



Coexisting with fire: The case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands

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ABSTRACT

Fire and fire management are recognized as important factors in biodiversity conservation. Measuring species-level demographic, behavioural and population responses to different fire regimes is essential for designing adequate management policies. Here we assessed the impact of fire on survival rates, reproduction and movement patterns in *Testudo graeca*, an endangered terrestrial tortoise inhabiting the Mediterranean region, a system in which fire plays a relevant role in the functioning of their ecosystems. Then we predicted the probabilities of quasi-extinction of *T. graeca* under several fire regimes and population sizes by means of stochastic population models. Our results showed that fire caused direct and delayed reductions in local survival, young individuals being the most affected. There were not differences in fecundity and movement patterns of tortoises between burned and unburned areas. Population models showed a strong variation in the probability of quasi-extinction of populations depending on the fire regime and the population size. Under fire frequencies similar to those occurring in the wild (<1 fire every 20–30 years) most tortoise populations seemed to buffer the effects of fires. However, when this threshold value of fire frequency was surpassed, the probability of quasi-extinction of populations exploded for all populations, except for those with the largest sizes. *T. graeca* populations may be able to cope with natural current fire frequencies, but the effects of more recurrent fires may severely threaten the species. Our results have straightforward applications for fire management purposes in those areas of the Mediterranean region where this endangered species is present.

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1. Introduction

The Mediterranean basin, an area where human activities have had a major impact and transformed its landscapes and ecosystems for more than 8000 years, is paradoxically one of the global biodiversity hotspots (Myers et al., 2000; Coll et al., 2010). Burning, cutting, clearing, terracing and grazing have been historically used to cultivate, establish and maintain grasslands throughout the Mediterranean region (Andreae, 1991; Blondel and Aronson, 1999). Fire is a widespread process that plays a key role in ecosystems' functioning (Pausas and Keeley, 2009). In addition to human-induced burning, natural fires have been a recurrent disturbance in Mediterranean climate regions for millennia (Pausas et al., 2008). However, over the last few decades, major socio-economic changes on the northern (European) rim of the Mediterranean (industrialisation, touristic development and rural exodus, see Martínez-Abraín

et al., 2009) and fire suppression policies have modified the ecosystems' functioning, natural fire regimes and their intensity (Keeley et al., 1999; Pausas, 2004; Moreira and Russo, 2007; Pausas et al., 2008). Although controversial, prescribed burning (i.e., controlled human-induced burning conducted during the cooler months to reduce fuel buildup) has been recommended as a suitable management tool to prevent extensive wildfires and to restore the dynamics of traditionally modified ecosystems (Moreira and Russo, 2007).

Ecological disturbances such as fires drive demographic and ethologic variation in many species (Pickett and White, 1985; Menges and Quintana-Ascencio, 2003). Mediterranean vegetation has been traditionally considered as fire prone (Andreae, 1991; Bond and van Wilgen, 1996). In fact, recent evidences suggest that Mediterranean coastal shrublands and oak forests are very resilient to current and past fire regimes (Pausas et al., 2008). Nevertheless, much work remains to be done to understand the effects of fire on fauna (Sutherland and Dickman, 1999; Lyon et al., 2000; Whelan et al., 2002; Lindenmayer et al., 2008; Jacquet and Prodon, 2009; Driscoll et al., 2010). In order to develop fire management strategies and achieve the successful conservation of biodiversity, an

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understanding of individual species' responses to fire regimes is essential (Driscoll et al., 2010). To gain an understanding of the long-term effects of fire in fitness components, which ultimately drive population dynamics (Williams et al., 2002), we need reliable measurements for those components (Converse et al., 2005; Sanz-Aguilar et al., 2010). The development of predictive population models based on robust estimates of life history traits and dispersal abilities is necessary for estimating extinction probabilities under different fire regimes linked to natural conditions, management strategies or climate scenarios (Driscoll et al., 2010).

Due to their low movement capabilities, reptiles are expected to be fire-sensitive species. Many reptile species are in decline due to habitat loss and degradation, introduced species, pollution, harvest, and climate change (Gibbons et al., 2000; Klemens, 2000), and wildfires have been mentioned as one of their main threats in some regions (Brooks and Esque, 2002). Several studies have evaluated the effects of prescribed fires and wildfires on terrestrial reptile populations (Stubbs et al., 1985; Greenberg et al., 1994; Hailey, 2000; Esque et al., 2003). Nevertheless, the impact that fires have on demography and population dynamics of reptile species is still controversial; both negative (fire-related mortality of individuals) and positive effects (fire-related habitat changes) have been documented (Smith et al., 2001; Esque et al., 2003; Yager et al., 2007; Ashton et al., 2008; Driscoll and Henderson, 2008; Lindenmayer et al., 2008; Santos and Poquet, 2010). Most studies concerning the effects of fire on reptile populations are based on local presence or abundance indices (Lindenmayer et al., 2008). Studies estimating the effects of fire on demographic parameters are scarcer (but see Hailey, 2000; Lyet et al., 2009) and, to our knowledge, no population model has been designed to predict the future responses of reptile populations to different fire regimes.

The aim of this study was to predict the resilience of spur-thighed tortoise (*Testudo graeca*) populations to different wildfire regimes. First we estimated the direct and delayed effects of fire on the local survival of juvenile, immature and adult tortoises of a studied population using multistate capture–recapture data and models (Lebreton and Pradel, 2002). Different non-exclusive mechanisms can cause a reduction in tortoises' survival during and after a fire. Direct mortality can be caused by contact with flames, exposure to lethal high temperatures and smoke inhalation (Smith et al., 2001). Short-term delayed mortality may occur linked to habitat degradation, i.e., reduced nutrient availability, loss of cover from predators or loss of thermal refugia (Lawrence, 1966; Sutherland and Dickman, 1999; Esque et al., 2003). Furthermore, the degradation of ecological conditions after a fire may induce a medium- to long-term emigration from the burned area (Lyet et al., 2009). Then, movement patterns and fecundity of adult tortoises located in a burned and an unburned area were compared. Finally, we used the resulting estimates to forecast the dynamics of spur-thighed tortoise populations under different fire scenarios using stochastic population models, including the frequency of fires, the surface burned and also testing for the potential effects of demographic stochasticity due to the natural variations in tortoise density (Anadón et al., 2009, 2010).

