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The limits of demographic buffering in coping with environmental variation

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Animal populations have developed multiple strategies to deal with environmental change. Among them, the demographic buffering strategy consists in constraining the temporal variation of the vital rate(s) that most affect(s) the overall performance of the population. Tortoises are known to buffer their temporal variation in adult survival, which typically has the highest contribution to the population growth rate λ, at the expense of a high variability on reproductive rates, which contribute far less to λ. To identify the effects of projected increases in droughts in its natural habitat, we use field data collected across 15 locations of *Testudo graeca* in southeast Spain over a decade. We analyse the effects of environmental variables on reproduction rates. In addition, we couple the demographic and environmental data to parameterise an integral projection model to simulate the effects of different scenarios of drought recurrence on λ under different degrees of intensity in the survival–reproduction tradeoff. We find that droughts negatively affect the probability of laying eggs; however, the overall effects on λ under the current drought recurrence (one/decade) are negligible when survival is constant (independent of the reduction of reproduction by drought events) and when survival increased as a tradeoff with the reduction of reproduction rates, with a threshold to population viability at three or more droughts/decade. Additionally, we show that, although some species may buffer current environmental regimes by carefully orchestrating how their vital rates vary through time, a demographic buffering strategy is insufficient to ensure population viability in extreme regimes. Our findings support the hypothesis that the demographic buffering strategy has a limit of effectiveness when adverse conditions occur frequently. Our methodological approach provides a framework for ecologists to determine how effective the management of environmental drivers can be for demographically buffering populations, and which scenarios may not provide long-term population persistence.

Keywords: climate change, drought, integral projection models (IPM), life-history traits, population growth rate, reproduction rates, *Testudo graeca*, tortoise

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Introduction

The impact of changing environmental conditions on persistence is one of the main challenges facing species worldwide (Tuljapurkar 1990). Environmental stochasticity is predicted to increase with global climate change (Alexander et al. 2006, IPCC 2014). This environmental stochasticity can cause the decline of natural populations and lead to their extinction due to the physiological and demographic responses of organisms to unexpected climate conditions (Chown et al. 2010, Selwood et al. 2014, Radchuk et al. 2019). Thus, understanding how extant life-history strategies may respond to future changes, such as projected increases of drought recurrence (Burke et al. 2006) is critical (Coumou and Rahmstorf 2012). This knowledge is particularly needed in threatened species because of their frequently small population sizes and constrained distributions (Lanfear et al. 2014). Demographic descriptors, such as population size (n), ultimately control the degree of environmental stochasticity that a population can undergo before becoming locally extinct (Lanfear et al. 2014). Reductions in n via the negative effects of environmental stochasticity on underlying vital rates (e.g. survival, fecundity, growth) can lead to a population collapse if n reaches values lower than the minimum viable population size of the species (Shaffer 1981, Tuljapurkar 1990).

Species have evolved a wide range of life-history strategies to persist in different environments (Pianka 1970, Southwood 1988, Stearns 1992, Morris and Doak 2004, Boyce et al. 2006, McDonald et al. 2017). Examples of such strategies include large offspring size and/or extended parental care, which enhances offspring recruitment (Shine 1978); or self-pollination in low-density populations, which increases short-term population viability (Kalisz et al. 2004). This diversity of strategies ultimately emerges from the limitations imposed by finite resources and physiological constraints, which result in vital-rate tradeoffs (Stearns 1992). During the last decades, researchers have focused on classifying such strategies according to investments in specific vital rates (e.g. fast–slow continuum, reproductive strategies continuum; Gaillard et al. 1989, Stearns 1992, Bielby et al. 2007, Salguero-Gómez 2017, Healy et al. 2019). However, these classifications do not explicitly consider how the investments in each vital rate may vary with time and the implications of this variation for population viability (but see Pfister 1998, Doak and Morris 2010).

Evidence is starting to emerge regarding a continuum of strategies to deal with environmental variation that ranks species from highly demographically buffered to highly demographically labile (Pfister 1998, Koons et al. 2009). Demographically labile species, such as some annual plant species (Levine and Rees 2004), persist in stochastic environments by allowing the most sensitive vital rate(s) (i.e. those with large effects on population growth rate λ) to vary with environmental conditions, thus 'tracking the environment' (Koons et al. 2009, Jongejans et al. 2010). In contrast, demographically buffered species, such as long-lived mammals (Gaillard and Yoccoz 2003, Campos et al. 2017), tend to constrain the temporal variation of the vital rates that most affect population growth rate λ (Pfister 1998, Boyce et al. 2006, Hilde et al. 2020). A next logical step in this research agenda is to identify limits beyond which populations along different points on this continuum may no longer be able to cope with increasing environmental stochasticity (Doak and Morris 2010).

Chelonians are known to demographically buffer their vital rates in adverse environmental conditions (Heppell 1998). This taxonomic group includes some of the longest-lived tetrapods, such as Testudinidae or Emydidae, with lifespans of over 100 years (Castanet 1994). Chelonians are ideal organisms to investigate the possibility of limits to population viability under harsh climate conditions because they are ectothermic and therefore their vital rates are strongly influenced by the environment (Ihlow et al. 2012). Terrestrial tortoises exhibit high temporal variability in their reproductive output, which typically has a low contribution to λ (Doak et al. 1994). The reproductive rate in chelonians is also usually diminished due to adverse environmental changes, such as reductions in precipitation or increases in temperature (Turner et al. 1986, Nieuwolt-Dacanay 1997). However, tortoise populations buffer such negative impacts on reproductive rates through constant-through-time high adult survival rates (Turner et al. 1986, Henen 1997). Here, the role of vital-rate tradeoffs may be critical in enabling species persistence (Stearns 1992). For instance, a reduction in reproductive rates in adverse conditions can be countered by a constant or increased survival rates (e.g. *Homopus signatus*: Loehr 2010, Loehr et al. 2011 and, bird like *Parus major*: Reed et al. 2013). However, the projected increases in the frequency of adverse environmental conditions (Seneviratne et al. 2012) poses novel challenges for the viability of tortoise populations. Thus, identifying the limits of environmental variation beyond which demographically buffering species cannot persist is crucial for their effective conservation.

