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A low cost approach to estimate demographic rates using inverse modeling

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ABSTRACT

Survival is a key parameter in species' management and conservation. Most methods for estimating survival require time series data, large sample sizes and, overall, costly monitoring efforts. Inverse modeling approaches can be less data hungry, however they are underused in conservation sciences. Here we present an inverse modeling approach for estimating relative survival rates of long-lived species that is mathematically straightforward and evaluate its performance under constraints common in conservation studies related to small sample sizes. Specifically, we (i) estimated the relative survival rates in a *Testudo graeca* population based on one-year monitoring, (ii) assessed the impact of sample size on the accuracy, and (iii) tested alternative hypotheses on the impact of fire on the survival rates. We then compared the results of our approach with capture-recapture (CRC) estimates based on long-term monitoring. Our approach (153 individuals within a single year) yielded estimates of survival rates overlapping those of CRC estimates (11 years of data and 1009 individuals) for adults and subadults, but not for juveniles. Simulation experiments showed that our method provides robust estimates if sample size is above 100 individuals. The best models describing the impact of fire on survival identified by our approach predicts a decrease in survival especially in hatchings and juvenile individuals, similar to CRC estimates. Our work proves that inverse modeling can decrease the cost for estimating demographic rates, especially for long-lived species and as such, its use should be encouraged in conservation and management sciences.

Key words: Pattern-oriented model, survival rates, demography, tortoise, disturbance, fire, *Testudo graeca*

1. INTRODUCTION

The estimation of demographic parameters such as survival and reproduction rates is key for accurate forecasting of the fate of wildlife populations and for evaluating alternative management actions (Boyce, 1992; Williams et al., 2002; Beissinger and McCullough, 2002). In ecology, several approaches have been developed to estimate demographic parameters of wild animal and plant populations (Williams et al., 2002; Gross et al., 2002; Thomson et al., 2009). The estimation of age dependent survival is especially difficult for long-lived species because current methods such as capture-recapture (CRC) methods typically require long-term monitoring of individuals (Lebreton et al., 1992), which involves intensive field effort (e.g. for tortoises the range is 3-22 years monitoring, Appendix 1) and consideration of imperfect detection (Lebreton and Pradel, 2002; Thomas et al., 2010; Sanz-Aguilar et al., 2016). The capture-recapture framework allows for dealing with imperfect detection and is now commonly used to estimate animal survival rates (e.g., Lebreton et al., 1992; Lebreton and Pradel, 2002; Giménez et al., 2007; Thomson et al., 2009; Sanz-Aguilar et al., 2016). During the last decades, technological development has allowed to track animals and obtain direct survival estimates using telemetry data that provide an accurate monitoring of individuals over time (Millspaugh and Marzluff, 2001), but batteries do not usually last long (Bridge et al., 2011). Although CRC and telemetry monitoring methods proved to be accurate and useful, they can often not be applied for species of conservation concern where long-term studies would be very costly or infeasible (Williams et al., 2002).

An alternative to direct estimation of demographic parameters is indirect estimation based on population-level data such as age structure estimates (e.g., Caughley, 1977; Michod and Anderson, 1980; Udevitz and Ballachey, 1998; Wiegand et al., 2004). For example, survival rates can be indirectly estimated from age distribution data by analysis of the underlying age-structured Leslie matrix model if additional pieces of information are available, for example population growth rate, recruitment rates, the age structure of natural deaths, or stability of the age structure (Caughley, 1977; Michod and Anderson, 1980; Tait and Bunnell, 1980; Sickle et al., 1987; Udevitz and Ballachey, 1998). Similar methods were also developed in fisheries where catch-age patterns provide population age structures that then allowed together with auxiliary information for stock assessment (for a review see Quinn, 2003). These approaches fit into the pattern-oriented modeling strategy (Wiegand et al., 2003; Grimm et al., 2005), a general modeling framework that relies on “inverse modeling” where the outputs of a model called “patterns” (e.g., in our context the emerging stable age distribution of a population or time-series data) are used to estimate the model inputs (e.g., the unknown parameters). In other words, inverse modeling estimates parameter values by optimizing the match between observed patterns and the corresponding model outputs. Inverse modeling has been traditionally used in several scientific areas like hydrology, oceanography, soil science or climatology (Tarantola, 1987; Gottlieb and DuChateau, 1996; Wunsch, 1996; Bennett, 2002), but less in ecological studies. Exceptions are applications to time-series data (e.g., Wiegand et al., 1998, 2004; Gross et al., 2002; Martínez et al., 2011, 2016; González and Martorell, 2013; White et al., 2014; González et al., 2016; Zipkin et al., 2014a,b) or other types of patterns (e.g., Revilla et al., 2004; Kramer-Schadt et al., 2007; Hartig et al., 2011; Anadón, et al., 2012; May et al., 2015).

However, inverse modeling is still underused in ecology and, particularly, in conservation studies, and the performance of these methods under different sampling efforts and their potential for hypothesis testing or model selection have not been fully assessed. Here we present an inverse modeling approach for estimating relative survival rates of long-lived species that does not require long-term monitoring (or time-series data) and, as such, circumvents time and funding constraints commonly encountered in conservation studies. We illustrate our approach using the spur-thighed tortoise (*Testudo graeca*) in the southeastern Spain as a case study. This population has been intensely studied in previous studies (Pérez et al., 2002; Rodríguez-Caro et al., 2013, 2016, 2017), including long-term monitoring studies and capture-recapture studies (e.g. Sanz-Aguilar et al., 2011).

Our specific goals are threefold. First, we aim to compare estimates of survival rates of *T. graeca* obtained by means of our inverse modeling approach using age-distribution data from just one year with estimates obtained by means of capture-recapture methods using long term monitoring data (i.e. 11 years; Sanz-Aguilar et al., 2011). Second, we aim to explore how sample size affects the accuracy and precision of the estimated relative survival rates and to identify a minimum sample size for our case study. Third, we illustrate how our approach can be used to test alternative hypotheses on factors affecting survival, which is in our particular case study the impact of fire on survival rates.

2. MATERIALS AND METHODS

2.1. General methodology

Our approach uses the observed age distribution of the population that can be obtained by short-term studies as pattern to indirectly estimate relative survival rates based on age-structured population projection matrix models (Caswell, 2001). While the pattern-oriented approach is in general flexible, our specific implementation relies on the assumptions that: a) the sampled population is stable and closed (i.e., no dispersal in or out of the study area); b) the observed age structure of the population contains signals of the demographic rates and detectability; and c) stochasticity is relatively unimportant.

First, an age-structured Leslie projection matrix (Caswell, 2001; Fig. 1b) is used to generate the expected stable age distribution (Fig. 1c) of hypothetical populations under different combinations of demographic parameters such as age-dependent survival rates S_i and fecundity F (Fig. 1a). To obtain the stable age distribution we used the R package popbio (Stubben and Milligan, 2007). To find the demographic parameters that produce the best match with the observed age structure (Fig. 1e), we varied them systematically over the parameter space (Fig. 1a) (Wiegand et al., 2004).

The age-structured Leslie transition matrix (A) takes the form

$$A = \begin{bmatrix} 0 & 0 & 0 & \ldots & 0 & F_r & \ldots & F_m \\ S_1 & 0 & 0 & \ldots & 0 & 0 & \ldots & 0 \\ 0 & S_2 & 0 & \ldots & 0 & 0 & \ldots & 0 \\ 0 & 0 & S_3 & \ldots & 0 & 0 & \ldots & 0 \\ 0 & 0 & 0 & \ldots & 0 & 0 & \ldots & 0 \\ 0 & 0 & 0 & \ldots & S_{r-1} & 0 & \ldots & 0 \\ 0 & 0 & 0 & \ldots & 0 & S_r & \ldots & 0 \\ 0 & 0 & 0 & \ldots & 0 & 0 & \ldots & 0 \\ 0 & 0 & 0 & \ldots & 0 & 0 & \ldots & S_m \end{bmatrix} \qquad (1)$$

where the S_i represent the survival rates for age $i = 1$ to m, with m being the maximal age, r the age when subadults become adults (i.e., be reproductive), and F_i the fecundity rate. Usually, the population is divided into o different age classes (e.g., one-year-old individuals, juveniles, subadults, and for adults) and the same survival rates S_i are assumed within each age class. The fecundity term varies depending on timing of the census (i.e., pre- or post-breading census). For the case of pre-breeding matrices as used here we obtain

$$F = SR \times BS \times S_\mathrm{h} \qquad (2)$$

where *SR* is the female sex ratio (note that the Leslie matrix is typically calculated only for females), *BS* the (age-independent) breeding success, and S_h is the survival from hatching to the first year.

Given that individuals of the different age classes (e.g., juveniles vs. adults) can differ in their detectability (e.g. Rodríguez-Caro et al., 2016, 2017), the predicted stable age distributions must be corrected. This can be accomplished by multiplying the predicted age distributions resulting from the projection matrix by age-dependent detection probabilities to obtain the "observable age distribution" of the simulated populations.

Our inverse approach could be applied in principle for all parameters of the age-structured Leslie transition matrix (eq. 1), however, because the effects of fecundity and mortality parameters typically cancel in this type of models, parameter identifiability problems may arise if no additional information is used (Wood, 1997). While survival parameters are usually difficult to estimate on the short-term, fecundity parameters are more often available for long-lived species such as the spur-thighed tortoise (Díaz-Paniagua et al., 1996, 1997). We therefore applied inverse modeling for the relative survival rates of the age-structured Leslie transition matrix (eq. 1) that are unknown, whereas we estimated age or stage-specific fecundity from independent information.

We identified the relative survival rates that fitted the observed age distribution data best by using a likelihood approach (Hilborn and Mangel, 1997; Burnham and Anderson, 2002). To define the match between observed and predicted age distributions, we calculated the likelihood of observing the observed age frequencies (x_1, x_2, x_3, x_4,…, x_m; where m is the maximal age) given the predicted age structure (p_1, p_2, p_3, p_4,…, p_m) that emerged from a parameterizations $\boldsymbol{\theta}$

of the population model. Given the multinomial nature of our variable and assuming independence, the log-likelihood function is given by:

$$l(\boldsymbol{\theta}, p_1, p_2, ..., p_m) = \log(\frac{n!}{\Pi x_i!}) + \sum_{i=1}^{m} x_i \log(p_i) \qquad (3)$$

where n is the total number of individuals, x_i ($i = 1, \ldots m$) is the observed number of individuals in age class i and p_i ($i = 1, \ldots m$) is the predicted proportion of individuals in age class i.

Because the stable age distribution P is the right eigenvector of the dominant eigenvalue λ of the Leslie transition matrix **A** (i.e., $A\ P = \lambda\ P$), multiplying the survival vector $\boldsymbol{\theta} = (S_1, ..., S_o)$ by a constant c with $0 < c < 1/\max(\boldsymbol{\theta})$ results in the same predicted stable age distribution and hence in the same likelihood. Therefore, we can identify only the relative survival rates $\boldsymbol{\theta}_{\mathrm{rel}} = (S_1/S_2, S_2/S_3, \ldots S_{m-1}/S_m)$, but use of additional information may allow us to restrict the range of the absolute survival rates.

There are different possibilities to find the maximum of the log-likelihood function over the parameter space; here we used an approach based on a rejection filter (e.g., Wiegand et al., 2004; Hartig et al., 2011) where we accepted in a first step all parameterizations $\boldsymbol{\theta}$ with $\Delta\mathrm{AIC} < 2$ (Burnham and Anderson, 2002). We use the rejection filter approach to obtain the full posterior distribution of the relative survival rates $\boldsymbol{\theta}_{\mathrm{rel}}$ and because we want to use the more flexible simulation approach to test alternative hypothesis on factors impacting survival (i.e., our third goal). However, as shortcut one may also fit the relative survival rates directly, for example using the *mle* function of *stats4* package in R (R Core Team, 2016).

