How far can a tortoise walk in open habitat before overheating? Implications for conservation

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ABSTRACT

Terrestrial chelonians are threatened worldwide by habitat destruction and illegal harvesting. Tortoises are slow moving animals susceptible to dehydration and overheating during movements in open habitats. Many species inhabit arid steppes where the availability of thermally buffered refuges (e.g. burrows) is a limiting factor. Determining the maximal distance between refuges that individuals can safely traverse during the active season is thus essential. We examined the relationship between body temperature variations and movement patterns in adult *Testudo graeca* in the arid steppes of Morocco. Using physical and mathematical models, our results suggest that during the active season adults cannot travel more than 1 km without serious risk of overheating. However, radio-tracking suggests that free-ranging individuals are behaviourally limited to 0.5 km trips between refuges. Overall, maintaining a distance less than 0.5 km between refuges (e.g. through bush planting) is essential to limit fragmentation and to retain healthy populations. This restoration would also benefit to many other species that depend on bush-refuges.

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Introduction

Habitat loss and fragmentation caused by global changes are major threats to animal populations. Monitoring the impact of habitat destruction and fragmentation on animal populations is thus important (Workman & Bos 2007). However, accurately assessing the population consequences of habitat changes can be an arduous task in the field. For instance, the impact of fragmentation on populations depends on the biological traits of the species (e.g. reproductive mode), population dynamics (e.g. number of individuals, age structure) and on various environmental factors (Caswell 2001; Legendre et al. 2008; Stevens et al. 2004). Moreover, the effects of fragmentation per se are often associated with other threats (e.g. resource depletion, invasive species) complicating analysis. In practice, fragmentation is often described in terms of connectivity between patches whereas habitat loss is characterised through the reduction of resources (e.g. food, shelter). For example the rapid extension of road networks and urbanised areas splits habitats and populations into more or less interconnected discrete functioning patches; but within patches, high quality habitats can be nonetheless retained (Votsi et al. 2012).

The degradation of habitat can provoke strong fragmentation of populations even when the landscape is not intersected by a network of barriers (e.g. roads, dams) (Pe'er et al. 2005). For example, many animal species depend on refuges to escape biotic (e.g. predation) and abiotic (e.g. dehydration) threats (Berryman & Hawkins 2006; Bonnet et al. 2013; Bulova 2002; Roper et al. 2001; Schwarzkopf & Alford 1996; Ultsch & Anderson 1986). Consequently, even in an apparently homogenous landscape, a rarefaction of appropriate refuges (e.g. bushes, logs, rocks) can generate inconspicuous barriers that isolate individuals or sub-populations (Pe'er et al. 2005). Decreasing refuge density can be detrimental as the distance between refuges would be expected to increase, leading to isolation of refuges. Especially in organisms with limited dispersal abilities that are dependent on the quality and density of appropriate refuges (Bonnet & Brischoux 2008; Grillet et al. 2010; Lagarde et al. 2012).

Terrestrial chelonians provide typical examples of poorly mobile species that depend heavily on the availability of suitable refuges (Bulova 2002; Lagarde et al. 2012; Pike & Mitchell 2013). Tortoises are declining worldwide, and many species live in arid steppes where the landscape is superficially homogenous (Buhlmann et al. 2009). During the active season individuals navigate between thermally buffered refuges to escape overheating and the density of these refuges is a major determinant for the presence of the tortoises (Lagarde et al. 2012). Assessing the degree of connectivity

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between refuges can require considerable field research (e.g. mark-release-recapture studies, long term radio-tracking) (Hailey & Coulson 1996a; Hailey 1989). Measuring the distance that individuals can safely traverse between refuges provides a direct means to address the importance of connectivity between refuges, and to propose potential conservation measures to improve habitat quality.

