

Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise

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Abstract

Climatic shifts may increase the extinction risk of populations, especially when they are already suffering from other anthropogenic impacts. Our ability to predict the consequences of climate change on endangered species is limited by our scarce knowledge of the effects of climate variability on the population dynamics of most organisms and by the uncertainty of climate projections, which depend strongly on the region of the earth being considered. In this study, we analysed a long-term monitoring programme (1988–2009) of Hermann's tortoise (*Testudo hermanni*) aimed at evaluating the consequences of the drastic changes in temperature and precipitation patterns predicted for the Mediterranean region on the demography of a long-lived species with low dispersal capability and already suffering a large number of threats. Capture–recapture modelling of a population in the Ebro Delta (NE Spain) allowed us to assess the effect of climate variability on the survival of tortoises. Winter rainfall was found to be the major driver of juvenile and immature survival, whereas that of adults remained high and constant across the study. Furthermore, local climate series obtained *ad hoc* from regional climate simulations, for this and 10 additional Mediterranean locations where tortoises occurred, provided us with reliable future climate forecasts, which were used to simulate the fate of these populations under three precipitation scenarios (mean, wet and dry) using stochastic population modelling. We show that a shift to a more arid climate would have negative consequences for population persistence, enhancing juvenile mortality and increasing quasiextinction risk because of a decrease in recruitment. These processes varied depending on the population and the climate scenario we considered, but our results suggest that unless other human-induced causes of mortality are suppressed (e.g. poaching, fire, habitat fragmentation), climate variability will increase extinction risk within most of the species' current range.

Keywords: climate projections, demography, extinction risk, population matrices, precipitation, survival, *Testudo hermanni*

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Introduction

Climate change, manifested through global warming and changes in the distribution, amount and frequency of precipitation, is a major cause of concern worldwide as its impacts on all ecosystems are becoming increasingly apparent (Parmesan & Yohe, 2003; IPCC, 2007). Observational evidence indicates that the average temperature of the globe has increased by about 0.74 °C over the last four decades, and that this trend is inducing some ecological responses such as changes in phenology, shifts in species distribution and changes in community composition (McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003).

Ecological responses to climate change are mediated by local rather than by global changes in temperature and precipitation patterns. The spatial heterogeneity of

climatic conditions across a species range calls for examining responses at the population level when studying species' responses to climate change (Grosbois *et al.*, 2006; Wolf *et al.*, 2010). Local changes have a direct impact on demographic rates (Forchhammer *et al.*, 1998; Saether *et al.*, 2000; Sillett *et al.*, 2000; Coulson *et al.*, 2001; Jenouvrier *et al.*, 2005), modifying local population dynamics and resulting population-specific responses across the geographic range of a species (McCarty, 2001). The species' inherent ability to withstand climatic shifts determines the type of responses displayed and thus the vulnerability of its populations to local environmental changes; species with low dispersal capability and with populations occurring in fragmented habitats will be unlikely to adapt to rapid environmental changes by shifting their geographic distribution and colonising new suitable areas in different altitudes or latitudes (Root & Schneider, 2006; Loss *et al.*, 2011; Foufopoulos *et al.*, 2011). Hence, their persistence will depend strongly on the degree of

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variation in local conditions, with potentially higher extinction risks in areas already suffering population declines because of nonclimatic stressors and where important changes in climate are predicted (Sala *et al.*, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Fofopoulos *et al.*, 2011).

As a consequence, it is essential to forecast the future responses of natural systems to changes in the climatic conditions to implement mitigation strategies aimed at increasing or maintaining the resilience of organisms to such changes (Hannah *et al.*, 2002; Coenen *et al.*, 2008; Hagerman *et al.*, 2010; Hansen *et al.*, 2010). Long-term datasets of populations occurring in relatively undisturbed areas enable us to correlate life-history parameters and population trends to climate variability without the confusing effects of other stressors in the underlying climatic trend (Parmesan & Yohe, 2003). However, these datasets are rare and many studies that investigate the regional consequences of climate change on the biota rely on species-specific climatic envelopes to forecast species distributions under future climatic scenarios (Rebelo *et al.*, 2010) rather than forecasting population responses to projected regional climate changes (but see (Jenouvrier *et al.*, 2009; Wolf *et al.*, 2010).

Reptiles have recently been considered a vulnerable taxonomic group, given that important population declines have been detected worldwide and that climate change is suspected to be one of the drivers of this global trend (Gibbons *et al.*, 2000). Among reptiles, land tortoises (family Testudinidae) are likely to be the most vulnerable, given their low dispersal capabilities, their occurrence in fragmented habitats and that most species are already threatened (26 of the 32 evaluated species; IUCN 2011). These features should be particularly important in arid and semiarid ecosystems, such as the Mediterranean region. Sala *et al.* (2000) classified the Mediterranean basin as one of the regions where the consequences of climate change will be more pronounced, forecasting dramatic losses in biodiversity. Indeed, recent observations reveal a surface warming trend of 0.25 to 0.35 °C per decade over the last 40 years and a decrease in annual precipitation amounts between 5% and 20% for the same period, and these trends are expected to continue in the future (IPCC, 2007), in addition to a higher frequency of drought events and heat waves (Piervitali *et al.*, 1997). Rainfall patterns are more difficult to predict than temperature because of the local variability imposed by topography, distance from the sea and land use (Gao *et al.* 2006), but precipitation is likely to increase its seasonal character, and occur in the form of intense events (Sánchez *et al.*, 2004). These predicted trends will contribute to a general increase

in aridity over the entire Mediterranean region (Christensen *et al.*, 2007).

Here, we examine the effects of climate variability on the population dynamics of Hermann's tortoise (*Testudo hermanni*), a threatened reptile species endemic to the Mediterranean region, to forecast the population responses to the regional climate changes predicted for this area. Hermann's tortoise occurs throughout the entire European Mediterranean region. Factors, such as habitat destruction, illegal collection for the pet trade, use of pesticides, forest fires and increase in predation pressure are generally thought to be responsible for the decline of Hermann's tortoises (Stubbs & Swingland, 1985; Stubbs *et al.*, 1985; Guyot & Clobert, 1997; Hailey, 2000; Cheylan, 2001; Matache *et al.*, 2006; Rozyłowicz & Dobre, 2009). Nevertheless, the role of climatic variability (which may be additive to the other drivers of population decline) in the population dynamics of tortoises and other reptiles remains poorly understood (but see Converse *et al.*, 2005; Chamaille-Jammes *et al.*, 2006), and to our knowledge, there is no information on the magnitude of the demographic responses to future regional climate changes in any ectothermic vertebrate. To shed some light upon the matter, we begin by assessing the correlation between local climate variability and survival rates using data from a long-term monitored population in the Ebro Delta (western Mediterranean) inhabiting a semiarid environment and lacking anthropogenic disturbances. Then, we will build stochastic population models to investigate the consequences of future climate variability for the whole geographical range of the species distribution. Instead of using general circulation models, which cannot resolve regional particularities of climate (Tabor & Williams, 2010), here we use a set of regional climate simulations for the 21st century and derive local series using an empirical calibration method that improves climate projections by accounting for local relevant factors for the study populations, allowing us to make more realistic predictions of their quasiextinction probabilities under several possible future climate scenarios.

