

1 **A low cost approach to estimate demographic rates using inverse modeling**

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18 Running heading: Low cost method to estimate demographic rates

1 ABSTRACT

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

20 **Key words:** Pattern-oriented model, survival rates, demography, tortoise, disturbance, fire,  
21 *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 (Millsbaugh 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

46 rates can be indirectly estimated from age distribution data by analysis of the underlying age-  
47 structured Leslie matrix model if additional pieces of information are available, for example  
48 population growth rate, recruitment rates, the age structure of natural deaths, or stability of the  
49 age structure (Caughley, 1977; Michod and Anderson, 1980; Tait and Bunnell, 1980; Sickle et  
50 al., 1987; Udevitz and Ballachey, 1998). Similar methods were also developed in fisheries where  
51 catch-age patterns provide population age structures that then allowed together with auxiliary  
52 information for stock assessment (for a review see Quinn, 2003). These approaches fit into the  
53 pattern-oriented modeling strategy (Wiegand et al., 2003; Grimm et al., 2005), a general  
54 modeling framework that relies on “inverse modeling” where the outputs of a model called  
55 “patterns” (e.g., in our context the emerging stable age distribution of a population or time-series  
56 data) are used to estimate the model inputs (e.g., the unknown parameters). In other words,  
57 inverse modeling estimates parameter values by optimizing the match between observed patterns  
58 and the corresponding model outputs. Inverse modeling has been traditionally used in several  
59 scientific areas like hydrology, oceanography, soil science or climatology (Tarantola, 1987;  
60 Gottlieb and DuChateau, 1996; Wunsch, 1996; Bennett, 2002), but less in ecological studies.  
61 Exceptions are applications to time-series data (e.g., Wiegand et al., 1998, 2004; Gross et al.,  
62 2002; Martínez et al., 2011, 2016; González and Martorell, 2013; White et al., 2014; González et  
63 al., 2016; Zipkin et al., 2014a,b) or other types of patterns (e.g., Revilla et al., 2004; Kramer-  
64 Schadt et al., 2007; Hartig et al., 2011; Anadón, et al., 2012; May et al., 2015).

65         However, inverse modeling is still underused in ecology and, particularly, in conservation  
66 studies, and the performance of these methods under different sampling efforts and their  
67 potential for hypothesis testing or model selection have not been fully assessed. Here we present  
68 an inverse modeling approach for estimating relative survival rates of long-lived species that

69 does not require long-term monitoring (or time-series data) and, as such, circumvents time and  
70 funding constraints commonly encountered in conservation studies. We illustrate our approach  
71 using the spur-thighed tortoise (*Testudo graeca*) in the southeastern Spain as a case study. This  
72 population has been intensely studied in previous studies (Pérez et al., 2002; Rodríguez-Caro et  
73 al., 2013, 2016, 2017), including long-term monitoring studies and capture-recapture studies (e.g.  
74 Sanz-Aguilar et al., 2011).

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

83

## 84 **2. MATERIALS AND METHODS**

### 85 **2.1. General methodology**

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

91 structure of the population contains signals of the demographic rates and detectability; and c)  
 92 stochasticity is relatively unimportant.

93 First, an age-structured Leslie projection matrix (Caswell, 2001; Fig. 1b) is used to  
 94 generate the expected stable age distribution (Fig. 1c) of hypothetical populations under different  
 95 combinations of demographic parameters such as age-dependent survival rates  $S_i$  and fecundity  $F$   
 96 (Fig. 1a). To obtain the stable age distribution we used the R package popbio (Stubben and  
 97 Milligan, 2007). To find the demographic parameters that produce the best match with the  
 98 observed age structure (Fig. 1e), we varied them systematically over the parameter space (Fig.  
 99 1a) (Wiegand et al., 2004).

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

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

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

$$107 \quad F = SR \times BS \times S_h \quad (2)$$

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

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

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

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

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

$$132 \quad l(\boldsymbol{\theta}, p_1, p_2, \dots, p_m) = \log\left(\frac{n!}{\prod x_i!}\right) + \sum_{i=1}^m x_i \log(p_i) \quad (3)$$

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

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

141 There are different possibilities to find the maximum of the log-likelihood function over  
 142 the parameter space; here we used an approach based on a rejection filter (e.g., Wiegand et al.,  
 143 2004; Hartig et al., 2011) where we accepted in a first step all parameterizations  $\boldsymbol{\theta}$  with  $\Delta\text{AIC} < 2$   
 144 (Burnham and Anderson, 2002). We use the rejection filter approach to obtain the full posterior  
 145 distribution of the relative survival rates  $\boldsymbol{\theta}_{\text{rel}}$  and because we want to use the more flexible  
 146 simulation approach to test alternative hypothesis on factors impacting survival (i.e., our third  
 147 goal). However, as shortcut one may also fit the relative survival rates directly, for example  
 148 using the *mle* function of *stats4* package in R (R Core Team, 2016).

149 For each accepted parameterization  $\boldsymbol{\theta}$  we calculated the ratios  $S_i/S_{i+1}$  to obtain their  
 150 posterior distribution. Because survival rates range between 0 and 1, the estimates of the relative  
 151 survival rates allow us to generate upper bounds for each survival rate  $S_i$ . To do this, we identify  
 152 the highest survival rate in relations to each other, define its value as one, and obtain the

153 corresponding values of the other survival rates as their upper bounds. In order to narrow down  
154 the possible range of the highest survival rate, we determine for different values of the highest  
155 survival rate the mean age of individuals that survived up to adult age the age only 1% of them  
156 reach and the longevity of the individuals (Castanet, 1994).

157 In theory, a population may reach a stable distribution, but in reality, it never arrives  
158 exactly at its stable distribution (Williams et al., 2011). It is thus critical to assess how far away a  
159 population is from the stable distribution. We therefore evaluated the distance between the  
160 observed age distribution and the stable age distribution of the best model using two common  
161 measures: Keyfitz's delta (Keifitz, 1968) and projection distance (Haridas and Tuljapurkar,  
162 2007). Keyfitz's delta is the sum of the differences between the predicted stable age distribution  
163 and the observed age distribution and the projection distance is the difference between the  
164 reproductive value of a population with the observed age structure and the reproductive value of  
165 a population with the predicted stable age distribution.

