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ORIGINAL PAPER

Immediate response to translocation without acclimation from captivity to the wild in Hermann's tortoise

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Abstract Survival, reproductive and recruitment rates, along with health status, of translocated and resident individuals should be evaluated. However, gathering this information poses logistical constraints and requires long-term studies. Considering the urgent nature of many species' situations where translocation would be appropriate, fast-assessment techniques should be tested. We assessed the immediate response to translocation of Hermann's tortoises (*Testudo hermanni hermanni*) directly from captivity to the wild. Individuals were maintained in captivity 2 to 8 years before being released in spring 2013 into a natural population impacted by fire. During the critical 3 months post-release period, we radio-tracked translocated individuals (N=12) and resident tortoises in spring 2013 (N=14), plus another batch of resident tortoises in spring 2012 (N=9). Movements, behaviours, body condition and body temperature were regularly recorded. All translocated tortoises acclimated well to their novel environment. We found no differences in movement, thermoregulation and body condition between translocated and resident tortoises. Body condition of all tortoises increased rapidly in spring. We found no sign of perturbation in resident tortoises. Contrarily, resident males mated with translocated females. Translocations should be further tested on larger spatial and time scales to improve population restoration programmes, especially in threatened species with limited dispersal ability.

Keywords Body condition · Translocation · Immediate response · Movements · *Testudo hermanni* · Thermoregulation

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Introduction

Conservation translocation is a fast technique to rescue threatened individuals and/or to restore populations (review in Griffith et al. 1989). Reinforcement is the intentional release of an organism into an existing population of conspecifics (IUCN/SSC 2013). Considering current rates of habitat loss and fragmentation, displacing organisms to favourable areas is often the last option to minimise population collapses. Therefore, translocation is a widely used tool for conservation (Seigel and Dodd 2002; Germano and Bishop 2009; Seddon et al. 2012). However, acclimation to novel environments can be challenging for displaced animals, and local populations and host ecosystems can be perturbed by the introduction of individuals, diseases, genes, etc. (Griffith et al. 1989). Consequently, translocations should be assessed through careful monitoring of released individuals and host populations.

Ideally, long-term monitoring of survival and reproductive rates of translocated animals coupled with health monitoring should be performed (Jacobson 1993; Jacobson et al. 1999; Fischer and Lindenmayer 2000; Sheean et al. 2012), notably, to identify relevant factors (e.g. age, number of individuals released, seasons, group composition, hard- versus soft-release) for translocation success (Bright and Morris 1994; Clarke et al. 2002; Field et al. 2007; Griffiths et al. 2012; Nichols et al. 2012; Sheean et al. 2012). Unfortunately, comprehensive long-term studies are often unrealistic due to logistical, financial and time constraints. Thus, a large proportion of conservation translocations remain inadequately monitored (Griffith et al. 1989; Seigel and Dodd 2002; Sheean et al. 2012). Further, translocation success has been insufficiently assessed in many taxa (Fischer and Lindenmayer 2000; Seddon et al. 2005), notably in reptiles (Dodd and Seigel 1991; Germano and Bishop 2009).

More importantly, the urgency of many situations means that we cannot wait to obtain the desired information to make decisions. On the other hand, launching release programmes in the absence of careful field monitoring is unacceptable scientifically, is potentially deleterious for both released individuals and resident host populations, and it entails risks in terms of public acceptance. Thus, using alternative fast procedures to assess the fate of released animals and host populations is essential (Griffiths et al. 2012).

Candidates for translocation can stem from various sources (e.g. natural populations, captivity and illegal trade). Suitable host areas can be natural, managed, degraded, and they may or may not be included in the species distribution range. This diversity of situations is associated with different definitions regarding translocation (e.g. relocation, repatriation, reintroduction; review in Dodd and Seigel 1991 or see Griffith et al. 1989; Seddon 2010). Whatever the case, assessing the compatibility between host area and translocated individuals is essential. Compatibility should increase if released individuals have experienced conditions similar to those found in the host area, a situation expected for relocation of free-ranging individuals displaced within the natural geographic area of the species (Dodd and Seigel 1991). Conversely, individuals from captive breeding programmes may face greater difficulties to acclimate to novel environments. Similarly, confiscated animals (e.g. illegal pets), injured, ill and orphaned individuals that are regularly maintained in captivity over long periods before release (Wimberger et al. 2009), as well as individuals withdrawn from areas undergoing urban development (Field et al. 2007), may face a greater acclimation challenge. In order to compensate for the lack of experience, individuals are kept in outdoor enclosures in the host area before release (Pedrono and Sarovy 2000; Tuberville et al. 2005). However, enclosure building and maintenance entail substantial logistical costs, whereas hard-release (i.e. translocation without acclimation) is simpler, faster and thus offers major advantages. Comparing the respective costs versus advantages of each approach, encompassing hard- and soft-release, relocation and reintroduction, and for each targeted species/population, is unfeasible. In practice, the most challenging situation should be tested first: if successful, the need to test the other options is greatly relaxed. Intuitively, hard-release of wild individuals kept in captivity for prolonged periods represents such a challenging situation.