We investigated these issues in the Moorish tortoise (*Testudo graeca soussensis*) in the arid steppes of central Morocco, where tortoise population viability is highly linked to shrub density (Lagarde et al. 2012), threatened by illegal trade (Dodd & Franz 1993; Znari et al. 2005) and where thermal refuges are destroyed by farmers through land use practices (Ben Kaddour 2005), overgrazing (El Mouden et al. 2006) and firewood production (Ben Kaddour 2005; El Mouden et al. 2006). Overheating represents the main threat for individuals during movements due to the open nature of the steppe habitat; the tortoises are directly exposed to solar radiation and they rapidly accumulate heat (Bailey & Highfield 1996; Lagarde et al. 2012; Spotila et al. 1973). Lethal overheating can theoretically occur within a few hours if the tortoise cannot reach a thermally buffered refuge (Gans & Dawson 1976). We estimated the maximum distance that a tortoise can move at different periods of the day using physical models (Lelievre et al. 2011; O'Connor et al. 2000; Shine & Kearney 2001; Vitt & Sartorius 1999) to estimate how long tortoises could be exposed to solar radiation, and coupled these results to tortoise locomotor performances as a function of their internal temperature. We then compared theoretical distance with distances moved by free ranging animals for which we estimated internal body temperature using a simple mathematical model we developed.

Methods

Study site

Fieldwork was conducted in April 2008 in the central Jbilet Mountains, 25 km north of Marrakech in Morocco (31°37′ N, 8°02′ W, 580 m a.s.l.). The region is arid (mean rainfall 240 mm) with precipitation falling essentially between September and February (Ben Kaddour 2005; Le Houérou 2001; Znari et al. 2005). In our study area, high (summer) and low (winter) ambient temperatures reduce tortoise activity (Legendre et al. 2008). In spring, the main active season, air temperatures are often >35 °C and the ground surface can reach much higher (>60° C). The evergreen vegetation where the tortoises can shelter is mainly composed of jujube shrubs (*Ziziphus lotus*), retams (*Retama monosperma*), acacia (*Acacia gummifera*) and oleanders (*Nerium oleander*) (El Mouden et al. 2006). Due to overgrazing and over-harvesting of fire-wood, many bushes have been destroyed and refuge availability is limited in most places (Lagarde et al. 2012). The substrate consists of a hard schistose surface that remains bare for the majority of the year. Following rainfall, an ephemeral herbaceous layer is present for only a few weeks (El Mouden et al. 2006).

Study species

In the central Jbilets, we have surveyed tortoises since 2000 and their occurrence is closely associated with jujube shrub density (Lagarde et al. 2012). In contrast to several other terrestrial tortoises, *Testudo graeca* does not dig burrows but shelters (sometimes half-buried) in thick vegetation (Ben Kaddour et al. 2006; Cloudsley-Thompson 1970; Hailey & Coulson 1996b; Lagarde et al. 2002, 2012; Nussear et al. 2007). Jujube bushes protect the herbaceous vegetation from overgrazing by livestock and thus provide food (Bailey & Highfield 1996; Ben Kaddour 2005; El Mouden et al.

2006). In addition, jujube shrubs retain a soft soil where the tortoises can lay their eggs (Lagarde et al. 2012). The Moorish tortoise is diurnal and activity is concentrated during spring and autumn when climatic conditions are relatively temperate as demonstrated via a continuous monitoring system using acceleration data-loggers (Legendre et al., 2008). Spring activity is maximal in April (our study period), corresponding to the mating and egg-laying seasons (Ben Kaddour, 2005; Legendre et al., 2008). Tortoises are thus exposed to strong habitat constraints during displacements: suitable refuges (i.e. large bushes) are highly scattered in the landscape, often separated by distances greater than 300 m or more (see Fig. 1 in Lagarde et al. 2008). This means that tortoises are forced to cross important distances in the open during the day to move between thermally suitable refuges.