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

173

## 174 **2.2. Case study**

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

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

196

### 197 **2.3. Application (a): Estimating survival**

198 We applied our inverse approach to estimate the survival in our population using one year of  
199 monitoring (before the fire, 2003;  $n=153$ , Appendix 2). In a first step, we generated all possible  
200 parameterizations  $\theta = (S_h, S_j, S_s, S_a)$  where the ranges of each of survival rate  $S_i$  varied between  
201 0.01 and 0.99 with steps of 0.02, thus assuming a conservative upper bound for all survival rates  
202 of 0.99. For each  $S_i$  we therefore tested 50 alternative values. This resulted in a total of  $50^4 =$   
203 6,250,000 parameter combinations. In a second step, we used a pre-breeding Leslie matrix with  
204 25 age-classes (eq. 1), but survival rates were estimated per stage. The fecundity parameter of the  
205 Leslie matrix was defined by equation 2, where first-year survival ( $S_h$ ) was inversely determined  
206 by our approach, the sex ratio (SR) in this population was 0.5 (a clutch contains on average half  
207 male and half females) (Graciá et al., 2017), and breeding success was estimated as  $BS =$   
208  $NC \times CS \times HS = 5.21$ . For the latter we used data on the number of clutches ( $NC = 2$ ) and clutch  
209 size ( $CS = 3.16$ ), estimated in study by Rodríguez-Caro et al., (2014), and data on hatching  
210 success ( $HS = 0.824$ ) was obtained from bibliography (Díaz-Paniagua et al., 1997).

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

214 In a fourth step, we calculated the likelihood (eq. 3) for each parameterization  $\theta$  using the  
215 corresponding detectability-corrected simulated age distribution (Fig. 1d) with the observed age  
216 distribution of the monitoring of 2003 (Fig. 1c), and accepted all parameterizations  $\theta$  with  $\Delta AIC$   
217  $< 2$  (Burnham and Anderson, 2002). Next, we calculated for all accepted parameterizations the  
218 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  
219 the upper bounds of the survival rates. We also tested the difference between the observed age

220 distribution and the stable age distribution (Williams et al., 2011). Finally, we compared our  
221 estimated survival rates with the mark-recapture estimates of Sanz-Aguilar et al., (2011).

222

#### 223 **2.4. Application (b): Impact of sample size.**

224 By means of simulation experiments, we assessed the impact of sample size on the precision and  
225 accuracy of the relative survival estimates obtained by our approach. Starting from the stable age  
226 distribution resulting from a pre-breeding Leslie matrix with known parameter values  $\hat{\theta}$  (known  
227 vector of survival rates), we simulated a population of 1000 individuals by scaling the right  
228 eigenvector associated with the dominant eigenvalue (that represents the stable age distribution)  
229 to a total abundance of 1000. We used the observed detection probabilities to obtain stochastic  
230 samples of the simulated population with different sizes  $N$ . The age distributions arising from  
231 this sampling process were then used in the same way as the *observed* data in our inverse  
232 modeling approach presented in Application 1. We repeated this procedure for different sample  
233 sizes  $N$  ( $N = 500, 400, 300, 200, 100, 75, 50, 25$ ). For each  $N$ , the sampling process was repeated  
234 30 times. To select the minimum sample size that yields acceptable estimates we compared the  
235 increase of the standard deviation when reducing the sample size  $N$ . We tested the differences in  
236 the variance of the survival rates between  $N = 500$  and the other samples size by Levene's test  
237 (Levene, 1960).

238

#### 239 **2.5. Application (c): Factors impacting survival**

240 Our approach also allows for testing alternative hypotheses on temporal variation in the survival  
241 and fecundity parameters of the Leslie matrix. We applied this feature to our case study by  
242 assessing the impact of a fire disturbance (that occurred in our population in 2004) on the

243 temporal variation of the survival rates. This allowed us to compare our results with a previous  
244 study that estimated survival rates after fire by means of capture-recapture approaches (Sanz-  
245 Aguilar et al., 2011) for the same population and disturbance.

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

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

258

### 259 **3. RESULTS**

#### 260 **3.1. Estimating survival**

261 Our rejection filter retained 5001 out of a total of 6,250,000 tested parameter combinations  
262 (0.08%). The relative survival rates were  $\theta_{rel} = (0.26, 0.98, 0.93)$  for  $S_h/S_j$ ,  $S_j/S_s$ , and  $S_s/S_a$ ,  
263 respectively (Fig. 2). The upper bound vector of survival rates was  $\theta_{upper} = (0.23, 0.87, 0.91,$   
264  $0.99)$  for  $S_h$ ,  $S_j$ ,  $S_s$  and  $S_a$ , respectively. To assess a biologically reasonable lower and upper bound  
265 for adult survival  $S_a$  (the highest survival rate). We found that a 9-year old individual reached for

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

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

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

286

### 287 **3.2. Impact of sample size**

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

294

### 295 **3.3. Factors impacting survival**

296 The observed age distribution after the fire was calculated with 117 tortoises of year 2009  
297 (Appendix 2). The hypotheses that received the least support were the null hypothesis H1 with  
298 no impact of fire on survival (Table 2). Hypothesis H5 that assumed more long-lasting effects of  
299 fire on survival (up to 5 years) represented the best model (Table 2). The estimate relative  
300 survival rates were  $\theta_{rel H5} = (0.11, 0.66, 0.94)$ . With the upper bound survival estimates  $\theta_{upper H5} =$   
301  $(0.07, 0.62, 0.94, 0.99)$  for  $S_h$ ,  $S_j$ ,  $S_s$  and  $S_a$ , respectively. We found a high reduction in one-year-  
302 old and juvenile survival after fire. Stable age distributions of the six hypotheses are available in  
303 Appendix 2.

