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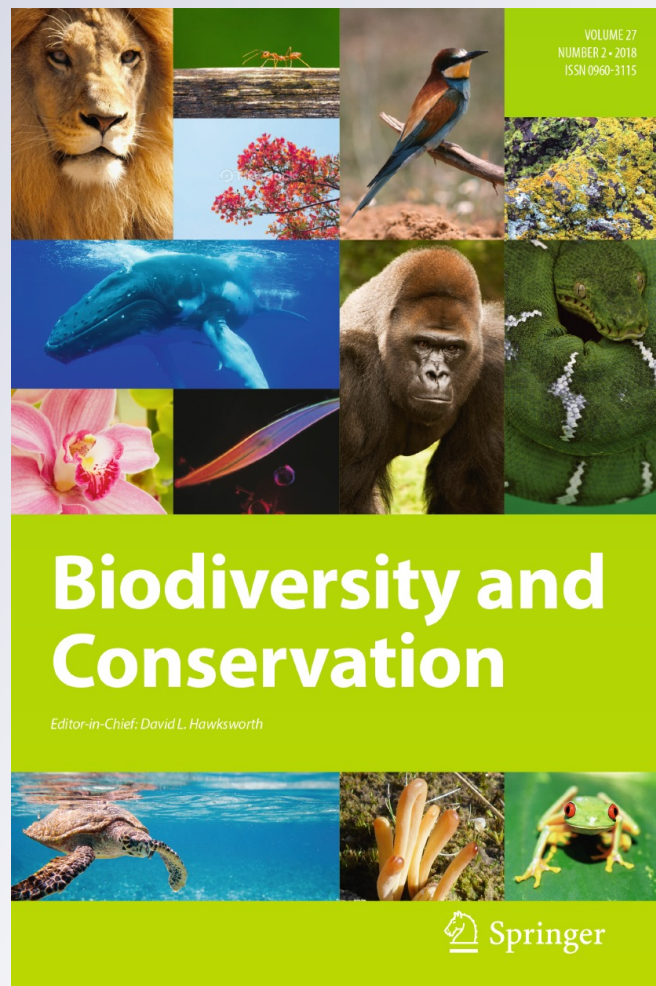
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Settlement pattern of tortoises translocated into the wild: a key to evaluate population reinforcement success

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Abstract A lack of long-term monitoring often impedes the evaluation of translocation used to reinforce populations. Crucial questions regarding the exact timing and place of possible settlement remain unanswered. To examine these issues we radio-tracked during three years 24 tortoises (*Testudo hermanni hermanni*) released to reinforce a resident population impacted by fire. Individuals from the resident population (N = 20) and from a distant control population (N = 11) were also radio-tracked. More than 11,000 fixes were collected, enabling us to precisely describe movement patterns. Most translocated tortoises first dispersed (> 500 m to > 3000 m away) in a random direction and sometimes crossed unfavorable areas. Later, a marked shift in movement pattern, from a relatively unidirectional course to multidirectional displacements indicated settlement. Movement patterns of translocated and resident individuals became undistinguishable after settlement. Most individuals settled during the first year after release but several settled in the second year. Mean annual survival rate (> 85%) remained within the range of the species but was lower compared to the resident (93%) and control tortoises (100%). Overall, most translocated individuals (~ 63%) settled and adapted well to their novel environment. This result is essential regarding current controversies that are unfounded and that limit conservation translocations. Yet, translocation sites should be large enough and/or surrounded by secondary favorable areas to limit the mortality associated with dispersal in hazardous environments. Large numbers of individuals rescued during urbanization works may easily supply conservation translocations to reinforce fragile populations.

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Introduction

Fragmentation and loss of habitats along with rapid environmental changes threaten animal populations; under low density thresholds populations might not be viable (Lennartsson 2002; Traill et al. 2007). One possible practical response is to assist displacements; for example to translocate individuals among areas to promote exchanges, or from unfavorable to favorable areas to reinforce populations. Genetically depressed and/or decimated populations living in appropriate habitats may benefit from reinforcement programs based on the release of individuals originating from captivity and/or from healthy populations (Madsen et al. 1999; Seddon et al. 2014). Consequently translocations can be an effective management strategy to stem the decline of threatened species (Griffith et al. 1989; Fischer and Lindenmayer 2000; Germano and Bishop 2009).

However translocation can be stressful for displaced individuals, these may over disperse and leave the target area, and it may also perturb resident populations; translocation failures have been reported (Seddon et al. 2012, 2014). In practice, in many translocation operations a lack of monitoring of both translocated individuals and of resident populations poses strong difficulties to obtain synthetic views and to derive general procedures (Dodd and Seigel 1991). Moreover, the peculiarities of each species and population imply that an adequate evaluation is essential to provide precise practical guidelines for wildlife managers (Sullivan et al. 2015).

Nonetheless outline key elements of an effective evaluation should be carefully considered. Selected resident areas should contain essential habitat features (Hambler 1994; Dodd and Seigel 1991; Bertolero and Oro 2009; Germano and Bishop 2009; Nafus et al. 2016). Monitoring during the short term post-release phase during which translocated individuals tend to over disperse is generally critical (Clarke and Schedvin 1997; Reinert and Rupert 1999; Attum et al. 2007; Hinderle 2011; Nussear et al. 2012). This initial dispersal phase has been attributed to homing behavior, aversion against unfamiliar habitat, or to aggressive interactions with resident individuals (Aragón et al. 2006; Stamps and Swaisgood 2007). Post release often entails over dispersion and high mortality risks, especially due to predation and starvation (Sullivan et al. 2004; Letty et al. 2007; Spinola et al. 2008; Attum et al. 2010). Aside from this post-release mortality, excessively dispersing individuals may not sufficiently contribute to population reinforcement (Le Gouar et al. 2012; Germano et al. 2015). To limit over dispersal, soft-release techniques where individuals are progressively accustomed with their novel habitat have been used (Tuberville et al. 2005; Knox and Monks 2014; Attum and Cutshall 2015; Attum and Rabia 2016), but rarely accurately evaluated (King et al. 2004; Attum et al. 2011; Attum and Cutshall 2015). Translocation success can be influenced by other factors: age, origin, number of released individuals and season of release (Fischer and Lindenmayer 2000; Germano and Bishop 2009; Attum and Cutshall 2015). Overall, translocation has a strong potential for conservation management but it requires precise assessment and thus it should be used in priority in species where important benefits are expected.

