

Maintained effects of fire on individual growth and survival rates in a spur-thighed tortoise population

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Abstract Fires strongly influence the ecology of reptiles and have both direct and indirect effects on population dynamics as they affect life history traits. Here, we examine the effects of fire on individual growth patterns and on the survival rates of a tortoise *Testudo graeca* population in south-eastern Spain. We compare the biometric data from recaptures 4 years before and after a fire which burned 31 % of our study area. The von Bertalanffy and Gompertz growth models best describe the individual growth patterns for males and females. In males, but not females, fire significantly decreased the time required to reach their asymptotic size (k parameter). However, adult survival analyses reveal that the local survival rates lowered for both sexes after fire. Our work evidences that the effects of fire can be complex and maintained over time, affecting different life history traits.

Keywords Disturbance · Fire effects · Growth models · Survival rates · *Testudo graeca*

Introduction

Stochastic disturbances are of particular importance in conservation and ecology inasmuch as habitat perturbations may

result in significant changes in population extinction probabilities (Greenberg 2001). Fire is one of the commonest disturbances that operates across multiple landscape scales to alter habitat structure and diversity (Russell et al. 1999; Esque et al. 2003). Three levels at which fires affect wildlife have been identified (Whelan et al. 2002): (1) direct or first-order effects that occur over a short time period lasting days or weeks; (2) second-order effects, indirect effects of fires that occur over a longer term which may affect key life history traits of individuals, such as growth, survival or reproduction; and (3) third-order effects, as evolutionary effects.

Reptile species are expected to be fire-sensitive species due to their low escape capabilities. In several regions, fires are one of their main threats (Couturier et al. 2011). In this study, we analysed fire effects on a population of the spur-thighed tortoise *Testudo graeca* in south-eastern (SE) Spain. In particular, we assessed second-order effects on individual growth and first- and second-order effects on survival by comparing population life traits before and after fire.

Materials and methods

Study system and data collection

The spur-thighed tortoise is a long-lived threatened species that lives in multi-successional Mediterranean shrublands with home ranges 2.56 ± 3.02 and 1.15 ± 0.15 ha for males and females, respectively (Anadón et al. 2006). This study was carried out in the biological reserve “Las Cumbres de la Galera” (Murcia, Spain; 34 ha). In the summer of 2004, a fire due to human activities burned approximately 250 ha. Although it started outside the reserve and was rapidly extinguished, 31 % of the study area was affected. This fire was one of the most extensive fires occurred in SE Spain in the last decade.

The tortoise population in the reserve was sampled visually, through captures–recaptures of individuals between 2000 and

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2009. Sex was determined according to external secondary characters. Unsexable immature individuals were classified as subadults. Individuals were measured for straight-line carapace length (CL) and marked by notching the marginal scutes. This sampling scheme included a 4-year period before the fire (females=16, males=20 and subadults=3) and another 4-year period after the fire (2005–2009, females=68, males=56 and subadults=5). Although the same area was sampled annually, the efforts made were more intensive after the fire.

Individual growth and survival

The effects of fire on individual growth were assessed using growth models from changes in individual sizes through time. To determine if the overall growth rates of either sex differed before and after fire, nonlinear regressions were used with four commonly used growth models (von Bertalanffy, Gompertz, Richards and a logistic model, as in Dodd and Dreslik 2007; see Electronic supplementary material 1). Having selected the most likely model, we formulate sex-specific growth curves for pre- and post-disturbance. These growth models were defined by two constant parameters, asymptotic size S_{∞} (millimetres) and parameter k (per year), in relation to the time required to reach their asymptotic size. The overall differences in growth curves were assessed using an F test (as in Lindeman 1999). The estimates of the parameters in the models (k and S_{∞}) were tested using a t test. Statistical analyses were performed using the R software (R Core Team 2012).

As previous studies have suggested, population viability in tortoises is sensitive to the survival of adults (Sanz-Aguilar et al. 2011). Consequently, we addressed their survival rates by using the method described by Beverton and Holt (1956). This method employs the mean of a size distribution and S_{∞} calculated previously (see ESM 2). We used a bootstrap to calculate the confidence interval (as in Oedekoven et al. 2013) and a t test to calculate the difference.

Results

The models that best described tortoises' population growth were the von Bertalanffy model and the Gompertz model, when considering the whole study period (see ESM 1). For further analyses, we selected the von Bertalanffy model as it is the most widely used model to describe chelonians population growth.