Materials and methods

Study area and population

This study was carried out at Punta de la Banya reserve, a protected area located in the Ebro Delta Natural Park (NE Spain, 40°37'N, 00°35'E; Fig. 1). Punta de la Banya is a flat sandy peninsula covering 2514 ha, connected to the mainland by a long, narrow natural isthmus. Its legal protection and relative isolation from the mainland guarantee a lack of human disturbances, fire events and, most of the time, intrusions of terrestrial predators into the area (for more details,

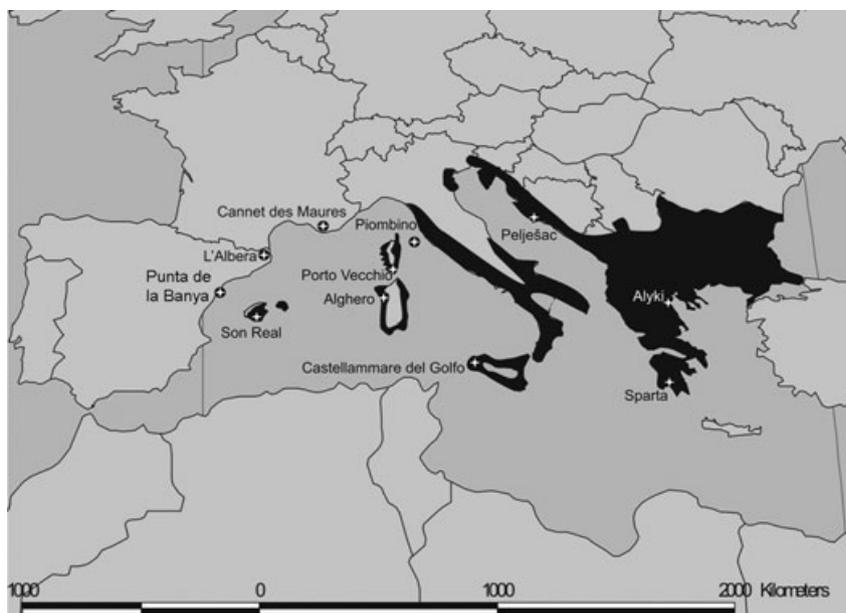


Fig. 1 Present-day geographic distribution of the Hermann's tortoise and location of the populations mentioned in this study.

see Bertolero *et al.*, 2007a,b). The area lies within the thermo-Mediterranean climatic zone, with more than a third of the annual precipitation being registered in autumn. Meteorological data collected in the Park (see next) show a mean daily temperature of 16.8 °C and a mean annual rainfall of 474.7 mm; these values are within the range of a semiarid ecosystem (Quézel & Barbero, 1982).

As part of a local conservation effort aimed at Hermann's tortoises, 44 individuals were released in the southern portion of the reserve between 1987 and 1988, with a second batch of 22 individuals released between 1997 and 1998 (see Bertolero, 2002; Bertolero *et al.*, 2007b). Prior to the first release, the Punta de la Banya lacked any established population of Hermann's tortoise although the area lies within the historical range of the species (Bertolero & Martínez-Vilalta, 1994). Reintroduced individuals were a mixture of adults and subadults from captive populations in different Spanish localities but all belonging to the western subspecies *T. h. hermanni*. All released tortoises were marked individually with notches in the carapace (see Bertolero *et al.*, 2007b for more details). Reproduction was recorded soon after the first release (Bertolero, 2002; Bertolero *et al.*, 2007a).

Capture–recapture data

Our capture–recapture monitoring was focused on those tortoises born in the wild at Punta de la Banya reserve (descendants of reintroduced adults). Tortoises were visually encountered by walking across the release area and surrounding patches of pine forest and vegetated dunes (suitable tortoise habitats), where individuals can potentially disperse (long distance dispersal is unlikely, given that most of the peninsula is marshland or unsuitable tortoise habitat). Tracks left on the sand and the hearing of tortoise's movement through the bush helped in our search. One person (A. Bertolero) was

involved in the surveys 85% of the days, whereas in the remaining 15%, surveys were performed by that person accompanied by 1–7 observers (mean: 2.0, SD: 0.1). When first encountered, tortoises were marked with notches in the carapace for future recognition and their age was estimated by carapace size and by counting the number of growth rings in the scutes, following Bertolero *et al.* (2005). Thanks to the annual monitoring of the population, those individuals showing deteriorated notches or those in their growth stages were re-marked to avoid tag loss or future misidentification of doubtful animals.

The first wild-born tortoises were detected in autumn 1988, but capture–recapture sampling did not start until 1991. Since then, continuous annual monitoring has resulted in a 19 year long capture–recapture dataset (1991–2009). Tortoises were captured or recaptured each year from April to June, a period of negligible length when compared with the between-captures interval (see Lebreton *et al.*, 1992), which ensures mortality to be more likely outside the sampling months. Here, we only included those individuals born in the wild since 1988, because they were the only known-age individuals, which allowed us to include age classes in the survival analysis. Most wild-born individuals (77%) were first encountered at age 0 and 1 (tortoises within their first and second years of life), but some of them were first encountered several years after birth. Individuals were sorted according to their age at first marking into 14 different groups (from age 0 to age 13, the oldest age at which one animal was first encountered). Considering that the first individuals were born in autumn 1988, a wild animal first caught in spring 1991 could be either 0, 1 or 2 years old, and since our dataset goes from 1991 to 2009, the maximum possible age attained by a monitored tortoise was 20 years. Thus, our age-at-first-marking groups were combined with the time since marking to build 20 age classes for survival analysis.

Local weather data

We obtained local meteorological records from 1991 to 2009 taken at the Ecomuseum Meteorological Station located in Deltebre, 17 km away from the study area. To test the effects of climate on tortoise survival, we used monthly values of temperature and accumulated rainfall. We were interested in year-round weather data, excluding the sampling months (April to June) for correlating the observed weather with the survival probabilities estimated for each year. Weather during hibernation (November to February), posthibernation (March) and summer months (July to September) may have consequences for the survival of tortoises (Díaz-Paniagua *et al.*, 2001; Converse *et al.*, 2005). In our analysis, we used the following environmental covariates: winter rainfall (total rainfall from November to February), summer rainfall (total rainfall from July to September), March rainfall (total rainfall in March), winter temperature (average minimum temperature from November to February) and summer temperature (average maximum temperature from July to September). Rainfall was supposed to be a biologically relevant covariate for our study species as it determines water and food availability, leading us to the prediction of a positive relationship between rainfall and tortoise's survival. More specifically, dry winters would be detrimental for Hermann's tortoise's survival by inducing mortality through dehydration during hibernation (Gregory, 1982) and through a reduction in the amount of food availability in the following spring. March rainfall may be critical for recovering hydration level after hibernation, whereas summer drought may increase tortoise's mortality by desiccation and starvation (Peterson, 1994). We did not consider rainfall during late spring (April–June) as a covariate because this period overlapped with sampling and survival was estimated out of the sampling months; the fact that these months corresponded to both the end and beginning of two consecutive annual intervals makes the effect of late spring rainfall on survival difficult to assess since it may affect simultaneously the survival estimated at both intervals. In terms of temperature, we expected that the coldest days would have the largest potential to reduce the survival of overwintering tortoises, so we used minimum temperatures to check our prediction of a positive relationship between winter temperature and survival. In summer, the highest temperatures would have the largest potential to reduce survival, so we used maximum temperatures to check for a potential negative relationship between summer temperature and survival.