Translocations are particularly well suited to alleviate the impact of habitat destruction in species with low dispersal abilities (Cushman 2006). Indeed, these organisms cannot easily escape events such as fires or flooding (Ayres et al. 2012; Baker et al. 2012; Lepeigneul et al. 2014; Ujvari et al. 2015). Further, long-lived species are particularly sensitive to rapid and marked environmental changes; low fecundity and late maturity are

incompatible with rapid population recovery. Terrestrial chelonians (i.e. tortoises) suffer from habitat destruction (fires notably), and population fragmentation (Lambert 1984).

Translocations have been tested in several tortoise species, notably in North America (Berry 1986; Tuberville et al. 2005; Rittenhouse et al. 2007; Field et al. 2007; Nussear et al. 2012; Hinderle et al. 2015) and in North Africa (Attum et al. 2007, 2010, 2011). In southern Europe most tortoise populations are threatened (Böhm et al. 2013; Tingley et al. 2016) but translocation operations have been limited to one very atypical and small area, a flat sandy salt marsh (Bertolero et al. 2007). Further evaluation is required to develop management tools applicable to the most general situation: most remaining tortoise populations live in dry semi-open scrubland landscapes which are highly fragmented. Indeed, illegal harvesting, forest fires, urbanization, and other causes (diseases, genetic ingression) have devastated many populations, especially in the western parts of the Mediterranean basin.

In this study we monitored Hermann tortoises that have been translocated to reinforce a resident population weakened by fires. Because many scientists and managers express a marked opposition to the translocation of Hermann tortoises, the current assessment is critical to ensure support for this conservation strategy. This study is a central element of a European Life program (LIFE08NAT/F/000475) that aims to set up and test different methodologies to protect and reinforce wild populations of Hermann tortoises. A previous investigation suggested that the very first step of translocation (hard-release, without acclimation during spring time) was successful; three months after release individuals were in good condition (Lepeigneul et al. 2014). But experimental translocations should also provide feedback relevant for long term objectives; a 3 months assessment is insufficient to evaluate annual survival rate, settlement *versus* dispersal patterns, and thus the actual success of establishment translocation. Tortoises are slow moving and robust animals; individuals may progressively leave the resident area over long time periods and/or may slowly waste away. An accurate appraisal of translocation success must be based on the characterization of post-release dispersal and settlement pattern. Some studies considered post-release movements (e.g. Attum and Cutshall 2015; Nussear et al. 2012), but none clearly integrated the crucial settlement phase. Close monitoring of the movements of both translocated and wild resident individuals is needed (Bauder et al. 2014). Because translocated tortoises may interact with residents, additional comparison with individuals from populations independent of translocations can be used as control.

On a daily basis, we radio-tracked during 3 years both exogenous translocated and resident tortoises in one population impacted by fire; we also monitored individuals from a distinct control population. Tortoises were translocated in spring and autumn to test seasonal effect. The close monitoring procedure enabled us to assess the following questions:

- Do translocated individuals settle in the resident area?
- Do they settle rapidly nearby the releasing site?
- Does translocation success vary with the season of release?

Methods

Study species

The Hermann tortoise (*Testudo hermanni hermanni*) is the only terrestrial chelonian living in metropolitan France. Historically, the spatial range of this previously abundant species

extended throughout the whole Mediterranean area from Italy to Spain. The species faces strong population declines across its distribution (red list endangered; IUCN et al. 2015). In France, Hermann tortoises are threatened by fires, urbanization and illegal pets trade (IUCN et al. 2015). Nowadays, few residual French populations persist in restricted areas in the Var district and in Corsica (Bertolero et al. 2011; Livoreil 2009). This species is characterized by typical life history traits of terrestrial tortoises; delayed sexual maturity of 10 years on average and low fecundity with females laying 3–8 eggs per year (Bertolero et al. 2011). The activity period broadly extends from March to mid-November (Bertolero et al. 2011; Huot-Daubremont and Grenot 1997). Females travel over long distances in search of nesting sites in spring (Swingland et al. 1986). Estimated home range size varies from 4.9 to 6.7 ha in males and females respectively (Ballouard et al. 2014).

Study site

The host site is situated in the National Nature Reserve (Plaine des Maures, <http://www.reserves-naturelles.org/plaine-des-maures>; Fig. 1), within the core of the residual distribution range of the species. The area covers 165 ha and is characterized by a mosaic of habitats dominated by Mediterranean scrublands (“maquis”) and forests. Scrublands vegetation is characterized by heather (*Erica arborea*), strawberry tree (*Arbutus unedo*) and filaires (*Phillyrea angustifolia*). Forests are composed by pines (*Pinus pinaster*) and cork oak trees (*Quercus suber*). Several intermittent and permanent watercourses cross the area. The southern part is more mountainous (127–490 m altitude). In 1978, a strong forest fire burned a great part of the area and destroyed many tortoises. Tortoises that survive fire can adapt to burned habitats (Lecq et al. 2014); but the population did not fully recover.