304 Our results partially match those obtained by Sanz-Aguilar et al., (2011) that also  
305 identified a large reduction in survival of young individuals. According to Sanz-Aguilar et al.,  
306 (2011), after fire, survival rates were 0.11, 0.62 and 0.95 for juveniles, subadults and adults,  
307 respectively.

308

## 309 **4. DISCUSSION**

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

316

#### 317 **4.1. Estimating survival**

318 Our comparison of the survival estimates from inverse modeling with that of capture-recapture is  
319 insightful. Our estimates based on data of 153 individuals that were captured during one year of  
320 monitoring are comparable to those obtained using capture-recapture analyses of 11 years (with  
321 >1000 captures) in the same population. Our estimates agreed with capture-recapture estimates  
322 for subadults and particularly adults, the age classes for which the species demography is more  
323 sensitive (Doak et al., 1994; Walker et al., 2012; Pérez et al., 2012). However, as one may  
324 expect, the uncertainty was somewhat higher when using only one year of data (Table 1). In our  
325 case, we directly estimate relative survival rates from the age distributions of 153 individuals  
326 captured during one year. However, biologically realistic values of survival rates (i.e.,  
327 information on longevity) of the adult life stage were used as additional information to improve  
328 parameter estimates.

329         The biggest difference in survival estimates between the capture-recapture method and  
330 our approach appears in juvenile survival. However, we suspect that this difference emerged  
331 largely because of methodological differences. Our approach divides juvenile survival into two  
332 groups: the first year and juveniles (until 4 years old), whereas the capture-recapture analysis

333 could not consider first year survival separately because hatchlings were not marked (they have a  
334 soft carapace). Interestingly, our estimate of first year survival ( $S_h$ ) is very similar to the capture-  
335 recapture estimate of juvenile survival ( $S_j$ ) (Table 1). Additionally, the capture-recapture estimate  
336 of juvenile survival may be low because of the low detectability and sample size of young  
337 individuals (Doak et al., 1994; Hailey, 2000; Tuberville *et al.*, 2008; Pike et al., 2008), because  
338 recapture probabilities of juveniles were not modeled separately, or because some juveniles may  
339 also lose the marks when growing carapace. However, beside of methodological differences, our  
340 approach may also overestimate juvenile survival because observed juvenile population sizes  
341 stay more or less equal from age 2 to age 4 (Fig. A2, Appendix 2). This effect can contribute to  
342 the unexpectedly high value of the juvenile survival. Clearly, stochastic effects can create this  
343 unusual pattern in juvenile age structure sizes because we used only one year of data and we  
344 have additionally considered a low detection probability of juveniles (27%).

345         A previous study by Fernández-Chacón et al., (2011) on the sister tortoise *T. hermanni*  
346 that modeled recapture probabilities including age effects found a first-year survival rate of 0.39  
347 (0.22-0.59) and an average of juvenile survival from age 1 to 4 years old of 0.69. These estimates  
348 are similar to the rates obtained here for *T. graeca*. Our estimate of first-year survival rate (0.24)  
349 was also lower than the estimate by Keller et al., (1997) for the population of *T. graeca* in SW  
350 Spain (0.39). This difference could reflect actual differences between the two populations and  
351 suggest that overall survival of juveniles in our study area could be lower than in other  
352 populations. In the Doñana National Park, the predation of hatchlings has been described as very  
353 low (Keller et al., 1997), whereas in the population in the southeastern Spain predation rates are  
354 higher (García et al., 2003).

355

356        **4.2.        Impact of sample size on robustness of survival estimates**

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

366  
367        **4.3.        Model selection and impact of fire on survival**

368        Our inverse-modeling approach was also successful in testing alternative hypotheses on factors  
369        affecting survival. We found evidence for a substantial decline of survival rates after the fire that  
370        lasted for several years. Our best supported hypothesis was H5, that predicted a 5 year effect  
371        after the fire and represents a long lasting effect of fire on survival. The capture-recapture study  
372        of Sanz-Aguilar et al., (2011), identified a faster recovery after the fire. As we did not estimate  
373        the recovery with our approach, we cannot compare in the same way both studies. However, both  
374        methods, with very different sampling efforts, identified the same general effects to describe the  
375        impact of fire on the survival of the different age classes. Both methods indicated that adult and  
376        subadult survival showed only a weak decrease after the fire. In contrast, our results suggest that  
377        juveniles and one-year-old tortoises suffered after the fire a notable decrease in survival.  
378        However, because of the different predictions of juvenile survival, results of our method and of

379 the capture-recapture estimates differed in the juvenile class. The ability of our approach to test  
380 the support of alternative hypotheses on how different ecological processes influences  
381 demography multiplies its usefulness and makes it more comparable to standard demographic  
382 estimation methods in ecology and conservation.

383

#### 384 **4.4. Accuracy vs. cost trade-offs**

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

401 with an optimization framework to inform on the trade-off between reduced cost vs. increased  
402 reliability in the parameter estimates (Field et al., 2004, Wildermuth et al., 2013).

403       Application of our approach requires that (i) individuals can be aged reliably, (ii) the  
404 population should be assumed to be closed and stable (e.g., Keyfitz's  $\Delta$  and the projection  
405 distance  $\alpha_0$  to if the age distribution is stable; Williams et al., 2011), and (iii) the minimal  
406 number of individuals needed for this study is around 100. Moreover, a priori information of  
407 survival rates of particular age classes (e.g. adults) or the longevity of the species can be very  
408 useful for obtaining absolute estimates of survival rates. We presented here a simple and straight-  
409 forward application of our approach that treats detectability and fecundity parameters as known,  
410 but focus on uncertainty in the unknown survival parameters. Extensions of our approach could  
411 adopt a Bayesian framework (e.g., Gross et al., 2002; Martínez et al., 2016) that considers also  
412 uncertainty in the estimates of fecundity parameters and a more complex observer model to  
413 describe detectability. However, such extensions would require more complex numerical  
414 optimization techniques for model parameterization. Future research should also consider the  
415 effects of stochasticity, especially at low population sizes, immigration and emigration, stage-  
416 structure populations and non-equilibrium dynamics. Overall, our work contributes towards  
417 broadening the toolbox in biodiversity conservation with a tool that is encouraged when long-  
418 term monitoring is not feasible.