Here, we evaluate the population viability of a chelonian species, the spur-thighed tortoise *Testudo graeca*, in southeast Spain. We hypothesised that the projected increase in adverse condition frequency in the region will jeopardise the persistence of species, and the tradeoff between reproduction and survival will delay the threshold of species persistence. Using field demographic data collected over a decade together with bibliographic information on this species, we parameterise an integral projection model (IPM; Easterling et al. 2000) to: 1) identify the effects of environmental conditions on reproductive rates; 2) evaluate the effects of current and projected droughts on its population growth rates (λ); and 3) identify the vital rate(s) that is(are) most responsible for a decrease in population performance due to droughts using a perturbation analysis.

Methods

Study system

The spur-thighed tortoise, *Testudo graeca* (Testudinidae) is a long-lived endangered species (Vulnerable, IUCN 2012).

This species is distributed across North Africa, southern Europe and Southwest Asia (Graciá et al. 2017a). The largest population of *T. graeca* in Spain is located in the southeast of the Iberian Peninsula (Fig. 1a). In this area, *T. graeca* are distributed across ~2600 km^2 of semiarid mountains, where annual precipitation ranges between 150 and 570 mm year^{-1}. This species has slow population dynamics (sensu Wilbur and Morin 1988), steady population growth rates (i.e. $\lambda \sim 1$, Rodríguez-Caro et al. 2016), delayed maturation (9–12 years, Graciá et al. 2020) and low offspring production (< 2 hatching per female per year, Jiménez-Franco et al. 2020). The life cycle of the species includes three stages: juveniles, subadults and adults (Fig. 1b). The survival of juveniles is typically low due to their soft carapace coupled with high predation by wild boars, rats or foxes (Hailey 1988, Díaz-Paniagua et al. 1997), whereas in subadults (4–8 years old) and adults (reproductive individuals) survival is much higher (Sanz-Aguilar et al. 2011, Rodríguez-Caro et al. 2013).

To obtain reproductive information for this species, we conducted fieldwork within a decade (2006–2007, 2010–2011 and 2014–2016) across 15 sites of 1 km^2 (Fig. 1a) sampling a total of 634 females (Supporting information). The 1-km^2 sites represented a subpopulation of the species according to the movement patterns and home ranges of the tortoises (Anadón et al. 2012, Graciá et al. 2020). The timing of the sampling coincided with the peak of the reproductive season, in spring (April–June), so that adult females could be assessed for their reproductive status (Díaz-Paniagua et al. 1996). We captured individuals manually along line transects of 2 km, repeated three times per site (Rodríguez-Caro et al. 2017). For each individual, we measured its carapace length (CL) and femoral width (FW) with digital callipers. Adults were sexed according to their morphological characteristics – juveniles and subadults do not show sexual dimorphism (López-Jurado et al. 1979). Females and subadults are morphologically indifferentiable other than by size, and so we identified the minimum size in femoral width (FW_m) above which females lay eggs. All females were radiographed dorsoventrally with a portable X-ray machine set at 60 kV (20 mAs) at a distance of 1 m (Hinton et al. 1997), following methods described in Gibbons and Green (1979). In the radiography, we identified whether females carried eggs to estimate the probability of reproduction (φ) and, if so, counted the number of eggs (χ; Fig. 1b). We considered only females larger than $FW_m = 61$ mm for further analysis ($n = 534$ females) because this was the minimum observed size in our radiographic examinations of a female with eggs.

To parameterise our demographic model, we used survival (σ) and growth (γ) estimates from previous studies at the Galera site (Sierra de la Carrasquilla, Murcia, Spain 37°32′N, 1°39′W; Fig. 1). At that location, Sanz-Aguilar et al. (2011) estimated survival rates using 11 years of capture–recapture data (1999–2009) containing 1009 observations across 675 individuals of the same species. For our study, we used the survival rates estimated for 1999–2004 by Sanz-Aguilar et al. (2011): 0.20 (0.08–0.42, 95% CI) for juveniles, 0.79 (0.57–0.90) for subadults and 0.98 (0.92–0.99) for adults. Rodríguez-Caro et al. (2013) studied body growth patterns at the same site in a similar period (2000–2004). In it, 36 individuals were measured between captures and recaptures, and growth rates were modelled using von Bertalanffy regression models. We used this information to quantify individual growth rates based on carapace length (CL). Regarding the environment, the climate at this site between 1999–2004 (when survival and growth was collected) and 2006–2016 (when the reproduction information was collected) did not differ significantly (Kruskal–Wallis test $\chi^2 = 0.04$, $df = 1$, $p > 0.05$, for spring precipitation, the variable used in the analysis). Thus, the 1999–2004 and 2006–2016 environments were not viewed as confounds when using these data to paramterise our demographic model.