2. Methods

2.1. Species and study area

The spur-thighed tortoise *T. graeca* is a long-lived threatened species living in Mediterranean shrublands (Anadón et al., 2006a,b). *T. graeca* spend most of their lives sheltered under the vegetation or in refuges underground. They use burrows, or bury themselves, to hibernate and aestivate, where they may be protected from extreme temperatures, predators and possibly from

Table 1

(a) and (b) Fire history data from areas inhabited by spur-thighed tortoise populations in the Murcia Region, SE Spain, 1995–2005. Sources: Dirección General del Medio Natural of the Region of Murcia, Dirección General de Protección Civil of the Region of Murcia and Anuario Estadístico de la Región de Murcia (2008) published by the Centro Regional de Estadística de la Región de Murcia of the Region of Murcia, Forestal area considered = 67 235 Ha.

Fire events in the region of murcia (SE Spain)	
(a)	
No. fires (1995–2005)	232
Burned area (Ha)	573.10
Burned area (Ha)/No. fires	2.47 (SD = 17.78)
Burned area (Ha)/year	52.10 (SD = 84.66)
No. fires/year	21.09 (SD = 6.27)
Burned area (Ha)/forestal area (Ha)* year	0.0008 (SD = 0.001)
Fire return time (years)	1 291
(b)	
Burned area (Ha)	% of fires
0–0.1	44.8
0.1–1	31.9
1–10	21.1
10–100	1.7
>100	0.4

fire. Their population dynamics are determined by late reproductive maturity, high and constant adult survival, low and variable juvenile survival and high fecundity (Hailey and Loumbourdis, 1988; Díaz-Paniagua et al., 2001). Along its range in SE Spain the species present strong variations in abundance due to climate constraints comprising various orders of magnitude (from 20 to <0.05 indv/ha; Anadón et al., 2009, 2010).

The study was conducted at the Cumbres de la Galera biological reserve (Sierra de la Carrasquilla, Murcia, Spain 37°32'N, 1°39'W) where a high density population of spur-thighed tortoise is located (20 indv/ha; Anadón et al., 2006a, 2009). The reserve has ca. 70 ha and the study area covered 35 ha. It has a mean annual rainfall and temperature of 295 mm and 18–19 °C, respectively. The altitudinal range of the reserve is 515–655 m.a.s.l. The relief of the reserve is characterised by a system of gullies separated by hillsides of moderate to steep slopes composed of metamorphic (schist) and calcareous materials. The landscape structure is composed by immature successional shrublands (*Anthyllis cytisoides*, *Rosmarinus officinalis*, *Artemisia barrelieri*), patches of tussock grass (*Stipa tenacissima*), and small non-irrigated fields at the bottom of the gullies. According to regional habitat models, the reserve contains the optimum habitat for the species in terms of climate, relief and lithology (Anadón et al., 2006b).

A fire occurred in the summer of 2004 (1st August) in the Sierra de la Carrasquilla, burning an area of 250 ha and affecting 31% of the study area. The fire began outside the study area due to human activities and was rapidly extinguished. It was one of the most extensive fires to have occurred in the Murcia Region in recent years (Table 1). Although no habitat recovery measures were carried out after the fire, vegetation rapidly recovered (pers. obs.).

2.2. Tortoise population monitoring

The Cumbres de la Galera tortoise population was monitored annually from 1999 to 2009. Tortoises were found by walking through the habitat in the springtime and the early summer, according to the activity patterns of the species (Pérez et al., 2002). The same area was evenly covered annually but the effort devoted to searching for tortoises (number of hours per year) was variable over the years. Individuals were handled, marked with an individual code by notching the marginal scutes and released immediately. Although different biometric measures of each individual were recorded, some of the individuals were not

accurately aged because the growth rings of many adults were too worn to be counted accurately. Consequently, tortoises were classified according to their external characteristics which can be used as a proxy of individual sexual maturity and vulnerability to local predators (i.e., individual with a rigid ossified shell being less vulnerable than individuals with a soft, not ossified shell, Henry et al., 1998). Sexable individuals (shell shape and tail length) were classified as adults and unsexable immature individuals were classified as subadults (individuals with a rigid and ossified shell) or juveniles (individuals with a soft and not ossified shell). The resulting classes were strongly correlated with age (juvenile 1–4 years old, subadult 5–8 years old, adult >8 years old, Ben Kaddour et al., 2005; authors, unpub. data).

2.3. Survival probabilities: multistate capture–recapture analyses

We used 11 years of capture–recapture data (1999–2009) to evaluate the influence of the tortoises' age-based individual state (juvenile, subadult and adult) and the effects of the fire occurred in 2004 on recapture and survival probabilities. A total of 1009 observations of 675 individuals were written in multistate encounter histories (Lebreton and Pradel, 2002). Only the first individual observation in each year was used. Multistate models were built and fit to the data using program M-SURGE (Choquet et al., 2004). These models include three types of parameters, noted and defined as follows:

- p_{rt} : the probability that a marked tortoise is recaptured at time t in state r , given that it is alive and present in the population at time t .
- Φ_{rt} : the probability that a tortoise in state r at time t locally survives until $t + 1$.
- $\Psi_{rs,t}$: the probability that a tortoise in state r at time t is in state s at $t + 1$, given that the individual survived from time t to time $t + 1$. In order to simplify our model selection, the structure of the transition probabilities was modelled to be constant over time. We constrained impossible transitions to zero (from an adult state to subadult or juvenile states, from a subadult state to a juvenile state, and from a juvenile state to an adult state).