For each accepted parameterization $\boldsymbol{\theta}$ we calculated the ratios S_i/S_{i+1} to obtain their posterior distribution. Because survival rates range between 0 and 1, the estimates of the relative survival rates allow us to generate upper bounds for each survival rate S_i. To do this, we identify the highest survival rate in relations to each other, define its value as one, and obtain the corresponding values of the other survival rates as their upper bounds. In order to narrow down the possible range of the highest survival rate, we determine for different values of the highest survival rate the mean age of individuals that survived up to adult age the age only 1% of them reach and the longevity of the individuals (Castanet, 1994).

In theory, a population may reach a stable distribution, but in reality, it never arrives exactly at its stable distribution (Williams et al., 2011). It is thus critical to assess how far away a population is from the stable distribution. We therefore evaluated the distance between the observed age distribution and the stable age distribution of the best model using two common measures: Keyfitz's delta (Keifitz, 1968) and projection distance (Haridas and Tuljapurkar, 2007). Keyfitz's delta is the sum of the differences between the predicted stable age distribution and the observed age distribution and the projection distance is the difference between the reproductive value of a population with the observed age structure and the reproductive value of a population with the predicted stable age distribution.

Our approach can be extended to test alternative hypotheses on the drivers of temporal variation in demographic rates. To this end, different model structures that correspond to alternative hypotheses can be implemented within a simulation framework. For each alternative model structure, we determined the best estimate of the parameter vector $\boldsymbol{\theta}_{\mathbf{rel}}$ using relative estimates and compared competing models structures based on their corresponding AIC values. Model structures with $\Delta\text{AIC} < 2$ were considered equally well supported (Burnham and Anderson, 2002).

2.2. Case study

We applied inverse modeling to estimate relative survival rates of a long-term monitored population of the endangered spur-thighed tortoise *Testudo graeca*. The spur-thighed tortoise is a small long-lived chelonian widely distributed in the Mediterranean basin. The "Cumbres de la Galera" population has been monitored during the last 15 years (Sanz-Aguilar et al., 2011; Anadón et al., 2012; Rodríguez-Caro et al., 2013, 2016). In summer of 2004, a fire burned 31% of the study area. Sanz-Aguilar et al., (2011) and Rodríguez-Caro et al., (2013) estimated survival and the effect of fire on survival rates by means of multistate capture-recapture models and, by comparing the individual growth models, respectively. These survival estimates were used to validate the results of our inverse modeling approach.

We examined the observed age structure of the population in two different years: just before the fire event (2003) and 5 years later in 2009 (age distribution in Appendix 2) when the cumulative effects of fire over time are expected to be ceased (Sanz-Aguilar et al., 2011). We approximated individual age using growth rings and the carapace length (see details in Appendix 3). This allows us to distinguish in total twenty-five age classes. The oldest age class included all individuals older than 24 years because the accuracy of age estimations for older individuals in our population is low (Rodríguez-Caro *et al*. 2015). To compare our estimates of the survival rates with those obtained by classical capture-recapture methods, we classified 1 to 4 year old tortoises as juveniles (S_j), those aged 5 to 8 as subadults (S_s), and older individuals as adults (S_a) (Sanz-Aguilar et al., 2011). In addition, we also included the survival from hatching to the first year (S_h). Our task is to find the best parameterization for our relative survival vector $\boldsymbol{\theta}_{\mathbf{rel}} = (S_h/S_j, S_j/S_s, S_s/S_a)$.

2.3. Application (a): Estimating survival

We applied our inverse approach to estimate the survival in our population using one year of monitoring (before the fire, 2003; n=153, Appendix 2). In a first step, we generated all possible parameterizations $\boldsymbol{\theta} = (S_h, S_j, S_s, S_a)$ where the ranges of each of survival rate S_i varied between 0.01 and 0.99 with steps of 0.02, thus assuming a conservative upper bound for all survival rates of 0.99. For each S_i we therefore tested 50 alternative values. This resulted in a total of $50^4 =$ 6,250,000 parameter combinations. In a second step, we used a pre-breeding Leslie matrix with 25 age-classes (eq. 1), but survival rates were estimated per stage. The fecundity parameter of the Leslie matrix was defined by equation 2, where first-year survival (S_h) was inversely determined by our approach, the sex ratio (SR) in this population was 0.5 (a clutch contains on average half male and half females; Graciá et al., 2017), and breeding success was estimated as $BS = NC \times CS \times HS = 5.21$. For the latter we used data on the number of clutches ($NC = 2$) and clutch size ($CS = 3.16$), estimated in study by Rodríguez-Caro et al., (2014), and data on hatching success ($HS = 0.824$) was obtained from bibliography (Díaz-Paniagua at al., 1997).

In a third step, we obtained age-specific estimates of detectability by distance-sampling procedures (Thomas et al., 2010). Detection probabilities were 0.27 for juveniles (age 1-4), 0.41 for subadults (age 5-8) and 0.47 for adults (age > 8; see Appendix 4 for details).

In a fourth step, we calculated the likelihood (eq. 3) for each parameterization $\boldsymbol{\theta}$ using the corresponding detectability-corrected simulated age distribution (Fig. 1d) with the observed age distribution of the monitoring of 2003 (Fig. 1c), and accepted all parameterizations $\boldsymbol{\theta}$ with ΔAIC < 2 (Burnham and Anderson, 2002). Next, we calculated for all accepted parameterizations the ratios S_h/S_j, S_j/S_s, and S_s/S_a to obtain their posterior distribution and expected values, as well as the upper bounds of the survival rates. We also tested the difference between the observed age distribution and the stable age distribution (Williams et al., 2011). Finally, we compared our estimated survival rates with the mark-recapture estimates of Sanz-Aguilar et al., (2011).

2.4. Application (b): Impact of sample size.

By means of simulation experiments, we assessed the impact of sample size on the precision and accuracy of the relative survival estimates obtained by our approach. Starting from the stable age distribution resulting from a pre-breeding Leslie matrix with known parameter values $\hat{\boldsymbol{\theta}}$ (known vector of survival rates), we simulated a population of 1000 individuals by scaling the right eigenvector associated with the dominant eigenvalue (that represents the stable age distribution) to a total abundance of 1000. We used the observed detection probabilities to obtain stochastic samples of the simulated population with different sizes N. The age distributions arising from this sampling process were then used in the same way as the *observed* data in our inverse modeling approach presented in Application 1. We repeated this procedure for different sample sizes N ($N = 500, 400, 300, 200, 100, 75, 50, 25$). For each N, the sampling process was repeated 30 times. To select the minimum sample size that yields acceptable estimates we compared the increase of the standard deviation when reducing the sample size N. We tested the differences in the variance of the survival rates between $N = 500$ and the other samples size by Levene's test (Levene, 1961).

2.5. Application (c): Factors impacting survival

Our approach also allows for testing alternative hypotheses on temporal variation in the survival and fecundity parameters of the Leslie matrix. We applied this feature to our case study by assessing the impact of a fire disturbance (that occurred in our population in 2004) on the temporal variation of the survival rates. This allowed us to compare our results with a previous study that estimated survival rates after fire by means of capture-recapture approaches (Sanz-Aguilar et al., 2011) for the same population and disturbance.

We used the most likely model parameterization $\hat{\boldsymbol{\theta}}$ determined in Application 1 (that was based on the observed age distribution of the year 2003) to generate the stable age distribution for the year 2004 of the fire. We then simulated the next 5 years using survival rates modified in accordance with a set of alternative hypotheses and compared the simulated age distribution for year 2009 to the corresponding observed distribution (i.e. 5 years after the fire).

For hypothesis H0 (*no effects of fire on survival*), the survival parameters did not change, they are constant before and after the fire. For hypothesis H1, H2, H3, H4 and H5, population dynamics was simulated with new relative survival rates $\boldsymbol{\theta}_{rel}$ applied only for one, two, three, four or five years after the fire, whereas we applied in subsequent years the pre-fire survival rates $\hat{\boldsymbol{\theta}}$. The fire disturbance did not have negative effects on fecundity (Sanz-Aguilar et al., 2011), so we assumed no change in fecundity. We finally compared our estimates of the survival rates and the most likely hypothesis with that obtained in the previous study of Sanz-Aguilar et al., (2011).

3. RESULTS

3.1. Estimating survival

Our rejection filter retained 5001 out of a total of 6,250,000 tested parameter combinations (0.08%). The relative survival rates were $\boldsymbol{\theta}_{\mathbf{rel}} = (0.26, 0.98, 0.93)$ for S_h/S_j, S_j/S_s, and S_s/S_a, respectively (Fig. 2). The upper bound vector of survival rates was $\boldsymbol{\theta}_{\mathbf{upper}} = (0.23, 0.87, 0.91, 0.99)$ for S_h, S_j, S_s and S_a, respectively. To assess a biologically reasonable lower and upper bound for adult survival S_a (the highest survival rate). We found that a 9-year old individual reached for

S_a = 0.85, 0.9, 0.95, 0.97, and 0.99 on average an age of 15, 18, 28, 41, and 106 years, and 1% of them reached at least an age of 37, 52, 98, 160, 467 years, respectively. With a maximum longevity of the species in captivity reported as 102 years (Castanet, 1994), adult survival rates between 0.90 and 0.97 seem reasonable. In a second rejection filter, we selected the parametrization for hatching, juveniles and subadults using S_a between 0.9 – 0.97 (second rejection filter retained 1256) and we estimated the range for each survival rate (0.17 – 0.33 for S_h, 0.71 – 0.99 for S_j and 0.75 – 0.97 for S_s) (Fig. 3).

Sanz-Aguilar et al., (2011) estimated the survival rates of the population using 10 years of monitoring and obtained $\hat{\boldsymbol{\theta}}$ = (*NA*, 0.20, 0.79, 0.98) for juveniles, subadults and adults, respectively (Table 1) (note that CRC estimates did not consider first year survival). Our estimates for adult and subadult survival are very similar, with 95% CI's overlapping that of Sanz-Aguilar et al., (2011) (Table 1). However, our estimates for juvenile survival differ from that of Sanz-Aguilar et al., (2011).

The measures of distance between observed and predicted age distribution showed that the population can be considered as stable. We found a value of Keyfitz's Δ = 0.148 and a projection distance α_0 = -0.028. A value of Δ = 0.148 means that just 14.8% of individuals are in other classes than expected (Keifitz, 1968). A projection distance α_0 = 0 represent a stable age distribution, and our slightly negative value implies that the population is somewhat more concentrated into stages with low reproductive values. The stable age distribution is available in Appendix 2.

3.2. Impact of sample size

Our estimates were robust for sample sizes larger than 100 individuals, but uncertainty increased quickly for smaller sample sizes (Fig. 4), especially for S_j/S_s. Within this range, the obtained estimates approximated the known survival rates well (Appendix 5). Below 100 individuals, estimates were more uncertain with larger standard deviations (Fig. 4). The Levene-test showed that the variance was different when the sample size was over or lower 100 ($W_{ShSj} = 49.89$, *p-value* = <0.001; $W_{SjSs} = 55.16$, *p-value* = <0.001; $W_{SsSa} = 55.57$, *p-value* = <0.001).

