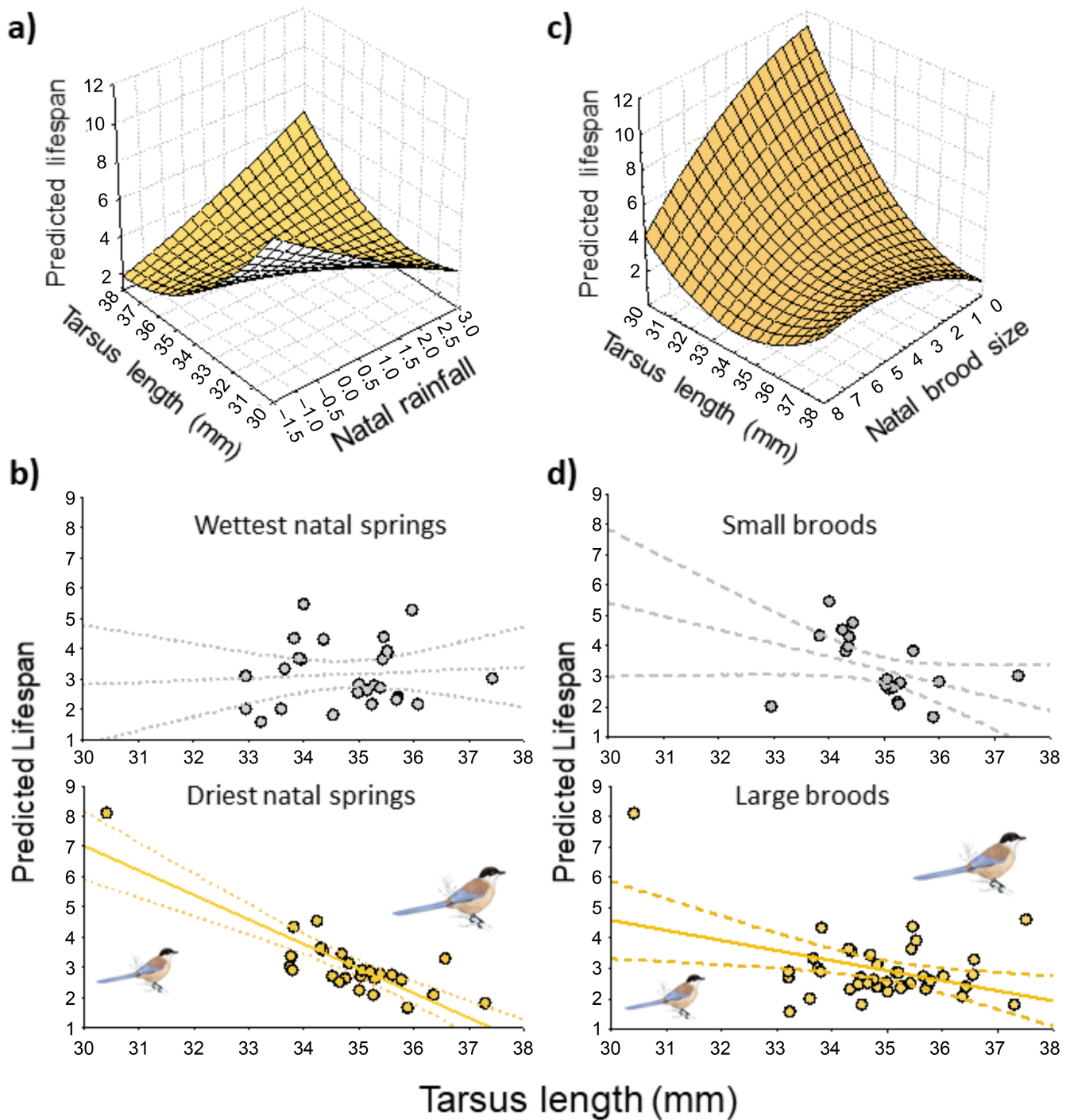


FIGURE 5 Lifespan depends on natal environmental conditions and body size in the Iberian magpie. (a) Relationship between lifespan and tarsus length in interaction with natal temperature. The predicted surface from a negative binomial general linear mixed model (GLMM) model is presented. (b) Detailed effects of body size on lifespan in the hottest and driest natal environments. Shown are the predicted values of lifespan in relation to tarsus length, regression lines (continuous lines reflecting significant associations), and 95% CI for hottest (i.e., above the third quantile of natal temperature [gray dots, $N = 26$ males]) and coldest (i.e., below the first quantile of natal temperature [orange dots, $N = 26$ males]) springs. (c) Relationship between lifespan and tarsus length in interaction with natal brood size. The predicted surface from a negative binomial GLMM model is presented. (d) Detailed effects of body size on the lifespan of broods with more and fewer nestlings. Shown are the predicted values of lifespan in relation to tarsus length, regression lines (continuous lines reflecting significant associations), and 95% CI for broods with more nestlings (i.e., above the median number of nestlings [gray dots, $N = 41$ males]) and fewer (i.e., below the median number of nestlings [orange dots, $N = 22$ males]). Illustration credit for the Iberian magpie picture: Juan Varela.

Indeed, we detected independent effects of natal climate and natal social environment on fitness, with the direction and magnitude of these effects being dependent on body size. These findings suggest that body size is a highly conserved trait that mediates the fitness consequences of natal environmental conditions in Iberian magpies.

We considered three theoretical scenarios to explain the fitness effects arising from the interplay between body size and natal and adult environmental conditions in the Iberian magpie (Figure 1). Our results revealed that fitness effects were not significantly influenced by the interaction between natal and adult environmental conditions. Additionally, the observed fitness effects mediated by the interplay between body size and natal environmental conditions were unaffected by adult environmental conditions. Therefore, the “environmental matching” scenario, which predicts higher