419

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425

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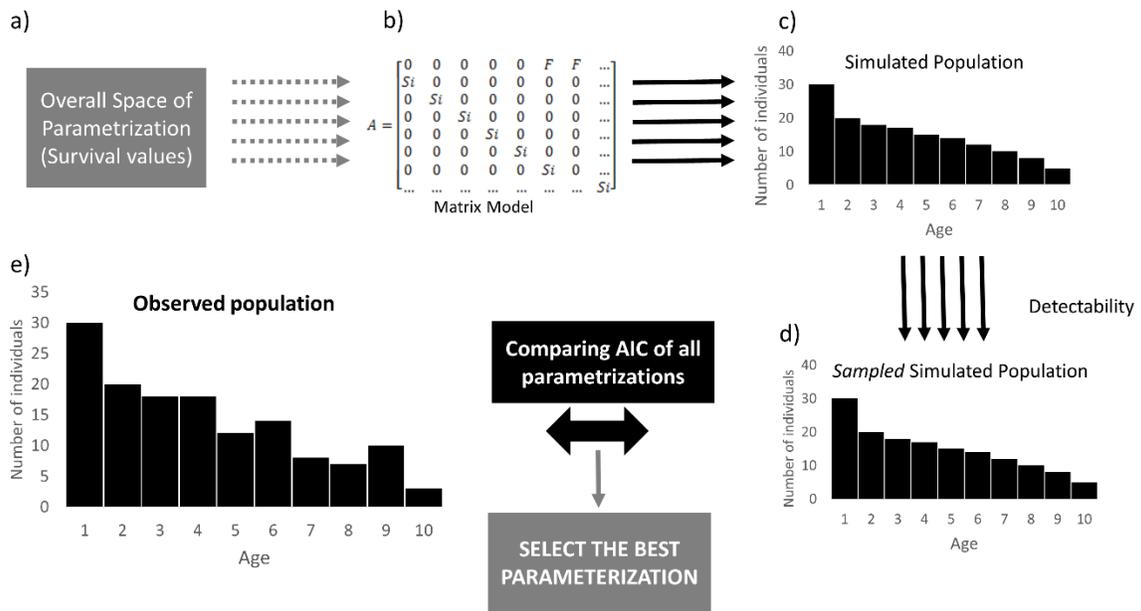
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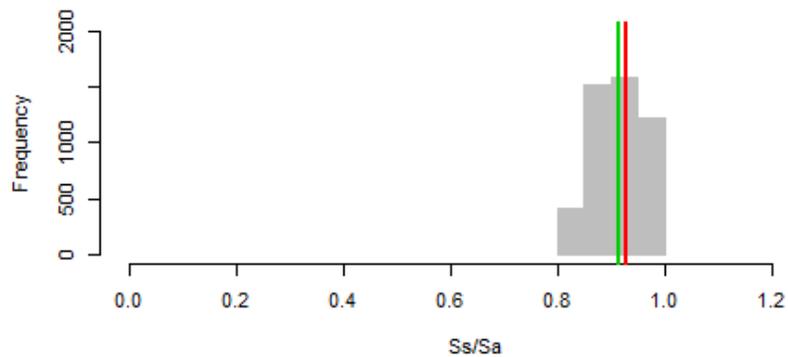
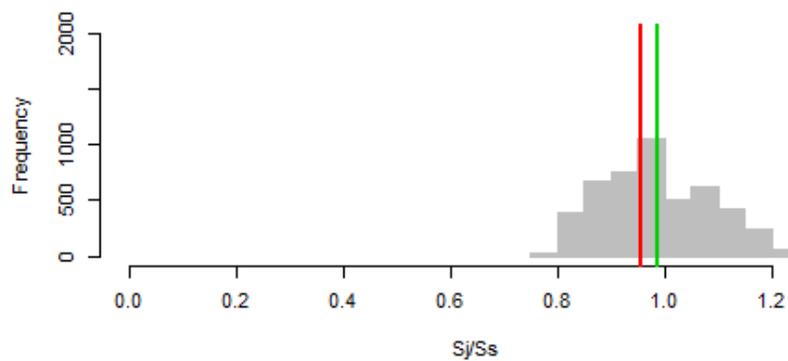
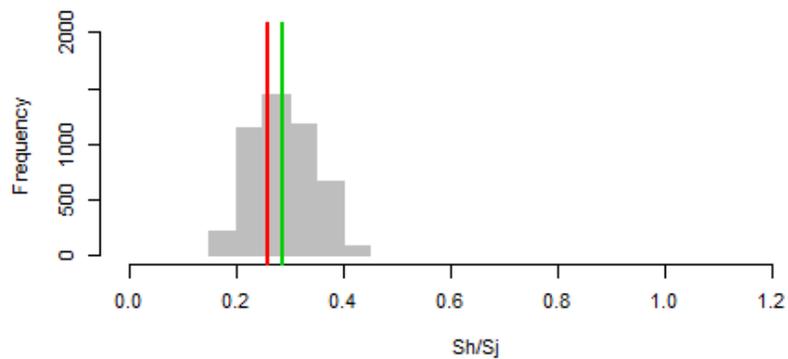