3.3. Factors impacting survival

The observed age distribution after the fire was calculated with 117 tortoises of year 2009 (Appendix 2). The hypotheses that received the least support were the null hypothesis H0 with no impact of fire on survival (Table 2). Hypothesis H5 that assumed more long-lasting effects of fire on survival (up to 5 years) represented the best model (Table 2). The estimate relative survival rates were $\boldsymbol{\theta}_{\text{rel H5}} = (0.11, 0.66, 0.94)$. With the upper bound survival estimates $\boldsymbol{\theta}_{\text{upper H5}} = (0.07, 0.62, 0.94, 0.99)$ for S_h, S_j, S_s and $S_{a,}$ respectively. We found a high reduction in one-year-old and juvenile survival after fire. Stable age distributions of the six hypotheses are available in Appendix 2.

Our results partially match those obtained by Sanz-Aguilar et al., (2011) that also identified a large reduction in survival of young individuals. According to Sanz-Aguilar et al., (2011), after fire, survival rates were 0.11, 0.62 and 0.95 for juveniles, subadults and adults, respectively.

4. DISCUSSION

Survival is a key parameter in studies regarding the conservation of populations, and as such, methods to estimate survival based on low sampling efforts are much needed. Approaches based on inverse modeling have been proposed as a low cost method alternative to classic methods (i.e. capture-recapture). However inverse modeling approaches are still underused in conservation and management disciplines. Our study assesses the performance of these methods under different sampling efforts and their potential for hypothesis testing.

4.1. Estimating survival

Our comparison of the survival estimates from inverse modeling with that of capture-recapture is insightful. Our estimates based on data of 153 individuals that were captured during one year of monitoring are comparable to those obtained using capture-recapture analyses of 11 years (with >1000 captures) in the same population. Our estimates agreed with capture-recapture estimates for subadults and particularly adults, the age classes for which the species demography is more sensitive (Doak et al., 1994; Walker et al., 2012; Pérez et al., 2012). However, as one may expect, the uncertainty was somewhat higher when using only one year of data (Table 1). In our case, we directly estimate relative survival rates from the age distributions of 153 individuals captured during one year. However, biologically realistic values of survival rates (i.e., information on longevity) of the adult life stage were used as additional information to improve parameter estimates.

The biggest difference in survival estimates between the capture-recapture method and our approach appears in juvenile survival. However, we suspect that this difference emerged largely because of methodological differences. Our approach divides juvenile survival into two groups: the first year and juveniles (until 4 years old), whereas the capture-recapture analysis could not consider first year survival separately because hatchlings were not marked (they have a soft carapace). Interestingly, our estimate of first year survival (S_h) is very similar to the capture-recapture estimate of juvenile survival (S_j) (Table 1). Additionally, the capture-recapture estimate of juvenile survival may be low because of the low detectability and sample size of young individuals (Doak et al., 1994; Hailey, 2000; Tuberville *et al.,* 2008; Pike et al., 2008), because recapture probabilities of juveniles were not modeled separately, or because some juveniles may also lose the marks when growing carapace. However, beside of methodological differences, our approach may also overestimate juvenile survival because observed juvenile population sizes stay more or less equal from age 2 to age 4 (Fig. A2, Appendix 2). This effect can contribute to the unexpectedly high value of the juvenile survival. Clearly, stochastic effects can create this unusual pattern in juvenile age structure sizes because we used only one year of data and we have additionally considered a low detection probability of juveniles (27%).

A previous study by Fernández-Chacón et al., (2011) on the sister tortoise *T. hermanni* that modeled recapture probabilities including age effects found a first-year survival rate of 0.39 (0.22-0.59) and an average of juvenile survival from age 1 to 4 years old of 0.69. These estimates are similar to the rates obtained here for *T. graeca*. Our estimate of first-year survival rate (0.24) was also lower that the estimate by Keller et al., (1997) for the population of *T. graeca* in SW Spain (0.39). This difference could reflect actual differences between the two populations and suggest that overall survival of juveniles in our study area could be lower than in other populations. In the Doñana National Park, the predation of hatchlings has been described as very low (Keller et al., 1997), whereas in the population in the southeastern Spain predation rates are higher (García et al., 2003).

4.2. Impact of sample size on robustness of survival estimates

The simulation exercise showed that survival estimates are robust provided samples sizes are larger than 100 individuals. We observed a notable decrease in the precision and accuracy of the estimates if the sample size was below 100 individuals. Moreover, our estimates were rather stable even with a low number of individuals. A sample size of 100 individuals from a single count or year represents a low sampling effort in comparison to the long-term monitoring effort usually needed in capture-recapture studies (in our study system, 11 years). Under what circumstances is this small decrease in the accuracy of the estimate acceptable? For many conservation efforts, where long-term monitoring programs are too expensive or infeasible, similar approaches as presented here will be extremely useful.

4.3. Model selection and impact of fire on survival

Our inverse-modeling approach was also successful in testing alternative hypotheses on factors affecting survival. We found evidence for a substantial decline of survival rates after the fire that lasted for several years. Our best-supported hypothesis was H5, that predicted a 5 year effect after the fire and represents a long lasting effect of fire on survival. The capture-recapture study of Sanz-Aguilar et al., (2011), identified a faster recovery after the fire. As we did not estimate the recovery with our approach, we cannot compare in the same way both studies. However, both methods, with very different sampling efforts, identified the same general effects to describe the impact of fire on the survival of the different age classes. Both methods indicated that adult and subadult survival showed only a weak decrease after the fire. In contrast, our results suggest that juveniles and one-year-old tortoises suffered after the fire a notable decrease in survival. However, because of the different predictions of juvenile survival, results of our method and of the capture-recapture estimates differed in the juvenile class. The ability of our approach to test the support of alternative hypotheses on how different ecological processes influences demography multiplies its usefulness and makes it more comparable to standard demographic estimation methods in ecology and conservation.

4.4. Accuracy vs. cost trade-offs

Our results suggest that inverse modeling approaches provide a suitable framework for estimating demographic rates and testing for its drivers (Gross et al., 2002, Zipkin et al., 2014a, González et al., 2016). Overall, we found that estimates from inverse modeling were reasonably accurate when compared with the more data hungry capture-recapture analyses (with a sampling effort ten times larger). However, it has to be noted that our approach uses not only the population size structure extracted from the 2003 monitoring data, but also detection probabilities (that were estimated from the same 153 individuals captured in 2003) and independent information on sex ratio (*SR*), number of clutches (*NC*), clutch size (*CS*), and hatching success (*HS*) to estimate the fecundity parameter *F* of the Leslie matrix. The fecundity parameters were estimated by radiography methods of females for 9 years (Rodríguez-Caro et al., 2014). Additionally, we used information on longevity to obtain reasonable bounds for adult survival (information about longevity can be found in open database such us *AnAge Database of Animal Ageing and Longevity* https://genomics.senescence.info/species/). As discussed above, there is a trade-off between accuracy and cost: to what extent should we compromise our conservation goals by trading accuracy in parameter estimates for costs? These trade-offs are often poorly explored in conservation biology. It would be necessary to couple our approach with an optimization framework to inform on the trade-off between reduced cost vs. increased reliability in the parameter estimates (Field et al., 2004, Wildermuth et al., 2013).

Application of our approach requires that (i) individuals can be aged reliably, (ii) the population should be assumed to be closed and stable (e.g., Keyfitz's Δ and the projection distance α_0 to if the age distribution is stable; Williams et al., 2011), and (iii) the minimal number of individuals needed for this study is around 100. Moreover, a priori information of survival rates of particular age classes (e.g. adults) or the longevity of the species can be very useful for obtaining absolute estimates of survival rates. We presented here a simple and straight-forward application of our approach that treats detectability and fecundity parameters as known, but focus on uncertainty in the unknown survival parameters. Extensions of our approach could adopt a Bayesian framework (e.g., Gross et al., 2002; Martínez et al., 2016) that considers also uncertainty in the estimates of fecundity parameters and a more complex observer model to describe detectability. However, such extensions would require more complex numerical optimization techniques for model parameterization. Future research should also consider the effects of stochasticity, especially at low population sizes, immigration and emigration, stage-structure populations and non-equilibrium dynamics. Overall, our work contributes towards broadening the toolbox in biodiversity conservation with a tool that is encouraged when long-term monitoring is not feasible.

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Highlights:

- We propose and evaluate an approach to estimate survival rates by inverse modeling
- Inverse modeling is underused in conservation and has not been adequately assessed
- Inverse modeling is less data hungry than current methods and yelds similar results
- This approach reduces the cost for estimating demographic rates.

A low cost approach to estimate demographic rates using inverse modeling

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Running heading: Low cost method to estimate demographic rates

ABSTRACT

Survival is a key parameter in species' management and conservation. Most methods for estimating survival require time series data, large sample sizes and, overall, costly monitoring efforts. Inverse modeling approaches can be less data hungry, however they are underused in conservation sciences. Here we present an inverse modeling approach for estimating relative survival rates of long-lived species that is mathematically straightforward and evaluate its performance under constraints common in conservation studies related to small sample sizes. Specifically, we (i) estimated the relative survival rates in a *Testudo graeca* population based on one-year monitoring, (ii) assessed the impact of sample size on the accuracy, and (iii) tested alternative hypotheses on the impact of fire on the survival rates. We then compared the results of our approach with capture-recapture (CRC) estimates based on long-term monitoring. Our approach (153 individuals within a single year) yielded estimates of survival rates overlapping those of CRC estimates (11 years of data and 1009 individuals) for adults and subadults, but not for juveniles. Simulation experiments showed that our method provides robust estimates if sample size is above 100 individuals. The best models describing the impact of fire on survival identified by our approach predicts a decrease in survival especially in hatchings and juvenile individuals, similar to CRC estimates. Our work proves that inverse modeling can decrease the cost for estimating demographic rates, especially for long-lived species and as such, its use should be encouraged in conservation and management sciences.

Key words: Pattern-oriented model, survival rates, demography, tortoise, disturbance, fire, *Testudo graeca*

1. INTRODUCTION

The estimation of demographic parameters such as survival and reproduction rates is key for accurate forecasting of the fate of wildlife populations and for evaluating alternative management actions (Boyce, 1992; Williams et al., 2002; Beissinger and McCullough, 2002). In ecology, several approaches have been developed to estimate demographic parameters of wild animal and plant populations (Williams et al., 2002; Gross et al., 2002; Thomson et al., 2009). The estimation of age dependent survival is especially difficult for long-lived species because current methods such as capture-recapture (CRC) methods typically require long-term monitoring of individuals (Lebreton et al., 1992), which involves intensive field effort (e.g. for tortoises the range is 3-22 years monitoring, Appendix 1) and consideration of imperfect detection (Lebreton and Pradel, 2002; Thomas et al., 2010; Sanz-Aguilar et al., 2016). The capture-recapture framework allows for dealing with imperfect detection and is now commonly used to estimate animal survival rates (e.g., Lebreton et al., 1992; Lebreton and Pradel, 2002; Giménez et al., 2007; Thomson et al., 2009; Sanz-Aguilar et al., 2016). During the last decades, technological development has allowed to track animals and obtain direct survival estimates using telemetry data that provide an accurate monitoring of individuals over time (Millspaugh and Marzluff, 2001), but batteries do not usually last long (Bridge et al., 2011). Although CRC and telemetry monitoring methods proved to be accurate and useful, they can often not be applied for species of conservation concern where long-term studies would be very costly or infeasible (Williams et al., 2002).