Capture–recapture modelling

Our capture–recapture dataset was analysed using Cormack–Jolly–Seber (CJS) and related models to obtain separate estimates of both survival and recapture probabilities (Lebreton *et al.*, 1992). This approach does not differentiate mortality from permanent emigration, so that the obtained survival estimates must be referred to as local or apparent survival rates. However, in our long-term monitoring programme, individuals that have not been detected in a previous year (because of dispersal to less surveyed sites; see fig. 1 in Bertolero *et al.*, 2007b) may be recaptured in subsequent sampling occasions

the following years, so a continuous monitoring allowed us to control for dispersal within the study area and obtain local survival rates that may be really close to real survival rates.

Prior to the modelling of our capture–recapture data, a goodness-of-fit (GOF) test was performed using program U-CARE (Choquet *et al.*, 2005) to make sure that the data followed the CJS model assumptions (Lebreton *et al.*, 1992). Owing to a high capture effort in the field (nearly all adult individuals were captured and/or recaptured each year, see Bertolero, 2002) and the low dispersal rates of tortoises, we expected a low proportion of transients (individuals caught once but never recaptured again).

The large number of age classes considered increased the complexity of model notation, because a given effect can be important for one age class or parameter, but not for others. We chose a model notation similar to the one used in Catchpole *et al.* (2000), in which each modelled parameter was separated by a '/' symbol. The model assuming a full age effect (20 age classes) for the survival probability, Φ , and recapture probability, p , was then denoted $\Phi_0/\dots/\Phi_{19}$, $p_0/\dots/p_{19}$. The subscript indicates the age of the tortoise and the symbol '/.../' indicates that all age classes in between were modelled separately. To simplify model structure, we grouped the age parameters that had similar values into a single class: the age classes were denoted by the first and the last age of the class joined by the underscore symbol '_'. For example, a model assuming the same survival for individuals from age 6 to 19 was noted as Φ_{6_19} . The effect of time was denoted in brackets after the parameter as (t); therefore, full age and time interactions were expressed as $\Phi_0(t)/\dots/\Phi_{19}(t)$, $p_0(t)/\dots/p_{19}(t)$. Additivity between parameters was denoted with the symbol '//', and when parameters were assumed to vary in parallel over time, with no interaction, the notation was $\Phi_0(t)//\dots//\Phi_{19}(t)$, $p_0(t)//\dots//p_{19}(t)$.

Models were built using program M-SURGE (Choquet *et al.*, 2004). We began with the modelling of the recapture probability p , considering a first model with full interaction of age and time in both survival and recapture. Once we found the best model for p , we kept this structure to model survival following the same procedure to obtain a consensus model, a parsimonious model for both recapture and survival. Afterwards, climatic covariates were introduced, and the amount of variation in survival explained by the covariate was assessed through an ANODEV test with a Fisher–Snedecor distribution, which compares the deviances of the constant model with the corresponding time-dependent model and the model including the covariate (Skalski *et al.*, 1993). Model selection was made following the Akaike information criterion (AIC) (Burnham & Anderson, 2004). We selected our best model as the one with the lowest AIC value, whereas models that differed in less than 2 values of AIC ($\Delta\text{AIC} < 2$) were considered statistically equivalent.

Climate projections

Climate projections for the 21st century were derived from the output of 13 regional climate models (RCMs) produced in the framework of the ENSEMBLES European project (Hewitt &

Griggs, 2004; further information at: <http://ensembles-eu.metoffice.com>). Simulations were run from 1951 to 2100 using the A1B emissions scenario (SRES) forcing, which is a scenario of intermediate emissions that considers a balanced use of fossil and nonfossil fuels. These RCMs operate at 25 km horizontal grid-length spatial resolution, allowing for a more explicit representation of local factors of climate than the most commonly used atmosphere-ocean general circulation models (Tabor & Williams, 2010). Here, we consider a multimodel approach to deal with the uncertainties arising from model error formulations (i.e. the representation of physical processes within RCMs) and also the inaccuracies found in their boundary conditions. Despite the enhanced representation of regional scale processes and geographical settings, RCM outputs still contain inaccuracies in climate representation at local scales. In order to generate data suitable for our analyses, we have applied to each RCM output a quantile–quantile statistical adjustment described in detail by Amengual *et al.* (2011).

In this study, for each tortoise population (see 'Population modelling'), the nearest available weather station within the World Meteorological Organization Global Telecommunication System database was used as the climatic historical record for the site. Regarding the future projections, daily-averaged simulated mean temperature and precipitation for each individual model were bilinearly interpolated to the individual sites from the grid points within a radius of 2° (Akima, 1978, 1996). Then, observed monthly mean temperatures and accumulated rainfall from 1980 to 2009 (the most complete historical record) were calculated and used as a baseline in the calibration method. In particular, the statistical calibration approach consists of calculating the changes in the continuous cumulative distribution functions (CDFs) of the monthly mean atmospheric variables between the 30 year simulated baseline period (i.e. 1980–2009) and successive 30 year simulated time slices from 2009 to 2099. These variations are corrected and then transferred to the observed CDFs for the baseline period. Thus, the new calibrated CDFs successfully convey the local climate signal for the subsequent time intervals (Amengual *et al.*, 2011). By doing this, we obtained 13 calibrated series of monthly mean temperature and accumulated rainfall spanning from December 2009 to November 2099 for each tortoise population. Since we were mainly interested in November to February precipitation (see 'Results'), we calculated yearly total winter rainfall values by adding up the monthly values from November to February. As a result, we obtained a time series of winter rainfall for the period 2009–2099 for each RCM and tortoise population.

To simplify the statistical treatment of the multimodel climatic projections, the ensemble mean together with an upper and lower confidence bound series (wet and dry, respectively) were considered in our population models. These upper and lower bound series were produced by either adding or subtracting the yearly winter intra-RCM standard deviation to or from the corresponding mean value. These three time series are assumed to encompass the set of most likely precipitation scenarios for each tortoise population: the most probable (represented by the ensemble mean), an upper

bound (i.e. favourable wet conditions) and a lower bound (i.e. representing very unfavourable dry conditions).

Population modelling

We built a 7-age class Leslie matrix based on the most parsimonious structure found in our population (see 'Results'), and considered a life cycle where only animals in the oldest age class were breeding (Fig. 2). Matrix entries for survival and fecundity were extracted from this study and the available literature (see next and Table 1).