Environmental variables: temperature, precipitation and vegetation greenness

To examine the relationship between environmental variables and reproductive rates, we used satellite data to obtain monthly information on temperature, precipitation and vegetation productivity at each of the 15 sampled sites (Fig. 1a). For each site, we also calculated mean monthly temperature (°C), total monthly precipitation (mm) and the monthly mean of normalised difference vegetation index (NDVI), a proxy of primary productivity and biomass (Rouse et al. 1974) and, thus, resources for herbivores (Pettorelli et al. 2011). These variables were calculated for each year between 1995 and 2017. The temperature data were obtained from the Oxford daytime land surface temperature dataset at a 5 km^2 spatial grid resolution (Weiss et al. 2014). This temperature product is based on the moderate resolution imaging spectroradiometer (MODIS) land surface temperature data (MOD11A2), which was gap-filled to eliminate missing data caused by factors such as cloud cover using methods described in Weiss et al. (2014). Precipitation data were obtained from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS, Funk et al. 2015), a quasi-global gridded precipitation time series with 0.05° spatial resolution. We calculated NDVI using the MYD13Q1 V6 product (NASA Land Processes Distributed Active Archive Center). This MODIS NDVI product (spatial resolution of 250 m) is computed from atmospherically corrected bi-directional surface reflectance that have been masked for water, clouds, heavy aerosols and cloud shadows. Per-pixel quality assessment metadata (Huete et al. 2002) were used to check product performance to measure NDVI among study sites and across years. We calculated the average of all these variables within a 500 m buffer radius around the centre of the coordinates at each study site. This buffer area was selected to represent the local conditions of the sampled tortoise sites (1 km^2) without diluting nearby areas with different land uses (Anadón et al. 2006). Because average precipitation and temperature usually do not show large variability within small areas (e.g. our buffer area), we assumed that the spatial resolution of our precipitation and temperature data is representative of the climatic variability within the buffer area.

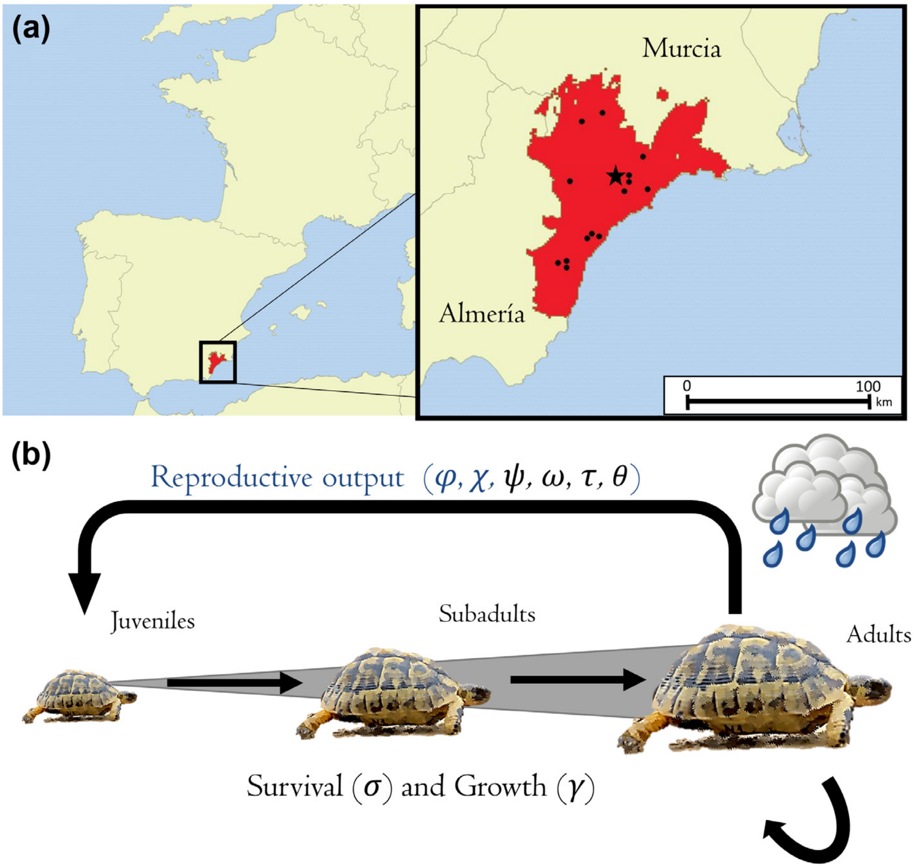

Figure 1. (a) Distribution of the spur-thighed tortoise *Testudo graeca* in the southeastern Iberian Peninsula (red). Black dots represent the locations of sampled sites, while the black star represents the location of the study site, Galera (Sierra de la Carrasquilla, Murcia, Spain 37°32′N, 1°39′W), for which we developed the drought simulations. (b) Life cycle of *T. graeca*, including three stages (juveniles, subadults and adults), and the different demographic processes used in our integral projection models. Individuals may grow to a given size with a probability γ if they survive (σ) from one year to the next. Only adults can reproduce. To quantify reproduction, we estimated the probability of reproduction (φ), the number of eggs produced per adult per clutch (χ), the number of clutches per year (ψ), the probability of hatching (ω), the probability of surviving to the one year (τ) and the size distribution of offspring the next year (θ) from field data. The vital rate parameters shown in blue are known to be affected by environmental conditions, and thus they are the focus of our study.

Statistical analysis of environmental variables

To identify the environmental drivers of population performance of *T. graeca*, we used a moving window approach (van de Pol et al. 2016). Briefly, this approach consists of testing the effect of a given environmental factor under different temporal windows on a chosen response variable and comparing these models to identify the factor that most affects the variable and the time window (Bailey and van de Pol 2016). We carried out this analysis using the package *climwin* (Bailey and van de Pol 2016) in R (<www.r-project.org>). We fitted each of the environmental variables (temperature, precipitation and NDVI) in different time windows to the reproduction data (probability of being reproductive, φ; and number of eggs, χ; Fig. 1a). We compared the models representing multiple (short- and long-lag) windows per each climatic variable. We determined a baseline model structure for reproduction (with the CL as a covariable) without environmental effects as a null hypothesis for φ and for χ, and we then tested the importance of several time windows. The time windows were measured in months, ranging in duration from 0 (i.e. same time as vital rate measurement) to 12 months (i.e. a year prior to the observation). We used an absolute time window method before the hypothetical censuses on 1 June of each year. We used generalised linear models with a binomial ('logit' link) and Poisson family ('log' link), for φ and χ, respectively. Lastly, we compared the *climwin* model outputs, and selected the best model as that with the lowest AIC (Burnham and Anderson 2002, Burnham et al. 2011).

