

Assessing the efficacy of reintroduction programmes by modelling adult survival: the example of Hermann's tortoise

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Keywords

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Abstract

Although reintroduction programmes are often implemented for recovering animal populations, projects seldom monitor the long-term survival of released animals. In addition, although many releases may occur in the same area, little is known about how the survival of successive release batches is affected by the presence of conspecifics and density dependence. Here, we use multi-state capture–recapture modelling (combining information from recaptures and recoveries) to analyse the survival of two batches of Hermann's tortoise *Testudo hermanni hermanni* released in a 10-year interval and monitored for 18 years at the Ebro Delta (western Mediterranean). We also tested whether the released animals experienced lower survival (i.e. a release cost) before becoming familiar with the new environment. Although we used a hard-release method, neither group experienced a short-term release cost. Annual survival of both groups differed and was not negatively affected by density-dependent factors. Annual survivorship of the first group of released tortoises was constant and very high (0.945, SE = 0.011), and similar to that estimated from several natural populations. The presence of a terrestrial predator in 1 year (before the release of the second group) significantly decreased the survival of tortoises (0.819, SE = 0.073). Strikingly, survival of the second batch was significantly lower than that of the first group after the first years of release (0.775, SE = 0.049). Although survivorship for the first group suggested that habitat quality was high, the second group seemed not to acclimate well to the new environment, possibly due to the presence of resident tortoises. From a management perspective, reintroduction programmes of the Hermann's tortoise are a successful strategy for its recovery. Nevertheless, it seems advisable to avoid: (1) the release of tortoises at the core of well-established populations and (2) areas with a high density of predators, which can jeopardize the reintroduction success, especially when the number of released individuals is small.

Introduction

Reintroduction is a valuable tool in wildlife conservation programmes attempting to reverse negative population trends (Griffith *et al.*, 1989). Despite their extensive use, reintroductions are expensive and many fail to recover populations (Griffith *et al.*, 1989; Dodd & Seigel, 1991; Wolf *et al.*, 1996; IUCN, 1998). The best way to assess the outcome of reintroductions is long-term monitoring, but this has seldom been accomplished (Dodd & Seigel, 1991; Sarrazin & Barbault, 1996; Sutherland, 2000). Despite a lack of empirical evidence to assess the efficacy of reintroductions, a large number of reintroduction projects have been carried out on mammals, birds and, to a lesser extent, on reptiles (Fischer & Lindenmayer, 2000; Seddon, Soorae & Launay, 2005).

It is assumed that a 'cost of liberation' (e.g. higher mortality) occurs in all reintroduction programmes before animals become familiar with their new environment (see

Sarrazin & Legendre, 2000 and references therein), but survival has seldom been estimated (Sarrazin *et al.*, 1994; Sarrazin & Barbault, 1996; Eastridge & Clark, 2001). If released animals show low survivorship, this may indicate that animals do not acclimate well, the habitat is not suitable, that causes of extinction are not totally eradicated in the release area or any combination of these factors. Less is known about whether the survival of released individuals is affected by the presence of resident individuals, or vice versa due to density-dependent or adverse social factors (e.g. Berry, 1986; Massot *et al.*, 1994; Mullen & Ross, 1997). Thus, the release of new individuals (i.e. reinforcement, after IUCN, 1998) can be ineffective if most animals die after being released or if they reduce the survival of the residents. These aspects are crucial for the practical design of reintroductions as well as for reinforcement projects.

