

Density dependence, climate and fires determine population fluctuations of the spur-thighed tortoise *Testudo graeca*

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Keywords

non-linear logistic models; *Testudo graeca*; endogenous; exogenous; disturbance; population density; climate; temperature.

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Editor: Nigel Bennett

Received 8 February 2016; revised 14 June 2016; accepted 24 June 2016

doi:10.1111/jzo.12379

Abstract

Population fluctuations are driven by a combination of multiple factors, which can be classified into endogenous and exogenous. Endogenous factors are directly related to density-dependent forces, whereas exogenous factors are environmental drivers (e.g. climate). Several studies have reported the effects of endogenous and exogenous factors using exponential population models in mammals, birds or insects, but few works have explored the effects on reptiles, specifically in tortoises. In this study, we developed logistic population growth models to decipher the role of these factors on the population dynamics of the spur-thighed tortoise *Testudo graeca*. The role of environmental drivers in the distribution, movement, survival, reproduction or individual growth has been described for this species in previous works, but no studies have examined the effects of both endogenous and exogenous factors in population growth rates. Using long-term data of *T. graeca* in southeastern Iberian Peninsula (1999–2013), we fitted non-linear logistic models with endogenous and exogenous effects. The results showed that endogenous processes are important drivers of the population dynamics of this species, and that exogenous factors, such as freezing hours in winter, also directly affect the population growth rate. Intolerance of extreme winter temperatures may especially affect hatchlings and juvenile tortoises. Our models also showed that perturbations (i.e. a fire occurred during the monitoring period) have a lasting impact by reducing the carrying capacity of the population. This study shows that simple quantitative approaches based on population dynamic theory are useful for deciphering the ecological mechanisms underlying dynamics of tortoise populations.

Introduction

Models based on population dynamic theory are simple tools to decipher the causes of population change and can provide reasonably accurate predictions (Royama, 1992; Berryman, 1999). These models, constructed from classical ecological principles, are helpful to develop conservation and management policies (Berryman, 1999; Saether *et al.*, 2000; Coulson *et al.*, 2001; Stenseth *et al.*, 2002; Lima & Naya, 2011). Recognizing the role of endogenous (i.e. density dependence) and exogenous factors (i.e. climate or disturbances) in the dynamics of natural populations is a central subject within the field of population ecology (Nicholson, 1933; Andrewartha & Birch, 1954; Royama, 1992). Endogenous factors are density dependent, and they cause changes in dynamic variables (e.g. the per capita growth rate). Consequently, these factors are affected by those changes. In contrast, exogenous factors are density independent and may influence the per capita growth rate, but are not affected in turn by those changes (Royama,

1992; Berryman, 1999; Turchin, 2003). Many authors have studied the effects of endogenous and exogenous factors using exponential or logistic growth models (Berryman, 1999). Studies with birds (Furness & Greenwood, 1993; Lima & Estay, 2013), mammals (Lima & Berryman, 2006; Lima, Previtali & Meserve, 2006; Previtali *et al.*, 2009) and insects (Estay & Lima, 2010) support this classical approach. Although previous studies analyze population trends of several species of reptiles (i.e. Reading *et al.*, 2010; Luiselli *et al.*, 2014), to the best of our knowledge, there are no previous studies using this approach within this group.

In this study, we developed population dynamic models to decipher the role of endogenous and exogenous factors on the population dynamics of the spur-thighed tortoise, *Testudo graeca*, a threatened terrestrial tortoise inhabiting Mediterranean landscapes. The strongest evidence of density-dependent factors (i.e. endogenous) in shaping population dynamics in tortoises is from giant tortoises in oceanic islands (Swingland & Coe, 1979; Gibson & Hamilton, 1984). However, the very