An alternative to direct estimation of demographic parameters is indirect estimation based on population-level data such as age structure estimates (e.g., Caughley, 1977; Michod and Anderson, 1980; Udevitz and Ballachey, 1998; Wiegand et al., 2004). For example, survival rates can be indirectly estimated from age distribution data by analysis of the underlying age-structured Leslie matrix model if additional pieces of information are available, for example population growth rate, recruitment rates, the age structure of natural deaths, or stability of the age structure (Caughley, 1977; Michod and Anderson, 1980; Tait and Bunnell, 1980; Sickle et al., 1987; Udevitz and Ballachey, 1998). Similar methods were also developed in fisheries where catch-age patterns provide population age structures that then allowed together with auxiliary information for stock assessment (for a review see Quinn, 2003). These approaches fit into the pattern-oriented modeling strategy (Wiegand et al., 2003; Grimm et al., 2005), a general modeling framework that relies on "inverse modeling" where the outputs of a model called "patterns" (e.g., in our context the emerging stable age distribution of a population or time-series data) are used to estimate the model inputs (e.g., the unknown parameters). In other words, inverse modeling estimates parameter values by optimizing the match between observed patterns and the corresponding model outputs. Inverse modeling has been traditionally used in several scientific areas like hydrology, oceanography, soil science or climatology (Tarantola, 1987; Gottlieb and DuChateau, 1996; Wunsch, 1996; Bennett, 2002), but less in ecological studies. Exceptions are applications to time-series data (e.g., Wiegand et al., 1998, 2004; Gross et al., 2002; Martínez et al., 2011, 2016; González and Martorell, 2013; White et al., 2014; González et al., 2016; Zipkin et al., 2014a,b) or other types of patterns (e.g., Revilla et al., 2004; Kramer-Schadt et al., 2007; Hartig et al., 2011; Anadón, et al., 2012; May et al., 2015).

However, inverse modeling is still underused in ecology and, particularly, in conservation studies, and the performance of these methods under different sampling efforts and their potential for hypothesis testing or model selection have not been fully assessed. Here we present an inverse modeling approach for estimating relative survival rates of long-lived species that does not require long-term monitoring (or time-series data) and, as such, circumvents time and funding constraints commonly encountered in conservation studies. We illustrate our approach using the spur-thighed tortoise (*Testudo graeca*) in the southeastern Spain as a case study. This population has been intensely studied in previous studies (Pérez et al., 2002; Rodríguez-Caro et al., 2013, 2016, 2017), including long-term monitoring studies and capture-recapture studies (e.g. Sanz-Aguilar et al., 2011).

Our specific goals are threefold. First, we aim to compare estimates of survival rates of *T. graeca* obtained by means of our inverse modeling approach using age-distribution data from just one year with estimates obtained by means of capture-recapture methods using long term monitoring data (i.e. 11 years; Sanz-Aguilar et al., 2011). Second, we aim to explore how sample size affects the accuracy and precision of the estimated relative survival rates and to identify a minimum sample size for our case study. Third, we illustrate how our approach can be used to test alternative hypotheses on factors affecting survival, which is in our particular case study the impact of fire on survival rates.

2. MATERIALS AND METHODS

2.1. General methodology

Our approach uses the observed age distribution of the population that can be obtained by short-term studies as pattern to indirectly estimate relative survival rates based on age-structured population projection matrix models (Caswell, 2001). While the pattern-oriented approach is in general flexible, our specific implementation relies on the assumptions that: a) the sampled population is stable and closed (i.e., no dispersal in or out of the study area); b) the observed age structure of the population contains signals of the demographic rates and detectability; and c) stochasticity is relatively unimportant.

First, an age-structured Leslie projection matrix (Caswell, 2001; Fig. 1b) is used to generate the expected stable age distribution (Fig. 1c) of hypothetical populations under different combinations of demographic parameters such as age-dependent survival rates S_i and fecundity F (Fig. 1a). To obtain the stable age distribution we used the R package popbio (Stubben and Milligan, 2007). To find the demographic parameters that produce the best match with the observed age structure (Fig. 1e), we varied them systematically over the parameter space (Fig. 1a) (Wiegand et al., 2004).

The age-structured Leslie transition matrix (A) takes the form

$$A = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 & F_r & \dots & F_m \\ S_1 & 0 & 0 & \dots & 0 & 0 & \dots & 0 \\ 0 & S_2 & 0 & \dots & 0 & 0 & \dots & 0 \\ 0 & 0 & S_3 & \dots & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & S_{r-1} & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 & S_r & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & S_m \end{bmatrix} \qquad (1)$$

where the S_i represent the survival rates for age $i = 1$ to m, with m being the maximal age, r the age when subadults become adults (i.e., be reproductive), and F_i the fecundity rate. Usually, the population is divided into o different age classes (e.g., one-year-old individuals, juveniles, subadults, and for adults) and the same survival rates S_i are assumed within each age class. The fecundity term varies depending on timing of the census (i.e., pre- or post-breading census). For the case of pre-breeding matrices as used here we obtain

$$F = SR \times BS \times S_{\mathrm{h}} \qquad (2)$$

where *SR* is the female sex ratio (note that the Leslie matrix is typically calculated only for females), *BS* the (age-independent) breeding success, and S_h is the survival from hatching to the first year.

Given that individuals of the different age classes (e.g., juveniles vs. adults) can differ in their detectability (e.g. Rodríguez-Caro et al., 2016, 2017), the predicted stable age distributions must be corrected. This can be accomplished by multiplying the predicted age distributions resulting from the projection matrix by age-dependent detection probabilities to obtain the "observable age distribution" of the simulated populations.

Our inverse approach could be applied in principle for all parameters of the age-structured Leslie transition matrix (eq. 1), however, because the effects of fecundity and mortality parameters typically cancel in this type of models, parameter identifiability problems may arise if no additional information is used (Wood, 1997). While survival parameters are usually difficult to estimate on the short-term, fecundity parameters are more often available for long-lived species such as the spur-thighed tortoise (Díaz-Paniagua et al., 1996, 1997). We therefore applied inverse modeling for the relative survival rates of the age-structured Leslie transition matrix (eq. 1) that are unknown, whereas we estimated age or stage-specific fecundity from independent information.

We identified the relative survival rates that fitted the observed age distribution data best by using a likelihood approach (Hilborn and Mangel, 1997; Burnham and Anderson, 2002). To define the match between observed and predicted age distributions, we calculated the likelihood of observing the observed age frequencies ($x_1, x_2, x_3, x_4,\dots, x_m$; where m is the maximal age) given the predicted age structure ($p_1, p_2, p_3, p_4,\dots, p_\mathrm{m}$) that emerged from a parameterizations $\boldsymbol{\theta}$

of the population model. Given the multinomial nature of our variable and assuming independence, the log-likelihood function is given by:

$$l(\boldsymbol{\theta}, p_1, p_2, ..., p_m) = \log(\frac{n!}{\Pi x_i!}) + \sum_{i=1}^{m} x_i \log(p_i) \qquad (3)$$

where n is the total number of individuals, x_i (i = 1,… m) is the observed number of individuals in age class i and p_i (i = 1, …m) is the predicted proportion of individuals in age class i.

Because the stable age distribution P is the right eigenvector of the dominant eigenvalue λ of the Leslie transition matrix **A** (i.e., $\boldsymbol{A}\,P = \lambda\,P$), multiplying the survival vector $\boldsymbol{\theta} = (S_1, ..., S_o)$ by a constant c with $0 < c < 1/\max(\boldsymbol{\theta})$ results in the same predicted stable age distribution and hence in the same likelihood. Therefore, we can identify only the relative survival rates $\boldsymbol{\theta}_{\mathrm{rel}} = (S_1/S_2, S_2/S_3, \ldots S_{\mathrm{m-1}}/S_{\mathrm{m}})$, but use of additional information may allow us to restrict the range of the absolute survival rates.

There are different possibilities to find the maximum of the log-likelihood function over the parameter space; here we used an approach based on a rejection filter (e.g., Wiegand et al., 2004; Hartig et al., 2011) where we accepted in a first step all parameterizations **θ** with ΔAIC < 2 (Burnham and Anderson, 2002). We use the rejection filter approach to obtain the full posterior distribution of the relative survival rates $\boldsymbol{\theta}_{\mathrm{rel}}$ and because we want to use the more flexible simulation approach to test alternative hypothesis on factors impacting survival (i.e., our third goal). However, as shortcut one may also fit the relative survival rates directly, for example using the *mle* function of *stats4* package in R (R Core Team, 2016).

For each accepted parameterization **θ** we calculated the ratios $S_{\mathrm{i}}/S_{\mathrm{i+1}}$ to obtain their posterior distribution. Because survival rates range between 0 and 1, the estimates of the relative survival rates allow us to generate upper bounds for each survival rate S_{i}. To do this, we identify the highest survival rate in relations to each other, define its value as one, and obtain the corresponding values of the other survival rates as their upper bounds. In order to narrow down the possible range of the highest survival rate, we determine for different values of the highest survival rate the mean age of individuals that survived up to adult age the age only 1% of them reach and the longevity of the individuals (Castanet, 1994).

In theory, a population may reach a stable distribution, but in reality, it never arrives exactly at its stable distribution (Williams et al., 2011). It is thus critical to assess how far away a population is from the stable distribution. We therefore evaluated the distance between the observed age distribution and the stable age distribution of the best model using two common measures: Keyfitz's delta (Keifitz, 1968) and projection distance (Haridas and Tuljapurkar, 2007). Keyfitz's delta is the sum of the differences between the predicted stable age distribution and the observed age distribution and the projection distance is the difference between the reproductive value of a population with the observed age structure and the reproductive value of a population with the predicted stable age distribution.

Our approach can be extended to test alternative hypotheses on the drivers of temporal variation in demographic rates. To this end, different model structures that correspond to alternative hypotheses can be implemented within a simulation framework. For each alternative model structure, we determined the best estimate of the parameter vector $\boldsymbol{\theta}_{\mathbf{rel}}$ using relative estimates and compared competing models structures based on their corresponding AIC values. Model structures with ΔAIC < 2 were considered equally well supported (Burnham and Anderson, 2002).

2.2. Case study

We applied inverse modeling to estimate relative survival rates of a long-term monitored population of the endangered spur-thighed tortoise *Testudo graeca*. The spur-thighed tortoise is a small long-lived chelonian widely distributed in the Mediterranean basin. The "Cumbres de la Galera" population has been monitored during the last 15 years (Sanz-Aguilar et al., 2011; Anadón et al., 2012; Rodríguez-Caro et al., 2013, 2016). In summer of 2004, a fire burned 31% of the study area. Sanz-Aguilar et al., (2011) and Rodríguez-Caro et al., (2013) estimated survival and the effect of fire on survival rates by means of multistate capture-recapture models and, by comparing the individual growth models, respectively. These survival estimates were used to validate the results of our inverse modeling approach.

We examined the observed age structure of the population in two different years: just before the fire event (2003) and 5 years later in 2009 (age distribution in Appendix 2) when the cumulative effects of fire over time are expected to be ceased (Sanz-Aguilar et al., 2011). We approximated individual age using growth rings and the carapace length (see details in Appendix 3). This allows us to distinguish in total twenty-five age classes. The oldest age class included all individuals older than 24 years because the accuracy of age estimations for older individuals in our population is low (Rodríguez-Caro *et al*. 2015). To compare our estimates of the survival rates with those obtained by classical capture-recapture methods, we classified 1 to 4 year old tortoises as juveniles (S_j), those aged 5 to 8 as subadults (S_s), and older individuals as adults (S_a) (Sanz-Aguilar et al., 2011). In addition we also included the survival from hatching to the first year (S_h). Our task is to find the best parameterization for our relative survival vector $\boldsymbol{\theta}_{\mathbf{rel}} = (S_h/S_j, S_j/S_s, S_s/S_a)$.