In this study, we monitored captive tortoises (*Testudo hermanni hermanni*) released into natural habitat without acclimation, and resident individuals of the host population, using a fast approach to assess translocation success during the critical post-release (i.e. establishment) phase. Immediately after translocation, tortoises are disorientated. Possibly perturbed by novel conditions, they may exhibit warning signs such as inappropriate and potentially haphazard behaviours and/or a decrease in body condition (Rich and Romero 2005). Indeed, finding appropriate shelters or feeding resources and conflicts with rivals generate chronic stress, perturb thermoregulation, entail excessive energy expenditure and may jeopardise survival (Bulova 2002; Lagarde et al. 2012; Attum et al. 2013; Bonnet et al. 2013). Resident tortoises may well be perturbed by the introduction of unknown individuals, diseases, and by a sudden modification of population density. Consequently, on a regular basis, we monitored daily displacements, behaviour, thermal profiles and body condition of tortoises during the 3 months following translocation in order to detect possible warning signs.

This study, framed into a conservation Life + program, aimed to test practical actions designed to promote the persistence of the endangered Hermann's tortoise (UICN France et al. 2009). In Mediterranean regions, frequent fires represent a major threat (Hailey 2000a; Popgeorgiev 2008; Couturier et al. 2011; Sanz-Aguilar et al. 2011; Santos and Cheylan 2013). Each year, several tens of tortoises accidentally injured by fires, dogs, vehicles or machines or illegally collected are brought to rescue centres where they are generally kept for prolonged periods, often years (Gagno et al. 2013). These tortoises represent potential candidates to supplement populations devastated by fires (Lecq et al. in press). In addition, releasing these tortoises in natural habitats would alleviate logistical costs associated with captivity (IUCN 2000). This study provides a rapid, rigorous assessment of acclimation by combining key ecophysiological traits.

Methods

Study species

Previously abundant in France, the Hermann's tortoise (*Testudo hermanni hermanni*) persists in Corsica and on the continent in restricted areas of the Massif des Maures and adjacent plains of southeastern France (Livoreil 2009; Bertolero et al. 2011). The mean body size of adults is 15–18 cm (straight carapace length, SCL) in females and 14–15 cm in males. This species exhibits a generalist diet (herbivorous to omnivorous) and marked philopatry (Calzolai and Chelazzi 1991).

Study site

The host site, situated in a National Nature Reserve (Plaine des Maures), covers 165 ha and belongs to the Conservatoire d'Espaces Naturels (Fig. 1). The area consists of small plains interspersed with small mountains (elevation ranges between 127 and 490 m). The site was severely burned in 1978, many tortoises were killed and the population never completely recovered (Livoreil 2009). Currently, 0.8 individuals can be observed per hour during standard surveys, whereas a score of two individuals per hour is considered typical of healthy populations (Livoreil 2009). However, the vegetation has regenerated and is now mainly composed of forests (40 %), maquis-shrubland (40 %), and grassy meadow (20 %). The study site offers a wide diversity of microhabitats, including open herbaceous areas alternating with shrubby and closed forest areas that provide important various refuges (litter, logs, large rocks). Plant species eaten by the tortoises, such as *Trifolium angustifolium*, *Taraxacum* sp., *Asparagus* sp. and *Rubus rubus*, are abundant in the area (in spring notably). A small river crosses the site, providing access to water year round (puddles in summer). The study site contains a mosaic of favourable habitats (Meek and Jayes 1982; Calzolai and Chelazzi 1991; Filippi et al. 2010).