fitness when natal and adult environmental conditions are similar, can be excluded (Figure 1), as this scenario requires, as a prerequisite, that fitness effects are mediated by the interaction between natal and adult environmental conditions (Monaghan, 2008). Furthermore, our results do not support the predictions of a pure “silver spoon” scenario (Figure 1), as the fitness effects of temperature, rainfall, and the social environment at the natal nest were dependent on body size. Instead, our findings align with the “size-dependent sensitivity” model (Figure 1), which proposes that the effect of adult environmental conditions depends on inherited body size, irrespective of natal environmental conditions. Specifically, we found strong evidence that larger males incur significant fitness costs when raised in poor natal environments. First, larger males raised during hotter years were globally less fecund than smaller males raised under the same conditions (Figure 3). Additionally, larger males had shorter lifespans than smaller ones when born during dry years or when raised in nests with many broodmates (Figure 5).

We do not yet know the exact mechanisms through which larger body size is penalized under adverse natal conditions. However, we can speculate that periods of early-life stress may have size-dependent effects on metabolic rates and energy expenditure in Iberian magpies. In sexually dimorphic species, the larger sex is generally considered more costly to rear and more susceptible to mortality due to its higher energetic needs and food requirements during development (Stamps, 1990). These factors make larger individuals particularly sensitive to unfavorable conditions (Chin et al., 2005). In Spain, higher temperature and lower rainfall during spring are associated with reduced insect availability (García & Arroyo, 2001; Salaberria et al., 2014). Additionally, brood-size manipulation studies have shown that sharing the nest with more siblings often impairs the development of nestlings in altricial birds (Boonekamp et al., 2014; Horak et al., 1999; Saino et al., 1997). Based on

these findings, we propose that larger Iberian magpie males, due to their greater energy demands, are disproportionately disadvantaged under nutritional stress caused by limited food availability or intense sibling competition in larger broods.