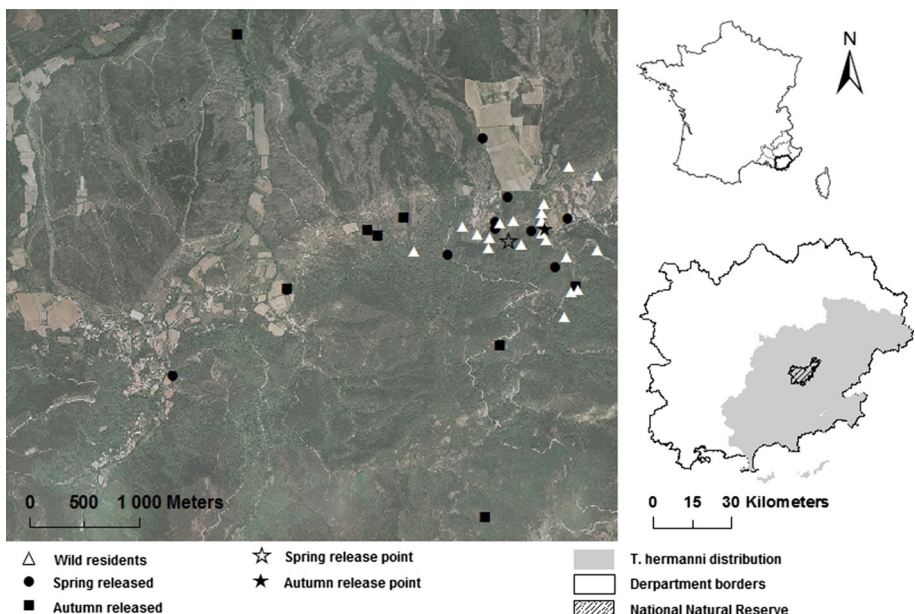


Fig. 1 Study site and final locations of monitored tortoises in early 2016. White triangles represent wild resident individuals. Translocated tortoises are represented with black symbols: spring released with circles and autumn released with squares. The two release sites are indicated with stars

Currently, in the study site the observation is 0.8 individual/hour rate (under favorable climatic conditions), approximately two times lower compared to healthy populations where at least 2 individuals/hour can be observed (Livoreil 2009). The study site provides abundant food items and shelters and thus is considered as favorable. We selected two release points: one in spring situated near a temporary river within a diverse semi-opened habitat, and one in autumn distant from 300 m was situated in the vicinity of a forest area where tortoise could find proper shelter for hibernation (Fig. 1).

Experimental groups: translocated and resident tortoises

Candidates for translocations stem from a pool of tortoises maintained in captivity in a rescue center devoted to the conservation of Hermann tortoises (SOPTOM) and located 8 km from the study site. Selected individuals were initially collected in the wild for various reasons such as recovery from accidental injuries or rescued from urban development (for details see Lepeigneul et al. 2014). Selected tortoises were kept in outdoor enclosures (7 m × 7 m) in groups of two to six individuals during prolonged periods (3–11 years, on average 7). Vegetation and shelters in the enclosure were relatively similar to those available in the release site. Fresh food items (e.g. lettuces, fruits) and fresh water were provided daily. The exact initial capture location was not available for all tortoises; however at least 10 km separated initial capture from release sites. We assumed that this distance would limit homing (Germano and Bishop 2009). Overall, tortoises experienced two translocations: first from capture site to captivity at the rescue center, and to the experimental field site.

We also monitored two groups of free-ranging tortoises, from the resident population (resident) and from another population (control). In total 4 groups of tortoises were monitored during the translocation operation, from early 2013 until late 2016 (Table 1):

- (1) Twelve spring translocated tortoises (5 Males, 7 Females) radio-tracked from the 23/04/2013 until late 2015.
- (2) Twelve autumn translocated tortoises (6 M, 6 F) from the 15/10/2013 until late 2016.

Table 1 Mean initial body mass and mean straight carapace length (SCL) for both sexes (M: Males; F: Females) of tortoises monitored during the pre-experimental phase (2012) and during the translocation experiment (2013–2015)

Group	N	Body mass (g)	SCL (mm)
Control 2012	3M	531 [492, 560]	137.8 [134.2, 140.0]
	3F	963 [890, 1066]	167.5 [164.2, 174.0]
Resident 2012	4M	500 [483, 520]	135.8 [134.1, 137.1]
	5F	811 [735, 914]	156.3 [148.3, 164.3]
2013–2015			
Control	5M	555 [463, 641]	139.8 [131.7, 147.2]
	6F	885 [805, 965]	163.8 [156.9, 171.3]
Resident	9M	512 [464, 558]	138.3 [132.0, 143.7]
	11F	862 [787, 938]	162.9 [158.7, 166.9]
Spring released	5M	446 [399, 494]	132.6 [127.0, 138.2]
	7F	799 [656, 937]	160.5 [149.9, 170.1]
Autumn released	6M	448 [381, 530]	132.2 [128.2, 137.4]
	6F	840 [749, 957]	162.8 [156.9, 170.1]

95% confidence interval are indicated into brackets

- (3) Twenty resident individuals (9 M, 11 F) in the resident population. They were captured within a 0.8 km radius from the release point and immediately released after being processed (measurements, device fitting). Some individuals were lost (i.e. cessation of radio-tracking emission) and they were replaced by other individuals. Monitoring occurred from spring 2013 to late 2016.
- (4) Eleven control individuals (5 M, 6 F) from another population situated 3 km from the release points (separated by roads impassable for tortoises) were monitored from 2013 to 2014.

In order to assess baseline movement patterns of free ranging resident and control individuals prior to translocation (Champagnon et al. 2012) we monitored two additional groups of tortoises in 2012: 9 in the resident population (4 M, 5 F) and 6 in the control population (3 M, 3 F).

Tortoise monitoring

All tortoises were identified with a notch code. Only adults large enough to be fitted with electronic devices were used (straight carapace length > 15 cm, body mass > 400 g). Each tortoise was fitted with a radio transmitter (AVM, Colfax, CA, USA) glued to the carapace with resin. The mass of equipment was less than 10% of individual body mass as recommended for tortoises (Lagarde et al. 2008). Location of the monitored tortoises was recorded on a daily basis (twice a day at the beginning) during the first year after release, every 2 days the second year after release, then once every 15 days during the last year of monitoring (third year). We precisely located individuals using a three-element Yagi antenna connected to aR4 10ATS receiver (Advanced Telemetry Systems, Isanti, MN, USA) and a hand-held GPS (margin of error 5 m). Tortoises were searched in random order. Under unfavorable climatic conditions (i.e. cold temperature, rain, hibernation) tortoises remained motionless and were not tracked. Dead tortoises were collected and carefully inspected in the laboratory in order to determine the cause of death.

Data analyses

Survival

Survival functions and annual survival rates were estimated with the staggered entry Kaplan–Meier method (Kaplan and Meier 1958; Pollock et al. 1989a, b). We then compared survival functions between groups using log-rank test (Pollock et al. 1989a) with 3 degrees of freedom for a period of 35 months. We computed 95% confidence intervals based on the method given by Pollock et al. (1989b).