Experimental groups: translocated and resident tortoises

Candidates for translocations stem from a pool of tortoises maintained in captivity in a rescue centre devoted to the conservation of Hermann tortoises (SOPTOM) and located 8 km from the study site. Selected individuals were those that had recovered from accidental injuries or that were rescued from natural habitats destroyed due to urban development. Individuals were also selected according to genetic- (all originated from French continental populations; Perez et al. 2013) and health-related criteria (blood screening, lack of faecal and blood parasites, mycoplasma and herpes virus test; Alberts et al. 1998; Woodford 2000; Mathes et al. 2001;

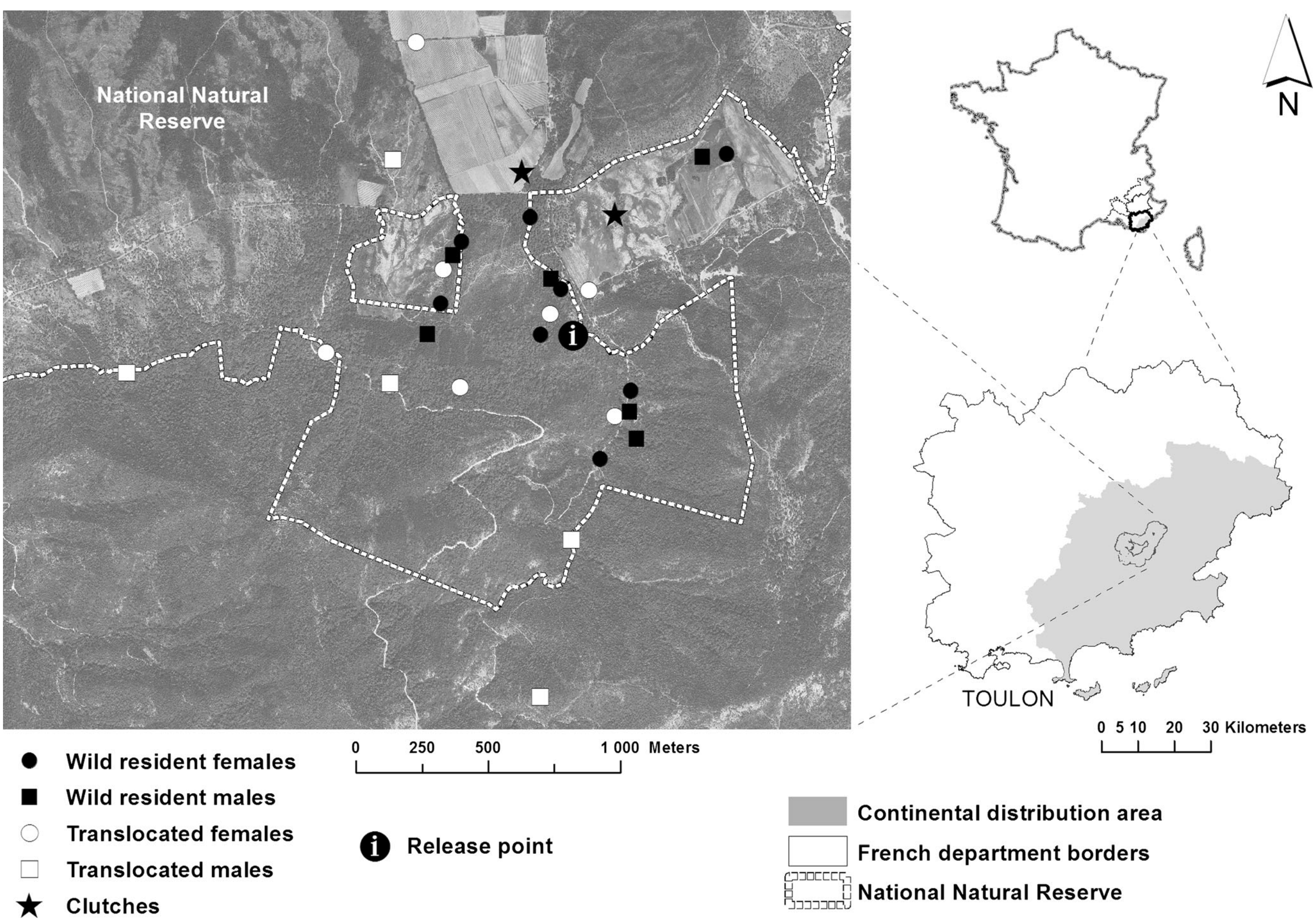

Fig. 1 The study site of the experimental translocation site (*left panel*) is in the National Natural Reserve des Maures. The large *black circle* (*i*) represents the release point. Each symbol represents the latest fix (19 July 2013) of each radio-tracked tortoises in spring 2013. Translocated tortoises are indicated with *open symbols*, resident individuals with *black symbols*. Females are indicated with *circles* and males with *squares*. The locations of two clutches laid by two translocated females are also provided (*stars*). The *right panel* indicates the situation of the study zone in France (*top graph*) and more precisely in the Var district (83, *down graph*)