1

2 Figure 1. Summary of general framework of the model.

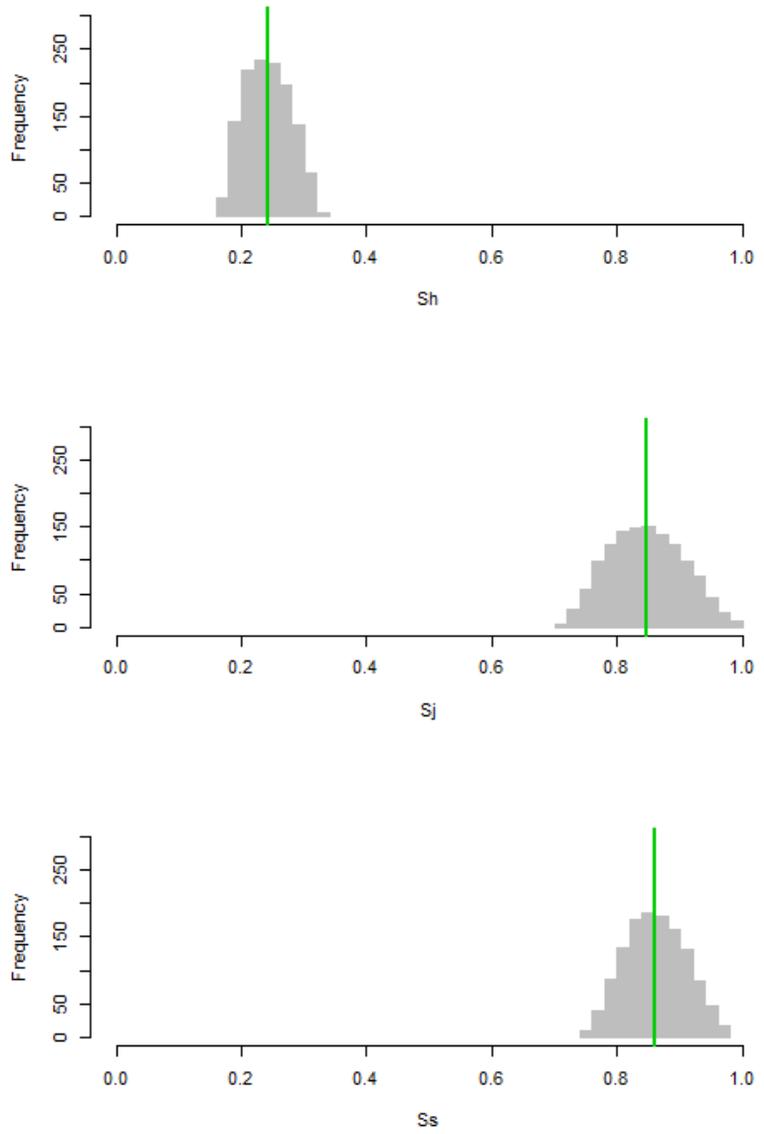
3



1  
 2 Figure 2. Histograms of the distribution of the relative survival rates  $S_h/S_j$  (left)  $S_j/S_s$  (middle) and  
 3  $S_s/S_a$  (right) for the 5001 parameterizations that yield  $\Delta AIC < 2$ .  $S_h$ ,  $S_j$ ,  $S_s$ ,  $S_a$  are the survival rates  
 4 of hatchlings, juveniles, subadults, and adults, respectively. The red lines are the maximum

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

3



4

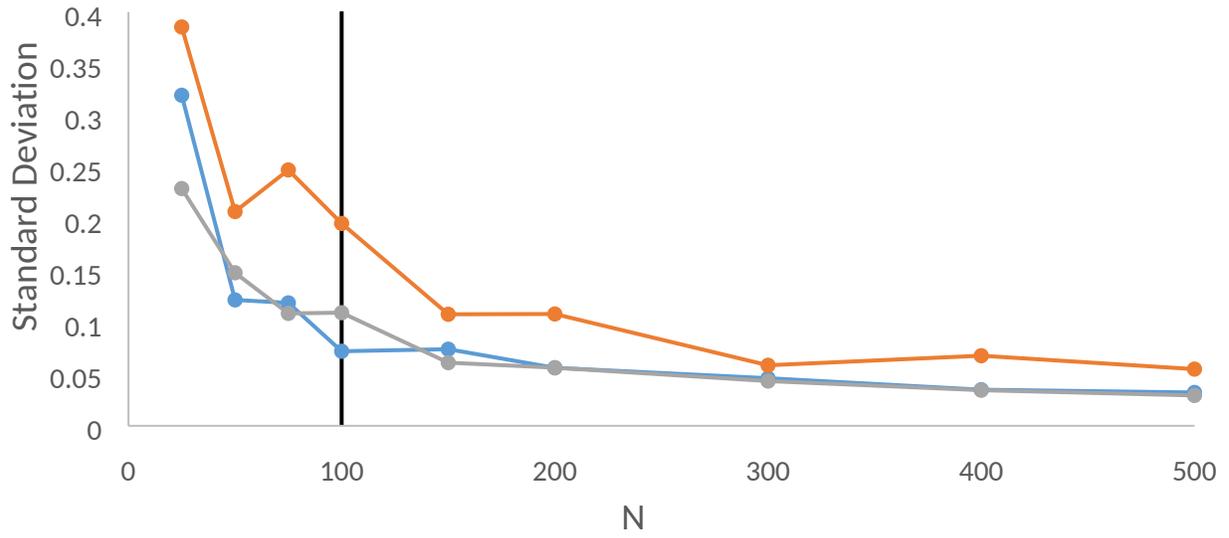
5 Figure 3. Histograms of the distribution of the absolute survival rates  $S_h$  of hatchlings (left),  $S_j$  of  
6 juveniles (middle), and  $S_s$  of subadults (right) for the 1256 parameterizations that yield  $\Delta AIC < 2$   
7 and where the adult survival rate  $S_a$  was within the plausible range (0.9, 0.97). The green lines

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

3

4

1



2

3 Figure 2. Reduction of the standard deviation (SD) through the increment of the sample size ( $N$ )

4 in the simulations (30 replicates) for  $S_i/S_j$  in blue,  $S_j/S_s$  in orange and  $S_s/S_a$  in grey. When the

5 sample size is lower than 100 the standard deviation increases substantially.