Body temperature estimate

To limit behavioural and physiological perturbation due to surgery (which could falsify our results), we decided not to implant thermal data loggers into the body cavity of the subjects (Edwards 2005). To estimate central body temperature (T_b) we built a simple mathematical model based on the easily recordable dorsal temperature (T_d) and the initial internal temperature. We used the approach previously developed by Delmas et al. (2008) to determine nest temperature of turtles. We implemented distinct heating (α) and cooling (β) conductivity coefficients for the heating and cooling phases (Christian et al. 2006; O'Connor 1999, 2000; Porter et al., 1973). Tortoises rapidly accumulate heat during sun basking episodes (active thermoregulation) but they cool down slowly when they retreat into their refuge (Lagarde et al. 2012; Porter et al. 1973). We also integrated individual body mass (m) as suggested by Christian et al. (2006) in Eq. (1) where Δt is the time step.

$$Tb_t = Tb_{t-1} + (Tb_{t-1} - Td_t)(e^{\alpha m^\beta \Delta t} - 1) \qquad (1)$$

Both coefficients α and β were fitted using maximum likelihood for heating and cooling patterns derived from measurements obtained from physical models (see below).

Lagarde et al. (2012) showed that temperature measured in physical models as described below, underestimate body (cloacal) temperatures recorded in living individuals by approximately 2 °C (comparisons between internal temperatures of six pairs of tortoises versus physical models of similar size: mean Pearson $r^2 = 0.79 \pm 0.2$, range 0.52–0.98), regardless of ambient temperature conditions (see Lagarde et al. 2012 for details). This difference is likely caused by the fact that (1) physical models and living individuals do not have the exact same body shape (Lagarde et al. 2012), (2) hydrogel does not have the same thermal properties as circulating fluids and living tissues, and (3) physical models cannot reproduce physiological regulations (Angiletta et al. 2002; O'Connor 1999; Vitt & Sartorius 1999). Therefore, we considered that an internal physical model temperature of 38 °C corresponded to a critical body temperature of 40 °C for a living specimen (Hutchison et al. 1966).

We tested the accuracy of the mathematical model by comparing internal physical model temperatures and estimated T_b (mathematical model) using 16 physical models fitted with both external and internal data loggers exposed to alternating shade and solar radiation over six days under various climatic conditions (cloudy and sunny days, in combination with presence or absence of wind). We used empty shells (consolidated with small amounts of resin) collected in the study site. The physical models were filled with a hydro-gel poured into a plastic bag placed inside the shell. The mass was adjusted according to the linear regression between body mass and shell length (both log-transformed) of free ranging tortoises captured in the study site over the last eight years (N > 200; see Lagarde et al. 2012). We used three
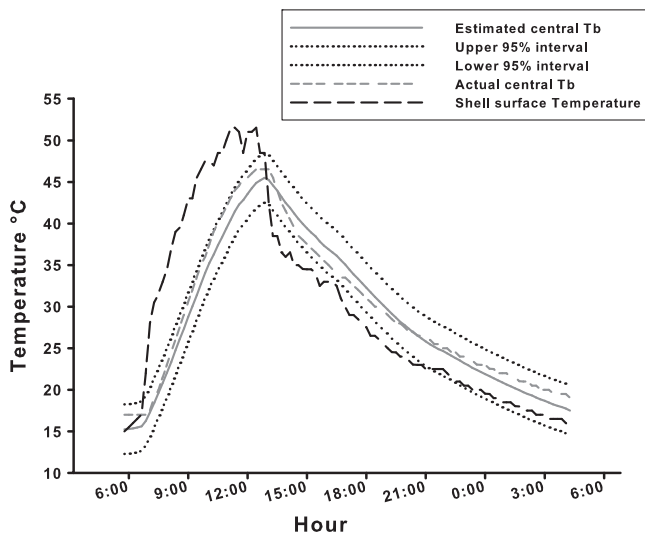
Fig. 1. Estimated central body temperature (T_b) of physical model of *Testudo graeca soussensis* using mathematical model (solid grey line) during a single day with 95% confidence interval (dotted lines). The estimated T_b was obtained using shell surface temperature (T_d) recorded with loggers glued on the back of the physical models (long dashes). The actual central body temperature of the models (using implanted loggers) is represented with the dashed grey line. All recorded central temperatures are comprised in the 95% confidence interval (see text).