Movements

Straight line distances from the point of release/capture and successive locations were calculated using the “geosphere” package on R software. We averaged straight line distances per period of 2 weeks in order to limit the influence of daily movements (e.g. due to foraging, thermoregulation). Residual normality was obtained with LOG transformation of the data. We used a linear mixed model (LMM) to account for pseudo-replication. We considered that distances varied differently through time and among individuals (random factors). We tested the effect of timing, sex, years and groups as fixed factors allowing

several interactions. Dispersal and settling phases were determined graphically by inspecting each individual pattern: during dispersal the distance from the release point increased regularly over time, inflexion point indicated when individuals settled (i.e. shift from unidirectional course to multidirectional displacements, fixes tend to aggregate spatially).

We checked for spatial autocorrelation of the fixes by computing means of Moran's I index (Moran 1950) for each group and for both movement phases (dispersal vs settling). This index varies between -1 (negative autocorrelation) and 1 (positive autocorrelation). No spatial autocorrelation occurs when this value is close to 0 .

We used turning angles between successive daily courses to study movement patterns (Claussen et al. 1997). This provided a clue to assess how individuals explore their habitat. To maximize dispersal, tortoises should select obtuse turning angles. Conversely, acute turning angles suggest that the tortoise tends to explore a given area. We also calculated movement speed based on a weekly basis. To avoid overestimation of speed, we did not include weeks with less than three fixes.

As translocated tortoises were displaced twice, homing was assessed considering the initial capture site and the captivity location at the SOPTOM. We used two indicators: (1) average directionality, which indicates the mean azimuth adopted, and (2) angular dispersion to estimate movement sinuosity (Estevez and Christman 2006; Hinderle et al. 2015). Average directionality was standardized to 0 in order to avoid the influence of the relative positions of the release and initial capture/captivity location. Angular dispersion was calculated using turning angles (i.e. angles between two successive directions; Estevez and Christman 2006). These parameters were estimated during dispersal (until the final settlement for individuals that re-dispersed after a first settling). Tortoises exhibiting perfect homing are expected to hit their home with an average directionality of 0.00° (scale $0-180^\circ$) and an angular dispersion of 1 (scale $0-1$). In order to avoid possible effect of daily movements on these indicators, we selected locations spaced by at least 6 days. Thus, one spring and one autumn released tortoise were removed from this analysis due to insufficient number of locations. We computed these indexes and distances between points using "adehabitatLT" package. Movement analyses did not include the data recorded in 2016 in the autumn released group when the other groups were not anymore monitored.

Habitat selection

Favorable habitats of the species have been previously described (Rozyłowicz and Popescu 2012; Vilardell-Bartino et al. 2015). Using recent aerial photos (2015), Natura 2000 habitat cartography, and direct observations in the field, the vegetation structure of the study site was implemented in geographic information system (GIS: ArcMap 10.0). Habitat types were classified as following: open forests, dense forests, sparse scrublands, dense scrublands, cultivated plots, habitations, uncultivated grasslands, and riparian forests. Habitat selection was assessed respectively for resident (2012 data included) and translocated tortoises (spring and autumn released pooled; 2013–2015) using Manly selectivity measure (Manly et al. 2002). We considered habitats included within individual home range, 100% MCPs (design III type analyses). We computed average of individual selection ratios and their confidence intervals for each habitat type concerned. Habitat types were considered as positively selected when selection ratio and associated CI (Confident Intervals) were above 1 , and avoided below 1 . We defined seasons based on the activity periods of the species: spring from early April to mid-June, summer from mid-June to mid-October, and winter

from mid-October to the end of March (Huot-Daubremont and Grenot 1997). Habitat selection analyses were performed using “adehabitatHS” package.

Statistics

The 95% confidence intervals (CI) of the means, estimates for slopes, and statistical tests were computed using bootstraps. We compared means using *t* or Mann–Whitney tests depending if the data were normality distributed or not. Cohen’s *d* tests were performed to complete results and count data were compared using Odds ratios (Nakagawa and Cuthill 2007).

Distribution of the data was assessed through Q–Q plots. Data were LOG transformed to obtain normal distributions if necessary. In linear mixed model (LMM; maximum likelihood estimator; “lme4” package) we estimated the variance explained by inter-individual variability using two types of R^2 : R^2_c (conditional R^2) is the proportion of variance explained by fixed and random factors cumulated. R^2_m (marginal R^2) indicates the proportion of variance explained by fixed factors only (Nakagawa and Schielzeth 2013). Effects of co-variables were assessed by computing 95% CI on slope estimates. A difference was considered significant when 95% CI did not include zero. For each model tested, Akaike Information Criterion (AIC) was computed. We selected the most parsimonious with the lower AIC and lower number of factors. Models were considered significantly different when $\Delta AIC > 2$.

All statistical analyses were performed using R 3.2.4.

Results

Almost all translocated and resident tortoises were monitored continuously (except during hibernation) until the end of the experimentation, or until death. In one translocated tortoise the transmitter failed to provide a signal after 1 year. In total 12,704 locations were recorded (mean number of location per individual = 180).

Survival

At the end of the experiment in October 2016, a total of nine tortoises have died (3 M and 1F from the spring group and 3 M and 2F from the autumn group). Amongst them, five were killed by predators (i.e. missing limbs and bites), one fell in a hole, and three died for unknown reason. In the resident group, three tortoises (1 M, 2F) were killed by predators. No mortality occurred in the control group. Mean annual survival rates were respectively 0.86 (95% CI 0.80–0.91) in spring released tortoises and 0.83 (95% CI 0.72–0.91) in autumn released tortoises. The values were 0.93 (95% CI 0.88–1.00) in wild resident tortoises and 1.00 (95% CI 1.00–1.00) in control tortoises. Despite differences in overall survival rates among the groups, log-rank tests comparing the survival curves did not reach statistical significance (log-rank test: $\chi^2 = 4.037$, d.f. = 3, $p = 0.26$).