Hermann's tortoise *Testudo hermanni hermanni* faces a number of threats, primarily habitat loss and poaching for

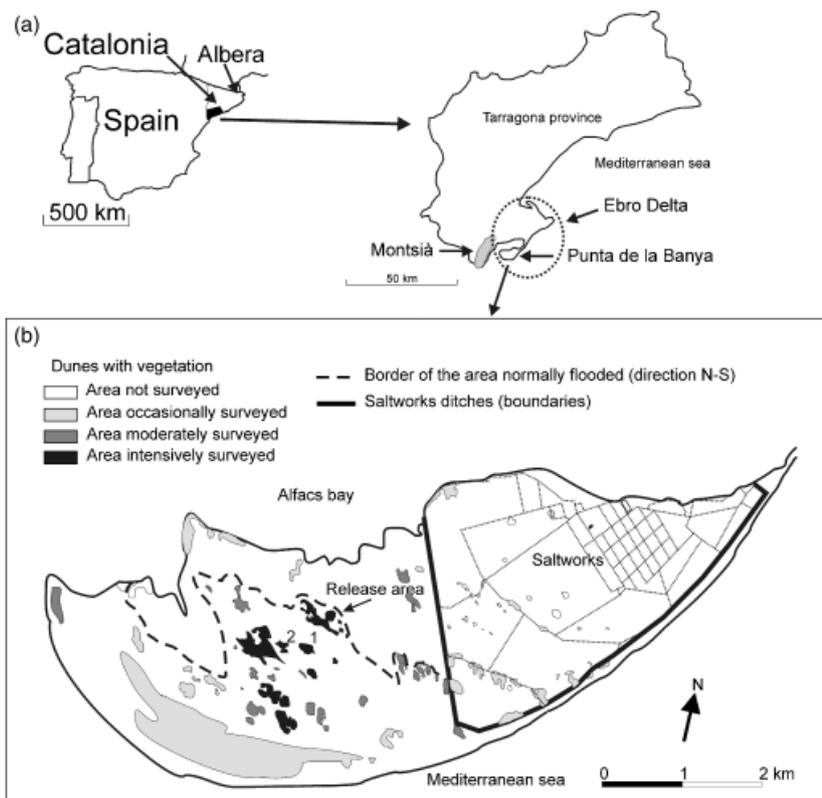


Figure 1 Map of Spanish localities cited in the text. The insets show: (a) map of the Tarragona province; (b) map of the Punta de la Banya peninsula (Ebro Delta Natural Park) showing the release dune and the surrounding dunes surveyed. In total, only four females of the first release batch (G1) dispersed from release dune to dunes 1 and 2 during 1987–2003.

the pet trade – poaching in particular has resulted in near eradication of this species. In an attempt to halt the decline in the Spanish population, where only one mainland population remains in north Catalonia (Albera population), a reintroduction project was started in the Ebro Delta Natural Park (south Catalonia; Fig. 1). Because two groups of tortoises were released 10 years apart, we were able to analyse whether survival of introduced individuals differed between the two groups: both residents (first released) and newcomers. Reintroductions of this species have been carried out throughout its geographical range, but little is known about their viability (Soler *et al.*, 2002). In contrast to many threatened species with reintroduction programmes, adult survival has been analysed in several natural populations of Hermann's tortoise (Hailey, 1990, 2000; Henry *et al.*, 1999; Willemsen & Hailey, 2001). We will use these estimated parameters as reference values to evaluate the success of the reintroduction project.

Methods

Background and study site

Western populations of Hermann's tortoises are listed as endangered in the IUCN's *Red Data List* and are critically

endangered in Spain, where populations are restricted to Catalonia and the Balearic archipelago (Pleguezuelos, Márquez & Lizana, 2002). To increase the number of populations (only one in Catalonia – Albera – at the end of the 1980s), a conservation introduction project was initiated at the Punta de la Banya reserve, Ebro Delta Natural Park ($40^{\circ}37'N$ $00^{\circ}35'E$, Fig. 1). Although tortoises are not known from this reserve, the Ebro Delta Natural Park is within the historical range of the species (Bertolero & Martínez Vilalta, 1994). The reserve is a peninsula legally and effectively protected from humans, safe from fire and, most of the time, from terrestrial predators. During the project, two releases took place 10 years apart: the first (herein denoted G1) during 1987–1988, involving 44 tortoises, and the second (herein denoted G2) during 1997–1998, consisting of 22 animals (Table 1). All released individuals were adults (with no clearly visible new growth laminae due to old age and wear) or subadults > 7 years old (known hatch year in captivity). The origin of both groups was mainly captivity, although for most individuals the exact time in captivity was unknown. We checked carefully that all individuals showed both morphological and colour features of the western subspecies *T. h. hermanni* (Cheylan, 2001). Individuals were marked individually with notches in the carapace (Plummer, 1989) and released without any previous habituation *in situ* (i.e. a hard release *sensu* Kleiman, 1989).