Models used here do not distinguish mortality from permanent emigration from the study area, and hence survival should be considered as local (Lebreton et al., 1992). The goodness-of-fit of the general model (Pradel et al., 2003) was calculated by building specific contingency tables for each recapture occasion using program U-CARE (Choquet et al., 2009). Model selection was based on Akaike's Information Criterion (Burnham and Anderson, 2002). Additionally, for each model j we calculated the Akaike weights, w_j , as an index of its relative plausibility (Burnham and Anderson, 2002). We began model selection with the general model assuming an effect of the individual state and the year on recapture and survival probabilities and a state effect on transition probabilities. Then, we tested the effects of time, age-based individual state, fire (a punctual effect the subsequent year "1Y" related to the reduced vegetation cover), searching effort (total search hours per year) and their interactions on recapture probabilities. Once we had selected the structure of the recapture probabilities that minimized the AIC value, we tested the effects of time, age-based individual state and fire on survival probabilities. Fire effect was tested following five different hypotheses that assumed different lengths of time (in years) for the effects of fire on survival probabilities:

1Y: a direct survival effect of fire (reduced survival rate from year 2004 to 2005).

2Y, 3Y, 4Y, 5Y: a direct and delayed survival effects of fire (reduced survival rate from 2004 to 2006, from 2004 to 2007, from 2004 to 2008 and from 2004 to 2009, respectively).

2.4. Reproduction and movement patterns

In order to compare movement patterns and fecundity between tortoises located inside and outside the burned area, 12 reproductive adult female tortoises (six inside and six outside the burned area) were fitted with radio-transmitters (Tinyloc S.L.) and radio-tracked from May 2005 to May 2006. They were located every other week during the activity periods of the year (spring, early summer and autumn, Pérez et al., 2002) and once a month in summer and winter. Each location was recorded with a Global Position System (GPS; error ± 3 m).

Radio-tracked females were X-rayed during the spring activity season in order to estimate the number of clutches (NC) and the total number of eggs (NE) laid each year. The time allowed between consecutive X-rays (2 weeks) ensured that all clutches developed by females were detected (Díaz-Paniagua et al., 1996). Differences in NC and NE between females in the burned and unburned areas were assessed by means of an ANOVA test.

Differences in home range size, home range perimeter and distances covered between tortoises inside and outside the burned area were tested with a t -test. We used the Minimum Convex Polygon (Mohr, 1947) as the home range estimator. The distances covered were measured as the mean distances between consecutive locations for the whole annual cycle and for the spring, autumn, summer and winter activity seasons (Pérez et al., 2002).

2.5. Quasi-extinction probabilities: population models

Stochastic population models were built to forecast the effects of fire on the probabilities of quasi-extinction of *T. graeca* populations subjected to different scenarios using program ULM (Legendre and Clobert, 1995). The variance of demographic parameters estimated from CMR modelling (for survival) and field records (for fecundity) were used to simulate environmental stochasticity. To avoid an inflation of the variance estimated from CMR modelling we disentangled sample and process variance of survival estimates (σ^2 , a measure of error variation and covariance in Φ_i). We calculated process variance using program MARK (White and Burnham, 1999) from a model considering temporal and state variation in survival (see Results) to introduce it in simulations as a more reliable measure of environmental stochasticity. This partially ensured that we did not incur a serious bias over-estimating quasi-extinction probability. Projection scenarios included the occurrence of natural catastrophes as the frequency of a fire event, as well as the proportion of burned surface; the former was incorporated as an annual probability of suffering a fire (setting a maximum upper limit at 0.30, i.e., suffering a fire every 3 years, which is the extreme value observed in the tortoise Spanish distribution range- Sierra de Cabrera in Almeria, Spain), and the latter assumed that the proportion of tortoises affected by the fire was the same as the proportion of burned surface (from 5% to 100%). Demographic stochasticity was also included in the population projections due to its potential effect on small populations; the binomial distribution, $B(N, p_i)$ of all vital rates i may have an important role when population size (N) is small. Density-dependence (either positive or negative) was not included in the models because no evidence of Allee effects or carrying capacity was available for the study population and also because we were not interested in the estimation of the final number of individuals at the end of the projections. A thousand Monte Carlo runs of stochastic population models were simulated over a 100-year period and quasi-extinction probabilities were calculated (when population size was below the threshold of 10% of original population size). We introduced the survival values, estimated using CMR modelling, for years with and without the effects of fire, into the models. The models included 3 age classes following the CMR

modelling approach: juveniles, subadults and adults (see above), the last-named being the only class able to breed. Recruitment was assumed to be completed for the adult age-class, which was an optimistic guess estimate for a long-lived species with delayed, age-dependent recruitment for sexually mature individuals. Fecundity was considered as the combination of clutch size, annual frequency of clutches, hatching rate and sex-ratio in the nests (set to a guess estimate of 0.5 in our case). Clutch size and laying frequency were estimated using field records from radio-tracked female tortoises (see results). Hatching rate was introduced using previous data from the literature (Swingland and Stubbs, 1985; Hailey and Loubourdis, 1990; Díaz-Paniagua et al., 1997). Even though survival of eggs in nests may be reduced in burned areas, we did not change this parameter when fire occurred because we had no data for it. The effects of fire on the ground are correlated with the combustible biomass and its humidity, which are extremely low in our study area (semiarid shrublands), and below 2–3 cm of the surface the temperature do not increase (Valette et al., 1994; Bradstock and Auld, 1995); consequently the projections were not likely to be biased by this parameter and in no case did they overestimate quasi-extinction probabilities. Nest predation was not introduced because previous studies recorded very variables rates depending on the aggregation of nests in particularly suitable areas (Díaz-Paniagua et al., 1997), which is not the case here because most of the available habitat is suitable for nesting (authors, unpub. data).