Soares et al. 2004; Salinas et al. 2011). Tortoises were kept in outdoor enclosures (7 m×7 m, two to six individuals per enclosure) for 2 to 8 years. The outdoor enclosures contained natural elements, notably local vegetation (few very small shrubs), refuges and were subject to similar climatic conditions to the release site. However, fresh water and various fresh foods were provided daily and home range was severely restricted. Although the exact capture location was not available for all tortoises, broad geographic information provided by collectors ensured that at least 10 km separated capture and release points. We assumed that this distance would limit homing (Germano and Nieuwolt-Dacanay 1999), a major source of failure in chelonian translocation (Germano and Bishop 2009). Overall, tortoises experienced two translocations: from various field sites to captivity in the rescue centre and then from captivity to the experimental field site.

To assess acclimation (i.e. establishment) success (i.e. very short-term or immediate response to translocation), we monitored three groups of tortoises: two groups of resident tortoises in the springs of 2012 and 2013 and one group of translocated individuals in spring 2013. In this study, because we focused on the establishment period, analyses were restricted to 3 months in spring (from 24 April to 19 July in both years).

1) A group of nine resident individuals (4 M, 5 F) was monitored in 2012, 1 year prior the experiment (R-2012). They were captured in the vicinity of the release point (within a 0.8-km radius), immediately processed in the field and released. This group was used to assess possible interannual variability (R-2012 vs R-2013) and possible negative effect of translocation on the host population (Berry 1986; Champagnon et al. 2012).
2) The translocated group (T-2013) consisted of 12 individuals (5 M, 7 F). They were simultaneously hard-released (i.e. without acclimation, Kleiman 1989) without any food or water supply, on 23 April 2013 (Fig. 1).
3) A group of 14 resident individuals (6 M, 8 F from the host population) was monitored (R-2013) in parallel to the translocated tortoises (T-2013). They were captured in the vicinity of the release point (within a 0.8-km radius), immediately processed in the field and released.

In the three groups of tortoises, we selected adults (SCL> 15 cm) with a body mass greater than 400 g to permit the fitting of electronic equipment. Each individual was sexed, weighed, measured (SCL) and marked with a notch code on the carapace. The three groups were not different in terms of mean body size (females, Kruskal-Wallis χ^2=1.29, df=2, p= 0.50; males, χ^2=1.96, df=2, p=0.37) or mean body mass (females, χ^2=0.44, df=2, p=0.80; males, χ^2=1.27, df=2, p=0.53).

Tortoise monitoring

Each tortoise was fitted with a radio transmitter (AVM, Colfax, CA, USA) and a temperature data logger (Thermochron iButtons, Dallas Semiconductor) glued to the carapace with resin. The overall mass of the equipment did not exceed 10 % of the tortoise's body mass and thus was unlikely to perturb daily activity (see Lagarde et al. 2008). Data loggers recorded shell temperature every 30 min. Carapace temperature provides a reliable estimate of body temperature (Lagarde et al. 2012). The tortoises were located on a daily basis (except during cold and rainy days, tortoises remain sheltered), twice a day when possible, with a three-element Yagi antenna connected to a R410 ATS receiver (Advanced Telemetry Systems, Isanti, MN, USA). The coordinates of each location were obtained using a hand-held GPS (N=2,746). Main behaviours (feeding, walking, basking, mating and fighting) were recorded when the animals were observed from a distance, hence, without disrupting normal behaviours. Tortoises observed sheltered were considered as inactive. Body mass was measured every 2 weeks for all tortoises.

To assess options available for body temperature control, we used 55 physical models (Lagarde et al. 2012; Moulherat et al. 2014). These consisted of empty carapaces (similar SCL range to the monitored tortoises) filled with hydrogel and prepared following the methodology of Lagarde et al. (2012). We placed them in various microhabitats representative of those used by tortoises: in the open, under the shade of trees, under small bushes, under large bushes and in litter. We recorded temperature every 30 min using a data logger glued on the shell of the models.

Statistical analyses

Straight line distance (an index of displacement) between consecutive locations was measured daily for each individual and averaged per week (N=12 weeks). The total distance travelled from the release point (a crude exploration index) was calculated as the cumulative distance between successive daily locations from the first position and was averaged per week. Data were log-transformed to meet distribution normality. We fitted a linear mixed model (lme4 package) to test the influence of sex (male, female), group (T-2013, R-2012 and R-2013) and time (weeks) on the mean daily distance travelled and the mean distance from the release point. Time was implemented as a continuous variable: 12 weeks from 24 April 2012/2013 to 19 July 2012/2013. We set individuals as a random variable to account for lack of independence among repeated measures.