Table 1 Tortoises and sampling information from the monitoring program of the introduced population of Hermann's tortoises *Testudo hermanni hermanni* in the Ebro Delta Natural Park

Year	RT	NTS	NDT	<i>e</i>	<i>d</i>
1987	7M + 17F				2.16
1988	9M + 11F	5 ^a	1	4	3.51
1989		7	1	1	3.42 ^b
1990		15	0	11	3.24
1991		20	0	9	3.42
1992		29	0	25	2.97
1993		23	2	11	3.33
1994		27	4	32	4.32
1995		20	5	25	4.68
1996		20	0	22	6.13
1997	6M + 5F	21 ^a	0	26	7.39
1998	5M + 6F	25 ^a	2	18	7.93
1999		35	0	24	8.02
2000		29	4	15	7.57
2001		25	3	11	7.48
2002		25	0	11	7.57
2003		14	2	10	6.58
2004		21	0	7	7.21

^aWithout including the released tortoises of the same year.

^bFor 1989 there were not enough data to estimate the population size by the capture–recapture method; the population size was calculated from the number of released tortoises found this year, plus the released tortoises found in the next years but not found in 1989.

RT, number of released tortoises per year (M, males; F, females); NTS, number of alive released tortoises found in spring (April–June) each year; NDT, number of released tortoises found dead each year; *e*, sampling effort, that is, the number of days sampled in spring per year; *d*, density of tortoises in the release dune (tortoises ha⁻¹).

Released tortoises reproduce regularly in the reserve (Bertolero *et al.*, 2007), where at least 448 tortoises were born to 2001 (Bertolero, Carretero & Llorente, 2005) and have established a self-sustained population (Bertolero, 2002). The mean age of maturity is 6.7 and 8.4 years for wildborn males and females, respectively (Bertolero, 2002 and unpublished results). Tortoises are active from February to November, but the main activity occurs from March to October (Bertolero, 2002). Hermann's tortoises show homing behaviour (Chelazzi & Francisci, 1979) with stable home ranges that can overlap between individuals (Bertolero, 2002). Nevertheless, territorial behaviour has been poorly understood to now. Adult and subadult densities vary greatly between western populations (2.7–19.1 tortoises ha⁻¹; see review in Cheylan, 2001).

The Punta de la Banya is a flat sandy salt marsh of 2514 ha with isolated dunes covered by psammophilous and halophilous vegetation. The habitat is similar to that occupied by some populations in northern Minorca (Balearic Islands), Tuscany (Italy) and Greece. All tortoises were released in the same place on a single dune of 11.1 ha isolated from other dunes (the closest dune was 247 m away) by a desert plain with no vegetation at all that may be flooded by seawater (Bertolero, 2002). Dunes were consid-

ered discrete patches with non-suitable habitat connecting them, although some tortoises (mostly subadults or adults born in the reserve) did disperse between dunes (Bertolero, 2002). The Ebro Delta is within the semi-arid bioclimatic zone (Quézel & Barbero, 1982), with the heaviest rain between September and October. During 1987–2004, the annual mean (\pm SE) temperature was 17.2 ± 0.2 °C, with a mean annual rainfall of 492 ± 31 mm.

Survival analysis

All parts of the release dune and surrounding dunes were searched annually from 1987–2004 (Fig. 1). In most years, monitoring was carried out during all the activity periods of the tortoises (Table 1). Nevertheless, survival analysis was limited for tortoises caught between April and June, and so the monitoring period (*i*) was much shorter than the interval between successive monitoring periods (*i* to *i* + 1, Lebreton *et al.*, 1992). Spring mean time devoted for monitoring tortoises was 15 days (SE = 2, *n* = 17; Table 1) and each sampling day averaged 326 min long (SE = 11, *n* = 241).