We found a strong positive effect of precipitation on the probability of reproduction (φ, the best eight models are described in the Supporting information). However, we did not find a significant effect of any of the three environmental variables (precipitation, temperature or NDVI) on clutch size (χ). We found that the range of action of each environmental variable (temperature, precipitation and NDVI) on the probability of reproduction φ was significantly different. The positive effects of precipitation on the probability of reproduction φ were most conspicuous during the three months prior to the field measurement, while the negative effects of temperature included the full year prior to the vital rate measurement. On the contrary, the positive effect of NDVI included the last 6–7 months prior to the observation. Out of these climatic variables, spring precipitation prior to the sampling month (*p*) raised a more parsimonious model (ΔAIC of best model was −62.3) than temperature (ΔAIC of best model was −45.6) or NDVI (ΔAIC of best model was −33.6; Supporting information). Based on these analyses, we decided not to build multivariate models to predict vital rates as a function of these environmental variables since these variables were highly correlated (Pearson's $r > 0.75$, p-value < 0.05). Instead, we used the spring precipitation as the factor that affect the probability of reproduction.

Demographic modelling

To determine a potential threshold of drought recurrence beyond which this species is not able to persist against environmental stochasticity, we parameterised a stochastic integral projection model (IPM, Easterling et al. 2000). An IPM describes the structure *n* and dynamics of individuals in a population classified by one or more continuous traits *z*'s during the time period t to $t+1$ (Eq. 1, Ellner and Rees 2006). We parameterised the IPMs coupling the field and bibliographic demographic data, together with climatological data (spring precipitation, *p*), as described above, to analyse the effects of projected environmental changes on population dynamics. The single continuous state variable *z* in our IPM was carapace length (CL, mm), which is continuous over the three life stages (Fig. 1), using the data of Rodríguez-Caro et al. (2013) on the same population. The overall IPM is described by Eq. 1, where the kernel *K* represents the overall dynamics of the population. The *K* kernel can be sub-divided in the subkernels *P* and *F* (Eq. 2). The limits of the integral of *K* in Eq. 1 and 2 were initially evaluated as the minimum observed size ($L = 27$ mm) to the maximum observed size ($U = 176$ mm) across all sites and years. Following Williams et al. (2012), we checked for potential accidental eviction of individuals that would be projected to fall outside of the integration range [L, U]. Eviction of large adults occurred at values > U, and so we fixed U =180 mm to prevent accidental eviction. Extending the range of the upper integration limit did not qualitatively modify our results nor did it produce biologically unrealistic size transitions.

$$n(z',t+1) = \int_L^U K(z',z)\,n(z,t)dy \tag{1}$$

$$n(z',t+1) = \int_L^U \left[P(z',z) + F(z',z,p)\right] n(z,t)dy \tag{2}$$

The subkernel *P* describes how individuals may change linearly in trait *z* value (γ, growth), conditional on survival (σ) (Eq. 3). The subkernel *F* describes the contribution of reproductive individuals of size *z* at time *t* to new recruits of a given size z at $t+1$ and the probability of reproduction affected by spring precipitation *p* (Eq. 4). Here, the subkernel *F* is defined by the six vital rate functions described in the reproductive route of Fig. 1b: probability of reproduction in year *t* dependent on *p* (φ), number of eggs per clutch (χ), number of clutches per individual in time *t* (ψ), probability of egg hatching in time *t* (ω), survival probability of the offspring from t to $t+1$ (τ) and size distribution of offspring in $t+1$ (θ). As we developed this model just for females, we halved egg production under the assumption that the female–male sex ratio is 1:1, because the sex ratio in populations of the southeast of Spain is typically 1:1 (Graciá et al. 2017b). The vital rates φ and χ were estimated empirically in this study, and the remaining four (ψ, ω, τ and θ) were obtained from previous studies on the same species in Spain (Díaz-Paniagua et al. 1997, Keller et al. 1997, Graciá et al. 2020). The vital rate φ was estimated with generalized linear mixed model (GLMM), which included the linear and quadratic value of the size of female (*z*), the spring precipitation (*p*) and the population site as a random variable.

$$P(z',z) = \sigma(z)\gamma(z',z) \tag{3}$$

$$F(z',z,p) = \varphi(z,p)\chi(z)\psi\omega\tau\theta(z') \tag{4}$$

Population simulations

To evaluate the threshold of population viability against projected climatic regimes, we examined the difference between the effect of current environmental conditions and simulated climate change conditions on the species' population stochastic growth rate (λ_s). We carried out the simulation for the Galera site because the available data on survival and growth came from this population (Sanz-Aguilar et al. 2011, Rodríguez-Caro et al. 2013, more information on vital rates in the Supporting information). Population trends were estimated by projecting the population model over a 100-year period in 100 separate runs with an initial population size $n_0 = 1000$ individuals. The initial population distribution of *n* in Eq. 1 was obtained from the stable size distribution of the kernel *K*. This approach is biologically pertinent here because most sampled natural populations of this species are close to their stationary equilibrium (Rodríguez-Caro et al. 2019). Still, the subsequent sensitivity analysis we carried out to examine the influence of the initial size distribution on our demographic projections showed that our estimates of stochastic growth rates under different climate scenarios were insensitive to the initial population structure conditions (Supporting information).