2.3. Application (a): Estimating survival

We applied our inverse approach to estimate the survival in our population using one year of monitoring (before the fire, 2003; n=153, Appendix 2). In a first step, we generated all possible parameterizations $\boldsymbol{\theta} = (S_h, S_j, S_s, S_a)$ where the ranges of each of survival rate S_i varied between 0.01 and 0.99 with steps of 0.02, thus assuming a conservative upper bound for all survival rates of 0.99. For each S_i we therefore tested 50 alternative values. This resulted in a total of 50^4 = 6,250,000 parameter combinations. In a second step, we used a pre-breeding Leslie matrix with 25 age-classes (eq. 1), but survival rates were estimated per stage. The fecundity parameter of the Leslie matrix was defined by equation 2, where first-year survival (S_h) was inversely determined by our approach, the sex ratio (SR) in this population was 0.5 (a clutch contains on average half male and half females) (Graciá et al., 2017), and breeding success was estimated as $BS = NC \times CS \times HS = 5.21$. For the latter we used data on the number of clutches ($NC = 2$) and clutch size ($CS = 3.16$), estimated in study by Rodríguez-Caro et al., (2014), and data on hatching success ($HS = 0.824$) was obtained from bibliography (Díaz-Paniagua at al., 1997).

In a third step, we obtained age-specific estimates of detectability by distance-sampling procedures (Thomas et al., 2010). Detection probabilities were 0.27 for juveniles (age 1-4), 0.41 for subadults (age 5-8) and 0.47 for adults (age > 8; see Appendix 4 for details).

In a fourth step, we calculated the likelihood (eq. 3) for each parameterization $\boldsymbol{\theta}$ using the corresponding detectability-corrected simulated age distribution (Fig. 1d) with the observed age distribution of the monitoring of 2003 (Fig. 1c), and accepted all parameterizations $\boldsymbol{\theta}$ with $\Delta\text{AIC} < 2$ (Burnham and Anderson, 2002). Next, we calculated for all accepted parameterizations the ratios S_h/S_j, S_j/S_s, and S_s/S_a to obtain their posterior distribution and expected values, as well as the upper bounds of the survival rates. We also tested the difference between the observed age distribution and the stable age distribution (Williams et al., 2011). Finally, we compared our estimated survival rates with the mark-recapture estimates of Sanz-Aguilar et al., (2011).

2.4. Application (b): Impact of sample size.

By means of simulation experiments, we assessed the impact of sample size on the precision and accuracy of the relative survival estimates obtained by our approach. Starting from the stable age distribution resulting from a pre-breeding Leslie matrix with known parameter values $\hat{\boldsymbol{\theta}}$ (known vector of survival rates), we simulated a population of 1000 individuals by scaling the right eigenvector associated with the dominant eigenvalue (that represents the stable age distribution) to a total abundance of 1000. We used the observed detection probabilities to obtain stochastic samples of the simulated population with different sizes N. The age distributions arising from this sampling process were then used in the same way as the *observed* data in our inverse modeling approach presented in Application 1. We repeated this procedure for different sample sizes N ($N = 500, 400, 300, 200, 100, 75, 50, 25$). For each N, the sampling process was repeated 30 times. To select the minimum sample size that yields acceptable estimates we compared the increase of the standard deviation when reducing the sample size N. We tested the differences in the variance of the survival rates between $N = 500$ and the other samples size by Levene's test (Levene, 1960).

2.5. Application (c): Factors impacting survival

Our approach also allows for testing alternative hypotheses on temporal variation in the survival and fecundity parameters of the Leslie matrix. We applied this feature to our case study by assessing the impact of a fire disturbance (that occurred in our population in 2004) on the temporal variation of the survival rates. This allowed us to compare our results with a previous study that estimated survival rates after fire by means of capture-recapture approaches (Sanz-Aguilar et al., 2011) for the same population and disturbance.

We used the most likely model parameterization $\hat{\boldsymbol{\theta}}$ determined in Application 1 (that was based on the observed age distribution of the year 2003) to generate the stable age distribution for the year 2004 of the fire. We then simulated the next 5 years using survival rates modified in accordance with a set of alternative hypotheses and compared the simulated age distribution for year 2009 to the corresponding observed distribution (i.e. 5 years after the fire).

For hypothesis H0 (*no effects of fire on survival*), the survival parameters did not change, they are constant before and after the fire. For hypothesis H1, H2, H3, H4 and H5, population dynamics was simulated with new relative survival rates $\boldsymbol{\theta}_{\text{rel}}$ applied only for one, two, three, four or five years after the fire, whereas we applied in subsequent years the pre-fire survival rates $\hat{\boldsymbol{\theta}}$. The fire disturbance did not have negative effects on fecundity (Sanz-Aguilar et al., 2011), so we assumed no change in fecundity. We finally compared our estimates of thesurvival rates and the most likely hypothesis with that obtained in the previous study of Sanz-Aguilar et al., (2011).

3. RESULTS

3.1. Estimating survival

Our rejection filter retained 5001 out of a total of 6,250,000 tested parameter combinations (0.08%). The relative survival rates were $\boldsymbol{\theta}_{\mathbf{rel}}$ = (0.26, 0.98, 0.93) for S_h/S_j, S_j/S_s, and S_s/S_a, respectively (Fig. 2). The upper bound vector of survival rates was $\boldsymbol{\theta}_{\mathbf{upper}}$ = (0.23, 0.87, 0.91, 0.99) for S_h, S_j, S_s and S_a, respectively. To assess a biologically reasonable lower and upper bound for adult survival S_a (the highest survival rate). We found that a 9-year old individual reached for

S_a = 0.85, 0.9, 0.95, 0.97, and 0.99 on average an age of 15, 18, 28, 41, and 106 years, and 1% of them reached at least an age of 37, 52, 98, 160, 467 years, respectively. With a maximum longevity of the species in captivity reported as 102 years (Castanet, 1994), adult survival rates between 0.90 and 0.97 seem reasonable. In a second rejection filter, we selected the parametrization for hatching, juveniles and subadults using S_a between 0.9 – 0.97 (second rejection filter retained 1256) and we estimated the range for each survival rate (0.17 – 0.33 for S_h, 0.71 – 0.99 for S_j and 0.75 – 0.97 for S_s) (Fig. 3).

Sanz-Aguilar et al., (2011) estimated the survival rates of the population using 10 years of monitoring and obtained $\hat{\boldsymbol{\theta}}$ = (*NA*, 0.20, 0.79, 0.98) for juveniles, subadults and adults, respectively (Table 1) (note that CRC estimates did not consider first year survival). Our estimates for adult and subadult survival are very similar, with 95% CI's overlapping that of Sanz-Aguilar et al., (2011) (Table 1). However, our estimates for juvenile survival differ from that of Sanz-Aguilar et al., (2011).

The measures of distance between observed and predicted age distribution showed that the population can be considered as stable. We found a value of Keyfitz's $\Delta = 0.148$ and a projection distance $\alpha_0 = -0.028$. A value of $\Delta = 0.148$ means that just 14.8% of individuals are in other classes than expected (Keifitz, 1968). A projection distance $\alpha_0 = 0$ represent a stable age distribution, and our slightly negative value implies that the population is somewhat more concentrated into stages with low reproductive values. The stable age distribution is available in Appendix 2.

3.2. Impact of sample size

Our estimates were robust for sample sizes larger than 100 individuals, but uncertainty increased quickly for smaller sample sizes (Fig. 4), especially for S_j/S_s. Within this range, the obtained estimates approximated the known survival rates well (Appendix 5). Below 100 individuals, estimates were more uncertain with larger standard deviations (Fig. 4). The Levene-test showed that the variance was different when the sample size was over or lower 100 (W_{ShSj} = 49.89, *p-value* = <0.001; W_{SjSs} = 55.16, *p-value* = <0.001; W_{SsSa} = 55.57, *p-value* = <0.001).

3.3. Factors impacting survival

The observed age distribution after the fire was calculated with 117 tortoises of year 2009 (Appendix 2). The hypotheses that received the least support were the null hypothesis H1 with no impact of fire on survival (Table 2). Hypothesis H5 that assumed more long-lasting effects of fire on survival (up to 5 years) represented the best model (Table 2). The estimate relative survival rates were $\boldsymbol{\theta}_{\text{rel H5}} = (0.11, 0.66, 0.94)$. With the upper bound survival estimates $\boldsymbol{\theta}_{\text{upper H5}} = (0.07, 0.62, 0.94, 0.99)$ for S_h, S_j, S_s and S_a, respectively. We found a high reduction in one-year-old and juvenile survival after fire. Stable age distributions of the six hypotheses are available in Appendix 2.

Our results partially match those obtained by Sanz-Aguilar et al., (2011) that also identified a large reduction in survival of young individuals. According to Sanz-Aguilar et al., (2011), after fire, survival rates were 0.11, 0.62 and 0.95 for juveniles, subadults and adults, respectively.

4. DISCUSSION

Survival is a key parameter in studies regarding the conservation of populations, and as such, methods to estimate survival based on low sampling efforts are much needed. Approaches based on inverse modeling have been proposed as a low cost method alternative to classic methods (i.e. capture-recapture). However inverse modeling approaches are still underused in conservation and management disciplines. Our study assesses the performance of these methods under different sampling efforts and their potential for hypothesis testing.

4.1. Estimating survival

Our comparison of the survival estimates from inverse modeling with that of capture-recapture is insightful. Our estimates based on data of 153 individuals that were captured during one year of monitoring are comparable to those obtained using capture-recapture analyses of 11 years (with >1000 captures) in the same population. Our estimates agreed with capture-recapture estimates for subadults and particularly adults, the age classes for which the species demography is more sensitive (Doak et al., 1994; Walker et al., 2012; Pérez et al., 2012). However, as one may expect, the uncertainty was somewhat higher when using only one year of data (Table 1). In our case, we directly estimate relative survival rates from the age distributions of 153 individuals captured during one year. However, biologically realistic values of survival rates (i.e., information on longevity) of the adult life stage were used as additional information to improve parameter estimates.

The biggest difference in survival estimates between the capture-recapture method and our approach appears in juvenile survival. However, we suspect that this difference emerged largely because of methodological differences. Our approach divides juvenile survival into two groups: the first year and juveniles (until 4 years old), whereas the capture-recapture analysis could not consider first year survival separately because hatchlings were not marked (they have a soft carapace). Interestingly, our estimate of first year survival (S_h) is very similar to the capture-recapture estimate of juvenile survival (S_j) (Table 1). Additionally, the capture-recapture estimate of juvenile survival may be low because of the low detectability and sample size of young individuals (Doak et al., 1994; Hailey, 2000; Tuberville *et al.,* 2008; Pike et al., 2008), because recapture probabilities of juveniles were not modeled separately, or because some juveniles may also lose the marks when growing carapace. However, beside of methodological differences, our approach may also overestimate juvenile survival because observed juvenile population sizes stay more or less equal from age 2 to age 4 (Fig. A2, Appendix 2). This effect can contribute to the unexpectedly high value of the juvenile survival. Clearly, stochastic effects can create this unusual pattern in juvenile age structure sizes because we used only one year of data and we have additionally considered a low detection probability of juveniles (27%).

A previous study by Fernández-Chacón et al., (2011) on the sister tortoise *T. hermanni* that modeled recapture probabilities including age effects found a first-year survival rate of 0.39 (0.22-0.59) and an average of juvenile survival from age 1 to 4 years old of 0.69. These estimates are similar to the rates obtained here for *T. graeca*. Our estimate of first-year survival rate (0.24) was also lower that the estimate by Keller et al., (1997) for the population of *T. graeca* in SW Spain (0.39). This difference could reflect actual differences between the two populations and suggest that overall survival of juveniles in our study area could be lower than in other populations. In the Doñana National Park, the predation of hatchlings has been described as very low (Keller et al., 1997), whereas in the population in the southeastern Spain predation rates are higher (García et al., 2003).