The modelling of survival combined live recaptures and recoveries of dead animals through a multistate approach, with two possible states: alive and newly dead (see Lebreton, Almeras & Pradel, 1999 and references therein). We estimated three different parameters: *S*, the annual survival probability; *p*, the annual recapture probability; *r*, the annual recovery probability (the probability of finding a dead tortoise). We sampled the whole study area (release and surrounding dunes), and there was no evidence of permanent emigration (i.e. 1-*S* equalled mortality). It is important to note that, despite surveys of the surrounding dunes, no individuals from *G*₂ were detected with the release dune, whereas four females from *G*₁ dispersed from this dune (Bertolero, 2002 and unpubl. data) and stayed in the new dunes (Fig. 1).

In the survival-transition matrix, the probability of staying in the state 'alive' from time *k*–1 to *k* was Ψ_k^{11} , the probability of changing from state 'alive' to state 'newly dead' was $\Psi_k^{12} = 1 - \Psi_k^{11}$, whereas the opposite transition was impossible ($\Psi_k^{21} = 0$). A dead tortoise obviated transitions to other states ($\Psi_k^{22} = 1$). Maximum likelihood functions were fitted using software M-SURGE 1.7 (Choquet *et al.*, 2005b).

Several variables, covariates and groups were used to test several biological hypotheses about adult survival: time (noted by *t*); group (*g*), to assess whether survival was equal between the two batches of release; sex (*s*, only considered for *G*₁ with sufficient sample size); release cost (*c*), to test whether survival was lower during the first year after release (a short-term cost; see Sarrazin & Legendre, 2000); terrestrial predator (*b*), to test whether a badger *Meles meles*, which entered the site in 1994 and seriously injured at least one female, affected survival; and density of conspecifics (*d*), to test whether survival decreased with an increase in the population density (e.g. Altwegg *et al.*, 2003). To estimate annual density, the population size of released tortoises plus born-free tortoises ≥ 5 years old (Bertolero *et al.*, 2005) was estimated using software CAPTURE for closed populations

(Otis *et al.*, 1978) implemented in MARK 4.0 (White & Burnham, 1999). We grouped samples monthly and, following the year, we selected groups from 4 to 7 months to calculate the annual population size. Following the selection criteria, we chose model M_{th} in 68.8% of the cases, model M_h in 18.8%, model M_{bh} in 6.2% and model M_{tb} in 6.2% (where the subscript th indicates that capture probabilities vary with time and individual animal; h indicates that capture probabilities vary only with individual animal; bh indicates capture probabilities vary with individual animal and behavioural response to capture; tb indicates that capture probabilities vary with time and behavioural response to capture: see Otis *et al.*, 1978).

Finally, we tested the influence of capture effort (number of monitoring days) each year on recapture and recovery probabilities in a linear or non-linear association (denoted by e and $e+e^2$, respectively, for recapture and ey for recovery, Table 1).

Factors and covariates were tested as interactions (noted by $*$) or as additive effects (noted by $+$) using the standard notation in Lebreton *et al.* (1992). For this particular model, with a mixture of recaptures and recoveries, there is no goodness-of-fit test (GOF) to assess the fit of the more general model, namely $[S_{t*g*s}, p_{t*g*s}, r_{t*g*s}]$. In the absence of GOF for models mixing recoveries and recaptures, we only performed a GOF on recaptures. This procedure is justified by the fact that the number of recaptures is much greater than recoveries and thus information in the model is mainly derived from recaptures. We used U-Care software (Choquet *et al.*, 2005a) to check the GOF of the recapture dataset $[S_{t*g*s}, p_{t*g*s}]$ and we found no deviations from the expected values for any of the component tests (assessing for transient effects or capture heterogeneity, $\chi^2_{32} = 35.17$, $P = 0.320$). For model selection, we used the Akaike information criterion adjusted for small sample sizes (AICc, Burnham & Anderson, 2004).