Population projections were run using the software ULM (Legendre & Clobert, 1995). We performed a projection for each of the 11 populations of Hermann's tortoises from several Mediterranean sites (see Fig. 7). For each model, we introduced in the population matrix all the demographic data available; adult survival and fecundity rates (clutch size and frequency) were available for Punta de la Banya (this study and Bertolero *et al.*, 2007a) and populations in Corsica (Henry *et al.*, 1999), Greece (Willemsen & Hailey, 2001) and mainland France (Guyot, 1996), whereas for the remaining sites, we used adult survival and fecundity rates averaged from those available in the literature for several populations, excluding the one at Punta de la Banya, because here the common environmental and anthropogenic threats for tortoises were absent (Table 1). Juvenile survival rates were defined as a function of the local precipitation scenarios predicted for each locality as found in our survival analysis (see 'Results').

The initial number of female tortoises was known only for Punta de la Banya (28 adult females in 1988). For the other ten populations, we started each projection considering an initial number of 200 females (a relatively optimistic scenario without strong demographic stochasticity), assuming an initial stable age distribution (SAD) as in Punta de la Banya (see 'Results'). We considered that a population was not viable when the number of females decreased to 10% of the initial number, so we set the quasiextinction threshold at $n = 20$ females.

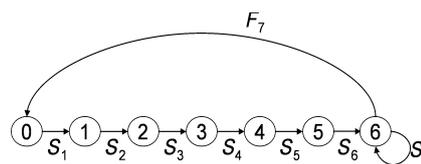


Fig. 2 Life cycle with prebreeding census for the Hermann's tortoise population occurring at Punta de la Banya reserve. Our capture period overlapped with mating and egg-laying, but hatching occurred a few months later; therefore, the number of female offspring present in the population the following year (F_7) was the product of the number of eggs laid per female (or mean clutch size, CS), the mean number of clutches laid by adult female in each season (or clutch frequency, CF), the sex ratio of the offspring (assumed to be $sr = 0.5$) and a survival rate of hatchlings from September to April (s_0), which was assumed to be the same as the survival of the first age class (s_1).

Table 1 Demographic rates (mean \pm SE) reported from several populations of Hermann's tortoise that were used in the population modelling

Population	Adult survival	Clutch size	Clutch frequency
Punta de la Banya (Ebro Delta, Spain)	0.97 \pm 0.01*	2.71 \pm 0.19†	1.38 \pm 0.16†
Porto-Vecchio (Corsica, France)	0.95 \pm 0.02‡	4.01 \pm 0.19†	1.67 \pm 0.17†
Maures (France)	0.92 \pm 0.02§	2.64 \pm 0.20**	1.4 \pm 0.1‡‡
Alyki (Greece)	0.91 \pm 0.02¶	3.60 \pm 1.50††	1.90 \pm 0.50††
Sparta (Greece)	0.80 \pm 0.03§§	–	–
Litochoron (Greece)	–	4.10 \pm 1.10††	2.40 \pm 0.80††
Deskati (Greece)	–	6.00 \pm 0.60††	2.40 \pm 0.80††
Average values¶¶	0.90 \pm 0.06	3.84 \pm 1.22	1.95 \pm 0.45

Complete data on adult survival and fecundity was only available for Punta de la Banya, Porto-Vecchio, Maures and Alyki populations. For the remaining sites (Sparta, Albera, Son Real, Alghero, Castellammare del Golfo, Piombino and Pelješac peninsula) we used averaged values for survival and fecundity when one or both rates were unknown. Litochoron and Deskati populations were not modelled but provided complementary clutch size and frequency values that were used to calculate average fecundity rates.

References: *This study, †Bertolero *et al.* (2007a), ‡Henry *et al.* (1999), §Guyot (1996), ¶recalculated from Hailey (2000), **Longepierre *et al.* (2003), ††Hailey and Loumbourdis (1988), ‡‡Fertard (1992), §§Willemsen & Hailey (2001).

¶¶The average is calculated using data from all populations, excluding Punta de la Banya.

We began by a deterministic population projection for Punta de la Banya and ran this simulation for three periods; 1988–1997, 1998–2009 and 2010–2099 (comprising the study periods after the first and second releases and our future time horizon). By doing so, we were able to calculate the SAD in our study area and the time needed for the population to reach it. We then performed a population projection introducing environmental stochasticity into both adult survival and fecundity parameters by means of probabilistic distributions (Beta and Gaussian, respectively; Samaranayaka & Fletcher, 2010). Juvenile survival was defined as a function of winter rainfall. To simulate population growth between 1988 and 2009, we used the actual local winter rainfall values recorded during this period, whereas from 2010 onwards, we used sequences of winter rainfall for the three future scenarios obtained from RCMs covering the study area. To obtain mean population growth rates, population sizes and quasiextinction probabilities, we ran 1000 Monte Carlo simulations for each scenario. By running simulations for the period 1988–2009, we were able to assess whether the obtained mean population size in 2009 was close to the size estimated for that year using capture–recapture techniques. Stochastic population projections conducted for the other 10 Mediterranean localities were run from 2010 to 2099 in the same way. Since these populations are subjected to many disturbances (pollution, habitat destruction, poaching, predation and fire events), environmental stochasticity was assumed to have only negative effects on adult survival and fecundity.

Results

Recapture and survival probabilities

Our data set comprised 255 encounter histories, with 19 capture occasions and 14 age-at-first-marking (called 'age' hereafter) groups. Significant trap-dependence and transient effects were detected by directional tests

(Z-tests; see Choquet *et al.*, 2005) in some of the age-groups, but the overall GOF statistic indicated that our model assuming time-dependent parameters on each age-group described the data adequately ($\chi^2 = 162.15$, $df = 191$, $P = 0.94$).

Model building began with the modelling of recapture probability (Table 2). We simplified the structure of the departure model and increased model parsimony when recapture probability was allowed to vary only with age (model 16 vs. model 17), but we finally obtained the best model structure when an additive effect of age and time was considered (model 17 vs. model 14). Survival was modelled following the same criteria: we also found an additive effect of age and time on survival, but model selection revealed the existence of only seven age classes in survival. The factorial 'time' effect describing the year-to-year variation in survival was then replaced by the climate covariates (temperature and rainfall) to assess their relationship to survival. Winter rainfall (November to February) was the best-supported environmental covariate. The ANODEV test showed a higher positive effect of winter rainfall on the survival of younger age classes than on older ones, with no rainfall effects on the survival of the oldest age class (aged 6 years and older). We kept survival for the oldest age class constant and left an additive effect between age and rainfall on the survival of the younger age classes (model 1): this was selected as the most parsimonious model, with a model weight of almost 90%. The model that was finally selected showed that recapture probability remained high most of the years and increased with age (Fig. 3 and Fig. S1). Survival showed a gradual increase from 0.39 (95% CI: 0.22–0.59) for 0 year old to 0.97 (95% CI: 0.95–0.98) for