As we found that the best moving window model showed a positive significant effect of spring precipitation (*p*) on the probability of reproduction φ, simulations of population viability included the effect of spring precipitation on φ. To simulate the effects of climate change on the viability of *T. graeca* populations, we quantified the current climate conditions, and then evaluated the effect of unusual increases in droughts on long-term demographic viability. The current regime of drought was estimated using standardised precipitation index (SPI) from 1961 to 2018 (Vicente-Serrano et al. 2017). We defined any precipitation values below the 10th percentile of SPI (−1.2) as a drought. Thus, the current scenario is characterised by one drought per decade. The harsher scenarios of climate models predict increases in droughts due to a ~20% reduction of precipitation in SE Spain (Amblar et al. 2017), with a consequent 1.5 droughts per decade. Next, we projected an increase in the decadal recurrence of droughts to identify the threshold of population growth rates of *T. graeca* against adverse conditions. We tested the recurrence of 1, 2, 3, 4 and 5 droughts per decade. For the simulations, we categorised two states of precipitation for the study site for further analyses: 1) drought years at 61 mm of spring precipitation (10th percentile of the historical records of precipitation at the Galera site, 1995–2017), and 2) normal years at 104 mm of spring precipitation (computed as the average of the historical records of precipitation without the 10th percentile). We simulated the recurrence of droughts from one to five droughts per decade probabilistically and randomly for each simulation (P(drought) = 0.1, 0.2, 0.3, 0.4 and 0.5, respectively).

To explore how the existence of tradeoffs between reproduction and survival may shape the outcomes of population-level responses to drought recurrence, we simulated vital rate combinations. These simulations were implemented to overcome a limitation in our data: empirical evidence regarding how droughts affect survival and reproduction come from the same population but different time windows (e.g. reproduction was quantified between 2006 and 2016, while survival between 1999 and 2004). Using the 2006–2016 data, we estimated the probability of reproduction in drought years at 0.48, and in normal years at 0.85 using the GLMM for the Galera site. We carried out simulations to explore the parameter space of extreme correlations between survival and reproduction, and thus the best- and worst-case scenarios for their correlations. Importantly, this approach provides a useful methodological pipeline for other researchers interested in these kinds of questions. Here, three combinations of vital rates were considered: 1) constant adult survival (mean value from Sanz-Aguilar et al. 2011: 0.98), regardless of how drought affects reproduction; 2) survival–reproduction tradeoff, whereby when reproduction decreases in drought years (probability of reproduction = 0.48), adult survival increases, reaching the upper bound of the 95th confidence interval (0.99) from Sanz-Aguilar et al. (2011). Here, for normal years, we used the mean value of adult survival (0.98) and the probability of reproduction estimate according to the precipitation (0.85); and 3) survival–reproduction positive correlation, which accommodates the fact that a bad environmental year releases less resources (Glazier 1999), and so both survival and reproduction should be affected negatively. This combination is based on the premise that tradeoffs will be unobservable if variance in resource acquisition is greater than variation in resource allocation; therefore, survival and reproduction would positively covary (Van Noordwijk and de Jong 1986). We carried out this scenario by using the lowest value from the 95th confidence interval of adult survival rate (0.92) from Sanz-Aguilar et al. (2011) under drought events, which affects the probability of reproduction (0.48). In normal years, both rates show the same values when compared to previous simulations.

For each of the simulations, we calculated the stochastic population growth rate (λ_s) as:

$$\log(\lambda_S) = \frac{\log(n_t) - \log(n_0)}{t} \tag{5}$$

where n_0 is the population size at time $t = 0$ and n_t the population size at time t (100 years for all simulations). Population size decreases when $\log(\lambda_s) < 0$ and increases when $\log(\lambda_s) > 0$, whereas $\log(\lambda_s) = 0$ indicates a demographically stable population.

We performed perturbation analyses in our IPMs to identify the different contributions of the vital rates parameters to population growth rate λ (Griffith 2017) under the different climate regimes: normal year (spring precipitation = 104 mm year^{-1}), or drought year (61 mm year^{-1}) with 1) constant adult survival, 2) survival–reproduction tradeoff and 3) survival–reproduction positive correlation, as defined above. We employed a brute-force method to calculate the elasticity of λ to parameter-level vital rates (Morris and Doak 2002). Briefly, this approach involves increasing the value of a particular vital rate parameter of interest (e.g. intercept or slope of the function relating size to survival) by an infinitesimal amount (here 0.001) while keeping all other parameters unaltered and calculating the effect on λ compared to its original, unperturbed value. We chose to carry out this elasticity analysis at the vital rate parameter-level rather than higher levels like whole vital rate or IPM mesh-discretised bin-level because a vital rate parameter-level elasticity provides a greater insight into the underlying mechanics of size-dependency in vital rates (Griffith 2017). We estimated the confidence interval of the elasticities of λ to the underlying vital rate parameters using 999 bootstraps of the individual-level data (Hall and Martin 1988). To develop the bootstrap, we used constant values for the rates from bibliography (survival, growth and the parameters of reproduction such as sex-ratio, hatchling size, number of clutches), and then we resampled the parameters related to reproduction with different subsets of the empirical data: probability of laying eggs (φ) and the number of eggs (χ).

Results

Simulations of drought recurrence

In our simulations of population performance, under the current climatic regime with either constant adult survival or a survival–reproduction tradeoff (i.e. high values of adult survival in drought events), the population is demographically stable. Our model under the current climatic conditions of one drought per decade produced an estimate of stochastic population growth rate $\log(\lambda_s) = 0.0000$ (-0.0001 to 0.0000, 95% CI) when the survival is assumed to be independent from reproduction (simulation with constant adult survival). Similar values are obtained under the survival–reproduction tradeoff scenario. On the other hand, the survival–reproduction positive correlation scenario produces negative declining populations, even when only one drought occurs per decade: $\log(\lambda_s) = -0.0011$ (-0.0012 to -0.0010, 95% CI; Fig. 2).