Results

The umbrella model (Model 1; all models in Table 2) was greatly improved when factors and covariates were introduced, especially when modelled in an additive way (Model 2). Recapture probabilities depended only on time and recovery was constant (Model 6), while only the release group influenced survival (Model 11). When considering a release cost on the first-year survival for the released batches (Models 13–16), only Model 15 was equivalent to Model 11. Nevertheless, in this model, survival was higher the first year, contrary to the release cost hypothesis.

We did not improve the model where survival was influenced by the group (Model 11) when density dependence was incorporated into both release batches simultaneously (Model 17) or into each one of them successively survival (Models 18 and 19). Besides, contrary to the hypothesis that density affects negatively, in these models survival increased with density. However, as Model 19 (survival of the $G1$ constant and survival of the $G2$ affected by density dependence) is a particular time dependent model

and performed similarly to the model with group effect (Model 11; $\Delta AICc < 2$ between this two models), we re-examined the effect of time for each group successively (Models 20 and 21). A model with $G2$ survival being time dependent and $G1$ survival constant (Model 21) was well supported. The AICc of the last model was lowered when we added the predator effect (Model 22). However, a model with only a predator effect (Model 23) did not perform similarly ($\Delta AICc = 2.18$). None of the models incorporating the effort of capture (Models 24 and 25) improved the AICc of the finally selected model.

The selected model (Model 22) had a group and predator effect in survival, and received 53.4% of the support (Table 2). For the $G1$, survival was high and constant (0.945, $SE = 0.011$), except in 1994, when it was significantly lower, presumably because of the presence of a badger (0.819, $SE = 0.073$; Fig. 2). For the $G2$ survival was time dependent, with two distinct periods: from 1997 to 2000 (mean value for this period: 0.699, $SE = 0.063$), with lower survival than $G1$, and from 2001 to 2003, when mortality was nil. Recapture probabilities changed only with time and recovery was constant (0.533, $SE = 0.074$; Fig. 3).

Discussion

To our knowledge, the present study is the first long-term survival analysis on one reintroduced or introduced species of chelonian. Although reintroduction projects are a common conservation strategy for many threatened animals (Fischer & Lindenmayer, 2000; Seddon *et al.*, 2005) and, in particular, for chelonians (e.g. Burke, 1989; Hambler, 1994; Pedrono & Sarovy, 2000), very few studies have assessed the long-term survival of released animals (e.g. Sarrazin *et al.*, 1994; Strum, 2005). Thus, the results from this study have a number of important implications for reintroduction programmes. First, survivals of the $G1$ and some of the $G2$ release groups were very high for most years ($G1$: 0.945 and $G2$: 1.000; Fig. 2), and values ranged above or within those obtained by previous studies on several species of wild tortoises (e.g. Iverson, 1991; Peterson, 1994; Kazmaier *et al.*, 2001; see also Table 3). Although environmental features and population trends vary among populations of Hermann's tortoises (mostly declining and some stable, Cheylan, 1984; Stubbs & Swingland, 1985; Hailey & Willmsen, 2003), annual adult survival seems to be a very conservative life-history trait (Table 3). The high survival of the first released tortoises suggested that they rapidly adapted to the new environment, which was probably of high quality (e.g. suitable refuges, food, absence of fire and free from terrestrial predators and poaching). It has been suggested that the success of reintroductions should be correlated with habitat suitability (Griffith *et al.*, 1989). Nevertheless, the success of a reintroduction programme is not guaranteed with high adult survival, but only when the population is viable and self-sustaining (Dodd & Seigel, 1991; Bertolero, 2002). Therefore, other factors such as fecundity, recruitment rates or the minimum number of released animals should also be investigated.

Table 2 Models of survival, recapture and recovery probabilities for Hermann's tortoises *Testudo hermanni hermanni* at the Ebro Delta Natural Park between 1987 and 2004, with number of estimable parameters (np), deviance of the model (Dev) and Δ AICc is the difference in AICc value when comparing current model with the selected best model. Akaike weight (ω_i) is the probability that a model is the best model of the set, discounting parsimony. Finally selected models are in bold.