The initial population values used for each age class in the simulations were set considering an initial stable age distribution calculated from a deterministic projection of 100 adults. Once the stable age distribution was reached, we scaled the initial population size to different values of N : 35, 70, 350 and 700 individuals. The largest value ($N = 700$) approximately equals the population size of the study area (35 ha and 20 indv/ha), whereas the remaining values of N can be assimilated to decreasing values of density in the same area. Given the characteristics of our stochastic population model, in order to assimilate different N sizes to different population density values we must made the next assumptions (e.g., Akçakaya et al., 1999): (i) no density-dependence effects (positive or negative) operate and (ii) individuals constitute a single and panmictic population (thus with homogeneous vital rates and density). The later condition is easily assumed given the small area (35 ha) relative to the movement patterns of individual (home range from 1 to 4 ha, Anadón et al., 2006a) and being individuals non territorial and with a promiscuous breeding system. In relation to the positive density regulation, our simulated population densities values ranges from 20 to 1 indv/ha whereas natural and viable tortoise populations in SE Spain present densities ranging from 20 indv/ha to 0.05 indv/ha (Anadón et al., 2009). Thus our simulated ranges of population density leave out the lowest abundance populations, where Allee effects may operate. Regarding negative density-dependence, it has not been described in *T. graeca* populations. However, in *Testudo hermanni* density regulation at very high densities (>40 adults/ha) has been suggested to act by means of biased sex-ratios (Hailey and Willemsen, 2000). In our population sex-ratio is unbiased (authors, unpub. data), pointing out that the mentioned density regulation process (the only one known for tortoises) likely do not operate.

Overall, our simulated density range comprises 5 out of the 9 described abundance classes of *T. graeca* in SE Spain (Fig. 1; Anadón et al., 2009, 2010), comprising the 46% of the species' range. It seems sensible not to include the lowest density populations in our models; in addition to the likely appearance of Allee effects, the vital rates of these populations may be not well represented by the parameters obtained in this study from a high density population inhabiting in a climatically optimal habitat (Anadón et al., 2006b).

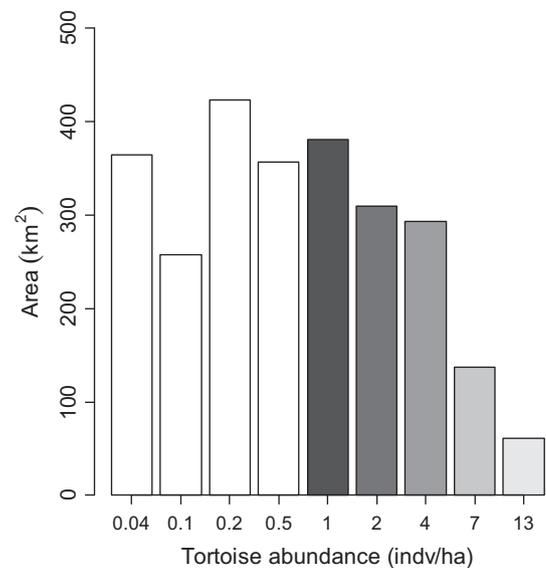


Fig. 1. Distribution of population densities of *Testudo graeca* in SE Spain (aprox. 2500 km²), after Anadón et al. (2009, 2010). The shaded bars represent the abundance classes covered in the stochastic population models for this work. Shade intensity matches abundance classes in Fig. 5.

3. Results

3.1. Capture–recapture modelling

The goodness-of-fit of the multistate model assuming a full time variation of recapture, survival and transition parameters fitted the data adequately ($\chi^2 = 30.92$, 41 df, $p = 0.87$).

We began our model selection with a model that considered the effects of time, age-based individual states and their interaction on both recapture and survival probabilities (Model 1, Table 2). A model in which recapture probabilities varied over time (Model 4, Table 2, Fig. 1) was preferred in terms of AIC over models including the effects of age-based individual states (Models 2–3, Table 2), search effort (Model 5, Table 2), fire (Model 6, Table 2) or no effects, i.e., a constant parameter (Model 7, Table 2). We used the structure of Model 4 (Table 2) for testing the effects of interest in survival probabilities. A model including an additive effect of the age-based individual state and time on survival greatly decreased the AIC value (Model 8, Table 2). Then we tested the effects of the age-based individual states (Models 9–11, Table 2), time (Model 12, Table 2), fire effects (Models 28–32), and the interactions between fire and state effects on survival (Models 13–27). The model including additive punctual effects of fire on the three age-based individual states (juvenile, subadult and adult) on survival probabilities (Model 13, Table 2) presented the lowest AIC value, although Model 13 was tied in terms of AIC with models including additive delayed effects of fire on the three biological states (Models 14–17, Table 2), models including the effects of fire on juveniles but not in subadults and adults (Models 23–24, Table 2), and a model considering state but not fire effects (Model 9, Table 2). Models in which survival probabilities were modelled in interaction between state and fire effects (Models 18–22, Table 2), were independent of the age-based individual state and dependent on the punctual or delayed fire effects (Models 28–32, Table 2) or to be constant (Model 33, Table 2) were not supported.

As several models were supported in terms of AIC in our model selection, we calculated model-averaged estimates of recapture (Fig. 2), survival probabilities (Fig. 3) and transition probabilities from models 9, 13–27 ($\Sigma w_i = 0.99$, Table 2). Model-averaged estimates of survival probabilities indicated that juveniles had a lower

Table 2
Modelling recapture 'p' and survival 'Φ' probability for spur-thighed tortoise at the Cumbres de la Galera biological reserve. Notation, np: number of estimable parameters; dev: relative deviance; QAICc: Akaike information criterion corrected for small sample size and overdispersion; Δ_i: the AIC difference between the current model and the one with the lowest AIC value; w_i: Akaike weight. Model notation: 't' = time effect, 'state' = biological state effect (a different value for juvenile 'juv', subadult 'subad' and adult 'ad' tortoises), 'effort' = search effort effect (total number of hours), '1Y' = direct punctual effect of fire, '2Y'-'3Y'-'4Y'-'5Y' = delayed effect of fire during the following two, three, four and five years, respectively, '+' = parallel variation between the effects considered (i.e. additive model), ':' = interaction between the effects considered. The model with the highest w_i is in bold.