temperature data loggers (thermochron iButtons, Dallas Semiconductor): one glued on the top of the shell, one under the shell (ventral position) and one inserted in the gel at the centre of the model. The models were then allowed to equilibrate for at least 12 h. For $\Delta t = 5$ min, α and β were fitted to -0.0217 and -0.8804 for the heating phase and -0.0490 and -0.9980 during cooling phases respectively (Fig. 1). As expected, the linear regression between measured (physical model) and estimated T_b (mathematical model) suggested that the model provided accurate estimates ($r^2 = 0.993$; slope $= 0.996$). The mean difference between estimated and observed values was $-0.24 \pm 0.02\,°C$ (mean $\pm$ SD), 95% of the differences were contained in a small interval ($-3.14\,°C$ to $3.84\,°C$), and they were normally distributed. The strongest differences usually occurred at the beginning of the cooling phases, where values generated by the mathematical model were influenced by greater thermal inertia than physical models (Fig. 1).

Locomotor performance

We measured walking speeds in the field around midday (10:00–15:00) during sunny days in spring, when the tortoises are naturally the most active (Sereau et al. 2010). We captured six adult females and eight adult males. The tortoises were kept in the shade (large bushes) at least 3 h before trials. For each trial we released the tortoise in a flat open area 5 m from a jujube bush, the head oriented towards the bush. Following 0–10 min latency, the tortoises walked away in search of a refuge. We then recorded the time required to reach the bush. The tortoises systematically moved in a straight line. We also recorded both cloacal temperature and air temperature 5 cm above ground. To monitor short term variations of T_b we repeatedly tested individuals: the tortoise was then replaced at the start point and the trial was repeated until body temperature stabilised or reached $37.5\,°C$ (2–37 consecutive trials performed/individual depending on weather conditions). The $37.5\,°C$ threshold corresponds to the maximum central body temperature measured in free-ranging individuals beyond which overheating can occur (Lagarde et al. 2012). This test provided standard measurements of walking speed in changes in T_b when a tortoise leaves a refuge and decides to undertake a movement in

the open. As the observer threatened the tortoise, we assumed that the walking speed would correspond to an elevated value.

Environmental thermal conditions

In the main microhabitats used by tortoises (see Lagarde et al. 2012 for details), we placed eight data loggers to record ambient temperatures and eight physical models to estimate tortoise T_b. We placed two physical models and two data loggers in the open, beneath small jujube bushes (height < 50 cm high), medium jujube bushes (height 50 cm to 2 m) and large jujube bushes (height > 2 m). The models were partially buried (half model shell's height) to mimic tortoise's behaviour when resting (Legendre et al., 2008).

Estimated body temperatures of tortoises leaving their refuge

Our central question was to determine the distance a tortoise can traverse in the open without overheating after having left a refuge. To answer to this question we half buried (half shell's height) 14 physical models under large jujube bushes for one night. The following day, we retrieved the models from the bush and placed them into the open to mimic a typical resting/activity behavioural sequence. We randomly tested various emerging times: 8:30; 10:00; 11:30; 14:00; 15:30; and, 17:00 to explore the natural activity range of the species (Legendre et al. 2008). When the dorsal temperature of the model exceeded $45\,°C$ for 30 min we stopped recording and the model was replaced into the bush. All models were left in the bushes between 19:00 and 8:30 to mimic the nocturnal activity of the species (Legendre et al. 2008). We measured the temperature of these physical models over 12 days (3 April 2008–15 April 2008).

Radio-tracking

In addition to the long term survey started in 2000 for which all found individuals are captured, measured, weighted and marked, we fitted 13 adult (shell length > 100 mm) Moorish tortoises (six males, seven females) with a radio transmitter (see Sereau et al. 2010 for details) and with a temperature data logger glued to the shell. Individuals were maintained for 3–6 h in the shade before release to ensure that internal temperature and shell temperature are initially the same. Individuals were located three times a day over 12 days (see Lagarde et al. 2003, 2008). For each location GPS coordinates, micro-habitat type and behaviour were recorded.