Table 2 Ranking of models performed in the survival capture–recapture analysis for Hermann’s tortoises at Punta de la Banya (Ebro Delta), showing the model structure for survival (Φ), recapture probability (p), number of parameters (np), deviance (DEV), and AIC values for each one

Model	Φ	p	np	DEV	AIC	Δ AIC	ω_i
1	Φ_0 (winter rain)//...// Φ_5 (winter rain)/ Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	45	1618.16	1708.16	0	0.876
2	Φ_0 (winter rain)//...// Φ_{6-19} (winter rain)	$p_0(t)$ //...// $p_{19}(t)$	45	1622.11	1712.11	3.950	0.122
3	$\Phi_0(t)$ //...// $\Phi_{6-19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	61	1599.66	1721.66	13.503	0.001
4	$\Phi_0(t)$ //...// $\Phi_{7-19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	62	1598.10	1722.10	13.940	0.001
5	$\Phi_0(t)$ //...// $\Phi_{8-19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	63	1597.86	1723.86	15.703	0.000
6	$\Phi_0(t)$ //...// $\Phi_{19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	73	1578.71	1724.71	16.548	0.000
7	$\Phi_0(t)$ //...// $\Phi_4(t)$ // $\Phi_{5-19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	60	1607.70	1727.70	19.542	0.000
8	Φ_0 (summer temp)//...// Φ_5 (summer temp)/ Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	45	1642.87	1732.87	24.714	0.000
9	Φ_0 (summer rain)//...// Φ_5 (summer rain)/ Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	44	1647.31	1735.31	27.150	0.000
10	Φ_0 /...// Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	44	1647.32	1735.32	27.160	0.000
11	Φ_0 (winter temp)//...// Φ_5 (winter temp)/ Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	45	1646.28	1736.28	28.124	0.000
12	Φ_0 (march rain)//...// Φ_5 (march rain)/ Φ_{6-19}	$p_0(t)$ //...// $p_{19}(t)$	45	1646.50	1736.50	28.347	0.000
13	Φ_0 /...// Φ_{19}	$p_0(t)$ //...// $p_{19}(t)$	56	1632.62	1744.62	36.464	0.000
14	$\Phi_0(t)$ /...// $\Phi_{19}(t)$	$p_0(t)$ //...// $p_{19}(t)$	55	1752.56	1862.56	154.401	0.000
15	$\Phi_0(t)$ /...// $\Phi_{19}(t)$	$p_0(t)$ //...// $p_{6-19}(t)$	42	1798.56	1882.56	174.401	0.000
16	$\Phi_0(t)$ /...// $\Phi_{19}(t)$	p_0 /...// p_{19}	38	1824.24	1900.24	192.076	0.000
17	$\Phi_0(t)$ /...// $\Phi_{19}(t)$	$p_0(t)$ /...// $p_{19}(t)$	35	1873.92	1943.92	235.761	0.000

Δ AIC is the difference in Akaike information criterion (AIC) value when comparing the current model with the selected best model. Akaike weight (ω_i) is the probability that a model is the best model of the set discounting parsimony.

≥ 6 years old tortoises (Table 3). Winter rainfall had a significant positive effect on survival of juveniles and immatures [Pearson correlation coefficient (95% CI) = 0.568 (0.120–0.824), $P = 0.017$]. The lower survival rates of the younger age classes fluctuated according to local winter rainfall, with increased survival in wetter years (Fig. 4), whereas in older age classes, we found a less pronounced variability in survival, which became constant in the oldest age class.

Climate projections

The winter (November to February) rainfall series predicted by the RCM’s reveal high spatial variability

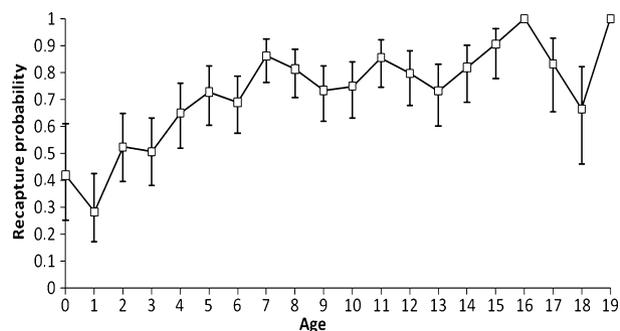


Fig. 3 Age-related recapture probabilities of tortoises at Punta de la Banya, drawn from the outputs of model 16.

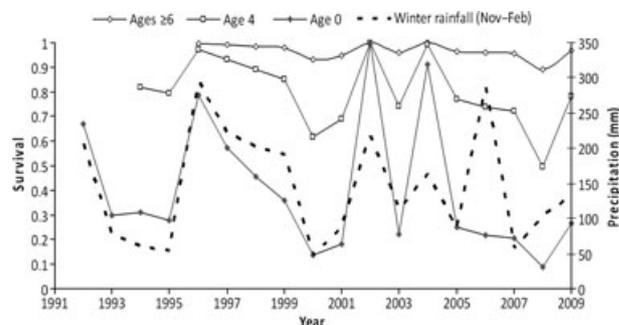


Fig. 4 Yearly fluctuations in survival (only mean values are shown) for ages 0, 4 and ≥ 6 at Punta de la Banya, taken from the survival time-varying model (see model 3 in Table 2). The dotted line shows the total winter rainfall (November to February) recorded at the Ebro Delta each year of the study period.

among geographical locations of Hermann’s tortoise throughout the Mediterranean (Fig. 5), owing to the strong modulation that local factors produce on the absolute accumulations (Lionello *et al.*, 2006). The Spanish sites show the lowest rainfall amounts, with annual winter values barely exceeding 200 mm, whereas French and Italian sites reach 300–400 mm per winter. The unique series for Pelješac exceeds a mean of 600 mm observed winter rainfall, arguably because of its surrounding rugged terrain.

The dry, mean and wet scenarios projected by the multimodel ensemble of RCMs depict a variety of

Table 3 Survival estimates for Hermann's tortoises at Punta de la Banya for each age; 95% confident intervals (in brackets) and SE are given. Results shown are from model 10 (see Table 2)

Age	Survival	SE
0	0.39 [0.22–0.59]	0.10
1	0.45 [0.31–0.60]	0.08
2	0.77 [0.59–0.89]	0.08
3	0.68 [0.53–0.80]	0.07
4	0.86 [0.70–0.94]	0.06
5	0.88 [0.76–0.95]	0.05
≥6	0.97 [0.95–0.98]	0.01

future evolutions with regard to the winter rainfall resource for Hermann's tortoise populations. Eastern-most sites tend to show diminishing amounts over the century for the three scenarios, with Sparta and Castellammare being the most severely affected locations with losses of up to 30% at the end of the century. In other areas, such as Punta de la Banya, Son Real and Alghero, none of the winter precipitation scenarios are projected to have statistically significant changes over the considered periods, meaning that, for the Spanish sites, future winter precipitation amounts are expected to continue being the lowest among the range of Mediterranean locations analysed here. Additionally, note the large uncertainty sites, such as Maures, Porto-Vecchio and Piombino display, with both increasing and decreasing amounts for the wet and dry scenarios, respectively.