6

7

1 **Table 1** Range of survival rates estimated for one-year-old individuals, juveniles, subadults, and  
 2 adults ( $S_h$ ,  $S_j$ ,  $S_s$ ,  $S_a$ , respectively) and the mean estimates and 95% confidence interval calculated  
 3 by Sanz-Aguilar (2011).  $N$  is the number of tortoises considered, the effort is the number of  
 4 hours searching for tortoises by person, and finally the period comprises the years of monitoring  
 5 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)
$S_s$	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)

6 \*173 tortoises found during the monitoring, but 20 discarded because were recaptures

1 **Table 2.** Relative survival rates after the fire with the standard error and AIC for each  
 2 hypothesis. H0 represent no effect of fire, the relative survival rates were the rates estimates in  
 3 Application 1, H1, H2, H3, H4 and H5, represent the maintained effect of fire of one, two, three,  
 4 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
<b>H5</b>	<b>0.11 (0.03)</b>	<b>0.66 (0.08)</b>	<b>0.95 (0.06)</b>	<b>98.35</b>

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## Appendix 1

**Table A1.1.** Sample size and time of monitoring of several species of terrestrial 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
<i>Astrochelys yniphora</i>	8 years	329	Madagascar	O'Brien et al. 2005
<i>Gopherus agassizii</i>	10 years	531	EEUU	Lovich et al. 2014
<i>Gopherus berlandieri</i>	10 years	2128	EEUU	Kazmaier et al. 2001
<i>Gopherus morafkai</i>	22 years	1186*	EEUU	Zylstra et al. 2012
<i>Gopherus popyphemus</i>	5 - 11 years	1667	EEUU	Tuberville et al. 2014
<i>Homopus signatus</i>	5 years	237	South Africa	Loehr 2010
<i>Pyxis arachnoides</i>	3 years	404	Madagascar	Walker et al. 2012
<i>Testudo graeca</i>	11 years	1389	Spain	Sanz-Aguilar et al. 2011 Bertolero et al. 2007 and Fernández-Chacón et al 2011
<i>Testudo hermanni</i>	18 years	361	Spain	2011
<i>Testudo hermanni</i>	9 years	6565	Greece	Hailey 2000
<i>Testudo hermanni</i>	7 years	401	France	Henry et al. 1998

\*N of marked individuals

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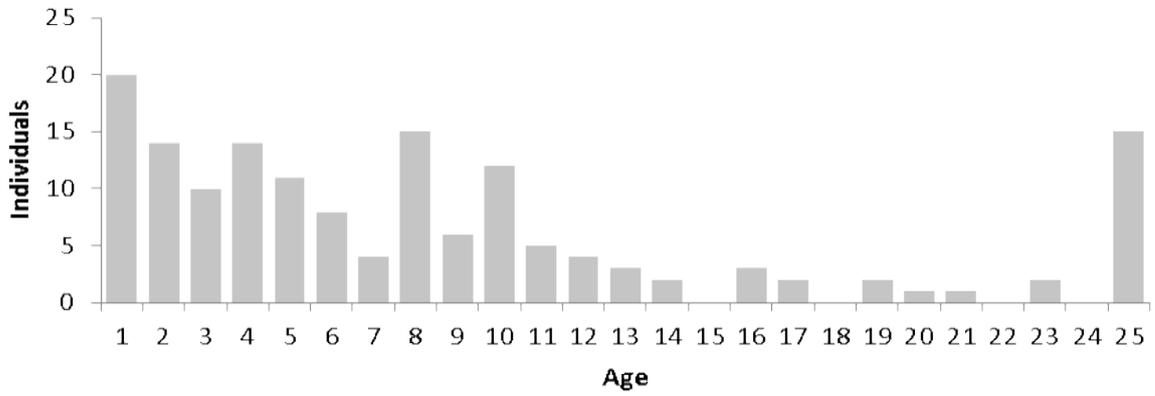
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Appendix 2

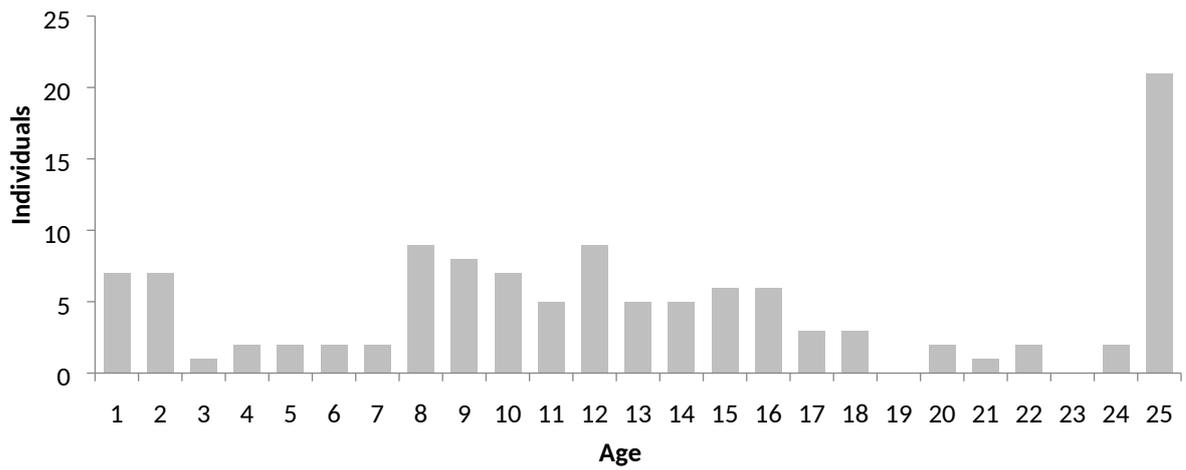
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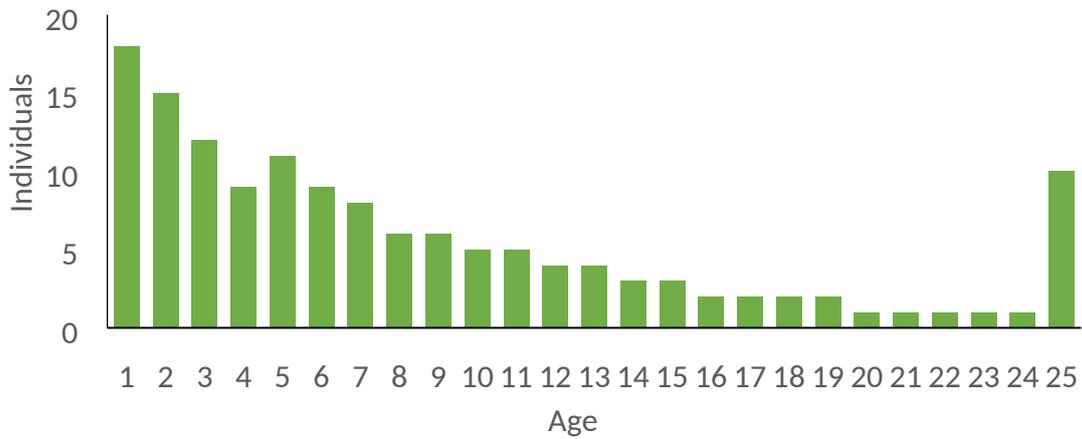
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6 Figure A2.1. Age distribution of the population in 2003 and 2009, before and after the