Statistical analysis

When necessary, data were normalised using log transformation. To analyse the walking speed recorded during locomotors performance tests, we used body size (straight shell length) and T_b as covariates in a linear mixed model (body size, T_b and the first order interactions as fixed factors and individual identity as a random factor). The distance travelled by free-ranging (radio-tracked) tortoises was analysed with a linear mixed model with the sex, date, period of the day (morning versus afternoon) as fixed explanatory variables and individual identity as a random factor. Model selection was based on Akaike criterion (AIC), we considered two models as different when ΔAIC > 2. This study does not aim to examine the thermoregulatory behaviour of the tortoises; instead we focused on one central question: how far can tortoises travel in the open without overheating? Consequently we do not present all the thermal readings recorded by the data loggers, we rather oriented the temperature analyses around the critical thresholds of $40\,°C$, corresponding to $38\,°C$ inside physical models as mentioned earlier. Unless specified, the results are presented as means $\pm$ SE. Statistical analyses were performed using R software (R Development
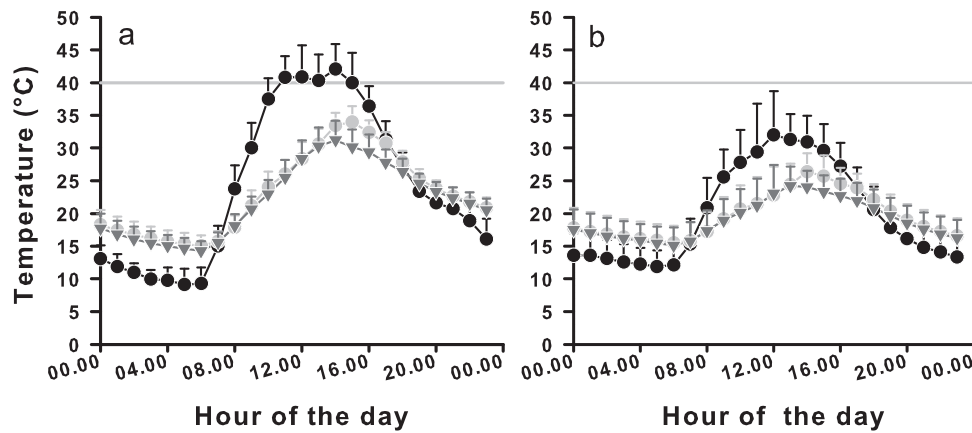
Fig. 2. Ambient temperatures recorded under small jujube shrubs (black circles), medium jujubes (light grey circles) and large jujubes (dark grey triangles) in the central Jbilets (Morocco) during sunny (a) and cloudy days (b) (mean + SD). The horizontal line indicates a high threshold (40° C).

[Core Team 2005](#)) with lme4 package ([Bates & Maechler 2004](#)) for generalised linear mixed model analysis.

Results

Environmental temperatures, body mass and overheating risk

During the study the mean ambient temperature averaged 22.7 °C and ranged between 4 °C and 50 °C. We considered two day types: cool/cloudy; and, hot/sunny days. During cool/cloudy days, both the air temperature and the T_b of the models suggested that the tortoises do not reach a T_b of 40 °C. During sunny days, the tortoises were exposed to potential overheating (i.e. model $T_b > 40$ °C with prolonged exposure to solar radiation) for at least an hour. Large bushes provided thermally buffered conditions while other habitats were potentially risky ([Fig. 2](#)). Females were observed to be less prone to overheating, presumably due to their larger size; mean body mass was 999.0 ± 34.4 g ($N = 64$) versus 463.3 ± 10.8 g ($N = 92$) in adult females and males respectively (2008 data) ([Fig. 3](#)).