Population projections

The deterministic population projection for Punta de la Banya yielded a population growth rate (λ) of 1.078 for the first 10 years after the first release (period 1988–1997), a λ of 1.027 for the study period after the second

release (1998–2009) and a λ of 1.016 when projected for the whole future time horizon (2010–2099). Departing from the initial time, the population reached a SAD after 28 years, with 43% of the individuals belonging to the oldest age class (Fig. 6). Under environmental stochasticity, Monte Carlo simulations yielded a mean population growth rate of 0.998 (SE: 0.0001) for the postreleases study period (1998–2009). The predicted number of female tortoises the year 2009, having considered both reintroduction events, was 76 ± 0.1 , meaning a total population size of 152 individuals that year, assuming a 1 : 1 sex ratio; this value was slightly lower than the population size estimated [182 tortoises (95% CI: 105–265); A. Bertolero, unpublished data] but within the 95% confidence interval for this estimate. Projections for the 21st century (2010–2099) showed a positive trend under future mean and wet scenarios, with mean population growth rates higher than 1, whereas a negative trend was obtained when projecting the population under a dry scenario (Table 4, Figs 7 and 8). Under this scenario, the population would reach the quasiextinction threshold after 89 years (Table 4, Fig. 9).

The stochastic population projections performed for the other 10 Mediterranean populations yielded mean population growth rates ≥ 1 for the mean and wet scenarios, whereas below 1 growth rates and negative population trends were detected in some populations when considering dry scenarios (Albera and Son Real in Spain and Alyki in Greece; Table 4, Figs 7 and 8). Under a dry scenario and starting from a population size of 200 females, the quasiextinction threshold was reached after 31 years in Son Real, 35 years in Albera and 62 years in Alyki (Table 4, Fig. 9).

Discussion

To our knowledge, this is the first study to assess the effects of climatic covariates on survival of Hermann's

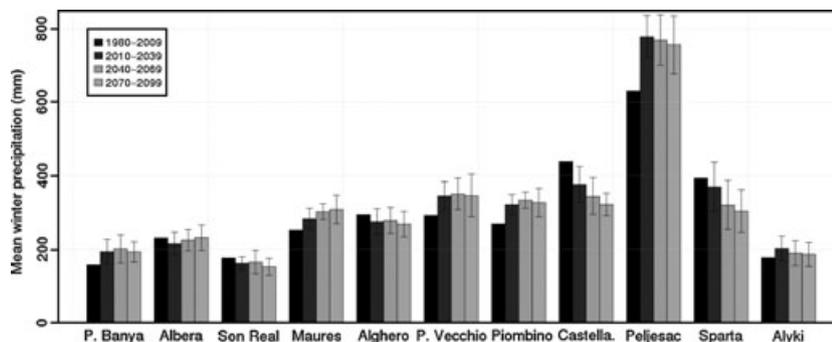


Fig. 5 Mean winter accumulated precipitation for 30 year periods spanning over present (1980–2009), early (2010–2039), mid (2040–2069) and late (2070–2099) 21st century. 'Present' values correspond to the nearest available SYNOP station to the 11 Hermann's tortoise population locations. Projected values result from the multimodel mean and vertical bars denote the intermodel standard deviation which define the mean, dry and wet scenarios used throughout the text. Note the west-east order of the sites for easier interpretation.

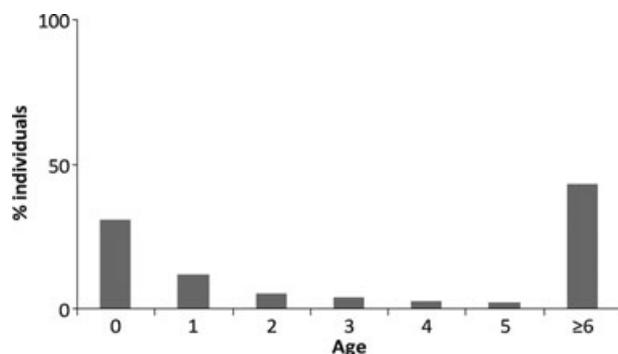


Fig. 6 Proportions of individuals when stable age distribution is reached in our study population of Hermann's tortoises.

tortoise and the first to forecast population responses under regional climate change scenarios for any species of reptile (but see Hawkes *et al.*, 2007). By obtaining robust estimates of demographic parameters and reliable regional climate projections, we were able to assess the consequences of predicted climate on the fate of several populations across the whole biogeographic range of the species. For Hermann's tortoises, winter rainfall was the main driver of juvenile and immature survival in populations that were free from other disturbances (natural and anthropogenic) and a potential increase in arid conditions would be detrimental to population persistence, especially for those also suffering from nonclimatic stressors. These results support the predictions that climate change will have negative

consequences for Mediterranean biodiversity (Sala *et al.*, 2000; Araujo *et al.*, 2006), and highlight the need to consider the effects of climate change, as well as other stressors, on population dynamics when implementing management efforts aimed at threatened species, especially for those with low dispersal capabilities.

The capture–recapture modelling conducted in our study allowed us to obtain robust age-related survival estimates, including juvenile and immature survival rates that are seldom recorded because of the low detectability of young individuals (Doak *et al.*, 1994; Hailey, 2000; Tuberville *et al.*, 2008; but see Congdon *et al.*, 1994; Keller *et al.*, 1998; Henry *et al.*, 1999). Pike *et al.* (2008) suggested that juvenile survival in reptiles may be often underestimated in capture–recapture analysis if offspring disperse from the study area. However, in our case, bias seems unlikely given that annual recapture rates were always higher than 40% and that we have observed most juveniles staying in the surveyed area through the monitoring of the colonisation process (Bertolero, 2002 and unpublished data). In addition, our mean juvenile survival (from 0 to 5 years old) was 0.64, which is close to the unbiased survival estimates for juvenile turtles (0.65) in Pike *et al.* (2008). Survival was found to increase with age, whereas the climate signal decreased. The oldest tortoises showed a high and invariable survival, whereas that of juveniles and immatures was much lower and influenced by climate (winter rainfall). These findings are typical life-history traits of long-lived species, such as chelonians