Model	p	Φ	np	dev	QAICc	Δ _i	w _i
1	t.state	t.state	51	1865.32	1972.86	34.93	0.00
2	t + state	t.state	42	1877.24	1964.98	27.04	0.00
3	state	t.state	29	1987.17	2046.95	109.02	0.00
4	t	t.state	38	1881.13	1960.19	22.25	0.00
5	Effort	t.state	29	1900.48	1960.26	22.33	0.00
6	F1Y	t.state	31	1987.46	2051.49	113.56	0.00
7	Constant	t.state	30	1991.91	2053.81	115.88	0.00
8	t	t + state	24	1895.59	1944.81	6.87	0.01
9	t	state	15	1908.44	1938.93	0.99	0.12
10	t	ad = sub/juv	14	1920.94	1949.37	11.43	0.00
11	t	ad/sub = juv	14	1928.86	1957.28	19.35	0.00
12	t	t	19	2008.33	2047.09	109.16	0.00
13	t	state + F1Y	16	1905.39	1937.93	0.00	0.20
14	t	state + F2Y	16	1907.53	1940.07	2.14	0.07
15	t	state + F3Y	16	1907.89	1940.44	2.51	0.06
16	t	state + F4Y	16	1907.67	1940.22	2.29	0.06
17	t	state + F5Y	16	1907.66	1940.21	2.28	0.06
18	t	state.F1Y	18	1904.79	1941.48	3.55	0.03
19	t	state.F2Y	18	1905.16	1941.85	3.92	0.03
20	t	state.F3Y	18	1907.66	1944.36	6.42	0.01
21	t	state.F4Y	18	1906.62	1943.31	5.38	0.01
22	t	state.F5Y	18	1906.96	1943.65	5.71	0.01
23	t	ad/subad/juv.F1Y	16	1907.87	1940.42	2.49	0.06
24	t	ad/subad/juv.F2Y	16	1905.99	1938.54	0.60	0.15
25	t	ad/subad/juv.F3Y	16	1908.41	1940.96	3.03	0.04
26	t	ad/subad/juv.F4Y	16	1908.42	1940.97	3.03	0.04
27	t	ad/subad/juv.F5Y	16	1908.44	1940.99	3.06	0.04
28	t	F1Y	14	2011.73	2040.16	102.22	0.00
29	t	F2Y	14	2015.44	2043.86	105.93	0.00
30	t	F3Y	14	2015.91	2044.33	106.39	0.00
31	t	F4Y	14	2014.80	2043.22	105.29	0.00
32	t	F5Y	14	2014.80	2043.22	105.29	0.00
33	t	Constant	13	2021.94	2048.30	110.37	0.00

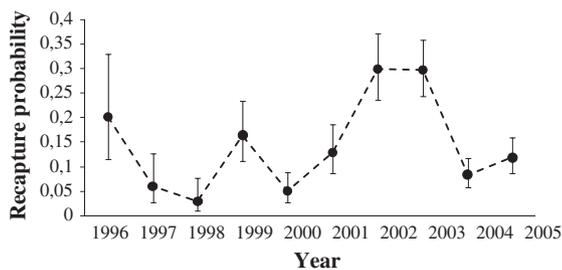


Fig. 2. Model-averaged estimates of annual recapture probabilities for spur-thighed tortoises at the Cumbres de la Galera biological reserve (Models 9, 13–27, Table 2).

local survival rate than subadults and adults (Fig. 3). Before the fire event that burned 31% of the tortoise habitat in the study area, adult, subadult and juvenile tortoises showed a mean local survival probability of 0.98 (95%CI = 0.92–0.99), 0.79 (95%CI = 0.57–0.90) and 0.20 (95%CI = 0.08–0.42) respectively (Fig. 3). From these values, assuming a constant survival rate of tortoises outside the burned area (69% of the tortoise population) and a homogeneous density of tortoises in the study population, we can approximate the average survival probabilities of tortoises inside the burned area. These values decreased following the fire, especially among juveniles and subadults (Fig. 3). The reduction in survival probabilities was higher the year immediately after the fire that reduced the average survival probabilities of adults, subadults and juveniles by 12.48%, 62.20% and 100% respectively. The recovery of the survival values observed prior to the fire was faster among adults than

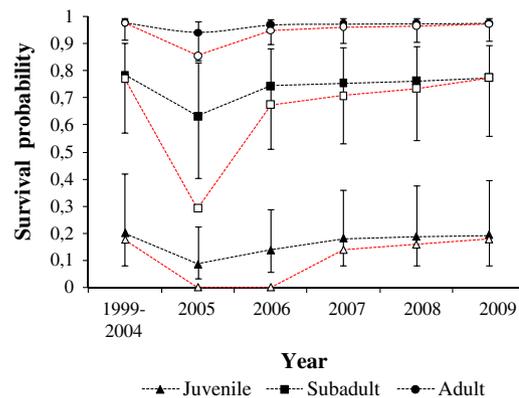


Fig. 3. Model-averaged estimates of survival probabilities for juvenile, subadult and adult spur-thighed tortoises at the 'Cumbres de la Galera' biological reserve before and after the wildfire occurred in the summer of 2004 (Models 9, 13–27, Table 2). Empty symbols represent the mean survival values estimated for the burned area.

among subadults and juveniles (Fig. 3). Transitions from a juvenile state to a subadult state, and from a subadult state to an adult state were 0.79 (95%CI = 0.26–1) and 0.30 (95%CI = 0.18–0.46), respectively.

Process variances of survival probabilities, calculated from Model 4 (Table 2) using program MARK were 0.10 (95%CI = 0.05–0.37), 0.07 (95%CI = 0.02–0.32) and 0.002 (0.00–0.03) for juveniles, subadults and adults, respectively. These decomposed variances (i.e., eliminating sampling variance) were used in population

models to simulate environmental stochasticity in survival parameters (see below).

3.2. Reproduction and movement patterns

Number of clutches and total number of eggs in radio-tracked females did not differ between unburned and burned areas the year following the fire (NC: ANOVA $F_{1,10} = 0.435$, $p = 0.525$; $NC_{burned} = 1.83 \pm 0.41$; $NC_{unburned} = 2.17 \pm 1.17$; NE: ANOVA $F_{1,10} = 0.553$, $p = 0.474$; $NE_{burned} = 5.33 \pm 2.80$; $NE_{unburned} = 6.83 \pm 4.07$).