Dispersal

Baseline movement patterns recorded prior to translocation (2012) in free ranging resident and control tortoises showed that individuals did not move farther away than a 500 m

radius distance from the first capture site (except for one female during one day, but she came back). None of the main factors used explained the variations of straight line distances from the first capture point; a null model was therefore retained for the resident and control tortoises in 2012 (Table 2).

After translocations, the most parsimonious model explaining straight line distances included interactions between groups, years, and releasing season (Table 2). Half of the variance was explained by fixed factors but inter-individual variability was important ($R^2c = 0.79$; $R^2m = 0.47$). Both spring and autumn released tortoises moved markedly far away compared to control and resident groups (Fig. 2). They eventually remained in a given place suggesting settlement. Control tortoises exhibited restricted movements and remained close to the first capture location (Fig. 2). A similar pattern was observed in resident tortoises; but several individuals moved more than 500 m away from the capture site (often temporarily). Notably, one male and one female moved more than 1000 m away. Graphical assessment of the patterns showed a high variability in settlement distance among individuals (Fig. 2). Control tortoises moved less far from the first capture point compared to the translocated groups.

Most movements of translocated individuals could be classified considering two phases: (1) dispersal with a fast increase over time of the straight line distance from the release point and (2) settlement with a marked reduction of this distance. This generated typical slopes/plateau trajectories (Fig. 2).

Positive autocorrelation of the fixes occurred in the control (Moran's $I = 0.15$, 95% CI 0.06–0.26) and resident (Moran's $I = 0.38$, 95% CI 0.26–0.51) groups. The same trend was observed in translocated tortoises but the positive autocorrelation was stronger during the dispersal phase (respectively for dispersal and settling phases; Moran's $I = 0.82$, 95% CI 0.73–0.90; Moran's $I = 0.53$, 95% CI 0.42–0.64; Cohen's $d = 1.28$, 95% CI 0.54–2.52; Mann-Whitney: $p < 0.001$).

Most translocated tortoises settled during the first year after release. Dispersal occurred mainly during spring. Settlement was delayed in the autumn compared to the spring group (Cohen's $d = 1.17$, 95% CI 0.26–5.82; $t = 3.30$, d.f. = 10.44, $p = 0.008$): occurring respectively 138.6 days (95% CI 70.0–222.8) versus 257.8 days (95% CI 236.1–277.9) after release. On average, most individuals of the spring group (11/12, 92%) settled 1103 m (95% CI 527–1814) away from the first capture point; in most of the autumn released group (7/12, 58%) this value was 1698 m (95% CI 1155–2284). However, no significant difference was detected between groups (Cohen's $d = 0.60$, 95% CI –0.29 to 2.27; $t = 1.24$, d.f. = 15.18, $p = 0.232$). Tortoises of the autumn released group hibernated into dense scrublands and forests nearby the release point with a mean distance of 96 m (95% CI 61–138).

We considered two types of dispersal based on the 500 m threshold distance from the first capture point exhibited by resident and control tortoises. Autumn released tortoises dispersed more often further from the 500 m threshold compared to the spring released tortoises (respectively 75% and 42% of individuals; Odds ratio = 0.09, 95% CI 0.00–0.51).

Movement and habitat selection during the settlement phase

Translocated tortoises were monitored during 158 days on average following settlement. Turning angles became more acute after settlement compared to the dispersal phase (Cohen's $d = 0.45$, 95% CI 0.31–0.60; Mann-Whitney: $p < 0.001$); and then they became undistinguishable compared to those displayed by resident tortoises (Cohen's $d = 0.07$,

Table 2 Table summarizing the GLMMs used to test for different between group for distances to starting locations

Data	Model	AIC	Δ AIC
2012 groups	Selected/null	528.7	0
	Full	533.53	4.83
2013–2015 groups	Selected	3839.5	0
	Full	3843.2	3.7
	Null	4137.9	298.4

Model selected, full and null models are indicated with respective AIC. Models with the lower AIC and the lower number of factor were selected. Random factors are indicated into brackets
ID individuals

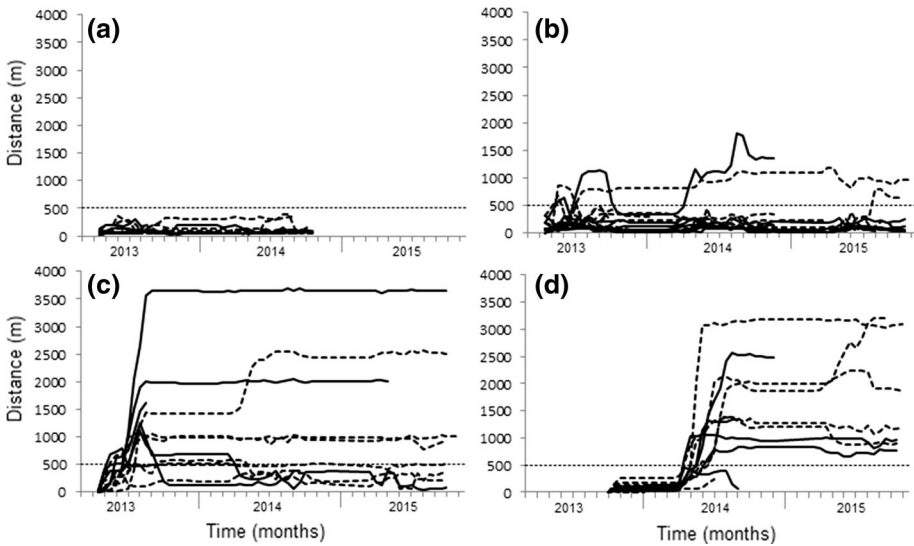


Fig. 2 Straight line distance travelled in function of time from the release/capture point by radio tracked tortoises. Each panel displays the results from a group: **a** controls; **b** host residents; **c** spring released; **d** autumn released. Males and females are respectively represented by continuous and dashed lines. The dotted horizontal line indicates a 500 m threshold. Major ticks on the X-axis represent the limit between years; the minor ticks indicate the limits between months

95% CI -0.02 to 0.17 ; Mann–Whitney: $p = 0.161$; Fig. 3). Tortoises travelled over longer distances during dispersal compared to settlement, especially in the spring group (Cohen’s $d = 1.05$, 95% CI 0.80 – 1.31 ; Mann–Whitney: $p < 0.001$ in the spring group, and Cohen’s $d = 0.23$, 95% CI 0.03 – 0.42 ; Mann–Whitney: $p = 0.647$ in autumn group). After settlement translocated tortoises moved over shorter distances compared to the resident tortoises (respectively for spring and autumn groups: Cohen’s $d = -0.40$, 95% CI -0.53 to -0.28 ; Mann–Whitney: $p < 0.001$ and Cohen’s $d = -0.29$, 95% CI -0.45 to -0.12 ; Mann–Whitney: $p < 0.001$; Fig. 4).