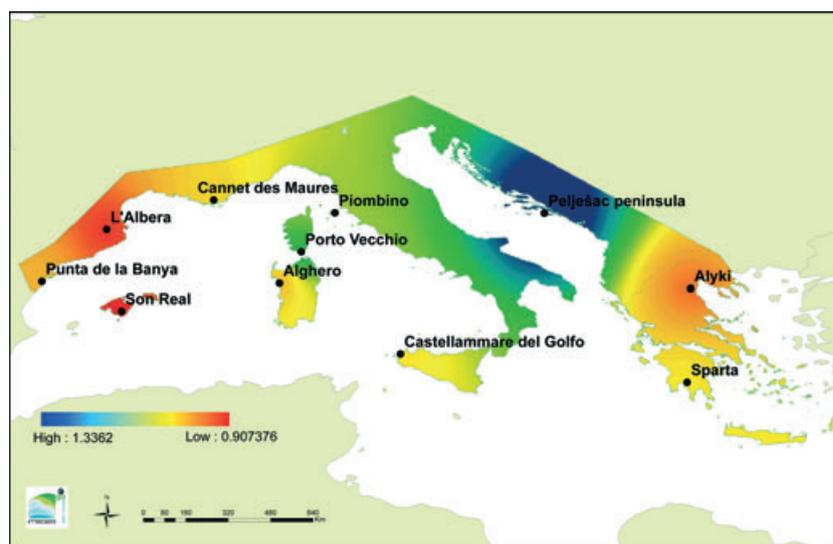


Fig. 7 Map showing the location of the populations selected for this study and the range of population growth projected under a dry precipitation scenario for the 21st century across the geographic distribution of the Hermann's tortoise. The colour shading of the figure emphasises the variation in population growth rates (λ) among the 11 populations under a dry scenario. For regions lying between two known populations, where no information was available, lambda values for the tortoise populations (if any) found there were interpolated using the inverse distance weighted (IDW) interpolation technique implemented in software ArcGIS 9.3 ESRI.

Table 4 Mean population growth rates (λ and SE in parenthesis) obtained under three future climate scenarios (dry, mean and wet) for the 11 populations considered

Population	Scenario			Time to reach $P_{q0(90)} = 1$
	Mean	Wet	Dry	
Punta de la Banya	1.055 (0.00004)	1.146 (0.00006)	0.985 (0.00018)	89
Albera	1.092 (0.00012)	1.229 (0.00014)	0.925 (0.00011)	35
Son Real	1.014 (0.00011)	1.133 (0.00013)	0.907 (0.00011)	31
Maures	1.158 (0.00005)	1.237 (0.00004)	1.018 (0.00005)	–
Alghero	1.212 (0.00014)	1.306 (0.00015)	1.002 (0.00011)	–
Porto-Vecchio	1.295 (0.00006)	1.360 (0.00005)	1.131 (0.00006)	–
Piombino	1.240 (0.00014)	1.319 (0.00015)	1.065 (0.00012)	–
Castellamare	1.305 (0.00015)	1.351 (0.00015)	1.026 (0.00012)	–
Pelješac	1.356 (0.00015)	1.359 (0.00015)	1.336 (0.00015)	–
Sparta	1.208 (0.00011)	1.287 (0.00015)	1.026 (0.00011)	–
Alyki	1.066 (0.00011)	1.180 (0.00015)	0.952 (0.00006)	62

In bold, mean growth rates for populations predicted to reach a quasiextinction probability ($P_{q0(90)}$) of 1 within a time horizon of 90 years. Expected times (in years) to quasiextinction are also given.

(Stearns, 1976): in these organisms, population dynamics are most sensitive to changes in adult survival, whereas changes in juvenile and immature survival have less impact on these dynamics (Doak *et al.*, 1994; Shine & Iverson, 1995; Heppel, 1998). In these species, juveniles and immatures may be less buffered against environmental stochasticity than adults, but in most situations population persistence seems ensured given the high and constant survival recorded for adults; however, these life-history traits may also constrain the ability of tortoise's populations to respond to chronic disturbances (see Congdon *et al.*, 1994). Mean adult survival in our study population (0.97) was considerably higher than that recorded in most other populations (ranging from 0.60 to 0.96; Bertolero *et al.*, 2007b). This was probably because of the lack of human disturbances, fire events and low predation rates in Punta de la Banya.

Our climate signal on juvenile and immature survival was driven by precipitation rather than by temperature, with decreased survival in dry winters. These results are congruent with recent findings that point to drought rather than global warming as the main threat for reptiles and amphibians inhabiting semiarid environments (Araujo *et al.*, 2006). Nevertheless, warming is still the main cause of species extinction in lizards (Sinervo *et al.*, 2010) and tropical ectotherms (Deutsch *et al.*, 2008). In temperate areas, low temperatures trigger hibernation in reptiles (Shine, 2005), which allows them to survive during the coldest months of the year. Thanks to this strategy, chelonian species living in high latitudes are able to withstand very low winter temperatures. Indeed, some turtle species even tolerate freezing without major consequences (Constanzo *et al.*,

1995) and lower winter temperatures have been correlated with higher survival in North American box turtles (Converse *et al.*, 2005). In contrast, precipitation regimes determine water and food supplies and a shortage in these vital resources might have serious consequences for tortoises and their hydration, ranging from poorer body condition to lower survival and fecundity rates (Gregory, 1982; Henen, 1997; Henen *et al.*, 1998). Given the low humidity retention of the sandy soils found in our study area, dehydration may be contributing to increase juvenile and immature mortality in dry years. Another plausible explanation for lower survival among younger age classes in dry years would be the decrease of available fresh vegetation after hibernation, causing higher mortality due to food scarcity.

At the level of overall geographic distribution of Hermann's tortoises, we detected some signs of population decrease and quasiextinction events when considering dry projection scenarios for the 21st century. Those populations located at the Western and Easternmost edges of the species' range might suffer the worst consequences of a shift to a more arid climate. Dry-scenario precipitation regimes expected for these areas may lead to a continuous reduction in juvenile survival that these populations seem unable to withstand for a long period of time despite the high and constant survival displayed by adults. These negative population trends would result from a chronic deficit in recruitment, also enhanced out of our study area by the lowered fecundity rates caused by negative environmental stochasticity. Recruitment of nonbreeders may be critical to ensure population persistence in long-lived species (Votier *et al.*, 2008).