To infer body temperature from shell temperature, we used a simple mathematical model validated in a related species with similar body size, *Testudo graeca* (Moulherat et al. 2014). Thermal profiles, both in models and free-ranging individuals, showed nychthemeral and seasonal patterns (mean temperature increased with time from April to July). Hence, we first eliminated autocorrelations by filtering the daily component from the shell and environmental temperature series. We used a Morlet wavelet analysis (Cazelles et al. 2008), allowing the detection of a cyclical structure in the signal across a temporal scale. It was then possible to determine the origin and periodicity of the cyclical structure by performing a multi-resolution analysis (Box and Jenkins 1976). This analysis assumes that the global signal consists of the addition of several signals at different temporal scales (Jenkins and Watts 1968). Thus, the separation of the signal into its different components allowed us to eliminate the daily cyclical variation due to environmental conditions.

Prior to analysis, Q-Q plots of the data were visually inspected to check the assumption of normality. We fitted a linear mixed model (log-likelihood maximisation) to test the effect of the following covariates: environmental temperature, group (T-2013, R-2012, R-2013), sex and interactions with body temperature, with individuals as the random variable to account for pseudo-replication.

Body condition

Body condition reflects the trophic (body reserves + developed follicles + gut content) and hydration status of individuals (Lagarde et al. 2002; Willemsen and Hailey 2002). Body condition was estimated using the standardised residuals of linear regression between log (body mass) against log (carapace length) (Bonnet et al. 2001a). The mean slope was 2.88±0.05 (R^2=0.93), and residuals were normally distributed. Body condition was calculated every 2 weeks. We used a linear mixed model to test the effect of group, sex and time on changes in body condition.

Model selection

We used a stepwise forward model selection using Akaike information criterion (AICc) to select the most parsimonious model (Burnham and Anderson 2002). We considered two models as significantly different when ΔAICc>2. All statistical analyses were performed on R (R-Development Core Team 2012) or MATLAB (MATLAB 2009), the wavelab toolbox was used for time series analyses (Donoho et al. 1999).

Results

Displacements

In 2013, 3 months after the onset of the field monitoring, all the 26 tortoises (12 T-2013+14 R-2013) were relatively close to the release point, i.e. within less than a 2-km radius and nine remained within a 0.8-km radius (Fig. 1). Pooling 2012 and 2013 observations, the most parsimonious model for the mean daily straight line distance travelled conserved all explanatory variables (group, sex, time) (Table 1 in the online supplementary files). However, model-based predictions indicated that 2013 resident (estimates of covariance β=−0.44±0.13) and translocated tortoises (β=0.57±0.14) displayed lower movement rates compared to 2012 resident tortoises, suggesting an interannual effect (Fig. 2). Mean distance travelled daily between consecutive locations tended to be greater in males compared to females (β=−0.19±0.11; Fig. 2), and movement rate for all tortoises increased over time (β=−0.09±0.01).

The same design linear mixed model applied to the mean distances from the release point confirmed the effect of time (β=−0.11±0.01), with tortoises moving further as the season progressed (Table 2 in the online supplementary files). Females remained closer to the release point than males (β=−0.32±0.26). A graphical inspection of the mean distance travelled suggested that translocated males tended to move further away from the release point (Fig. 1 and Fig. 4 in the online supplementary files).

Behaviours

In 2013, resident and translocated tortoises were monitored simultaneously, facilitating comparison. The translocated tortoises were observed active more often (i.e. moving, walking, mating, feeding or basking) than the resident tortoises (37 % in T-2013 vs 32 % in R-2013; χ^2=5.18, *df*=1, *p*=0.02). The most common observed activity was basking (21 % in R-2013 vs 26.9 % in T-2013; χ^2=7.91, *df*=1, *p*=0.005) whereas displacements (4.2 % in R-2013 vs 3.1 % in T-2013; χ^2=1.89, *df*=1, *p*=0.16) and feeding were more seldom recorded (1.3 % in R-2013 vs 2.7 % in T-2013; χ^2=5.34, *df*=1, *p*=0.03). Overall, although several differences between translocated and resident tortoises were significant, they remained modest. On few occasions, tortoises were observed mating (*N*=4, resident males mounting translocated females); no combat was observed.