7 disturbance.  $N = 153$  and  $N = 117$ , respectively

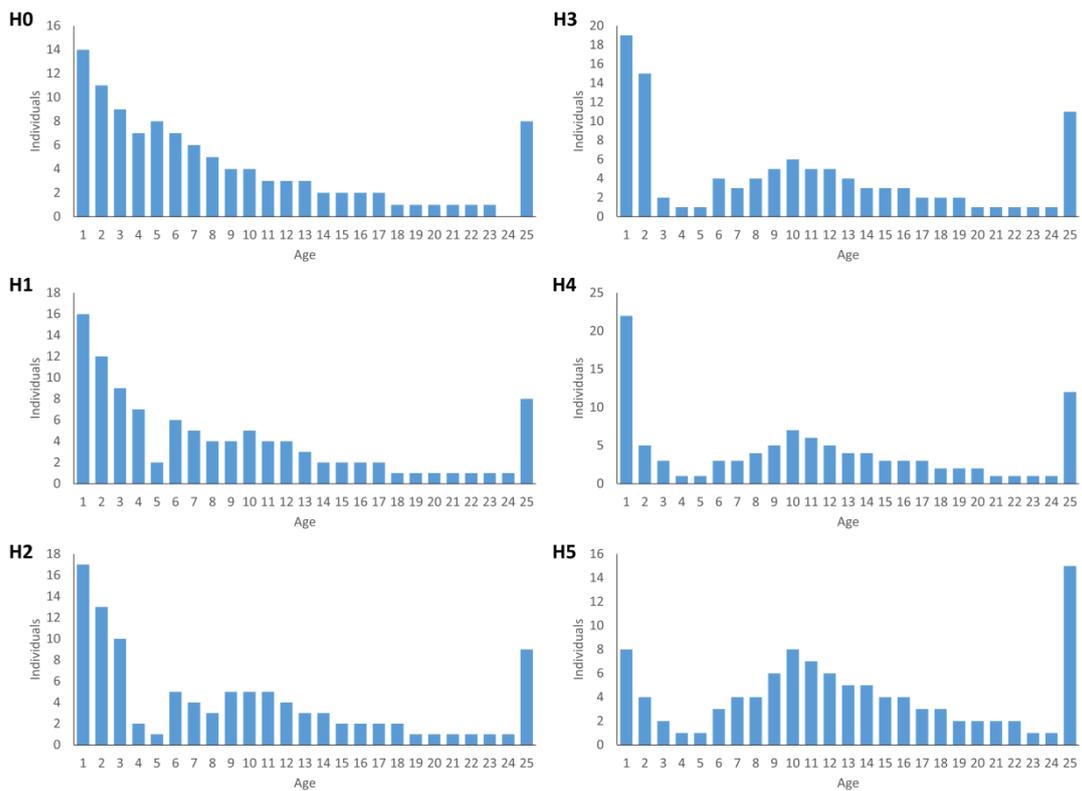
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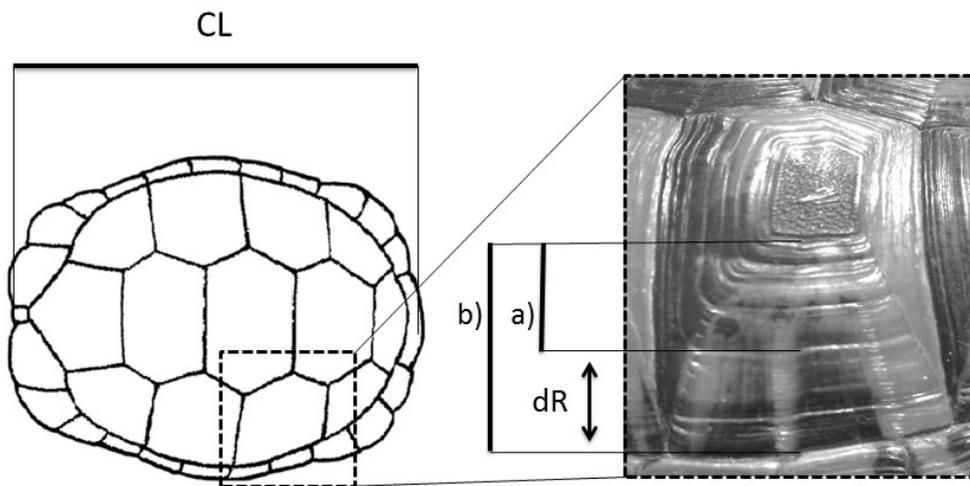
13 Figure A2.2. . Stable age distribution of the population in 2003 according to the model  
14 and simulated age distribution in 2009 for the 6 hypothesis. H0 represent no effect of  
15 fire; H1, H2, H3, H4 and H5, represent the maintained effect of fire of one, two, three,  
16 four and five years,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

### Appendix 3

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2 We estimate the age of the individuals using two methods; 1) counting de number of rings  
3 (Rodríguez-Caro *et al.* 2015) and measuring the carapace length (Rodríguez-Caro *et al.*  
4 2013).