To explore the limit of this tortoise species' ability to deal with increasingly adverse conditions, we simulated different recurrence intervals of droughts per decade. The performance of the population under a projected scenario of two droughts per decade in the constant adult survival scenario also results in demographic viability: $\log(\lambda_s) = -0.0002$ (-0.0003 to 0.0000). The simulation of three droughts per decade results in a negative stochastic population growth rate $\log(\lambda_s) = -0.0004$ (-0.0004 to -0.0003), as is also the case for any scenario with a greater drought recurrence (Fig. 2). In the same vein, when there is a survival–reproduction tradeoff scenario, the population maintains similar results as with the constant adult survival scenario, resulting in a declining population under three droughts per decade ($\log(\lambda_s) = -0.0003$; -0.0004 to -0.0002) or more.

Perturbation analyses

To examine the role of vital rates on the population performance of this endangered species under different climatic conditions, we examined the elasticity of the population growth rate. Under normal conditions (no drought; green bars in Fig. 3), the slope of growth (γ slope) shows the largest and positive effect on λ. This result highlights the importance of the growth of larger individuals, which grow faster than smaller ones when γ slope increases. In other words, when the slope increases (while keeping the growth intercept unaltered), smaller individuals grow less than the larger individuals. Next, the parameters with larger elasticity values are the slope and the quadratic slope of the size in the probability of reproduction (φ slope and φ slope 2) and the slope of survival (σ slope). The relatively large and positive elasticity of λ with respect to the slope of the probability of reproduction (φ slope) is related to a direct increase in the reproductive values (larger females are more likely to reproduce.). The quadratic slope of the probability of reproduction (φ slope 2) is negative, which means that increasing φ slope 2, the values of the parameter is more negative and the probability to reproduce is lower. The effects of the remaining parameters related to reproduction are negligible (Fig. 3).

The vital rate parameter elasticity profile for this species under drought conditions remains similar to that under normal conditions with constant adult survival (grey bars, Fig. 3) and survival–reproduction tradeoff (gold bars, Fig. 3). Key differences between normal years and drought years with constant adult survival emerge with the reduction of all the vital rate parameters, making this reduction in elasticity values higher under the survival–reproduction tradeoff scenario. On the other hand, larger differences in all parameters are found in the survival–reproduction positive correlation scenario (beige bars, Fig. 3), where the elasticities to growth and survival increase, especially for the slope of growth (γ slope). This result highlights the disproportionally important role of

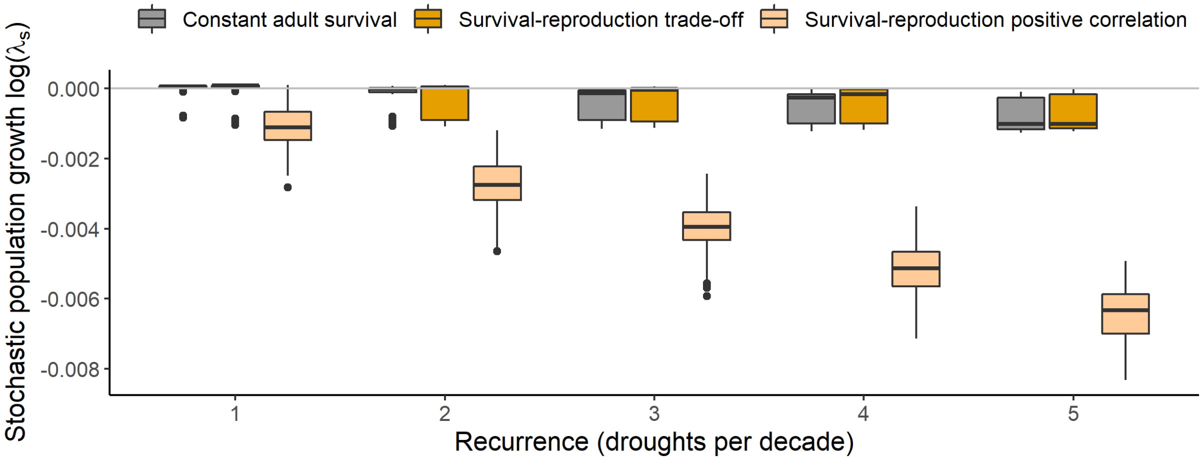

Figure 2. Simulated stochastic population growth rates ($\log(\lambda_s)$) of the spur-thighed tortoise at the Galera population (Fig. 1) under the current precipitation regimes (1 drought per decade) and under different drought recurrence intervals with different combination of survival and reproduction. The three combinations are: constant adult survival, the adult survival is constant and independent of the reproduction rates; survival–reproduction tradeoff, the adult survival increases with decreasing probability of reproduction; and survival–reproduction positive correlation, adult survival and probability of reproduction both decrease in droughts events. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values of the 95% of the interquartile range, and dots are the outlier values, defined as data outside this range. The grey line represents a stable population ($\log(\lambda_s) = 0$). All scenarios of survival–reproduction positive correlation and any scenario of constant adult survival and survival–reproduction tradeoff where droughts occur three or more times per decade produce a statistically unviable stochastic population growth rate.