Manly’s selection ratios for design III analysis suggested that habitat selection was overall similar among groups: tortoises avoided urbanized areas, cultivated plots and dense

Fig. 3 Turning angles exhibited by radio tracked tortoises during their displacements. The left panel (1) displays the results of the translocated tortoises (spring and autumn released groups pooled) during the dispersal and settlement phases. The right panel shows the results of the resident tortoises. The boxes represent medians, 25 and 75% percentiles. The whiskers extend to the minimal and maximal values

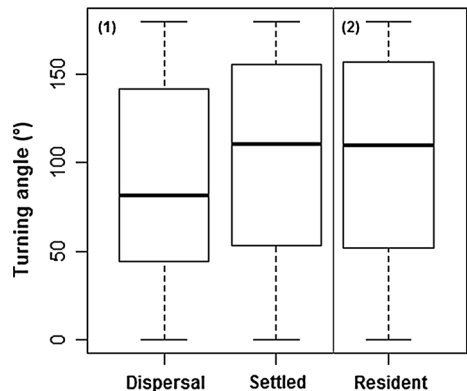


Fig. 4 Mean daily distance moved by (1) spring released tortoises, (2) autumn released tortoises and (3) resident tortoises, considering translocated dispersal (D) and settled phases (S). Error bars indicate 95% CI. Letters indicate significant differences

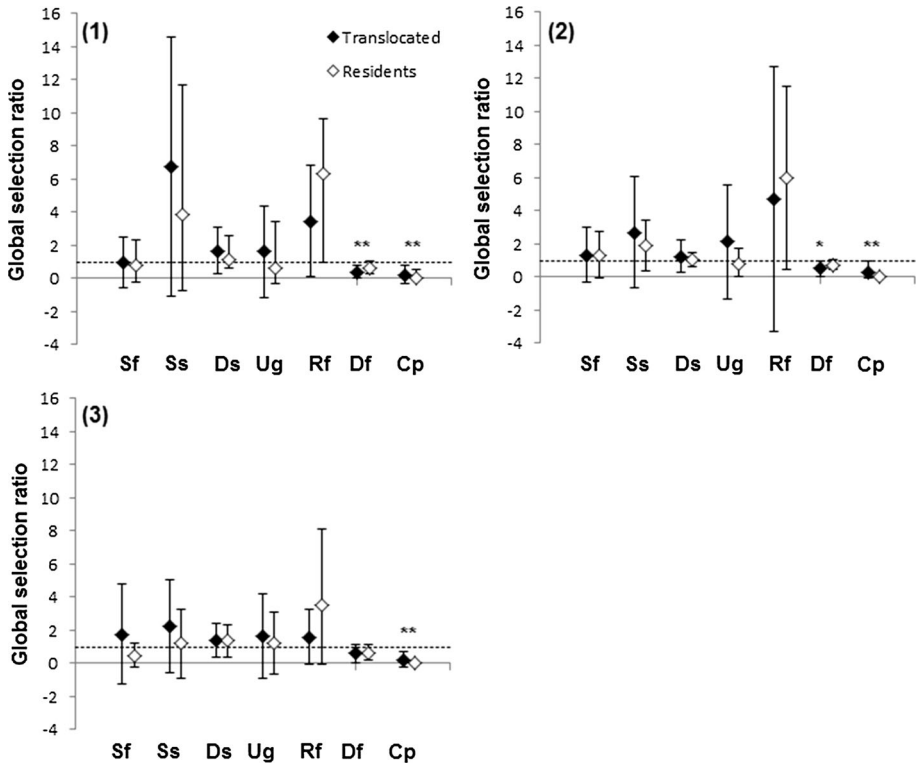
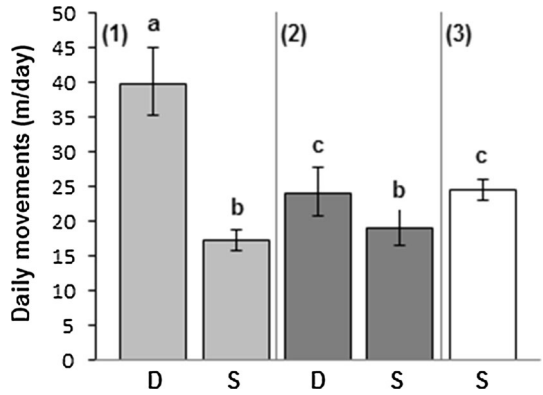


Fig. 5 Global selection ratios and 95% Confidence Intervals calculated for each habitat type and each season in resident and translocated (spring + autumn released) tortoises. Each panel provides the results for a season: (1) spring, (2) summer and (3) autumn. Habitat types were *Sf* sparse forests; *Df* dense forests, *Ss* sparse scrubland, *Ds* dense scrubland, *Ug* uncultivated grasslands, *Rf* riparian forests, *Cp* cultivated plots. Translocated and resident tortoises are respectively indicated with opened and dark symbols. A given habitat type is considered as positively selected when the 95% CI is above one, randomly used if one is included into the 95% CI and avoided when the 95% CI is below one. Significant habitat preference or avoidance are represented with *

forests in spring. However, dense forests were avoided in summer only by translocated individuals (Fig. 5). Several translocated tortoises ventured into cultivated plots. Some habitats were avoided but we did not find evidence for positive habitat selection. During dispersal tortoises crossed various habitats, including presumably unfavorable (e.g. dense close forest in north-facing slopes); but they settled in favorable habitats (e.g. semi open scrubland).