Thermoregulation

The mean body temperature of free-ranging tortoises was 23.0±0.1 °C (range 6.9–35.2 °C) in the R-2012 group, 20.6±0.1 °C (range 6.5–34.5 °C) in the R-2013 group and 21.5±0.1 °C (range 7.8–35.4 °C) in the T-2013 group. Mean environmental temperature of the operative models was 21.9±0.03 °C (range 2.9–60.2 °C) in 2012 and 19.7±0.03 °C (range 5.9–51.4 °C) in 2013. The model selection suggested that environmental temperature, sex, and their interaction were the best explanatory variables of the body temperature of free-ranging tortoises (Table 3 in the online supplementary files). Body temperature was positively correlated with

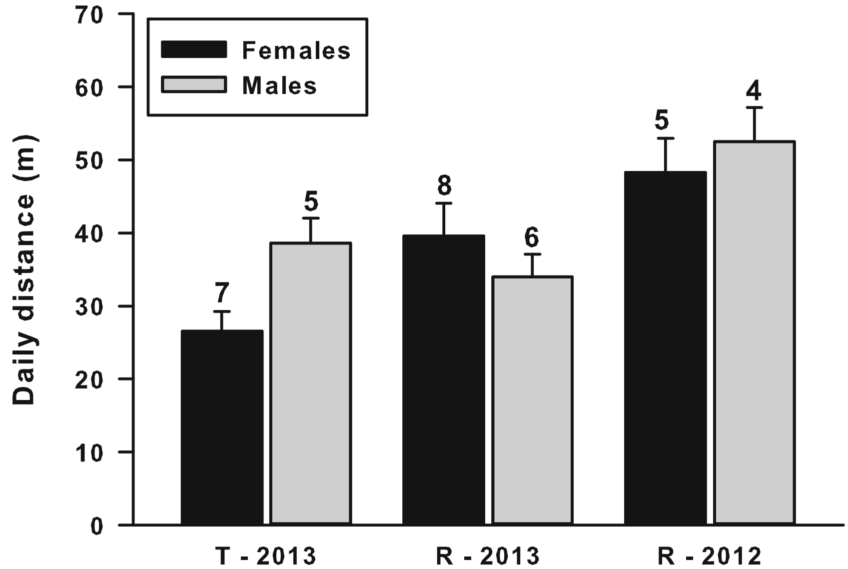

Fig. 2 Mean daily distances (averaged per week, N=12 weeks) travelled by translocated (*T-2013*), resident (*R-2013* and *R-2012*) tortoises radio-tracked during 3 months. Means are presented with SE and sample size. In 2012, tortoises travelled over longer distances on average; translocation status or sex effects were not significant. See text for statistical details

environmental temperature (β=0.1±0.001). A significant interaction term (Table 3 in the online supplementary files) suggested higher temperatures in males compared to females (Fig. 5 in the online supplementary files).

Body condition

During the study period, body mass was successively measured seven to eight times for each individual. In all groups and in both sexes, body condition increased significantly over time (Fig. 3). Time was the most important factor influencing body condition, whereas group and sex were not retained in the model selection (Table 4).

Discussion

Results of the current experiment clearly show that Hermann's tortoises translocated from captivity to the wild without acclimation adapted well and rapidly to their novel environment. Indeed, (1) we observed no sign of physiological or behavioural disorder in the translocated tortoises, (2) we found no major difference between the group of translocated and resident tortoises monitored simultaneously in 2013, and (3) we observed greater interannual differences between the two groups of resident tortoises monitored in 2012 and 2013. This latter result suggests that natural environmental variations played a greater role in fluctuations in key life history