particular nature of these case studies may limit any generalization. For *T. graeca* there are no works describing density-dependent processes regulating its population dynamics, and only one work suggests density-dependent processes in the genus *Testudo* (Hailey & Willemsen, 2000; for *T. hermanni*). In contrast to endogenous factors, there is much more evidence for the role of exogenous factors in the population dynamics of tortoises. Specifically, for the *Testudo* genus, most works indicate a key role of positive effect of winter and autumn precipitation in the survival of the younger individuals (Díaz-Paniagua, Keller & Andreu, 2001; Fernández-Chacón *et al.*, 2011 for *T. graeca* and *T. hermanni*, respectively). Our work was carried out in the population of *T. graeca* in south-eastern Iberian Peninsula. In this population, previous studies have shown the effects of climate or other habitat disturbances (such as fire) on the species' distribution and abundance (Anadón *et al.*, 2006a,b, 2012a), on individual movement patterns (Anadón, Wiegand & Giménez, 2012b) and on individual growth, survival and reproduction rates (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Specifically, climate has been described as the most important factor shaping the species' distribution (Anadón *et al.*, 2006a). Main climate constraints are related to autumn rainfall and the number of freezing days in winter. These two factors could be related to limitations imposed by the length of the annual activity period (Anadón *et al.*, 2006a). Fires have also been described as a factor that causes direct and delayed reductions in local survival in the years after the fire (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013).

According to previous works, we expect both endogenous and exogenous factors to affect the population dynamics of *T. graeca* in south-east Iberian Peninsula. Due to the scarcity of studies on endogenous factors, the relative weight of this driver remains an unknown *a priori*. We hypothesize that exogenous forces could play an important role, specifically the rainfall in autumn could have a direct effect on abundance and the extreme temperatures in winter could affect negatively the abundance of tortoises. We also hypothesize that as a consequence of fire, the density of tortoises may be reduced in the years after the disturbance.

Materials and methods

Study system

The spur-thighed tortoise, *T. graeca*, is a long-lived species inhabiting multi-successional Mediterranean shrublands (Anadón *et al.*, 2006a,b). Like other *Testudo* species, its population dynamics are characterized by delayed reproductive maturity and high and constant adult survival (Hailey & Loumbourdis, 1988; Díaz-Paniagua *et al.*, 2001; Sanz-Aguilar *et al.*, 2011). This study was carried out in a natural reserve 'Cumbres de la Galera' in the Region of Murcia in south-eastern Spain (37°32'N, 1°39'W). The area is a typical coastal semiarid Mediterranean shrubland. The reserve (70 ha) is surrounded by continuous and suitable habitat for the species (Anadón *et al.*, 2006a). Our study area within the reserve covered 35 ha. The mean annual rainfall and temperature are 295 mm and 18–

19°C, respectively. According to regional models based on climate, relief and lithology, the reserve contains the optimum habitat for the species (Anadón *et al.*, 2006a). In summer of 2004, a fire affected approximately 31% of the study area (10.8 ha). Although fire events in this region are quite common (232 recorded fires between 1995 and 2005), most fire events, around 76%, burned less than 1 ha (Sanz-Aguilar *et al.*, 2011). However, the 2004 fire burned more than 250 ha and was one of the most extensive fires recorded in south-east Spain within the last decade.

Data collection

The tortoise population at the reserve 'Cumbres de la Galera' was monitored annually from 1999 to 2013. Tortoises were sampled in the spring, according to their annual activity patterns (Díaz-Paniagua, Keller & Andreu, 1995; Pérez *et al.*, 2002) and under adequate weather conditions (i.e. not with rain or with temperature below 18°C). The same area was evenly covered by walking along annual line transects through the habitat. Relative abundance of the species was estimated from the number of tortoises found per hour and per person, although the sampling effort was variable over the years. The minimum sampling effort in a year was 40 h. We could not assume that detection was the same in different months during spring because the activity of tortoises assumes a seasonal pattern. For this reason, we used data from a previous radiotelemetry study to obtain an estimate of the percentage of surface-active tortoises during the sample months (March = 38.1%; April = 52.9%; May = 48.5%; using the per cent of active tortoises from the total of radiotelemetry tortoises, data from Pérez *et al.*, 2002). Detection might also vary with the year, size and stage of the individuals, with the experience of the observer, or sampling effort (e.g. Anderson *et al.*, 2001). To quantify these effects and correct for these potential biases, we performed a distance sampling analysis (Buckland *et al.*, 2001) using the software Distance 6.0 (Thomas *et al.*, 2010). Our results indicated that, out of these potential confounding factors, only size (adults vs. non-adults) had an effect on the detectability of tortoises in our population (see Appendix S1 for further details). Accordingly, relative abundance of adults and non-adults was corrected according to their detection probabilities (adults: 0.452, non-adults = 0.215).