Locomotor performance

We recorded a mean velocity of 6.88 ± 0.34 m min^{-1} (mean $\pm$ SD). Selection procedure conserved a single model (AIC = -149.7 and all ΔAIC > 2) with body size (LMC) and central body temperature as the main explanatory variables for the

variations in velocity. As expected, tortoise speed was positively correlated with body size and T_b (slopes were 6×10^{-5} m s^{-1} mm^{-1} and 0.16 m s^{-1} °C^{-1}, $r^2 = 0.42$ respectively). Therefore, we used T_b and shell size to predict tortoise speed. Taking these variables into account enabled us to accurately predict individual walking speed as assessed through a leave-one-out procedure and regressing predicted against actual values ($r^2 = 0.91$, slope is 0.91) ([Remm 2004; Stevens et al. 2012](#)).

Temporal windows of activity and maximum distance

We focused on the periods characterised by a moderate overheating risk: when T_b of at least one physical model reached 38 °C. For simplicity, we considered half-day periods, morning (8:00–13:00) versus afternoon (15:30–19:00). We estimated that during hot periods, the tortoises could safely travel 882.1 ± 37.5 m in the open, and that this excursion required on average 178.5 ± 12.0 min. However, these values were variable and dependent on the time of emergence ([Fig. 4](#)). The estimated safe distance rapidly decreased from 8:00 to 13:00, and then tended to stabilise after 15:30; reflecting the reducing intensity of solar radiation in the afternoon and concomitant decreasing overheating risk (however individuals must shelter before night). In addition, in the afternoon the T_b of the sheltered tortoises was already elevated, thereby improving locomotors performance compared to individuals leaving their refuge in the morning and
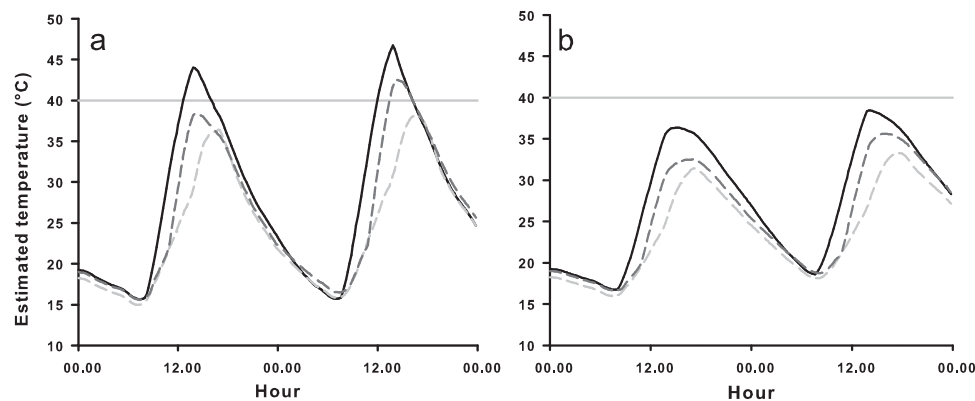

Fig. 3. Estimated central body temperature during two sunny days for adult male (a) and female (b) tortoises situated in a refuge. The females are larger than males (~450 g for males and ~1000 g for females). Three situations were considered: the tortoises could shelter under small (solid line); medium (black dashed line); or, large jujube bushes (grey dashed line). Central body temperature was estimated using the temperatures recorded on the shell surface of physical models placed in the different refuge types. Confidence interval has not been drawn for readability. Jujubes bushes prevent from overheating during cloudy days. However, during hot days, only large shrubs are able to protect tortoises against overheating.
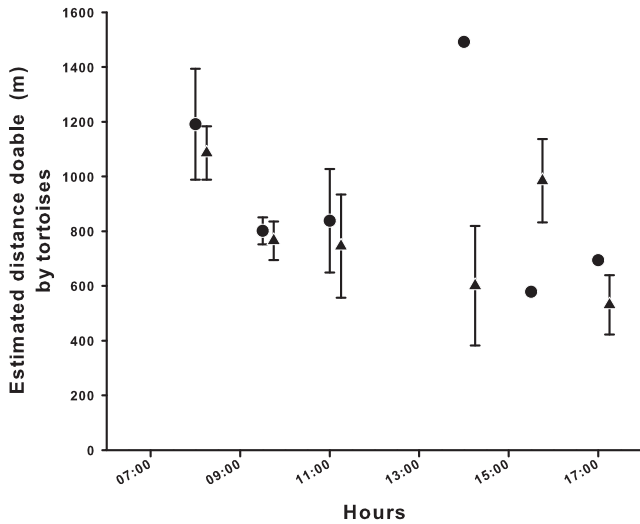
Fig. 4. Estimated cumulative distances that Moorish tortoises can travel (Y axis) during sunny days. In this species, individuals are diurnal, active during sunny days, and they move in the open during displacements because bushes are scattered. Solar radiations can entail overheating risks; the tortoises must cease displacements and shelter in a refuge. The mean estimated maximal distances for females (circles) and for males (triangles) were derived from the temperature measured in physical models, locomotors performances measured in the field on tortoises and from the change in body temperature over time (see text for details).