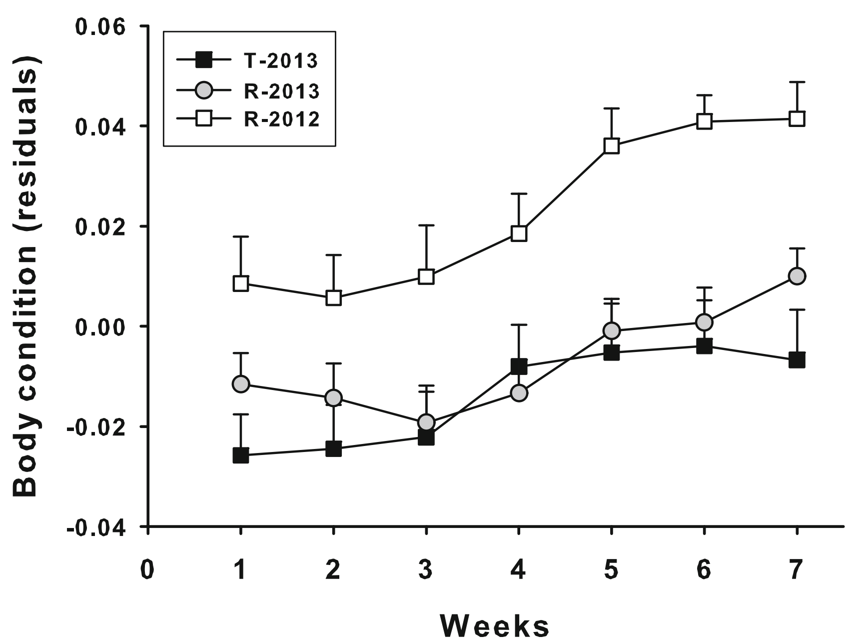

Fig. 3 Changes in mean body condition calculated weekly in translocated (*T-2013*), resident (*R-2013* and *R-2012*) tortoises radio-tracked during 3 months. Body condition increased significantly over time without a significant effect of group or sex

traits compared to the translocated status per se, a result in agreement with other chelonian studies (Field et al. 2007; Rittenhouse et al. 2007).

We acknowledge that the relatively short time period of the current study imposes limitations; however, we also emphasise that the use of the ecophysiological approach offers advantages considering the trade-off between the necessities to perform rapid assessments versus the need to base translocations on comprehensive information. Below, we discuss these issues.

Usefulness of ecophysiology to rapidly assess acclimation

Integrating physiological mechanisms is becoming increasingly useful in conservation biology (Wikelski and Cooke 2006; Cooke and O'Connor 2010; Cooke et al. 2012, 2013). Considering conservation translocations more specifically, different authors recommended combining physiology and behaviour for rapid assessment of acclimation success (Kahn 2006; Pinter-Wollman et al. 2009; Besson and Cree 2011; DeGregorio et al. 2012). This is especially important when making quick decisions and to accurately identify mechanisms underpinning demographic changes (Wingfield et al. 1997). For instance, rapid decrease in body condition, an integrative index of health status and energy budget that correlates with reproductive success and survival, is one of the warning signs that must be monitored (Bonnet et al. 2001b; Lagarde et al. 2008; Besson and Cree 2011). Similarly, individuals failing to acclimate to novel habitats may face difficulties in finding appropriate shelters, displaying chronic stress, perturbed thermoregulation and behavioural and possible haphazard displacements (Bulova 2002; Lagarde et al. 2012; Attum et al. 2013; Bonnet et al. 2013; Golubović et al. 2013).

Ecophysiological traits in translocated and resident Hermann's tortoises

Body condition increased significantly in spring and at the same rate in both resident and translocated tortoises. This lack of difference between resident and translocated experimental groups was an important result because body condition should increase following hibernation emergence (Jackson 1980; Hailey 2000b; Willemsen and Hailey 2002; Lagarde et al. 2002, 2008). Conversely, difficulties in locating feeding and thermal resources and in maintaining the hydro-mineral balance or possible sickness would have entailed a rapid decrease in body condition. Thus, our results suggest that translocated tortoises displayed adequate foraging and thermoregulatory behaviours, and they adapted well to their novel (natural) diet.

Body temperature was positively influenced by ambient temperatures (as expected). The total hours of sun were five times greater in spring 2012 compared to 2013, possibly explaining the higher body temperature and greater displacement activity of the tortoises in 2012. In 2013, translocated and resident tortoises displayed similar thermoregulation patterns. Translocated individuals seemed to counterbalance their unfamiliarity with their environment by a slight increase in their activity budget, notably in basking, but without interference with other activities (e.g. feeding). Likely, the wide range of microhabitats enabled all tortoises to select preferred body temperatures. These results differ from another experiment, performed in a different habitat however (Chelazzi and Calzolai 1986). Further investigations regarding habitat quality are thus required.

Several translocated males moved away from the release point (Fig. 1) but the lack of significant difference between groups suggests that these tortoises did not exhibit exaggerated exploratory behaviours, at least during the establishment phase. Males tended to be more active and maintained a higher mean body temperature compared to females, in accordance with other studies (Chelazzi and Francisci 1979; Calzolai and Chelazzi 1991; Mazzotti et al. 2002; Rozylowicz and Popescu 2012). No male-to-male combat was observed, perhaps due to the low population density, limiting encounter rate between rivals. Interestingly, during the study, we observed four resident males mating with translocated females, two of which were observed laying their eggs. Thus, although translocation suddenly increased local density, this did not markedly (if at all) perturb the main behaviours of the resident tortoises and translocated individuals behaved normally.