Environmental data

Climatic data for our study period (1998–2013) were provided by the Agricultural Information System of Murcia from the Research Institute of Agricultural and Alimentary Development of Murcia (siam.imida.es). We used the two climate factors directly associated with our hypothesis (e.g. temperature and precipitation), as well as potential evapotranspiration. Precipitation and potential evapotranspiration were described by their cumulated values, whereas temperature was described by four different metrics (total mean, means of the maximum and minimum monthly temperatures and extreme temperatures were described as the number of hours below 0°C; Table 1). In turn, each one of these six climatic descriptors was calculated for

Table 1 Climatic variables used in this study. These six variables were used in six temporal frameworks [current spring (spr), previous year (py), previous spring (pspr), previous summer (psum), previous autumn (paut) and previous winter (pwin)]

Climatic Variables	Value of variable	ID
Temperature	Mean	T_{mean}
	Mean minimum	T_{min}
	Mean maximum	T_{max}
	Hours below 0°C	H
Precipitation	Cumulated	P
Potential Evotranspiration	Cumulated	PET

six different time frameworks: current spring (spr), previous year (py), previous spring (pspr), previous summer (psum), previous autumn (paut) and previous winter (pwin). In total, we tested 36 variables describing climate.

Diagnosis

We modeled endogenous and exogenous influences based on the R-function (Berryman, 1999). The R-function represents the realized per capita population growth rates (R_t) which reflects the processes of individual survival and reproduction (Berryman, 1999). Defining $R_t = \log(N_t) - \log(N_{t-1})$, where N_t is the relative abundance of tortoise at time t , we can express it as (Berryman, 1999):

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = f(N_t, N_{t-1}, \dots, N_{t-i}, \varepsilon_t) \quad (1)$$

Where ε_t is a random normally distributed variable and i represents the lag in years (1–8). This model represents the density-dependent population dynamics.

To understand the endogenous structure of our tortoise population, we first determined the time delay in density-dependent effects of this time series. Following Berryman & Turchin (2001), we carried out an autoregressive analysis using the partial rate correlation function (PRCF). We fitted a multiple regression between the per capita growth rates (R_t) and lagged population density ($X_{t-i} = \ln N_{t-i}$) to estimate the PRCF _{$t-d$} coefficients at each lag ($i = 1, 2, \dots$), for statistical convenience we assumed a linear relationship (Royama, 1977). The population was dominated by first-order density-dependent effects (see below Results, Fig. 1); therefore, we used a non-linear version of the simple Ricker's (1954) equation as a starting point to model the R-function (Berryman, 1999).

Models of population dynamics

Assuming that population dynamics of tortoises are influenced by endogenous process, we used the non-linear logistic population model proposed by Royama (1992), derived from the logistic equation of Ricker (1954).

$$R_t = R_m - e^{(aX_{t-1}+c)} \quad (2)$$

where R_t is the realized per capita population growth rate, R_m is a positive constant representing the maximum finite

reproductive rate (related to the maximum growth rate), X_{t-1} is the logarithmic population density in time $t-1$, c is a constant representing competition and resource depletion and a indicates the effect of interference on each individual as density increases (Royama, 1992); $a > 1$ indicates that interference intensifies with density and $a < 1$ indicates habituation to interference. As the three parameters R_m , a and c have an explicit biological interpretation, we can include environmental perturbations in each parameter using the framework of Royama (1992). To model the effects of exogenous factors (climate) on the endogenous model (Equation 2), we added extra terms representing vertical and/or lateral effects (Royama, 1992). Simple additive environmental changes can be represented as vertical effects, which deflect vertically with proportional alterations in R_m . Vertical perturbations may affect survival and reproduction directly, causing changes in the maximum finite growth rate and can be expressed as:

$$R_t = R_m + d(Z_t) - e^{(aX_{t-1}+c)} \quad (3)$$

Where d is a simple linear function (positive or negative) of the different climatic variables (Z_t).