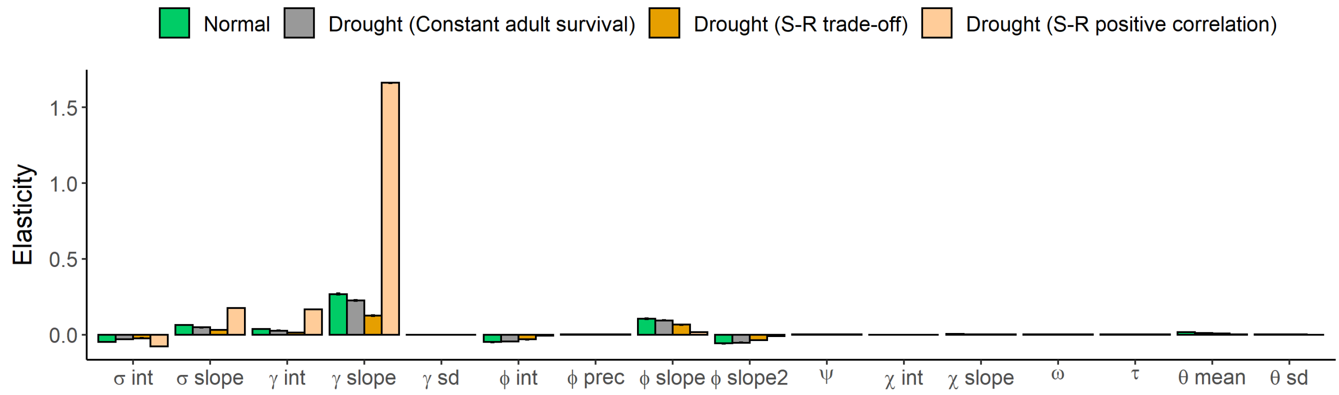

Figure 3. Elasticity of population growth rate λ with respect to the different vital rates parameters involved in the life cycle of *Testudo graeca* (Fig. 1b) under a regime of normal precipitation (green), drought with constant adult survival (grey), drought with survival–reproduction trade-off (gold) and survival–reproduction positive correlation (beige). Normal years are defined as those with a spring precipitation of 104 mm, the average precipitation of the long-term weather data at the Galera population (Fig. 1a); Drought years are defined as those with a spring precipitation of 63 mm (10th percentile at the same location). The vital rates parameters are: survival intercept (σ int), and slope (σ slope); growth intercept (γ int), slope (γ slope) and variability in growth rate using the standard deviation (γ SD); probability of reproduction intercept (φ int), slope of linear size effect (φ slope), quadratic size effect (φ slope2) and precipitation effect on the intercept (φ prec); the constant of number of clutches per year (ψ), number of eggs produced per adult per clutch intercept (χ int) and slope (χ slope); the probability of hatching (ω); the probability of surviving to the next year (τ); the mean of the size distribution of offspring of the next year (θ mean) and its standard deviation (θ SD).

growth under adverse conditions. In contrast, the elasticity to vital rate parameters depended on the probability of reproduction decrease with drought regimes under the assumption of survival–reproduction positive correlation. Thus, in the scenarios where adult survival is at its lowest value (drought conditions and correlation between reproduction and survival), the relative importance of reproduction for the performance of the population decreases.

Discussion

Demographically buffered species cope with environmental stochasticity by allowing vital rates (e.g. survival, reproduction) with low importance for population growth to vary with environmental conditions (Pfister 1998, Forcada et al. 2008, Morris et al. 2008, McDonald et al. 2016). A significant amount of demographic research has focused recently on determining when species can buffer demographically (Boyce et al. 2006, Hilde et al. 2020) but have not considered environmental limits to which this strategy remains advantageous (but see Doak and Morris 2010). Here, we hypothesised that projected climate conditions will jeopardise species with a demographic buffering strategy once environmental variation exceeds some limits. We used an integral projection model parameterised with 10 years of field data in the endangered *Testudo graeca* species to estimate the effect of drought in reproduction rates, combined with bibliographic information of growth and survival rates. Our results demonstrate that a reduction in adult survival due to drought conditions (simulations where both adult survival and probability of reproduction rates decrease in drought years) does not allow for the viability of its populations under any drought recurrence scenario. Although this scenario can be possible in other populations, this result does not seem realistic because the current population trend in the studied population is stable (Rodríguez-Caro et al. 2016, 2019). However, when adult survival was high (scenarios with a tradeoff where reproduction decreases and survival increases in drought events) and/or constant (survival remains constant and independent of drought events), the population showed stable trends. Our modelling exercise also provides strong evidence for the existence of a limit beyond which our study species cannot persist. In simulated conditions with too high recurrence of drought, the population dynamics showed negative, unviable trends. Even the simulation with the highest value of adult survival (in the tradeoff scenario where reproduction decreases while survival increases due to drought events) offered the same limit, wherein populations become unviable under three or more droughts per decade.

The increase in extreme droughts recurrence is one of the main threats of climate change for species (Burke et al. 2006, Seneviratne et al. 2012). Specifically, dryland ecosystems in the Mediterranean Basin are highly threatened by climate change and desertification with potentially irreversible impacts on populations (Maestre et al. 2012a, b). Such increases in the recurrence of adverse environmental conditions have been extensively documented to reduce the viability of populations (Beissinger 1995), change life history strategies (Haaland and Botero 2019, Lyberger et al. 2021) and to even cause their eventual extinction (Griffiths and Williams 2000). Population collapses due to droughts have already been reported in several species, including amphibians (Walls et al. 2013), mammals (Duncan et al. 2012) or invertebrates (Oliver et al. 2015). Our results suggested that the capability of maintaining the stable population growth rates against drought events has a limit. This limit only became evident when the drought recurrence was greater than that predicted by harsher climate change scenarios.