Limitations of this study

The time span of this study does not permit the estimation of key parameters such as annual survival or longer term dispersal/exploratory behaviours of translocated individuals. Thus, we do not know if the immediate acclimation success recorded during the first critical post-release period will translate into short- (2 to 3 years) or medium- (>3 years) term acclimation success. However, this assessment represents the first step. The establishment phase is critical because animals are exposed to unfamiliar conditions and to various costs such as predation (Armstrong et al. 1999; Bertolero et al. 2007; Bradley et al. 2012). Moreover, intensive monitoring provided a means to assess important elements of the annual activity of the tortoises. Monitoring encompassed half of the annual activity season, including vitellogenesis, egg laying, most of the foraging period and roughly half of the mating period (Lagarde et al. 2003; Sereau et al. 2010; Bertolero et al. 2011). Long-term population surveys (e.g. Bertolero et al. 2007) have an irreplaceable value in the appraisal of (re-) introduction programmes. However, to make rapid decisions, rapid assessments are also invaluable. The major interest of our study was the rapidity and accuracy of the evaluation.

The relatively small number of animals released in this study ($N=12$) represents another limit. However, intensive individual monitoring is incompatible with large numbers. More importantly, it is not always necessary to release or displace large numbers of animals.

Comparison with other studies

Most post-release monitoring studies focused on survival and movement (Tuberville et al. 2005; Attum et al. 2007, 2011; Hester et al. 2008; Nussear et al. 2012); few investigated physiological parameters (Kahn 2006; Field et al. 2007; Besson and Cree 2011; Drake et al. 2012; Hinderle 2012). Previous translocations yielded mixed results in chelonians (Hambler 1994; Attum et al. 2007, 2011; Riedl et al. 2008; Tuberville et al. 2008; Bertolero and Oro 2009; Drake et al. 2012; Nussear et al. 2012). Ranging from unsuccessful (Wimberger et al. 2009) to successful studies (Field et al. 2007; Griffiths et al. 2012). Most failures were apparently due to the unsuitability of novel habitats (Hambler 1994; Bertolero and Oro 2009; Germano and Bishop 2009), and high mortality in released cohorts was associated with excessive stress caused by captivity, capture, handling, transport and release per se (Teixeira et al. 2007; Dickens et al. 2010). These results suggest that immediate acclimation to novel habitats during the establishment phase is essential.

Conclusion

The practical outcomes of the current study have important implications for conservation management, especially regarding population restocking. The release of tortoises within a population depopulated by fire did not entail immediate negative consequences for resident individuals and translocated tortoises exhibited normal behaviours, movement and thermoregulation patterns. This study involved individuals kept for a number of years in captivity, in high density, artificially fed and unfamiliar with the host site though the fact that these animals were kept in outdoor enclosures with slightly similar vegetation and similar climate provided at least a small amount of acclimation. The very short-term success of the translocation without acclimation on the field before release was possibly due to the high quality of the host habitat. Other studies in tortoises rather recommended soft-release procedure (i.e. in situ enclosure acclimation before release or before aestivation release) to limit dispersal risk (Tuberville et al. 2005; Attum et al. 2011) or to not use areas with predators or with already established populations (Bertolero et al. 2007).

Although further investigations are clearly needed, we advocate considering a more flexible, pragmatic and proactive approach, depending upon each situation (e.g. urgency, logistical constraints). Extremely dense populations of different *Testudo* species (up to >80 individuals/ha; Djordjević et al. 2013) suggest that exceeding habitat-carrying capacity is unlikely in these low-energy specialists. Thus, the risk of causing resource depletion through translocations is likely minimal, especially as most tortoise population density has been severely reduced by anthropogenic activities, fire or illegal trade (Livoreil 2009; Popgeorgiev and Kornilev 2009; Rozylowicz and Dobre 2010; Ljubisavljević et al. 2011). The presence of natural predators should be considered as a natural element, not as an unsurmountable barrier. Overall, instead of focusing on potential hindrances automatically linked to translocation (success is never guaranteed), we suggest promoting practical actions to increase habitat quality, increasing shelter availability for juveniles, for example (Ballouard et al. 2013). Finally, implementing ecophysiological variables into demographic studies would provide robust means to identify underlying causes of translocation successes versus failures.

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