Differences in growth curves between sexes were observed, which were due to the asymptotic size parameter S_{∞} ($t_{40}=9.380$, $P<0.001$); females had a larger S_{∞} than males (161.84 ± 8.23 and 121.17 ± 2.83 mm, respectively). In relation to fire effects, growth curves were depressed in females and males, but significantly so in the latter (females, $F_{2, 76}=1.83$, $P=0.167$; males, $F_{2, 96}=5.79$, $P=0.004$). After the fire, the differences

were located in parameter k ($t_{94}=3.002$, $P=0.003$; Fig. 1), which decreased for the male population from 0.23 to 0.11 year⁻¹.

Survival rates lowered for both sexes after the fire from 98.43 ± 2.67 to 95.10 ± 1.09 for males and from 94.65 ± 2.27 to 90.09 ± 2.95 for females ($P<0.001$ in both cases).

Discussion

There have been many studies which have addressed the effects of fire on herpetofauna (e.g. Russell et al. 1999; Lindenmayer et al. 2008), and Mediterranean tortoises are specially sensible to this disturbance affecting important traits as mortality or small-scale movements (Hailey 2000; Couturier et al. 2011). However, due to the unpredictability of such events, there are very few works that compare the same population before and after disturbance (Sanz-Aguilar et al. 2011; Dodd et al. 2012).

Fire may alter food availability or may cause loss of shelter from predators and thermal refugia after the disturbance (Esque et al. 2003). After the fire, growth was slower in both males and females, although with a difference only significant in males (Fig. 1). These results were supported by a posterior correlation between weight (W) and CL before and after the fire, revealing a significant decrease in

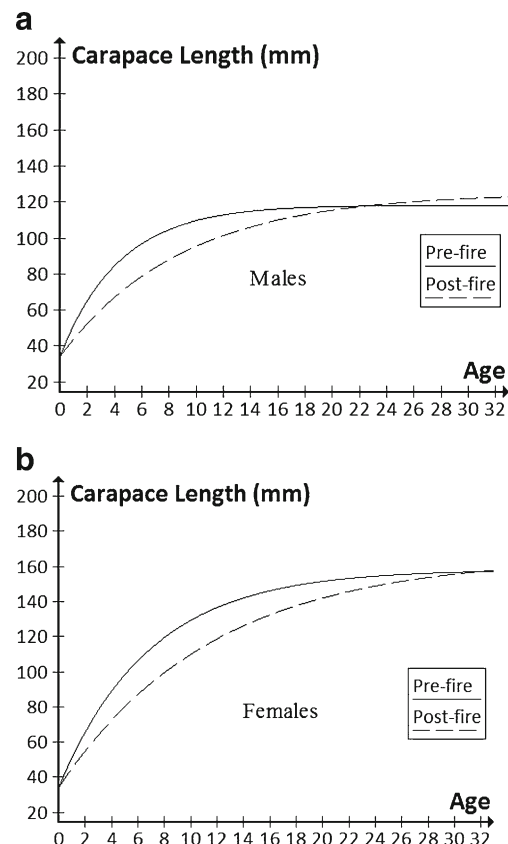


Fig. 1 Von Bertalanffy's growth curves for males (a) and females (b) by disturbance, relating individual sizes and the inferred age from the model

the W of males (MANOVA; W =FIRE+CL; females, $P=0.347$; males, $P=0.0118$). Sex-specific reproductive traits could be responsible of differences in energy requirements (i.e. males spend energy in bigger home ranges as a consequence of active search of females; Anadón et al. 2006).

Very few studies have focused on how the second-order effects of fires affect survival rates of animal populations. Sanz-Aguilar et al. (2011) studied first- and second-order effects on the survival of *T. graeca* by considering our same study system, but they employed capture–recapture models. Their work revealed that the survival probabilities of adults lowered from 98 % before fire to 86 % during the first year after fire, 95 % in year 2, 96 % in year 3 and 97 % in years 4 and 5 (an average of 4 % over the 5-year period). Our results report similar reductions in this population's survival rates (4 % for females and 3 % for males) using a different approach. From an applied and methodological point of view, our work demonstrates that the study of individual growth patterns can yield similar survival estimates to those offered by capture–recapture techniques.

For terrestrial tortoises, the effects of fires strongly depend on species and population and also on fire characteristics. Several studies have shown that fire can even have beneficial repercussions for tortoise populations (Russell et al. 1999; Yager et al. 2007). However, as shown by Sanz-Aguilar et al. (2011), despite some populations being able to coexist with fires, high recurrences or small population sizes can lead to local extinctions of spur-thighed tortoises.

In this sense, our work provides complementary results to current knowledge of the effects of fires on *T. graeca*. We did not only find effects on the survival rates of individuals but also detected that fire has relevant effects on their growth, which have consequences for population dynamics (i.e. number of eggs or clutches, size at maturity or even changes in survival). For this reason, we suggest that the effects of disturbance are complex and variable because they affect several life history traits.

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