An alternative process occurs when exogenous factors influence certain limiting resources, called lateral or non-additive effects (Royama, 1992). Lateral perturbations are normally expected from changes in an essential resource such as food or nesting sites (Berryman, 1999) and can only be evaluated jointly with the effect of population density. It can be expressed as:

$$R_t = R_m - e^{(aX_{t-1}+c+d(Z_t))} \quad (4)$$

Parameters were estimated by non-linear convergence (i.e. Marquardt/Newton-Raphson algorithm) using non-linear regression from the nls library in the program R (Bates & Watts, 1988). We calculated the Akaike information criterion corrected for small-sample bias (AICc), and differences in AICc (ΔAICc) for each model (Burnham & Anderson, 2004). In addition, for each model we calculated the Akaike weights, w_i , as an index of its relative plausibility (Burnham & Anderson, 2002). Predictive performance of the models was also assessed by means of root-mean-square error values (rmse; Sheiner & Beal, 1981). Rmse represents the standard deviation of the residual values (i.e. the difference between the observed and the values predicted by the model) and thus smaller rmse values represent better predictive performance. In addition, we used Pearson's correlation coefficient between the observed and predicted values. The best model, as assessed from the AIC values, was selected to draw inferences and run deterministic predictions. We used total trajectory (annual predictions calculated by the information of the exogenous variable using the best model) and one-step-ahead deterministic predictions (annual prediction calculated by the information of the exogenous variable and the abundance of the previous year using the best model) to simulate the dynamic behavior of the fitted models and correlations between observed and predicted values of population abundance to assess the performance of each of them.

Results

Population dynamics showed numerical fluctuations with a sudden decrease after the fire, which happened in 2004 (Fig. 1a). Results from the PRCF strongly suggested a first-order dynamics (Fig. 1b), which was also evident from the observer R-function (Fig. 1c). As there is a shift in the R-function before and after the fire (Fig 1c), we corrected these effects calculating the difference between the average of N_t before and after the disturbance (1.19 and 0.80 tortoises per hour, respectively). The difference (0.39) was added to the relative abundance after the disturbance to remove fire effects, the results are shown in Fig. 2a. It should be noted that

including the fire effects into the model (i.e. as a dummy variable) would yield the same results. The PRCF after the correction also indicated strong density-dependent effects (Fig. 2b) and the R-function showed a clear relationship between the relative abundance and the per capita population growth.

Of the 72 candidate climatic models (36 variables with lateral and vertical effects), 10 improved the AICc of the endogenous model (Table 2). The model with the largest support included the endogenous effects and the number of hours below 0°C in winter with an additive negative effect (Table 2, model A2). The rmse was very low (0.0381) and the Pearson correlation was very high (0.9531) and the predicted effects in