Interestingly, body size also mediated the effects of temperature experienced during adulthood. Larger Iberian magpie males that experienced hotter springs as adults produced more fledglings over their lifetimes. However, under colder spring conditions during adulthood, it was the smaller males that achieved greater reproductive success (Figure 4). One possible explanation is that in the resource-limited environments of hotter springs, larger body size confers advantages such as superior access to food or the ability to secure prime breeding sites by dominating smaller males (Blanckenhorn, 2000). Furthermore, there is extensive empirical evidence across many species showing that body size in males is a trait under strong sexual selection (Andersson, 1994; Andersson & Iwasa, 1996). Larger males may gain reproductive advantages either through improved success in male–male competition, where they can subdue smaller rivals (Andersson & Iwasa, 1996), or by being preferred by females as an indicator of high quality (Calsbeek & Sinervo, 2004). Although the exact mechanisms underlying the effects of warming on the viability and fecundity of Iberian magpies remain to be elucidated, our findings align with the third theoretical scenario (Figure 1) suggesting that the magnitude and direction of adult climate effects are mediated by structural body size.

Our population-level analyses revealed that the average tarsus size of male Iberian magpies has not changed over the past three decades, despite an observed temperature increase of $0.04^{\circ}\text{C}/\text{year}$ (Appendix S1: Figure S3). Numerous studies spanning several decades have documented reductions in bird body size in response to global warming across regions such as North America (Weeks et al., 2020; Youngflesh et al., 2022), the Amazon (Jirinec et al., 2021), Australia (Gardner et al., 2019), Israel (Dubiner & Meiri, 2022), and the United Kingdom (Yom-Tov et al., 2006). These studies have contributed to a generalized perspective that body size reduction in response to warming is a universal rule of climate change (Gardner et al., 2011). However, an increasing number of studies challenge this general pattern, reporting either an increase in body size concurrent with rising temperatures or no discernible trend. For example, body size increases have been observed in bird communities inhabiting the Usambara Mountains of Tanzania (Neate-Clegg et al., 2024), central California, United States (Goodman et al., 2012), and Australia (Gardner et al., 2014). Conversely, a lack of size change has been reported in South African birds (Lee et al., 2020). These deviations from the body size

reduction paradigm have been attributed to factors such as enhanced primary productivity and food availability in warmer conditions (Goodman et al., 2012; Neate-Clegg et al., 2024), or reduced energy expenditure for thermoregulation, allowing resources to be allocated toward growth (Gardner et al., 2014). In southern Spain, however, rising temperatures are associated with reduced insect availability (García & Arroyo, 2001), making such explanations unlikely for Iberian magpies. Our findings, which examine the effects of natal and adult environments on fitness through the lens of structural body size, provide an alternative mechanistic explanation for the observed stability in body size. Specifically, we demonstrate that the direction of climate effects differs between developmental and reproductive stages and depends strongly on genetic variation in body size within the population.

CONCLUSIONS

To better understand animal responses to climate warming, there is an urgent need for comprehensive studies examining patterns of body size change across diverse regions and ecological contexts (Ocampo-Peñuela, 2024). Despite focusing on a single bird species, our study identifies two previously unrecognized aspects of the context dependence of animal responses to climate change:

1. Climatic effects on a single species may differ—and even oppose one another—during developmental and reproductive stages.
2. Climatic effects may vary between individuals of different sizes within the same sex and population.

Globally, these findings provide a mechanistic framework for understanding body size stasis in the face of warming. They suggest that climate variation may favor different optimal body sizes for development and reproduction, cautioning against dismissing structural body size as a critical mediator of future climate impacts on animals.

AUTHOR CONTRIBUTIONS

Carlos de la Cruz and Juliana Valencia collected the data. Jesús M. Avilés, Carlos de la Cruz, Erick González-Medina, Auxiliadora Villegas, and José A. Masero conceptualized the study. Jesús M. Avilés led the analysis and writing. Erick González-Medina contributed to data analysis. Carlos de la Cruz, Erick González-Medina, Auxiliadora Villegas, Juliana Valencia, and José A. Masero revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Avilés, 2025) are available in Zenodo at <https://doi.org/10.5281/zenodo.15256198>.

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SUPPORTING INFORMATION

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

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