4.2. Impact of sample size on robustness of survival estimates

The simulation exercise showed that survival estimates are robust provided samples sizes are larger than 100 individuals. We observed a notable decrease in the precision and accuracy of the estimates if the sample size was below 100 individuals. Moreover, our estimates were rather stable even with a low number of individuals. A sample size of 100 individuals from a single count or year represents a low sampling effort in comparison to the long-term monitoring effort usually needed in capture-recapture studies (in our study system, 11 years). Under what circumstances is this small decrease in the accuracy of the estimate acceptable? For many conservation efforts, where long-term monitoring programs are too expensive or infeasible, similar approaches as presented here will be extremely useful.

4.3. Model selection and impact of fire on survival

Our inverse-modeling approach was also successful in testing alternative hypotheses on factors affecting survival. We found evidence for a substantial decline of survival rates after the fire that lasted for several years. Our best supported hypothesis was H5, that predicted a 5 year effect after the fire and represents a long lasting effect of fire on survival. The capture-recapture study of Sanz-Aguilar et al., (2011), identified a faster recovery after the fire. As we did not estimate the recovery with our approach, we cannot compare in the same way both studies. However, both methods, with very different sampling efforts, identified the same general effects to describe the impact of fire on the survival of the different age classes. Both methods indicated that adult and subadult survival showed only a weak decrease after the fire. In contrast, our results suggest that juveniles and one-year-old tortoises suffered after the fire a notable decrease in survival. However, because of the different predictions of juvenile survival, results of our method and of the capture-recapture estimates differed in the juvenile class. The ability of our approach to test the support of alternative hypotheses on how different ecological processes influences demography multiplies its usefulness and makes it more comparable to standard demographic estimation methods in ecology and conservation.

4.4. Accuracy vs. cost trade-offs

Our results suggest that inverse modeling approaches provide a suitable framework for estimating demographic rates and testing for its drivers (Gross et al., 2002, Zipkin et al., 2014a, González et al., 2016). Overall, we found that estimates from inverse modeling were reasonably accurate when compared with the more data hungry capture-recapture analyses (with a sampling effort ten times larger). However, it has to be noted that our approach uses not only the population size structure extracted from the 2003 monitoring data, but also detection probabilities (that were estimated from the same 153 individuals captured in 2003) and independent information on sex ratio (*SR*), number of clutches (*NC*), clutch size (*CS*), and hatching success (*HS*) to estimate the fecundity parameter *F* of the Leslie matrix. The fecundity parameters were estimated by radiography methods of females for 9 years (Rodríguez-Caro et al., 2014). Additionally, we used information on longevity to obtain reasonable bounds for adult survival (information about longevity can be found in open database such us *AnAge Database of Animal Ageing and Longevity* https://genomics.senescence.info/species/). As discussed above, there is a trade-off between accuracy and cost: to what extent should we compromise our conservation goals by trading accuracy in parameter estimates for costs? These trade-offs are often poorly explored in conservation biology. It would be necessary to couple our approach with an optimization framework to inform on the trade-off between reduced cost vs. increased reliability in the parameter estimates (Field et al., 2004, Wildermuth et al., 2013).

Application of our approach requires that (i) individuals can be aged reliably, (ii) the population should be assumed to be closed and stable (e.g., Keyfitz's Δ and the projection distance α_0 to if the age distribution is stable; Williams et al., 2011), and (iii) the minimal number of individuals needed for this study is around 100. Moreover, a priori information of survival rates of particular age classes (e.g. adults) or the longevity of the species can be very useful for obtaining absolute estimates of survival rates. We presented here a simple and straight-forward application of our approach that treats detectability and fecundity parameters as known, but focus on uncertainty in the unknown survival parameters. Extensions of our approach could adopt a Bayesian framework (e.g., Gross et al., 2002; Martínez et al., 2016) that considers also uncertainty in the estimates of fecundity parameters and a more complex observer model to describe detectability. However, such extensions would require more complex numerical optimization techniques for model parameterization. Future research should also consider the effects of stochasticity, especially at low population sizes, immigration and emigration, stage-structure populations and non-equilibrium dynamics. Overall, our work contributes towards broadening the toolbox in biodiversity conservation with a tool that is encouraged when long-term monitoring is not feasible.

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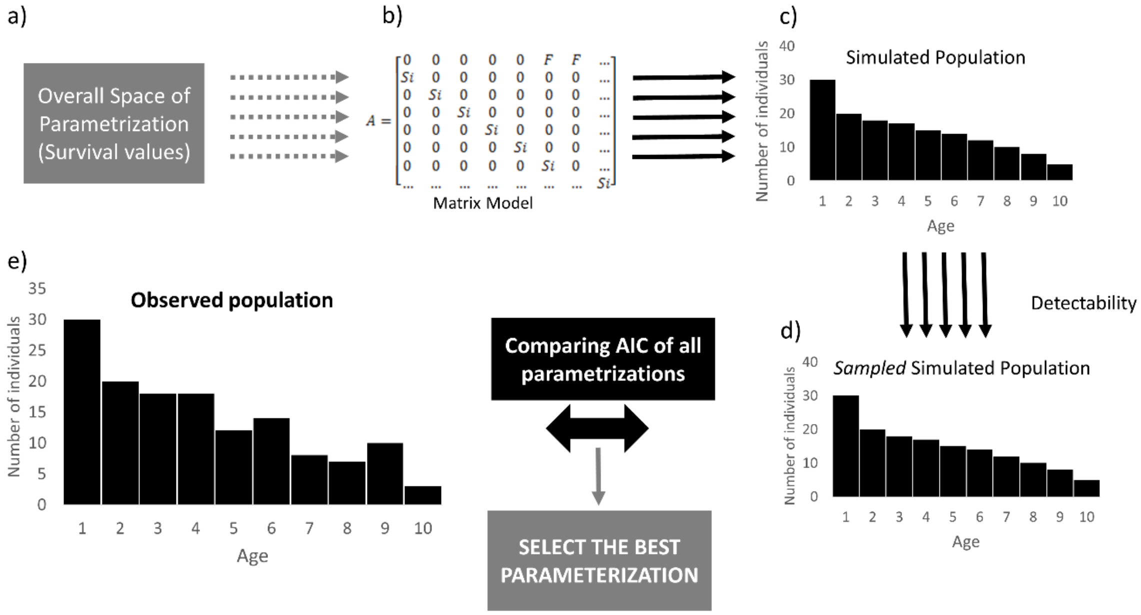

Figure 1. Summary of general framework of the model.

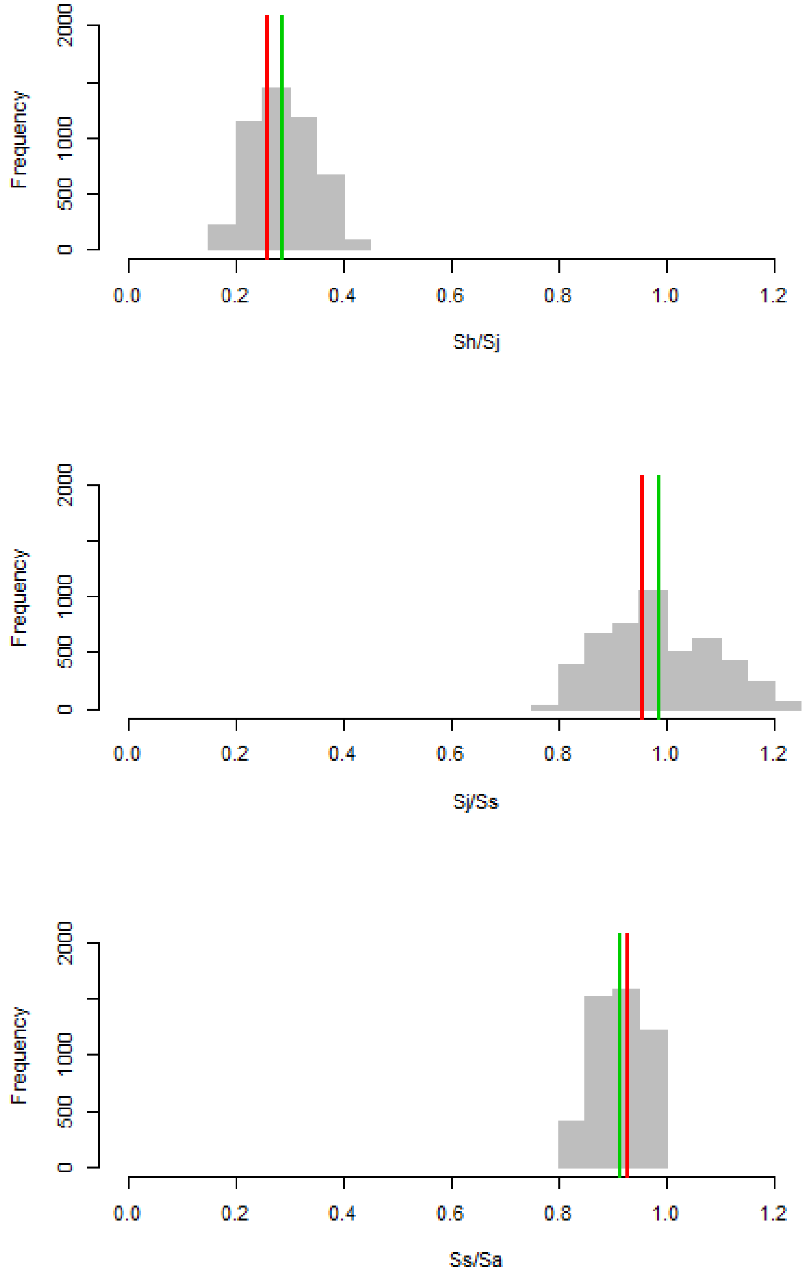

Figure 2. Histograms of the distribution of the relative survival rates S_h/S_j (left) S_j/S_s (middle) and S_s/S_a (right) for the 5001 parameterizations that yield ΔAIC < 2. S_h, S_j, S_s, S_a are the survival rates of hatchings, juveniles, subadults, and adults, respectively. The red lines are the maximum

likelihood estimates of the relative survival rates and the green lines represent the average of the distributions.

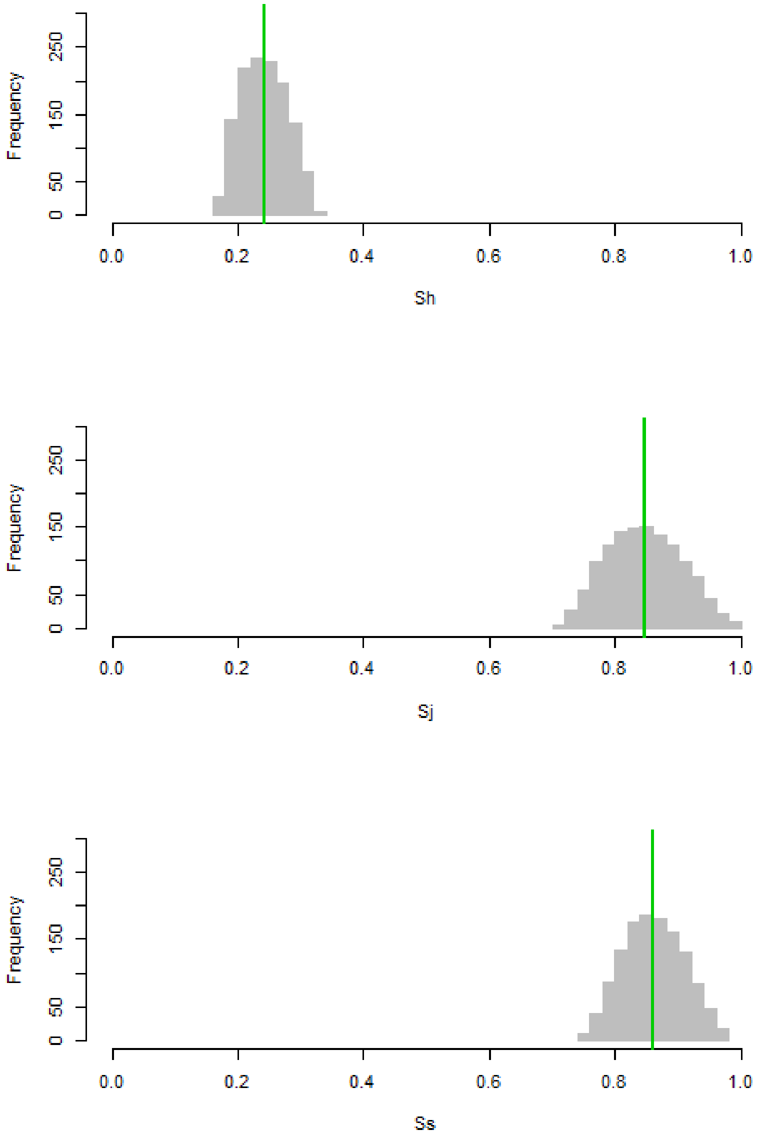

Figure 3. Histograms of the distribution of the absolute survival rates S_{h} of hatchings (left), S_{j} of juveniles (middle), and S_{s} of subadults (right) for the 1256 parameterizations that yield ΔAIC < 2 and where the adult survival rate S_a was within the plausible range (0.9, 0.97). The green lines

are the average values of the distributions. We obtain $S_h = 0.24$ (range 17 – 0.33), $S_j = 0.85$ (range 0.71 – 0.99) and $S_s = 0.86$ (range 0.75 – 0.97).