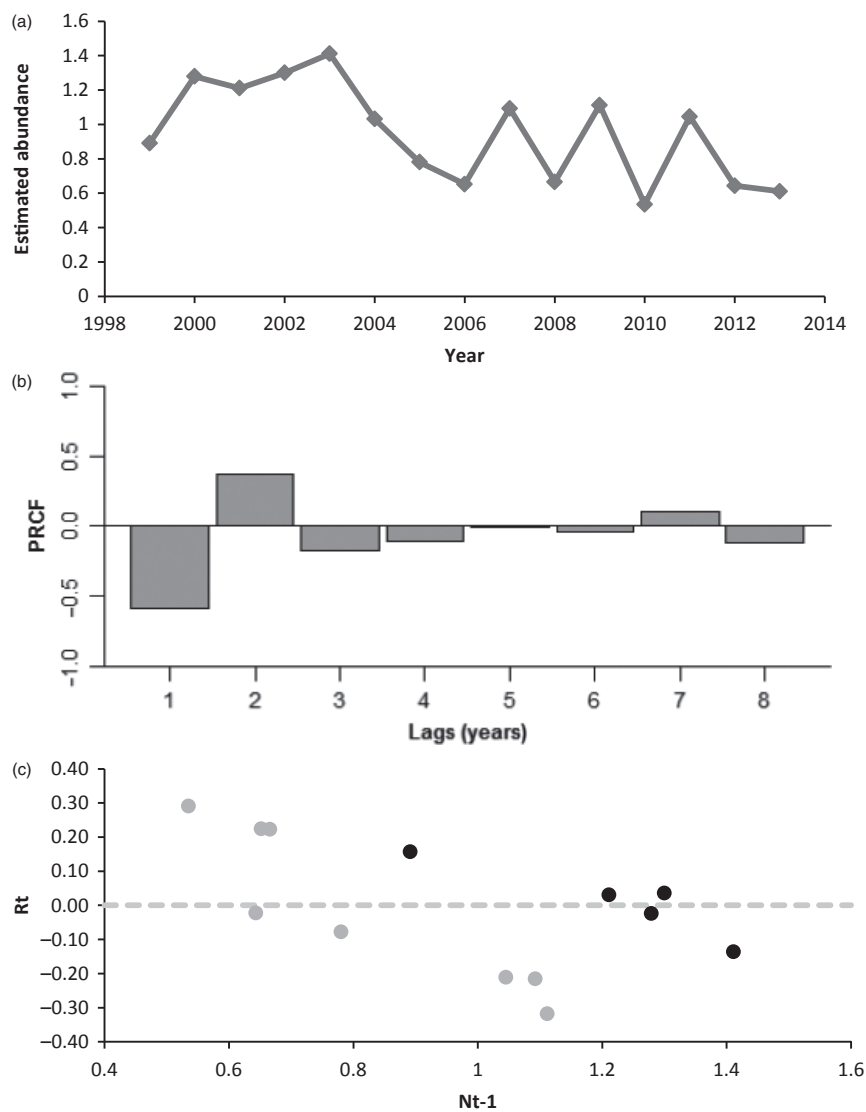


Figure 1 (a) Annual estimate abundance of spur-thighed tortoises, (b) partial rate correlation function (PRCF) and (c) relationship between the logarithmic annual per capita rate of change (R_t) and population abundance (N_{t-1}). In black and gray are the years before and after the fire, respectively.