As we expected for long-lived species, growth and survival were key vital rates for their demographic performance (Heppell 1998), followed by parameters related to the probability of reproduction. Growth was the most important demographic process in the elasticity analysis to maintain the population growth rate. Indeed, growth patterns are central to life-history theory, influencing other life-history traits such as survival and reproduction (Roff 2002), since size at maturity has been described as one of the most important life history traits for turtles and tortoise (Shine and Iverson 1995). Meanwhile, survival rates showed a lower effect than growth on the demographic performance of the species (unlike other chelonians; Cunnington and Brooks 1996). Finally, out of all the reproductive processes, probability of reproduction had the greatest effect on population growth rate (Fig. 3). In drought scenarios we found two patterns, when adult survival is constant or high in drought events (due to a tradeoff between reproduction and survival, because reproduction decreases in drought years), the contributions of all parameters to population growth rate decreased, this could be a direct consequence of the buffering strategy of the species to maintain population growth rate (Heppell et al. 2000). However, with a survival–reproduction positive correlation, where both rates had the lowest values when a drought occurs, there was an increase in importance of growth and survival parameters, neglecting the effect of reproduction rates. Our results are an example of how trait-based analyses provide accurate insight into the life cycle of the species (Ozgul et al. 2012). Although the uncertainty in model parameters is useful to understand the life history strategy of the species, structural model uncertainty can also be important when conducting population viability analysis (Stephens et al. 2002, Radchuk et al. 2014).

Despite the importance of existing theory to predict demographic responses to environmental variability, most of the existing studies have focused on the vital rates that greatly affect the growth rate of populations (Pfister 1998), such as adult survival in the case of long-lived species (Rotella et al. 2012, Becker et al. 2018, Graciá et al. 2020). However, the effect of reductions in reproductive rates of long-lived species on the population viability have been less studied (but see, Turner et al. 1984, Capdevila et al. 2019, Jiménez-Franco et al. 2020). Thus, it is important to note that in our simulations, the effect of environmental conditions on reproduction, and survival rates were simulated in three different scenarios: constant adult survival, survival–reproduction tradeoff and survival–reproduction positive correlation. Negative effects of drought on survival have been described in other related species (Longshore et al. 2003, Mitro 2003) and positive or non-effects have also been found (Loerh 2010). According to previous studies in our studied population, environmentally-driven reductions in adult survival would heavily reduce population growth rates and drive local extinctions (Graciá et al. 2020). Our approach highlights the importance of the less studied vital rates for the conservation of species.

Here, we have shown that the effect of climate change on the reproduction of the spur-thighed tortoise was driven via a lack of precipitation. Although our results support that the species can be stable under current levels of drought events, harsher environments or the interaction with other factors (such as high temperature or fire), could increase the risk of local extinction (Díaz-Paniagua et al. 2006, Sanz-Aguilar et al. 2011). These harsher conditions could already be present in certain locations within the range of this species due to microhabitat conditions, particularly in south-facing slopes (Quero et al. 2006), and could result in local extinctions. Additionally, the synergistic effects of droughts and fires have been described as a threat for endangered animal populations such as reptiles (Lunney et al. 1991), especially in Mediterranean ecosystems (Mouillot et al. 2002). In terms of reproduction specifically, increases in temperature are well known to affect the sex ratio determination in the eggs of reptiles, with hotter years resulting in more females (Pieau 1975). The sex-ratio bias in the offspring can significantly reduce the matting encounters for further generations, affecting its demographic viability (Graciá et al. 2020) or even cause the disappearance of one gender (Janzen 1994).

Our work contributes to a growing body of literature that uses demographic approaches on long-term, detailed demographic monitoring, coupled with high-resolution climatic data and bibliographic information to investigate demographic responses to environmental variation (Gaillard et al. 1989, Campos et al. 2017, Paniw et al. 2018, Capdevila et al. 2019). The challenges involved in measuring population dynamics from empirical studies of wildlife animals are numerous, often requiring various data from different resources to obtain all the necessary parameters to adequately describe the life cycle of the species of interest (Forcada et al. 2008, Graciá et al. 2020). Our model may also be used in an approach with climate variable as a continuum covariate in the IPM to gain a more detailed insight of climate change scenarios. Here, however, we used just categorical scenarios (drought versus normal years) to help guide the management of endangered species in conservation policies with a clearer message. The integration of multiple sources of detailed data into a single demographic model allowed us to look beyond the demographic effects of current environmental stochasticity and to reveal thresholds of environmental variations which can negatively affect endangered species.

Our modelling approach can be readily applied to other long-lived demographically buffering species. Researchers can also consider including means to evaluate and determine breakpoints for buffering such as interactive effects (e.g. temperature, disturbances; Darling and Côté 2008) or temporal autocorrelation (Tuljapurkar and Haridas 2006, Paniw et al. 2018). Multiple environmental variables may interact to exacerbate, or cancel out in some cases (Paniw et al. 2017), their effects on natural populations (Darling and Côté 2008). These variables can be explicitly included in the

IPM simulations by testing their effects on each vital rate (Capdevila et al. 2019). On the other hand, temporal environmental autocorrelations, which realistically incorporate important aspects of future climatic projections (Paniw et al. 2018), can be included in these models using Markov chain approaches. When accounting for autocorrelation, one identifies the different environmental states and the frequency of changes among them and then couples them with demographic models, parameterised under each environmental state, to finally simulate different walks through these chains (Tuljapurkar and Haridas 2006).

Conclusions

This study contributes to our understanding of how species with demographic buffering strategies can cope with stochastic environments and provides a useful modelling framework to predict population responses to environmental change. Moreover, through perturbation analyses, this framework allows us to identify the demographic mechanisms that mediate environmentally-driven population decline. Although here we have found that *Testudo graeca* is currently demographically stable, there is a limit of population viability to frequent adverse conditions which could jeopardise their long-term viability.

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Author contributions

Roberto C. Rodríguez-Caro: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Writing – original draft (equal). **Pol Capdevila**: Formal analysis (equal); Writing – review and editing (equal). **Eva Graciá**: Conceptualization (equal); Data curation (equal); Writing – review and editing (equal). **Jomar M. Barbosa**: Data curation (equal); Formal analysis (supporting); Writing – review and editing (equal). **Andrés Giménez**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Writing – review and editing (equal). **Rob Salguero-Gomez**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q83bk3jhs> (Rodríguez-Caro et al. 2021).

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