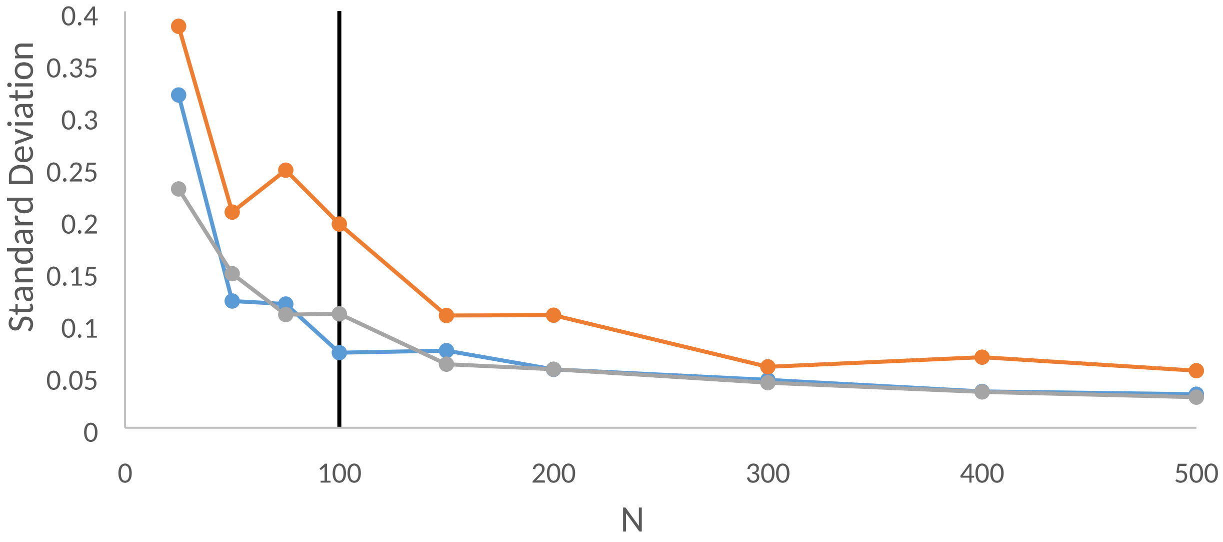

Figure 2. Reduction of the standard deviation (SD) through the increment of the sample size (N) in the simulations (30 replicates) for S_h/S_j in blue, S_j/S_s in orange and S_s/S_a in grey. When the sample size is lower than 100 the standard deviation increases substantially.

Table 1 Range of survival rates estimated for one-year-old individuals, juveniles, subadults, and adults (S_h, S_j, S_s. S_a, respectively) and the mean estimates and 95% confidence interval calculated by Sanz-Aguilar (2011). *N* is the number of tortoises considered, the effort is the number of hours searching for tortoises by person, and finally the period comprises the years of monitoring used to collect data and reach the estimates.

	Present study	Sanz-Aguilar et al., 2011
S_h	0.17 – 0.33	-
S_j	0.71 - 0.99	0.20 (0.08 – 0.42)
$\mathrm{S_s}$	0.75 – 0.97	0.79 (0.57 – 0.90)
S_a	0.90 – 0.97	0.98 (0.92 – 0.99)
N	173*	1389 (675 recaptures)
Effort	196 hours searching	1600 hours searching
Period	1 year (2003)	11 years (1999 – 2009)

*173 tortoises found during the monitoring, but 20 discarded because were recaptures

Table 2. Relative survival rates after the fire with the standard error and AIC for each hypothesis. H0 represent no effect of fire, the relative survival rates were the rates estimates in Application 1, H1, H2, H3, H4 and H5, represent the maintained effect of fire of one, two, three, four and five years, respectively. In bold the best model according AIC selection.

Hypothesis	S_h / S_j	S_j / S_s	S_s / S_a	AIC
H0	0.260	0.957	0.928	157.54
H1	0.07 (0.04)	0.71 (0.20)	1.07 (0.26)	148.36
H2	0.07 (0.04)	0.72 (0.12)	1.01 (0.13)	140.05
H3	0.06 (0.03)	0.71 (0.09)	0.97 (0.08)	122.40
H4	0.11 (0.03)	0.68 (0.08)	0.96 (0.07)	115.15
H5	**0.11 (0.03)**	**0.66 (0.08)**	**0.95 (0.06)**	**98.35**

Appendix 1

Table A1.1. Sample size and time of monitoring of several species of terrestial tortoises to estimate survival by capture-recapture methods. Time is the length of study and N is the sample size.

Species	Time	N	Place	Citation
Astrochelys yniphora	8 years	329	Madagascar	O'Brien et al. 2005
Gopherus agassizii	10 years	531	EEUU	Lovich et al. 2014
Gopherus berlandieri	10 years	2128	EEUU	Kazmaier et al. 2001
Gopherus morafkai	22 years	1186*	EEUU	Zylstra et al. 2012
Gopherus popyphemus	5 - 11 years	1667	EEUU	Tuberville et al. 2014
Homopus signatus	5 years	237	South Africa	Loehr 2010
Pyxis arachnoides	3 years	404	Madagascar	Walker et al. 2012
Teatudo graeca	11 years	1389	Spain	Sanz-Aguilar et al. 2011
Testudo hermanni	18 years	361	Spain	Bertolero et al. 2007 and Fernández-Chacón et al 2011
Testudo hermanni	9 years	6565	Greece	Hailey 2000
Testudo hermanni	7 years	401	France	Henry et al. 1998

*N of marked individuals

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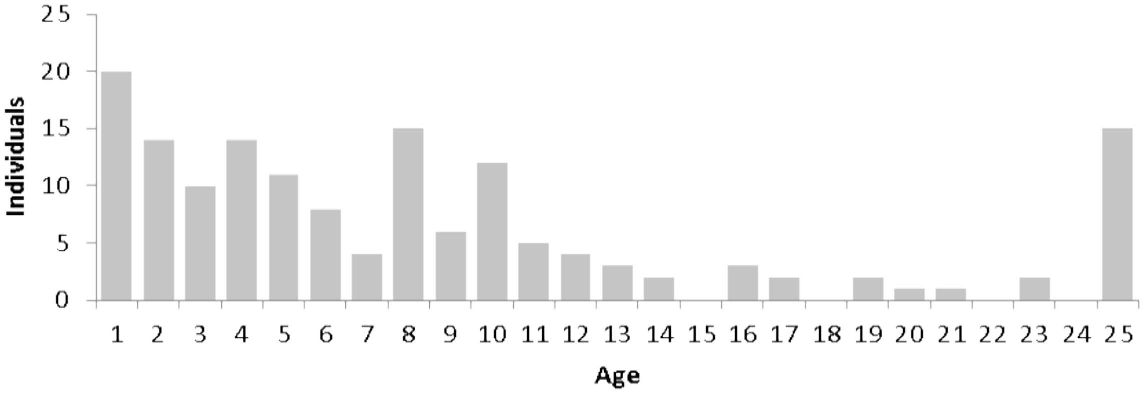
Appendix 2

2003



2009

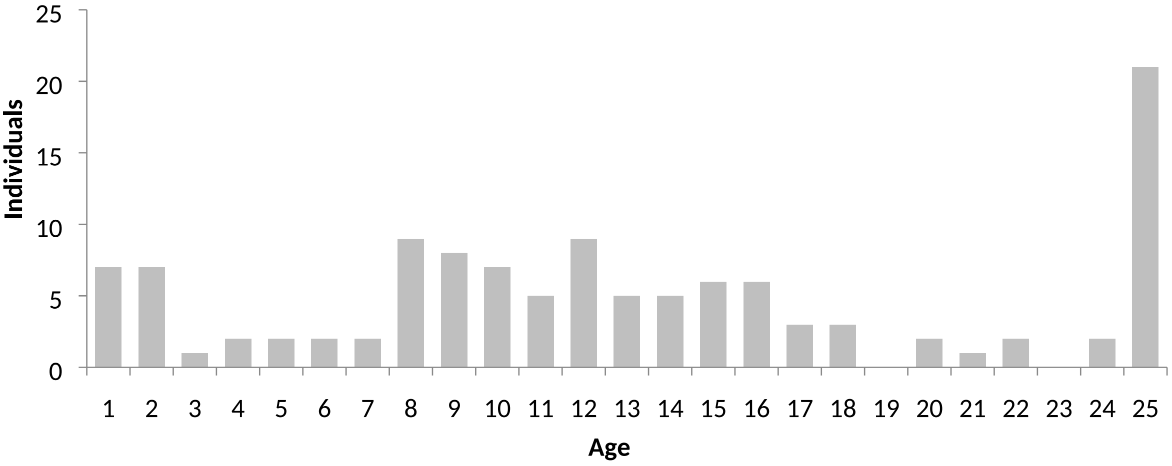
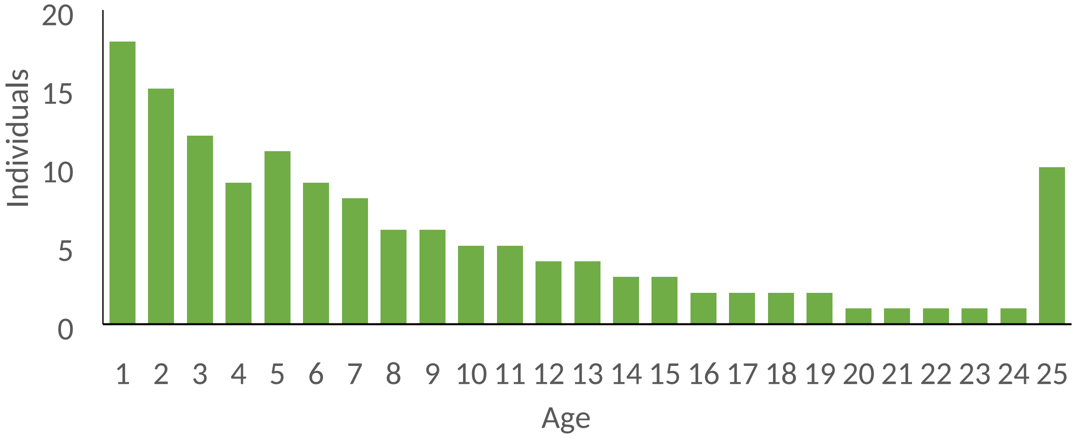