Homing

None of the translocated tortoises returned to the SOPTOM rescue center or to its initial capture site. The two proxies used suggested a lack of homing. Indeed, mean standardized values of directionality were close to 90° and close to 0.25 for the angular dispersions (Fig. 6).

Regarding possible homing toward the SOPTOM rescue center, mean standardized directionalities were 90.67° (95% CI 81.08–102.83) and 83.5° (95% CI 75.83–91.17) respectively for the spring and autumn groups. Considering the initial capture site the values were respectively 79.08° (95% CI 48.73–117.93) and 69.25° (95% CI 40.08–109.01). There were no differences between groups considering the SOPTOM rescue center (Cohen's $d = 0.43$, 95% CI -0.53 to 1.22 ; $t = -1.020$, d.f. = 20.07, $p = 0.320$) or initial capture site (Cohen's $d = 0.16$, 95% CI -0.74 to 1.02 ; $t = -0.553$, d.f. = 21.95, $p = 0.586$).

Mean angular dispersions were 0.26 (95%, CI 0.21–0.30) and 0.23 (95%, CI 0.15–0.31) for spring and autumn groups respectively; without significant difference between them (Cohen's $d = 0.26$, 95% CI -0.57 to 1.56 ; $t = -0.591$, d.f. = 14.65, $p = 0.564$).

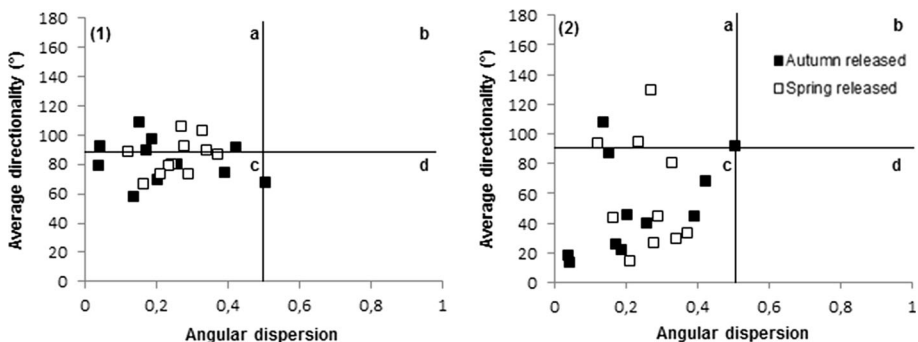


Fig. 6 Average directionality and angular dispersion of translocated tortoises during dispersal phase. Homing is tested for (1) the SOPTOM rescue center and (2) initial capture sites. Quadrants correspond to four kinds of movement patterns; a: moved in wrong or random directions without concentration in movement bearings; b: moved in wrong or random directions with concentration in movement bearings; c: moved with apparent directionality; d: moved with directionality and concentration in movement bearings (i.e. potential homing)

Discussion

The detailed information collected through an intensive and long-term monitoring of different groups of individuals provided practical responses to the three questions posed in the introduction. Moreover, none of these responses could have been derived from a short-term assessment. Indeed, a relatively accurate appraisal of the fate of translocated tortoises became available only at the end of the second year of the field experiment; and one additional year prior translocations was necessary to obtain baseline values. Broadly, the current robust assessment provided encouraging results for the use of translocation in the conservation of threatened Mediterranean tortoises, but it also revealed several complications that should be considered by field managers. Below we briefly discuss the main results.

Survival

Previous studies emphasized that translocated animals may face difficulties that can compromise their survival (Germano et al. 2015). Displaced individuals are relatively naïve, they must rapidly accustom to new habitats that may substantially differ from the conditions where they originated. This behavior involves avoiding unknown predators, finding suitable food items, freshwater, but also places for thermoregulation and appropriate shelters (Lagarde et al. 2012; Moulherat et al. 2014). In addition, the stress caused by handling, translocation, and settling may alter behaviors (Dickens et al. 2010; Teixeira et al. 2007).

Although the effect did not reach statistical significance, the survival rate of the translocated tortoises was lower compared to resident and control individuals: more than one-third of the translocated tortoises eventually died after 3 years. A preliminary short term month assessment did not detect any mortality (Lepeigneul et al. 2014). The close monitoring enabled us to identify the causes and precise timing of mortality. Predation by mammals was the main source of death and 66% of mortality occurred during dispersal (Armstrong et al. 1999; Bradley et al. 2012). Because dispersal and settlement were slow processes, the period during which translocated individuals were particularly at risk was prolonged and important to monitor. Therefore, this delayed mortality should be considered to better evaluate the initial number of individuals to release that are needed to effectively reinforce fragile populations.

Following settlement, annual survival rate remained high and consistent with previous estimates in free ranging populations (Bertolero et al. 2007; Couturier et al. 2011). Some authors recommended to control predators at the release site (Calvete and Estrada 2004), or to not translocate individuals in area frequented by predators (Bertolero et al. 2007). However, in this study natural predators (i.e. stone marten [*Martes foina*], Badger [*Meles meles*] and fox [*Vulpes vulpes*]) were involved (unpublished DNA identification results). Therefore predation might be inevitable and should be considered as a natural element of the environment. Our results suggest that following the critical dispersal phase, survival was established to a normal rate. We acknowledge that predation on nests and juveniles was not examined, but adult survival is the first parameter to consider in long live species (Sæther et al. 1996).

Dispersal versus settlement

Post translocation dispersal is commonly observed in chelonians (Attum and Cutshall 2015; Attum et al. 2011; Nussear et al. 2012). Yet, in terms of management it is more crucial to determine if, when, and where individuals eventually settle. The precise movement patterns we obtained enabled us to precisely distinguish dispersal from settlement. Distances from the release point and analyses of the turning angles provided consistent complementary information. Notably, the distinction was associated with a clear behavioral shift. During dispersal individuals adopted a unidirectional route, thereby consistently moving away from the release point, and sometimes crossing unfavorable habitats. A sudden change with multidirectional movements indicated settlement: individuals patrolled a selected favorable area. Specific movement patterns following reintroduction and behavioral shift between dispersal and settlement have been documented respectively in a lizard and in a bird species (del Mar Delgado et al. 2009; Christie et al. 2011).