Attending to the radio-tracking data, movement analyses for both groups of tortoises (located inside and outside the burned area) did not show differences either in the area and perimeter of the Minimum Convex Polygon ($p = 0.31$ and $p = 0.33$, respectively) nor in the distances covered in the annual cycle ($p = 0.49$), in spring ($p = 0.79$), in summer ($p = 0.30$) or in autumn ($p = 0.17$). We only found significant differences in the distances covered in winter ($p = 0.02$), with tortoises in burned areas covering larger areas at the beginning of the winter season, delaying their entry into hibernation. No individual moved between the burned and unburned areas.

3.3. Population models

Stochastic population projections showed that the effects of fire frequency (introduced as an annual probability of fire) and the surface burned (i.e., the proportion of tortoise population affected) had a similar effect on quasi-extinction probabilities (see Fig. 4). When fire did not occur, population growth rates even at the

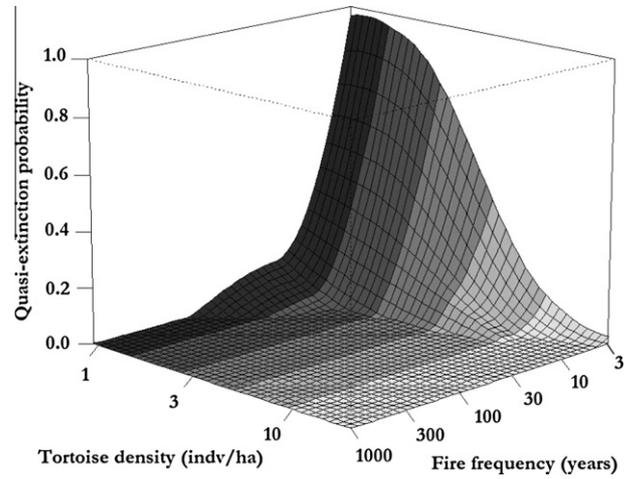


Fig. 5. Effects of population size and frequency of fire on quasi-extinction probabilities for spur-thighed tortoises in scenarios where the surface occupied by individuals was totally burned (100% of surface burned in Fig. 3). Different shades of grey represent different abundance classes of *T. graeca* present within the species' range as described in Anadón et al., 2009 (see Methods).

lowest initial population sizes (35 females) were high ($\lambda = 1.0861$, $SE = 0.0013$). Tortoises showed a relatively high capacity for buffering the effects of fire because quasi-extinction probabilities remained relatively low even with frequent fires affecting large surfaces. However small populations were more affected by the combination of fire impact and demographic stochasticity; quasi-

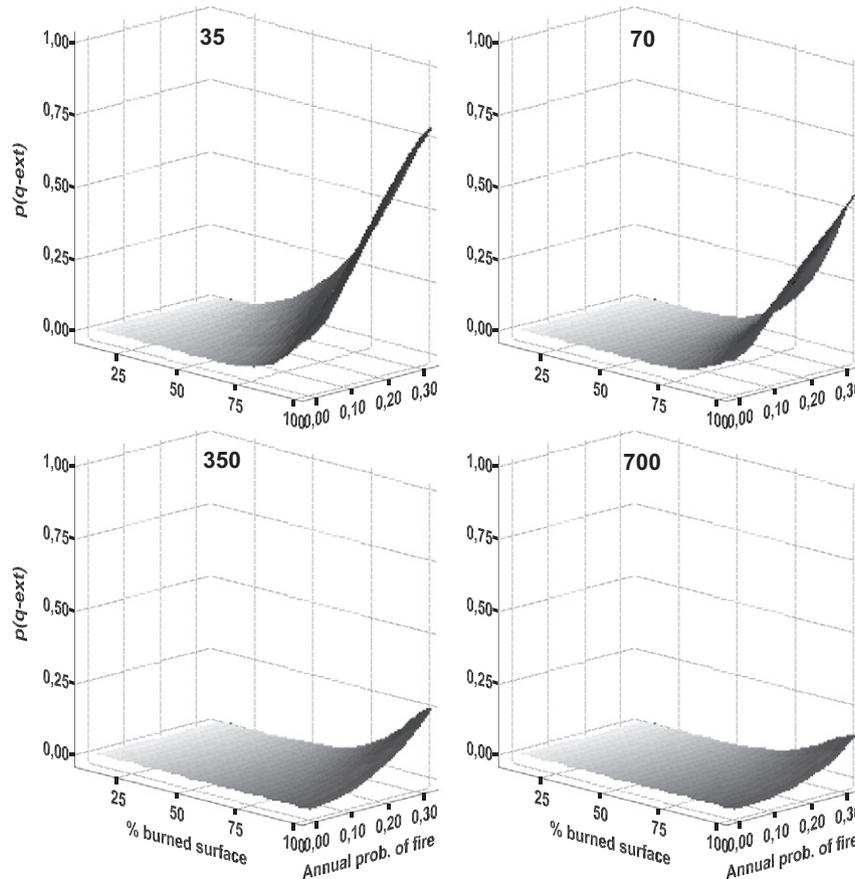


Fig. 4. Quasi-extinction probabilities for populations for spur-thighed tortoises under different scenarios of fire occurrence (i.e., annual probability of fire) and impact (as proportion of surface burned). The four panels show different initial total population sizes (number above each panel). Monte Carlo simulations were projected over a 100-year period.

Table 3
Survival estimates for several terrestrial tortoise populations and for the *Testudo graeca* study population before the fire event. *Rates corresponding to intermediate adult and subadult size classes.