	Model ^a	np	Dev	AICc	Δ AICc	ω_i
General models						
(1)	$S_{t*g*s}, p_{t*g*s}, r_{t*g*s}$	89	577.29	802.41	70.97	0.000
(2)	$S_{t+g+s}, p_{t+g+s}, r_{t+g+s}$	53	630.01	751.23	19.79	0.000
(3)	$S_{t+g+s}, p_{t+g}, r_{t+g}$	52	633.81	752.43	20.99	0.000
(4)	$S_{t+g+s}, p_{g+s}, r_{g+s}$	25	834.15	887.37	155.93	0.000
(5)	S_{t+g+s}, p_t, r_t	51	638.60	754.63	23.19	0.000
(6)	S_{t+g+s}, p_t, r	37	661.31	742.48	11.04	0.002
(7)	S_{t+g+s}, p, r	21	859.61	903.87	172.43	0.000
(8)	S_{t+g}, p_t, r	36	661.47	740.24	8.80	0.007
(9)	S_{g+s}, p_t, r	21	694.22	738.49	7.05	0.016
(10)	S_t, p_t, r	35	675.38	751.78	20.34	0.000
(11)	S_g, p_t, r	20	694.34	736.40	4.96	0.045
(12)	S, p_t, r	19	710.54	750.39	18.95	0.000
Release cost						
(13)	S_{g+c1}, p_t, r	22	693.82	740.31	8.87	0.006
(14)	S_{g+c2}, p_t, r	21	701.02	745.29	13.84	0.001
(15)	S_{g+c3}, p_t, r	21	693.96	738.22	6.73	0.018
(16)	S_{g+c4}, p_t, r	21	694.21	738.47	7.03	0.016
Density-dependence						
(17)	S_{g+d}, p_t, r	20	712.18	754.23	22.80	0.000
(18)	$S_{[G1+d]+G2}, p_t, r$	20	711.57	753.63	22.19	0.000
(19)	$S_{G1+[G2+d]}, p_t, r$	20	694.95	737.01	5.57	0.033
(20)	$S_{[G1+\eta]+G2}, p_t, r$	36	666.79	745.57	14.13	0.000
(21)	$S_{G1+[G2+\eta]}, p_t, r$	26	678.68	734.16	2.72	0.138
Predator						
(22)	$S_{[G1+b]+[G2+\eta]}, p_t, r$	27	673.68	731.44	0.00	0.534
(23)	$S_{[G1+b]+G2}, p_t, r$	21	689.34	733.61	2.18	0.182
Recapture effort						
(25)	$S_{[G1+b]+G2}, p_{e_t}, r$	12	768.03	792.78	61.34	0.000
(26)	$S_{[G1+b]+G2}, p_{e+e_t}, r$	15	760.31	791.47	60.03	0.000

^aParameter notations in the models are: S , survival; p , recapture; r , recovery. Subscripts: t , time; g , group ($G1$ =for first release batch; $G2$ =for second release batch); s , sex for group 1; $c1$, different release cost for each group; $c2$, equal release cost for both groups; $c3$, release cost only for group 1; $c4$, release cost only for group 2; d , density of conspecifics; b , predator; e , capture effort for recaptures; e_t , capture effort for recovery (e^2 and e_t^2 tested for quadratic relationships, respectively). Parameters without subscripts indicated no time variation (i.e. constant).

AICc, Akaike information criterion adjusted for small sample sizes.