Using the 500 m distance threshold from the first capture point (a value provided by the resident and control tortoises) we observed that 25% of the translocated tortoises settled rapidly in the area effectively targeted during the planning of the experiment. However all the others settled further, often 1500 m from the release point, and even further away with a maximal value of 3500 m. This proportion of long distance settlers should be taken into account in the planning of conservation translocations.

Dispersal determinants

It has been suggested that homing explains dispersal in translocated tortoises (Chelazzi and Francisci 1979; Field et al. 2007; Rittenhouse et al. 2007). We found no evidence for homing; therefore this behavior could not explain the post-release dispersal we observed. Our study supports the notion that a release distance greater than 10 km might be sufficient to limit homing (Hinderle et al. 2015).

Likely, most dispersing translocated tortoises attempted to cross unfamiliar environments, favorable or not, using the most efficient strategy: a unidirectional route to rapidly leave the area. For unknown reasons (e.g. weariness, accustoming to novel environment) they eventually settle in favorable habitats as suggested by the fact that the habitats selected by settling translocated tortoises were overall similar to those selected by wild resident individuals and included key features (Rozyłowicz and Popescu 2012; Vilardell-Bartino et al. 2015).

In tortoises, heterogeneous and patchy habitats limit dispersal and individuals tend to settle earlier and thus close to the release site if they encounter habitats that include favorable types of vegetation (Attum and Cutshall 2015; Cook 2004; Nussear et al. 2012; Stamps and Swaisgood 2007). The wide range in the settlement process we observed in the Hermann tortoise revealed complex patterns that likely reflect marked inter-individual differences. Indeed for most translocated individuals being released in favorable habitat was insufficient to trigger rapid settlement. Several individuals underwent long crossing of unfavorable zones before establishment.

Seasonal effect of releases

Translocations performed shortly prior to hibernation (or aestivation in hot countries) limit post-release activity and thus dispersal; this technique was called “forced inactivity soft release” (Attum et al. 2011). Presumably, the period of immobility increases site fidelity through acclimation to novel habitat (Attum and Cutshall 2015; Attum and Rabia 2016; Eastridge and Clark 2001; King et al. 2004). Our results do not support this scenario. The tortoises released in autumn effectively hibernated when ambient temperatures decreased and remained motionless during approximately 5 months; but they did not settle at emergence. Moreover, none of the autumn released tortoises exhibited fidelity to the forced hibernation site; instead they all abandoned the hibernation site and exhibited marked dispersal. The spring release tortoises settled more rapidly. Thus, results obtained in an Egyptian tortoise (*Testudo kleinmanni*) where pre-aestivation releases hastened settlement (Attum et al. 2011; Attum and Rabia 2016) are not necessarily applicable to the hibernation context of another *Testudo* species.

Independent to the season of release, dispersal occurred in spring. We suggest releasing translocated Hermann tortoises at the beginning of the active season when environmental conditions are favorable. These spring conditions favor the expression of exploratory behavior when the environment provides high resources availability (Bright and Morris 1994). Conversely, releasing Hermann tortoises in autumn before inactivity period or before a drought summer period would automatically expose individuals to additional and unnecessary stress and deleterious difficulties (e.g. to finding appropriate thermally buffered refuges).

Inter-individual differences in settlement patterns were marked despite the forced inactivity of autumn released tortoises, and in spite of prolonged captivity periods before translocation. Previous study showed that a prolonged captivity period does not significantly alter anti-predator behaviors (Micheli et al. 2014). It is thus unlikely that soft-release techniques would obliterate behavioral diversity and thus reduce the high post-release dispersal profile of most individuals (Eastridge and Clark 2001; Attum et al. 2011). Soft releases are usually based on the use of enclosures to keep individuals for several weeks or months (Tuberville et al. 2005; Hardman and Moro 2006; de Milliano et al. 2016). This approach is financially and logistically very costly compared to hard releases. Our results militate for the hard release technique in spring (Lepeigneul et al. 2014; this study). The most cost/efficient translocation methods must be retained to optimize conservation actions in the field, to limit handling and associated stress, and to facilitate monitoring.

Resident population

Prior translocations, monitoring of resident and control tortoises (in 2012) along with comparison with the control population during the experiment suggest that translocations did not impact negatively the resident population.

The behavior and body condition of resident tortoises was not affected (this study, unpublished results). Moreover, close monitoring enabled us to observe 43 mating involving pairs of translocated and resident tortoises (66% of translocated tortoises were observed mating); revealing cross-breeding between translocated and resident tortoises (unpublished results). This result suggest that translocated tortoises expressed the potential to effectively reinforce the resident population; however, a longer term survey is required

to ensure that these encouraging results translate into population increase through enhanced recruitment.

Conclusions

Further studies are needed to better understand the underlying causes of the strong inter-individual differences in settlement patterns we observed. Then major technical improvements could be derived and implemented as practical guidelines. Nonetheless, our results provided answers to the three main initial questions.

- Most translocated individuals settled in the resident area or in nearby connected areas, and therefore increase the recovery potential of the resident population(s).
- Most individuals did not settle rapidly; but most of them eventually settled within 2 years after release.
- Translocation success weakly varied with the season of release. Spring release provided the best results.

Overall, although predators impacted translocated tortoises during dispersal most of the released individuals adapted to their novel environment and eventually settled. They notably find shelters, fresh water and food, and mated with the resident tortoises. Translocations is therefore a suitable method to reinforce fragile populations of Hermann tortoises, and likely of other *Testudo* species with similar ecology. Large pools of Hermann tortoises are held in captivity or must be rescued during urbanization works. This study provides a strong argument in favor of releasing them into wild populations, or in appropriate areas that have been totally depopulated, rather than keeping them into captivity for years (as currently recommended) and without conservation value. Yet translocation cannot compensate for habitat lost. Thus, it should be combined with other crucial conservation actions to promote partly open mosaic scrubland areas, to set-up water ponds, and to increase the availability of diverse shelters required for females to lay their eggs and for juveniles (Ballouard et al. 2013, 2016; Celse et al. 2014).

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