Specie	Adult survival	Subadult survival	Juvenile survival	Reference
<i>Testudo graeca</i>	0.98 (0.92–0.99)	0.79 (0.57–0.90)	0.20 (0.08–0.42)	This study
<i>Testudo graeca</i>	0.90–0.92		0.01–0.09	Díaz-Paniagua et al., 2001
<i>Testudo graeca</i>			0.39	Keller et al., 1998
<i>Testudo hermanni</i>	0.95 (0.91–0.98)	0.88 (0.79–0.93)	0.52 (0.29–0.75)	Henry et al., 1998
<i>Testudo hermanni</i>	0.89 (0.80–1.00)			Willemsen and Hailey, 2001
<i>Testudo hermanni</i>	0.95 (SE: 0.01)			Bertolero et al., 2007
<i>Gopherus berlandieri</i>	0.73–0.83		0.25	Hellgren et al., 2000
<i>Gopherus agassizii</i>	0.87 (SD: 0.13)*	0.84 (SD: 0.18)*		Doak et al., 1994

extinction probabilities increased markedly (above 0.75) when the probability of fire and surface burned increased and were at their highest ($\lambda = 0.9599$, SE = 0.0001, see Fig. 4). When we simulated scenarios of 100% of burned surface and a range of tortoise population sizes, only fire frequencies lower than one fire every 20–30 years did not yield a strong increase in quasi-extinction probability (Fig. 5). Above this threshold value of fire frequency, only very high populations (>10 indv/ha, i.e., >300 individuals) were not affected by fires.

4. Discussion

Rigorous monitoring of animal species is essential for knowing the overall status of populations and predicting the short- and long-term consequences of events such as wildfires (McCoy et al., 2006; Hailey, 2000; Driscoll et al., 2010). Most studies concerning the effects of fire on reptile populations are based on presence–abundance estimates (Stubbs et al., 1985; Esque et al., 2003; Ashton et al., 2008; Lindenmayer et al., 2008; but see Hailey, 2000; Lyet et al., 2009). These methods do not allow studying the mechanisms responsible of population changes, such as survival or movement. Consequently, there is a clear need to understand the mechanisms behind species' responses to fire in order to forecast the population trajectories and ultimately estimate extinction probabilities under different climate or management scenarios (Williams et al., 2002; Driscoll et al., 2010).

4.1. Tortoise survival in the absence of perturbations

We provide robust estimates on recapture and state-dependent survival probabilities of the spur-thighed tortoise (Table 3). Surprisingly, we did not find any effect of the tortoise age-size individual state on recapture, in contrast with other studies in which juveniles were poorly detected and recaptured (Henry et al., 1998; Hailey, 2000). In accordance with previous evidence on tortoises, we found a positive effect of age/size on survival probabilities (Table 3, Henry et al., 1998; Díaz-Paniagua et al., 2001; Willemsen and Hailey, 2001; but see Pike et al., 2008), probably due to differences in their vulnerability to predators and their thermoregulatory abilities (Henry et al., 1998; Bertolero et al., 2007; but see Pike et al., 2008). Annual adult and subadult survivals seem to be a more conservative life history trait among chelonians than juvenile survival (Table 3).

4.2. Fire effects on local survival, reproduction and movement patterns

Fire-related mortality was higher among juveniles and subadults than among adults, in accordance with the results found by Hailey (2000). Direct age-differential mortality could be related to age-related differences in burrowing behaviour during the season when fires occurred (summer). Adult tortoises spend the sum-

mer and winter periods mostly inactive underground in burrows or by burying themselves, avoiding extreme temperatures and providing protection from predation. On the other hand, younger individuals, particularly juveniles, employ more superficial burrows or simply seek under the vegetation (authors, pers. obs.), most likely because their digging capabilities are physically limited. During fire on grasslands, the heating of soil does not generally exceed a few centimetres in depth (Valette et al., 1994; Bradstock and Auld, 1995), and thus most adults were probably less exposed to high temperature and smoke than younger individuals. Besides, small individuals may have suffered higher mortality from lethal heating than adults because of their higher surface-to-volume ratio, which allows heat to penetrate their vital organs relatively quickly (Brooks and Esque, 2002). Hailey (2000) found higher reductions of adult survival than our results. Direct impact of fires on tortoise populations may vary seasonally. Fires occurring during tortoise activity seasons (spring and fall), when most tortoises seek shelter under the vegetation, may have a much stronger impact on survival, such as that experienced by juveniles or subadults according to this study. In the same vein, fires may have a stronger impact on populations where burrow availability or digging is limited (e.g., calcareous areas), which are common within the species' range (Anadón et al., 2006b).

A fire related delayed mortality was observed among juveniles. Our results showed a drastic mortality of juveniles inside the burned area during the first and the second year after the fire (Fig. 3). The strong reduction in vegetation cover after a fire could have increased the visibility of young and vulnerable individuals to predators (Brooks and Esque, 2002; Lyet et al., 2009). In fact, Lawrence (1966) found an increase in the density of large predators due to movements from unburned to burned areas during the months following a fire occurred in the foothills of the Sierra Nevada, EEUU. In addition, the reduction of vegetation after a fire could also have hampered thermoregulatory behaviour, which in reptiles is based on switching between sunny and shaded areas (Blouin-Demers and Weatherhead, 2001), and that is more important among smaller individuals because of their lesser thermal inertia (Harlow et al., 2010). The reduction in food availability could be a third cause of delayed mortality, however grass cover in the burned area growth rapidly after the fire (pers. obs.) and tortoises have low metabolic rates and low energy costs for maintenance, being able to survive long periods with scarce resources (Shine, 2005).

The lack of differences in movement patterns between the burned and the unburned areas suggests that individuals located in the burned areas had not increase their territories to feed. Similar results have been found for the Orsini's viper *Vipera ursinii* (Lyet et al., 2009) or the gopher tortoise *Gopherus polyphemus* (Yager et al., 2007). We did not find differences in female reproductive output between burned and unburned areas, which suggest that food availability after the fire event was not a constraint for female egg formation and laying.

4.3. Tortoise population dynamics: implications for conservation and management

Local population dynamics are determined by survival, dispersal and reproductive rates (Williams et al., 2002). Population growth rates of long-lived tortoises are more sensitive to variation in adult survival than in fecundity-related fitness components (Doak et al., 1994; Heppell, 1998; Bowen et al., 2004; Reed et al., 2009).