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



8

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

11

12 For tortoises older than 10 years old, we calculate their age using an inverse regression  
13 by the equation 1 of Von Bertalanffy Model (Fabens, 1965) from Rodríguez-Caro *et al.*  
14 (2013).

$$15 \quad S_{\infty}(1 - be^{-kt}) = CL \quad \text{eq. 1}$$

16  $S_{\infty}$  is asymptotic size,  $b$  is a parameter associated with the amount of growth remaining,  
17  $k$  is the growth rate,  $t$  is the age of the individual and  $CL$  is the size (carapace length). We

18 used the inverse of eq. 1 to calculate t (age of the tortoises) using CL (Rodríguez-Caro *et*  
19 *al.* 2013; table S1.1)

20

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

Sex	$S_{\infty}$	$b$	$k$
Females	156.26	-0.7843	0.145
Males	118.23	-0.7112	0.228

23

24

25 When the tortoises are older than 26 years old, the growth of the individual is asymptotic.

26 Thus, estimate the age when the tortoises are older than 26 is impossible by this method.

27 Therefore, we categorized all individuals in the last group (more than 25 years old).

28

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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  $\omega$ ) 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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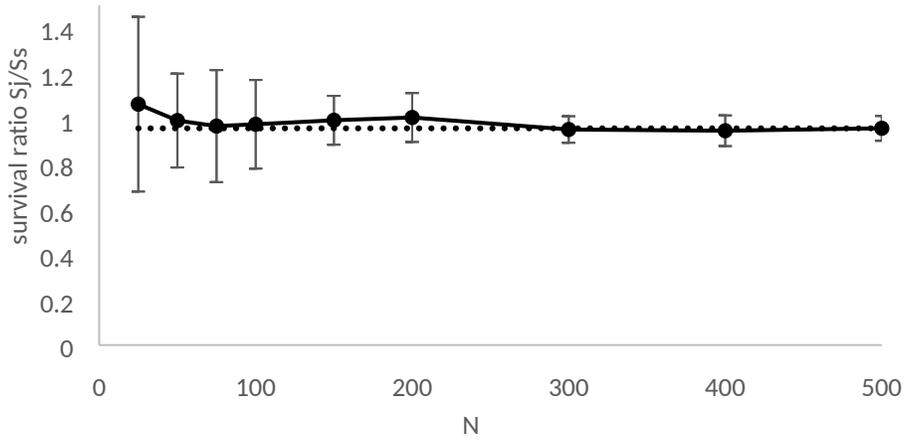
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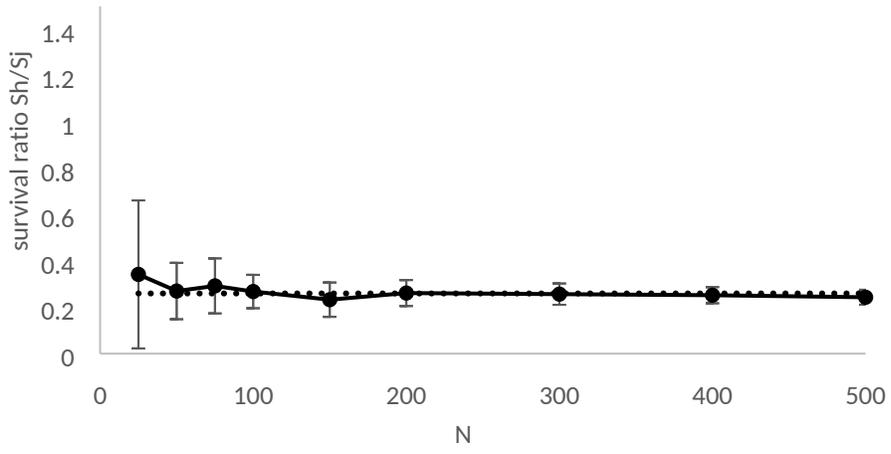
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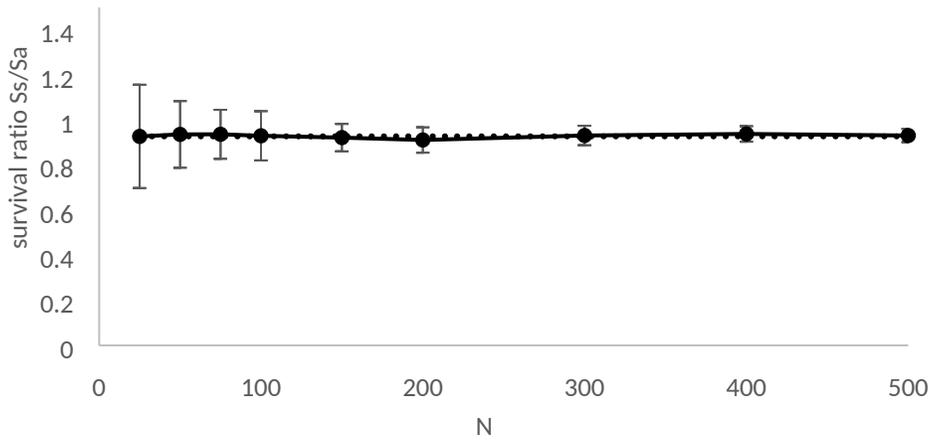
### Appendix 5



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- 1 Figure A6. Number of individuals in the simulation ( $N$ ) and the estimate relative survival rates
- 2 (black lines) and their standard simulations between simulations. Black dotted lines are the
- 3 known relative survivals rates.
- 4