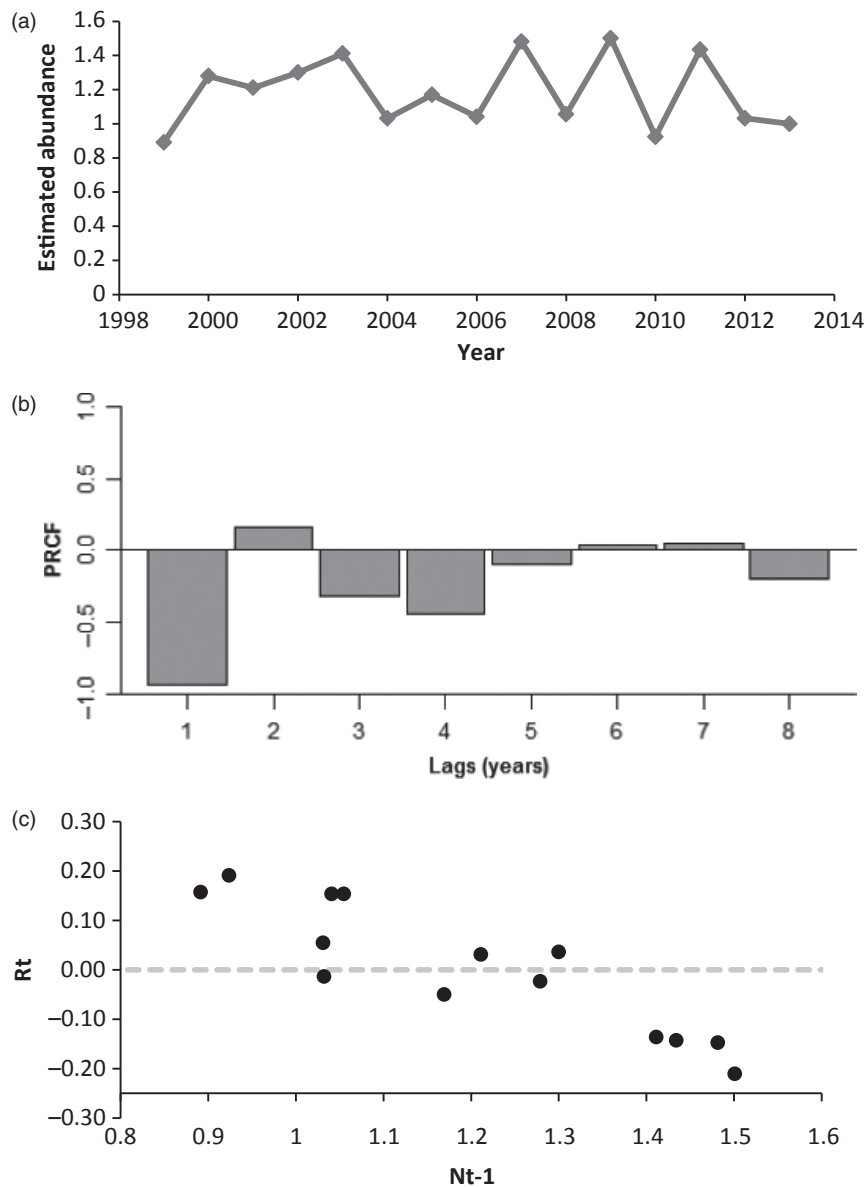


Figure 2 Data corrected by effects of fire. (a) Annual estimate abundance of spur-thighed tortoises, (b) partial rate correlation function (PRCF) and (c) relationship between the logarithmic annual per capita rate of change (R_t) and population abundance (N_{t-1}).

R_t are showed in Fig 3. This model seems to capture the observed dynamics effectively (Fig. 4). Correlations between observed and predicted values of density were 0.54 for total trajectory predictions and 0.73 for one-step-ahead predictions, respectively (Fig. 4). Two models had a similar statistical support than model A2, as their difference in AIC values was less than 2 units (Burnham & Anderson, 2002). These models included the number of hours below 0°C as lateral effects and T_{maxspr} with vertical effects (Table 2). The two models with the largest support, vertical and lateral effects of the number of hours below 0°C (Table 2, A2 and A3) actually yielded very similar predictions, as shown by the similarity in their response curves (Fig. S1).

Discussion

Our results indicate that endogenous processes are relevant forces in the dynamics of *Testudo graeca* and that climate factors also help account for variability in species population dynamics. To the best of our knowledge this is one of the few, and the most direct, evidence of intrinsic population regulation in continental tortoises (i.e. not in oceanic islands). With regards to exogenous factors, although the influence of climate in tortoises has been widely reported elsewhere (Díaz-Paniagua *et al.*, 2001; Anadón *et al.*, 2006a,b, 2012a; Attum *et al.*, 2011), most of these studies are based on statistical correlation between estimates of population size and environmental

Table 2 Optimal population dynamic models for spur-thighed tortoise using the exponential form of logistic growth (Royama, 1992)

ID	Model	Parameters estimates				AICc	Δ AICc	w_i	rmse	r_p
		a	b	C	d					
A1	$R_t = b - \exp(a X_{t-1} + c)$ Endogenous + climatic effects	3.73	0.43	-1.1583		-33.80	5.54	0.02	0.0536	0.9046
A2	$R_t = b - \exp(a X_{t-1} + c) + d H_{pwin}$	4.93	0.43	-1.4882	-0.0003	-39.34	0.00	0.25	0.0381	0.9531
A3	$R_t = b - \exp(a X_{t-1} + c + d H_{pwin})$	3.89	0.43	-1.3537	0.0007	-38.57	0.76	0.17	0.0391	0.9504
A4	$R_t = b - \exp(a X_{t-1} + c) + d T_{max_{spr}}$	1.39	0.43	-0.0009	0.0323	-37.40	1.94	0.10	0.0401	0.9491
A5	$R_t = b - \exp(a X_{t-1} + c) + d T_{max_{spr}}$	3.59	0.43	0.3699	-0.0719	-36.79	2.55	0.07	0.0417	0.9435
A6	$R_t = b - \exp(a X_{t-1} + c) + d PET_{pspr}$	1.74	0.43	-0.1402	0.0015	-36.13	3.21	0.05	0.0427	0.9406
A7	$R_t = b - \exp(a X_{t-1} + c + d T_{min_{pwin}})$	3.73	0.43	-0.8648	-0.0434	-34.96	4.37	0.03	0.0445	0.9353
A8	$R_t = b - \exp(a X_{t-1} + c) + d T_{min_{pwin}}$	2.93	0.43	-0.8237	0.0190	-34.55	4.79	0.02	0.0452	0.9333
A9	$R_t = b - \exp(a X_{t-1} + c) + d PET_{pyear}$	0.94	0.43	0.4647	0.0009	-34.16	5.18	0.02	0.0458	0.9313
A10	$R_t = b - \exp(a X_{t-1} + c + d T_{mean_{pwin}})$	4.04	0.43	-0.1552	0.0923	-34.08	5.26	0.02	0.0459	0.9309
A11	$R_t = b - \exp(a X_{t-1} + c + d PET_{pspr})$	3.39	0.43	-0.1315	-0.0028	-33.90	5.44	0.02	0.0462	0.9301

Parameters values were estimated by non-linear regression analysis. The best model was chosen by using Akaike information criteria for small sample size AICc. R^2 = proportion of the variance explained by the model, Δ AICc = increments of AICc. The model notations are as follows: R_t , per capita population growth rate; b , maximum per capita growth rate; a , effect of interference on each individual as population size increases; c , d , f constants for the model; X_{t-1} = \ln population abundance at time $t-1$.