Our stochastic population projections showed that the effects of fire may be especially worrisome among small or low-density populations of *T. graeca*, which are also affected by demographic stochasticity when fire frequency or the surface burned is high. Under fire recurrences under 1 fire every 20–30 years, the studied range of tortoise density seems to buffer the effects of fire, although the greater the population density, the better the species copes with fires. However, with a frequency greater than 1 fire every 20–30 years, the probability of extinction explodes, particularly for the smallest populations. The strong increase in the probability of quasi-extinction among small or low-density populations is particularly relevant in the case of *T. graeca*, which presents a wide range of densities (Fig. 1). Only those large populations with the highest density (>10 indiv/ha), which in SE Spain comprise <3% of the range (Anadón et al., 2010), seem not to be seriously threatened by recurrent fires. In the remaining abundance range (97%) the effects of highly recurrent fires might be severe and could threaten the persistence of tortoise populations.

The threshold fire frequency value obtained in this work (1 fire every 20–30 years) matches the estimates for fire frequency in natural Mediterranean shrublands (Mouillot et al., 2002) and it is much higher than current fire frequency estimated in most part of the *T. graeca* range in SE Spain (1 fire every 1000 years, Table 1). This current very low frequency of fires is likely due to the fact that current vegetation in the species range in SE Spain is composed by simplified successional shrublands (*A. cytisoides*, *R. officinalis*, *Helianthemum almeriense*) originated from the abandonment of traditional croplands in the 1960s (Anadón et al., 2006a). Because of their low biomass, fires in these shrublands are rare and cover small areas (Table 1, see also Fernandes, 2001). All in all, our results indicate that most populations of *T. graeca* (at least the densities considered in this study, which comprise the upper half of the abundance range of the species) can coexist with natural or current fire regimes. Nevertheless, along some areas of the species' range where livestock economy is important (e.g., Sierra de Cabrera, Almería, SE Spain), human-induced fires have been traditionally used for increasing the grazing quality of the pastures and fire frequency can approach the maximum considered in this study (0.30, own data). In these areas, tortoise populations may be severely threatened. From a management perspective, nowadays prescribed fires have been advocated for the maintenance of biodiversity (Moreira and Russo, 2007), including some terrestrial tortoises (Yager et al., 2007; Ashton et al., 2008). Our results suggest that fires as a biodiversity management tool may have a strong negative impact on *T. graeca* populations, unless a frequency of less than one fire every 20–30 years were considered. In addition to fire frequency, population size or density is also a key parameter that should be taken into account when discussing the impact of prescribed fires on tortoise populations. Furthermore, for the lowest density populations not included in this work (<1 indiv/ha) the impact could be severe even at much lower frequencies than the 20–30 years threshold value.

As with any other population model, the results here obtained should be read cautiously and bearing in mind the underlying assumptions (Morris and Doak, 2002). In this sense, stochastic models developed in this work could be improved to increase their reliability. First, further information on important parameters such

as recruitment, age-dependent or environmentally-dependent reproduction, hatching success in burned areas or nest predation is needed to complete a more robust population model. Second, our models neither account for density regulation that, if present, could condition the behaviour of the populations dynamics (Henle et al., 2004), nor they include dispersal processes from surrounding populations and thus our models describe the dynamics of isolated populations. Third, as we pointed out above, fires coupled with the activity period of the species, in areas with lower burrow availability due to lithology, or in landscapes with higher vegetal biomass, may be potentially more threatening (Hailey, 2000). Fourth, our models have not addressed those populations with the lowest density (<1 indiv/ha), which in SE Spain comprise 54% of the species range. These populations, which can show different population dynamics (i.e., appearance of Allee effects), are expected to be more sensitive to fire due to demographic stochasticity. Lastly, the potential long-term positive effects of fires on tortoise population dynamics have not been considered in this work (Santos and Poquet, 2010). Fires yield successional immature shrublands that are optimal for the species by reducing canopy cover and increasing grass cover (Anadón et al., 2006a; but see Lindenmayer et al., 2008 for a general discussion on reptiles). Furthermore, burning delivers a pulse of nutrients to soil and plants (Bond and van Wilgen, 1996) and immatures may particularly take advantage of the fast increase in food availability brought by the fire, and grow faster, accelerating the onset of sexual maturity (Stubbs et al., 1985). Considering the positive effects of fires on tortoise populations yields a broader overall vision of the role that fires are likely to have played in the population dynamics of *T. graeca* for millennia. The current landscape structure in the range of the species in the Mediterranean basin, dominated by successional immature shrublands of optimal quality and a very low frequency of fires, has only appeared in the last centuries, and probably does not resemble the ecological conditions where the species originally came from. In the original mature Mediterranean shrublands, with a high canopy cover and thus sub-optimal habitat for *T. graeca*, disturbances (e.g., fires) would open patches of successional shrublands with low canopy cover and high annual grass cover (Anadón et al., 2006a). At a landscape scale, fires would thus lead to bloom-like dynamics of temporary patches with a high density of tortoises inside a matrix of low-density patches due to sub-optimal habitat. In this sense, the current negative role of fire in the population dynamics of the species should be seen within the context of current highly human-modified landscapes, a recent exception in the history of the species.

5. Conclusions

Having a sound knowledge and understanding of species' population biology and dynamics is crucial for implementing appropriate conservation management policies (Pullin et al., 2004). Wildfires have shaped our world since long before humans emerged, and species may be adapted to a particular fire regime (Pausas and Keeley, 2009). Our study shows that medium to large sized populations of the terrestrial tortoise *T. graeca* may coexist within a certain range of fire frequency, which includes natural and current Mediterranean fire regimes. Nevertheless, at planetary level, it is estimated that biomass burning for agricultural reasons has increased by 50% since 1880, and that ca. 500×10^6 ha of savannas and shrublands burn each year (Levine, 1991; Levine et al., 1999), with little known consequences for terrestrial fauna, particularly reptiles. Furthermore, most scenarios for future climate change predict an increase of the environmental variability and the frequency of extreme events such as extreme droughts that may facilitate the spread of fires and shifts in fire regimes involving

higher fire occurrence and larger and more intense fires (Solomon et al., 2007), which could jeopardize the future viability of many spur-thighed tortoise populations.

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