Figure A2.1. Age distribution of the population in 2003 and 2009, before and after the disturbance. *N* = 153 and N = 117, respectively

2003



2009

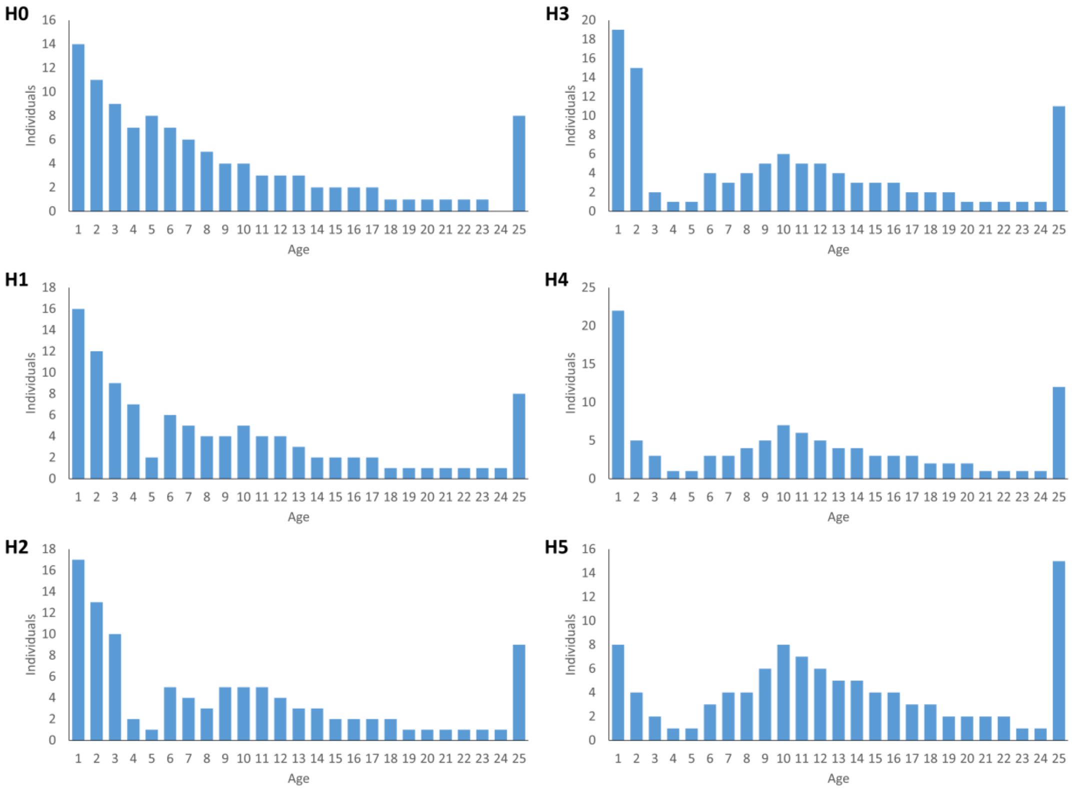


Figure A2.2. . Stable age distribution of the population in 2003 according to the model and simulated age distribution in 2009 for the 6 hypothesis. H0 represent no effect of fire; H1, H2, H3, H4 and H5, represent the maintained effect of fire of one, two, three, four and five years, respectively.

Appendix 3

We estimate the age of the individuals using two methods; 1) counting de number of rings (Rodríguez-Caro *et al.* 2015) and measuring the carapace length (Rodríguez-Caro *et al.* 2013).

The method of counting growth rings was described in Rodríguez-Caro *et al*. (2015). We used this method for tortoises aged up to 10 years old, the period in which counting growth rings is plausible.

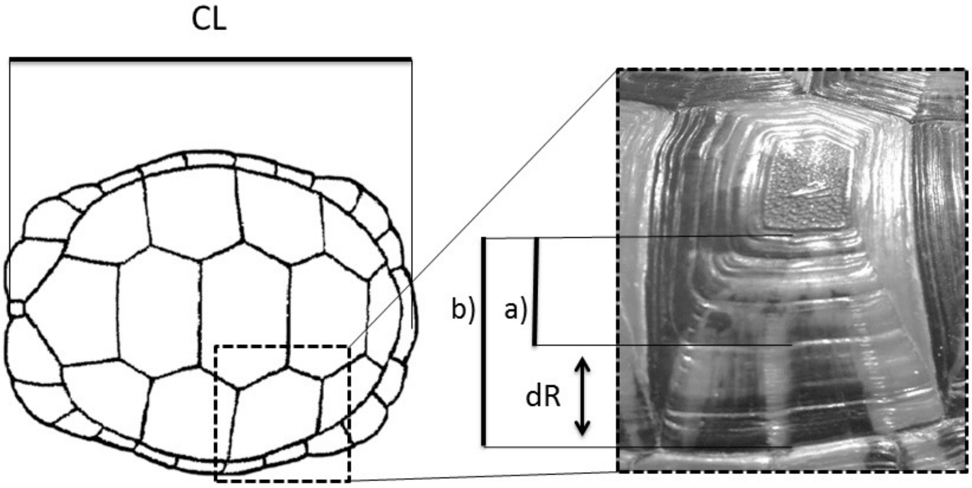


Figure A3. Example of number of rings and measure of the carapace length (CL) from Rodríguez-Caro *et al.* (2015)

For tortoises older than 10 years old, we calculate their age using an inverse regression by the equation 1 of Von Bertalanffy Model (Fabens, 1965) from Rodríguez-Caro *et al.* (2013).

$$S_\infty(1 - be^{-kt}) = CL \qquad \text{eq. 1}$$

S_∞ is asymptotic size, b is a parameter associated with the amount of growth remaining, k is the growth rate, t is the age of the individual and CL is the size (carapace length). We used the inverse of eq. 1 to calculate t (age of the tortoises) using CL (Rodriguez-Caro *et al.* 2013; table S1.1)

Table A2. Values of the parameters of Von Bertalanffy model according to Rodriguez-Caro *et al.* (2013) for males and females.

Sex	S_∞	*b*	*k*
Females	156.26	-0.7843	0.145
Males	118.23	-0.7112	0.228

When the tortoises are older than 26 years old, the growth of the individual is asymptotic. Thus, estimate the age when the tortoises are older than 26 is impossible by this method. Therefore, we categorized all individuals in the last group (more than 25 years old).

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Appendix 4

We used the Distance Sampling method (Thomas et al., 2010) to calculate the detectability of the individuals. This method assumes that detectability decreases as a function of the perpendicular distance from the line and it uses the observed distances to model the detection function. We use the same 153 individuals captured in 2003. The detection function was fitted to the distance data using Distance 6.0 (Thomas et al. 2010). Upon preliminary inspection of the fit, we removed perpendicular distances beyond 4.25m (truncation distance, hereinafter ω) where detection probabilities generally fell to 0.1 or lower (Buckland et al. 2001). Due to the observers' tendencies to round distances, we grouped the detections into five distance intervals (cutpoints: 0, 0.75, 1.5, 2.25, 3.25, 4.25 m), similar to other studies (Rodríguez-Caro et al., 2017). We evaluated the fits of the half-normal (HN) with multiple covariate distance sampling techniques (MCDS) including STAGE as a covariate (three factors: juvenile, subadults and adults). We found that the detection probability was 0.47 for adults, 0.41 for subadults and 0.27 for juveniles. Our results are similar to previous studies (Rodriguez-Caro et al., 2016, 2017)

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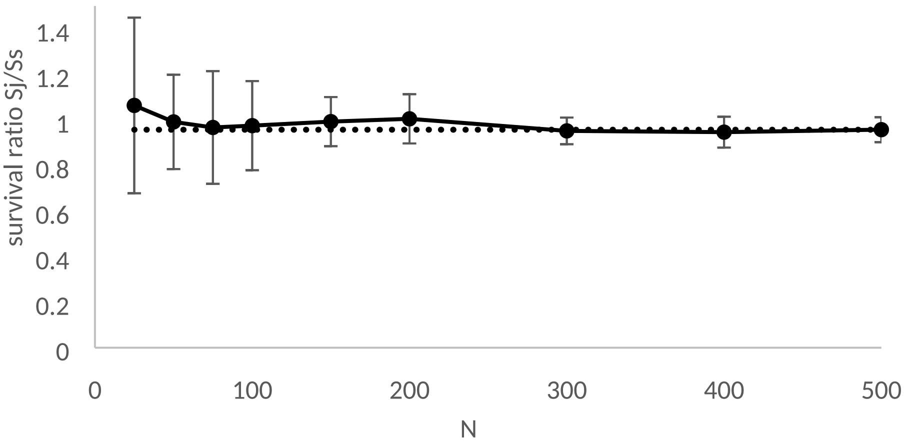
Appendix 5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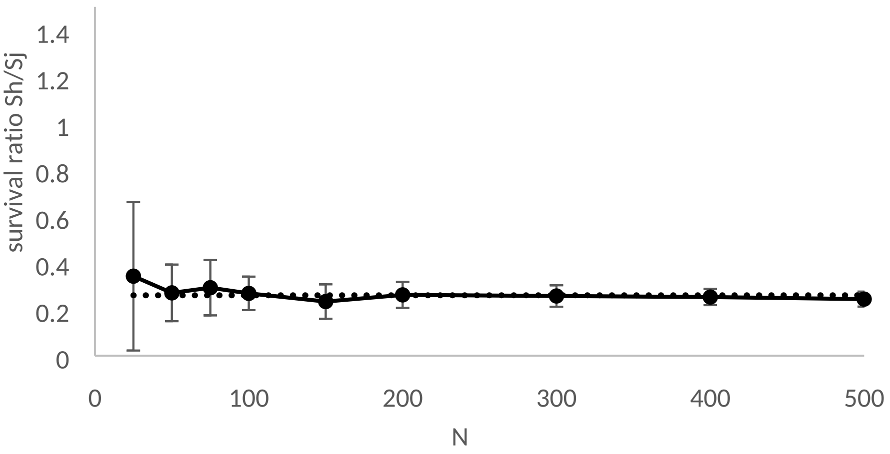
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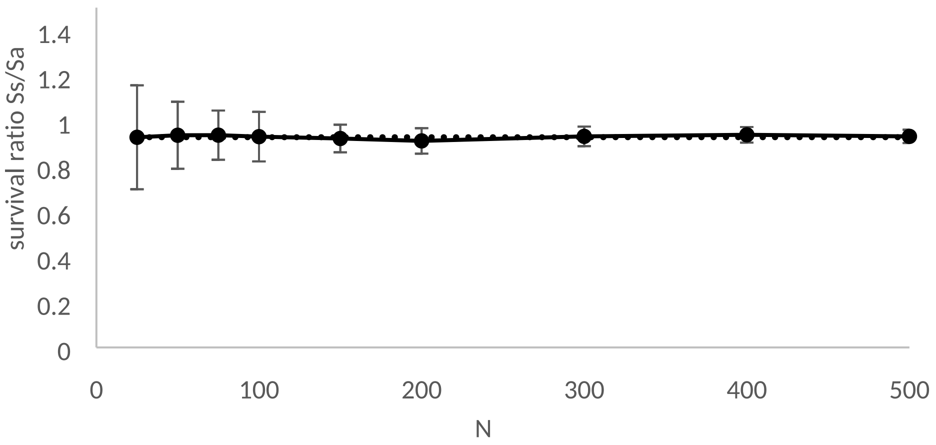
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Figure A6. Number of individuals in the simulation (N) and the estimate relative survival rates (black lines) and their standard simulations between simulations. Black dotted lines are the known relative survivals rates.