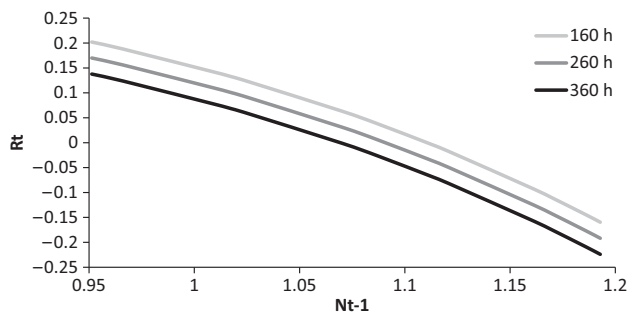


Figure 3 Relationship between the logarithmic annual per capita rate of change (R_t), population abundance (N_{t-1}) and number of hours below 0°C in winter, according to the model with vertical effects (A2). The mean of hours below 0°C was 266 h during the study.

variables. Here, we deduced the structure of the population processes, which is a central issue in population dynamics (Royama, 1992).

Our work indicates that the population dynamics of *T. graeca* in south-eastern Iberian Peninsula show fluctuations that are largely associated with density-dependent processes. These results show that the species' dynamics are regulated by intra-specific mechanisms, such as intra-specific competition (Berryman, 1999). Mechanisms put forward to explain this pattern are territoriality, aggressive behavior and nutrient limitation at carrying capacity (Berryman, 1999). As in most terrestrial tortoises, the studied populations of *T. graeca* present a promiscuous mating system with overlapping home ranges (Anadón *et al.*, 2006b) and, unlike other *Testudo* populations, male–male combats are extremely rare (R. Rodríguez-Caro & E. Graciá; pers. obs.). Thus, resource limitation at carrying capacity is the most plausible mechanism driving intra-specific competition in this population. Interestingly, this density-dependent mechanism is different from the only

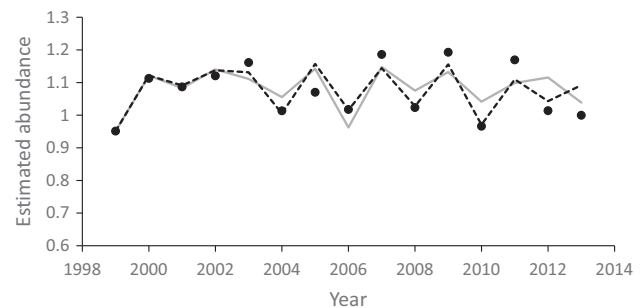


Figure 4 Comparisons between observed abundances (points) and deterministic predictions (lines) for the best model (A2). Total trajectory prediction is represented by the gray solid line and one-step-ahead prediction by the black dotted line. Estimated abundances (tortoises per hour searching) were adjusted by detection probability without fire effects.

previous work reporting intrinsic population regulation (Hailey & Willemsen, 2000). These authors suggested that population regulation in a studied population of *T. hermanni* occurs via sex ratio, with population with high densities showing a sex ratio strongly biased toward males. In any case, further studies are needed to identify the density-dependent mechanisms acting in the studied population in south-east Spain.