The second important result was the lack of a short-term release cost (first year) in either release batch. It was expected that released animals in a site should face new environmental features and challenges (a lack of knowledge on the abundance and location of refuges, food, water or predators). This constraint may lower survival during the habituation period, as it has been recorded in several species of birds (e.g. Sarrazin *et al.*, 1994; Sarrazin & Legendre, 2000), reptiles (Mullen & Ross, 1997) and mammals (e.g. Short & Turner, 2000; Eastridge & Clark, 2001; Bar-David *et al.*, 2005). This detrimental effect can be avoided with several reintroduction strategies (Bright & Morris, 1994; Eastridge & Clark, 2001), for instance soft releases, which should reduce dispersal (Tuberville *et al.*, 2005) and increase survival (Kleiman, 1989). However, a release cost has been found even in soft releases (Sarrazin *et al.*, 1994; Eastridge & Clark, 2001; Towns & Ferreira,

2001), whereas the present study is the first hard release to record high adult survival (of the first released batch) immediately following release. The physical structure of the study site, a dune isolated by surrounding non-suitable habitat, may have precluded dispersal and its commonly associated survival costs (Rousset & Gandon, 2002). Thus, not only habitat quality but also its features can be an important factor for the settlement of released animals.

A third and most striking result was the significantly lower survival of the second release batch during their first 4 years after release (Fig. 2). A different sex ratio or age structure did not explain this difference, because survival was equal for males and females and for tortoises of known and unknown age ($\chi^2_1 = 0.13$, $P = 0.72$). Increasing density from the $G2$ plus wild-born tortoises (≥ 5 years old) did not affect the survival of either release group (Models 17–19), suggesting that density-dependent effects were not operating

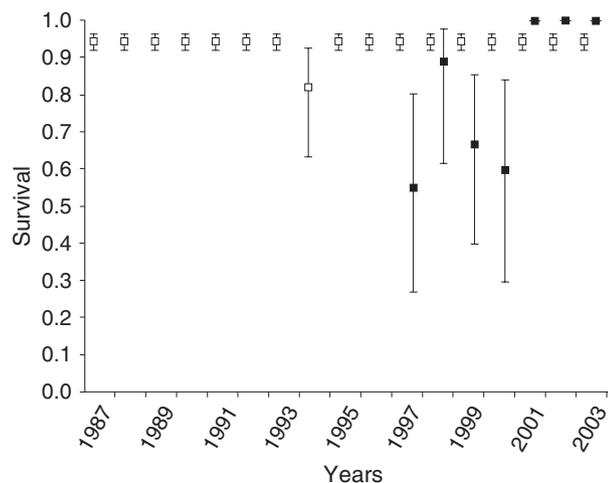


Figure 2 Survival probabilities of Hermann's tortoise *Testudo hermanni hermanni* in the Ebro delta according to the model $S_{(G1+b)+(G2+r)}$, p_r , r , with data from 1987–2003 for the first release batch (G1, hollow squares), and from 1997–2003 for the second release batch (G2, filled squares). Survival estimates are shown with 95% CI.

at such a population density (well below the maximum value reported in Cheylan, 2001) or with the amounts of available resources. Also, if density-dependent factors affected survival, they would have affected both groups of tortoises simultaneously (G1 and G2) and not just only one (G2). Thus, there are two potential explanations for the lower survival of the G2 during the first 4 years. One possibility is that the presence of resident tortoises affected the acclimatization process of newly introduced individuals. Another possibility is that the period of acclimatization of newcomers elapsed during the first 4 years (i.e. a release cost), although this seems to be a rather long period of time.

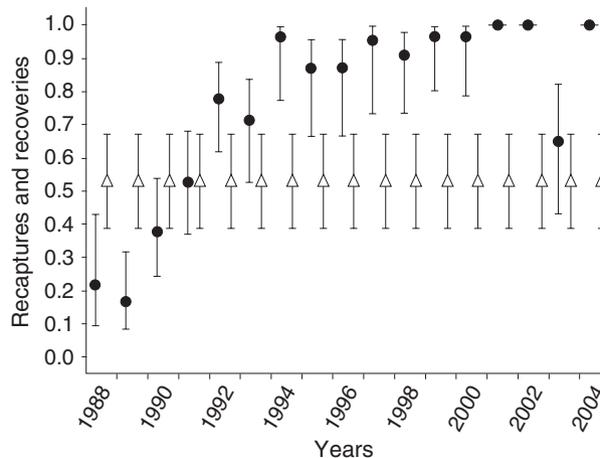


Figure 3 Recapture (filled circles) and recovery (triangles) probabilities from 1988 to 2004 of Hermann's tortoises *Testudo hermanni hermanni* at the Ebro delta according to the final model ($S_{(G1+b)+(G2+r)}$, p_r , r). Parameter estimates are shown with 95% CI.