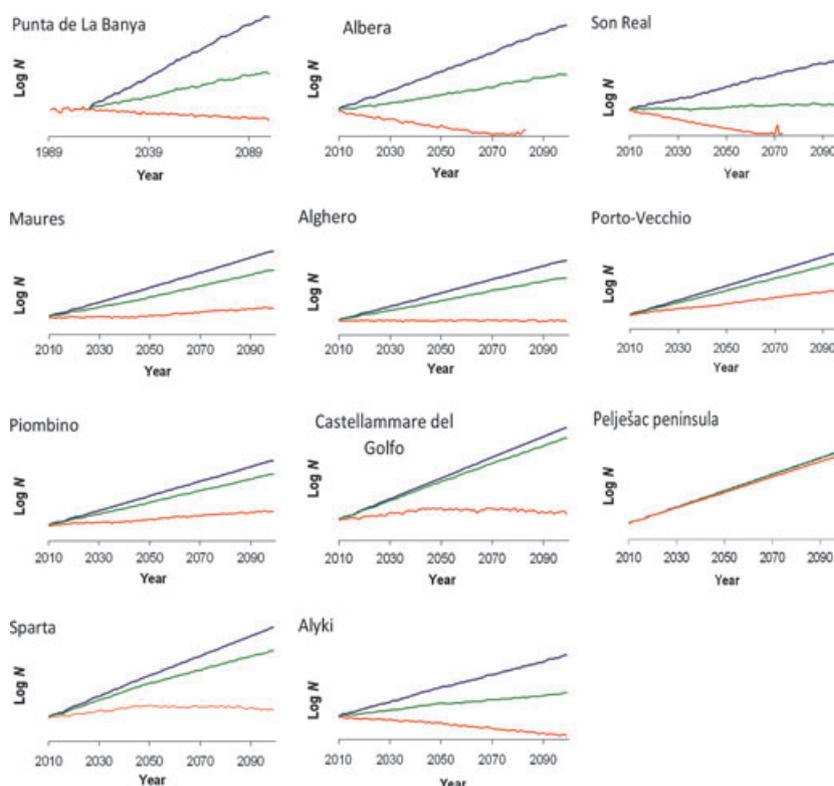


Fig. 8 Population trajectories projected under future dry (in red), mean (in green) and wet (in blue) scenarios for each Mediterranean population of Hermann's tortoises considered. Only the mean trajectory for all the Monte Carlo runs performed are shown. Y-axis numbers are not shown because simulation results are log-scaled and departing from an initial (theoretical) population size of 200 females. Trajectories do not stabilize at any carrying capacity because no density dependence was considered in our population modeling. Note that simulations for Punta de la Banya included the retrospective model of the population dynamics for the period 1988–2009.

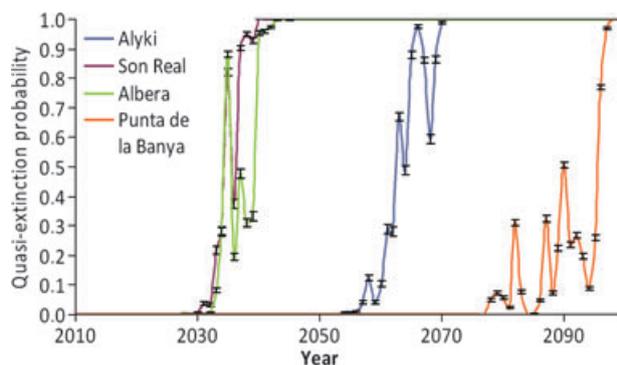


Fig. 9 Quasiextinction probabilities, with corresponding standard errors (bars), obtained for the next 90 years when projecting the Alyki, Son Real, Albera and Punta de la Banya populations under a dry scenario.

Low levels of recruitment because of harvesting of old juveniles in the snapping turtle *Chelydra serpentina* have been found to be unsustainable (Congdon *et al.*, 1994), highlighting the limited capability of turtles to

withstand continuous increases in mortality on this life stage. Previous studies on Hermann's tortoises in mainland France have also documented population decreases with low adult mortality (Stubbs & Swingland, 1985; Henry *et al.*, 1999) and these trends could be attributed to extremely low levels of recruitment caused by high levels of nest predation (95% nest predation in Maures; Stubbs & Swingland, 1985). Strikingly, we predicted the quasiextinction of our study population in the long term, providing evidence that even the best habitats are not necessarily safer from the consequences of regional climate changes (Pounds *et al.*, 1999). We suspect that tortoises in the Spanish sites may already be living under precipitation regimes close to suboptimal levels for the species. Therefore, a reduction (although not statistically significant) of the amount of winter rainfall in the future (as predicted by the dry scenario) may enhance a negative population trend. However, compared with other tortoise's populations in Spain, our study population reached the quasiextinction

threshold much later when projected under a future dry scenario for the next 90 years, a result otherwise consistent with the expected more deleterious impact of local climate change on populations already suffering from other sources of mortality (McCarty, 2001; Walther *et al.*, 2002). Population decline elsewhere was also enhanced by the additive negative environmental stochasticity of mortality factors (e.g. poaching, fire, habitat fragmentation) that are absent in Punta de la Banya reserve. These nonclimatic disturbances were worked into our population models by considering a negative effect of environmental stochasticity on adult survival and fecundity, but we were unable to introduce an effect of these sources of mortality on the estimation of juvenile or immature survival, since these rates were defined as a function of rainfall. Therefore, our projections should be considered very conservative, and the obtained population growth rates treated as optimistic, as we did not take into account many potential sources of egg, juvenile and immature mortality, such as predation or anthropogenic habitat destruction, to which these life stages are especially sensitive (Stubbs & Swingland, 1985; Hailey, 2000). We also ignored the role of density dependence in our projections because of the lack of information on the carrying capacity for each tortoise population, as well as the important effects of demographic stochasticity in small and fragmented populations (Sanz-Aguilar *et al.*, 2011). Projections for populations with more demographic data available (i.e. Maures, Porto-Vecchio, Alyki) were probably more reliable, although still optimistic since the effects of nonclimatic disturbances, density dependence and its interactions were not fully worked into the population modelling. However, our population projections are based on local future scenarios generated from the outputs of 13 RCMs developed for each location, and this approach provides more reliable forecasts of future local conditions than previous approaches based on global circulation models (Tabor & Williams, 2010) or the application of a single RCM (e.g. Wolf *et al.*, 2010). Therefore, despite the limitations of our population modelling, the mean growth rates and quasiextinction risks reported here should provide insights as to the potential impact that spatially heterogeneous climate change may have on several isolated populations of Hermann's tortoise across the species' entire geographic range.

Conclusions

This study is a first assessment of the effects of climate change on Hermann's tortoise's demography and population persistence. Our main goals have been to determine the role that climate variability plays in the

population dynamics of Hermann's tortoise and the negative consequences that a shift to a more arid climate in the Mediterranean would have for the species, ranging from lowered population growth rates to local extinction events. Our findings are expected to be useful for wildlife managers working with the species and should contribute to design climate-smart conservation efforts. Conservation in the 21st century requires integrating climate change in conservation plans and implementing climate adaptation strategies, especially for those systems already suffering the impacts of multiple nonclimatic stressors (Hagerman *et al.*, 2010; Hansen *et al.*, 2010). Hermann's tortoise is threatened by a great diversity of factors, all related to human activities either directly, such as poaching and habitat destruction, or indirectly, such as increasing predator abundance and changes in landscape configuration. Management efforts focused on the elimination or reduction of these causes of mortality at all life stages (e.g. increasing protection, habitat management) are likely to increase the resilience of the species to future environmental changes in the Mediterranean region. However, as we have seen for our study population, even when human-driven mortality is suppressed and effective protection is reached, populations might continue decreasing at some areas owing to local climatic trends. In these cases, a climate change-integrated conservation strategy (Hannah *et al.*, 2002; Heller & Zavaleta, 2009) should be applied, primarily focused on enhancing reserve expansion and connection as a way to facilitate range shifts, and increasing genetic diversity as a way to allow for local adaptation to future environmental changes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Variability in the recapture probability of tortoises at Punta de la Banya during the study period (1992–2009). For each year, mean values and corresponding standard errors (bars) are given. Results are drawn from the outputs of the time-varying model 17 (see Table 1).

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