Our results indicate that temperature, and not rainfall, is the most important climatic factor determining the dynamic of the spur-thighed tortoise. Our models indicate that the number of freezing hours during winter (extreme temperatures) is the climate variable with the largest impact on the dynamics of the studied tortoise population; extreme cold winters reduce the population growth rates. Main climate effects for this variable are vertical, which indicates that they induce changes in the maximum per capita growth rate (R_m). However, the model with the same variable as a lateral affect also fitted the data

very well, which means that, alternatively, differences in temperature might promote changes in the availability of essential resources, such as food or nesting sites. Regarding the role of temperature, the ability of reptiles to cope with lower temperatures remains limited. Reports of widespread mortality among hatchlings due to extreme minimum temperatures are common (St. Clair & Gregory, 1990; Lindeman, 1991; Packard, 1997; Packard *et al.*, 1997; Andreas & Paul, 1998; Nagle *et al.*, 2000) and demographic studies have shown that winterkill may contribute significantly to mortality in the first age classes (Tinkle, Congdon & Rosen, 1981). In cold temperate regions, winter mortality may significantly constrain recruitment and limit population size (e.g. Tinkle *et al.*, 1981; MacCulloch & Secoy, 1983; St. Clair & Gregory, 1990; Rozycki, 1998; Schneeweiss, Andreas & Jendretzke, 1998). The population of *T. graeca graeca* in south-eastern Spain inhabits in the northern limit of the distribution of this species in the western Mediterranean (Graciá *et al.*, 2013). This subspecies is widely distributed in the north of Africa, where the climate is warmer. Thus, in the Spanish population, colder winters may constrain the growth of the population.

According to Anadón *et al.* (2006a, 2012a) the distribution and abundance of *T. graeca* in south-eastern Iberian Peninsula and North Africa is largely controlled by rainfall variables, especially winter and autumn precipitation, followed by the number of freezing days in winter. The key role of rainfall before the active season of tortoises (i.e. spring, Pérez *et al.*, 2002) has been also indicated in demographic studies for *Testudo* species (Díaz-Paniagua *et al.*, 2001 for *T. graeca*, Fernández-Chacón *et al.*, 2011 for *T. hermanni*). However, rainfall variables did not show effects in our models. As such, the relative role of rainfall versus temperature factors on the population dynamics of the species remains to be clarified.

Fire events also had a clear effect on the dynamics of the studied population, as it has been described in previous works (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Previous works show that although reproduction rates were not affected, survival rates decrease in the years after the fire (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Accordingly, our results indicate that fire disturbance reduces abundance of tortoises and this effect is prolonged because the species is long lived. The models show that disturbance also reduces the carrying capacity of the system. Fire may alter food availability or cause loss of shelters from predators and thermal refugia after the disturbance (Esque *et al.*, 2003). The studied tortoise population seems to be trapped in a low equilibrium density point after the fire event, suggesting that the changes in the ecosystem structure and function cause a large impact on this reptile population.

Our approach supports the notion that simple models based on population dynamics can be used to disentangle the effect of different environmental variables. Current studies provided examples where these simple models are helpful to understand the causes of population fluctuations and make accurate predictions (Berryman & Lima, 2006; Lima & Berryman, 2006; Lima *et al.*, 2008a,b; Previtali *et al.*, 2009; Lima & Naya, 2011; Lima & Estay, 2013). This study also supports their accuracy for long-lived reptiles, as our results are consistent

with previous studies on the species, and shed light into the relative role of endogenous and exogenous factors in the population dynamics.

Acknowledgments

We thank all the people who participated in the fieldwork. Financial support was granted by the Spanish Ministry of Science and European Regional Development Fund (projects CGL2012-33536, CGL2015-64144; MINECO/FEDER) and Regional Government of the Community of Valencia (RGCV, ACOMP/2014/080 and ACOMP/2015/046). R. R.-C. was supported by a postgraduate grant from the RGCV (ACIF/2010/133) and a grant 'Scholarships for Young Researchers' by Santander Universities. E. G. was also supported by the RGCV with a postdoctoral grant (APOSTD/2015/048). Permits for the field work and capture animals were provided by 'La Delegación General de Medio Natural de la Comunidad Autónoma de la Región de Murcia' (FA/AUT/cap-06, AUT/FA/UND/186-08, AUT/ET/UND/48/2010). We also wish to thank ACUDE for allowing us to work in its reserve. We thank the anonymous reviewers for their valuable comments on an earlier version of this manuscript.

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Supporting Information

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

Appendix S1. Factors that affect the detection of tortoises.

Table S1. Models with the possible variables which affect detectability.

Figure S1. Effects of abundance of tortoises (N_{t-1}) and number of hours below 0°C in winter according to (a) the model with vertical effects (effects in the maximum growth rate, R_m) in population growth (R_t), and (b) the model with lateral effects (exogenous factors influence some limiting resources).