Because these two explanations are not mutually exclusive, they cannot be seen strictly as alternatives. However, survival of the resident tortoises was not affected by the presence of newcomers (no density effect). A similar result was found by Mullen & Ross (1997) on desert tortoise *Gopherus agassizii*, whereas Berry (1986) argued that relocated desert tortoises can disrupt the resident social system, although the latter was not based on experimental data. Nevertheless, until now, there is no published evidence to support the alteration of the social system in Chelonia after the release of newcomers and it is not clear how residents can affect the survival of newcomers.

Finally, although this is the first time that a badger is recorded as a predator of adult Hermann's tortoises

Table 3 Annual survival estimates for several natural populations of Hermann's tortoise *Testudo hermanni hermanni* and for the introduced population in the Ebro Delta Natural Park, all calculated with capture–recapture methods

Population	Mean survival	Range ^a	Years	Reference
Greece				
Alyki	0.914 M	0.813–0.982	1982–1986	Hailey (1990)
	0.877 F	0.839–0.955	1982–1986	Hailey (1990)
	0.884 ^{b,c}	0.796–0.966	1982–1989	Hailey (2000)
Mean of eight populations	0.886 ^b	0.800–1.000	1981–1990	Willemsen & Hailey (2001)
France				
Les Mayons (Maures)	0.922	0.879–0.951	1993–1995	Guyot (1996)
Pardiguière norte (Maures)	0.60	–	1993–1995	Guyot (1996)
Pardiguière sur (Maures)	0.78	–	1993–1995	Guyot (1996)
Collobrières (Maures)	0.96	–		Cheylan (2001)
Porto-Vecchio (Corsica)	0.95	0.91–0.98	1990–1996	Henry <i>et al.</i> (1999)
Spain				
Ebro delta, first release	0.945	0.920–0.963	1987–2004	This study
Ebro delta, second release	0.775	0.664–0.858	1997–2004	This study

^aFor Greece, ranges are minimum and maximum values; for France and Spain, ranges are 95% confidence intervals.

^bIncludes all tortoises of known sex (> 10 cm, may include sub-adults).

^cRecalculated from Table 3 in Hailey (2000).

M, males; F, females.

(previously badgers have only been recorded as predators of nests; Swingland & Stubbs, 1985; Guyot, 1996; Cheylan, 2001), a single event was sufficient to reduce their survival significantly. In the same way, Short & Turner (2000) found that reintroduced burrowing bettong *Bettongia lesueuri* experienced major mortality events following incursions of foxes *Vulpes vulpes*. Thus, protocols for reintroduction projects must take into account that predators (even at very low densities) can jeopardize a reintroduction programme, especially when few individuals are released.

Implications for reintroduction programmes of tortoises

The application of standard protocols for reintroduction programmes should be modified on a case-by-case basis. Nevertheless, our results should help to establish more thorough protocols for reintroduction (and also for reinforcement programmes) of tortoises. The success of the hard release probably resulted from the special features of the habitat, particularly a relatively small, suitable and isolated patch preventing dispersal and its associated risks. However, it is still possible that in continuous habitat, a soft release would be preferable over a hard release (Tuberville *et al.*, 2005). Furthermore, and more importantly, it seems that it is not advisable to release tortoises within a well-established population, not only because of the risk of disease transmission (Seigel & Dodd, 2000) or potential social system disruption (Berry, 1986), but because the presence of residents may disrupt the acclimatization process of newcomers. Finally, the presence of predators, even at low densities, can jeopardize the reintroduction project when the number of released individuals is small.

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