that must bask in the sun prior movements (night temperatures were often low), but this also accelerated overheating risk. Finally, tortoises leaving the bushes after 17:00 could not travel far because they faced a major time constraint (activity stopped around 19:00–19:30). The large body size of the females provided a buffering advantage and they were able travel farther than males (Student's test, $T = 1.588$, $p = 0.06$). For example, during the hottest periods (at 11:00), the estimated theoretical maximum distance, a tortoise can move is 493.90 m for males and 673.08 m for females.

Radio-tracking

The model selection suggested that the effects of sex and date were the main determinants of the distance travelled by the tortoises. Importantly, both males and females

remained motionless during cool days and were located moving only during warmer periods (date effect). During hot days, although the occurrence of movement was not different between sexes ($W = 66.2$, $p = 0.77$), females travelled longer distances (79.95 ± 10.98 m, max = 570.71 m) than males (38.80 ± 6.91 m, max = 154.48 m, $W = 1557$, $p = 0.0036$; Fig. 5) and walked during longer periods ($W = 16{,}038.5$, $p = 0.01$).

The maximal T_b of the free-ranging tortoises estimated by our model was 34.7 °C for males and 33.6 °C for females. In both cases these high values were recorded in tortoises walking in the open. The mean maximal body temperature was 32.09 ± 0.56 °C (all individuals, hence sexes, pooled). Males exhibited higher maximum T_b than females (33.06 ± 0.84 °C versus 31.26 ± 0.69 °C; $W = 34$, $p = 0.037$). Maximal estimated T_b were recorded between 16:00 and 19:36. Half ($N = 6$) of the maximal estimated T_b were obtained from tortoises that undertook relatively short trips (43.93–320.16 m) and that broke up movements with episodes of refuge use.

Discussion

The first outcome of this study is methodological. Accurately assessing body temperature variations and physiological limits is essential in ectotherms (Angiletta et al. 2002; Bennett 1980; Hertz et al. 1993; Pike & Mitchell 2013; Stevenson 1985). The simple model we developed and tested provided estimates of the central body temperature (T_b) of free-ranging tortoises. The T_b estimates were derived from shell temperatures easily collected with miniaturised data loggers. Notably, our model adequately smoothed the strong temperature elevations of the dorsum part of the shell exposed to sunrays during sun basking periods (Fig. 1). This smoothing procedure was essential to correctly estimate maximal body temperatures and to discard misleading values (i.e. false very high T_b). As our model also integrates body mass, it could be adapted to other tortoise species and possibly on other taxa (e.g. large lizards). This approach represents a safe potential alternative to the use of surgically implanted loggers. However both the α and the β coefficients should be re-estimated to encompass variations in body shape, physiology and possible yet untested allometric size effects (Christian et al. 2006; O'Connor et al. 2000; Vitt & Sartorius 1999). The maximal estimated T_b we calculated in free ranging tortoises fits well with available information concerning thermal biology of tortoises and reptiles in general (Cloudsley-Thompson 1970; Hailey & Coulson 1996c; Huey 1982; Nussear et al. 2007). This
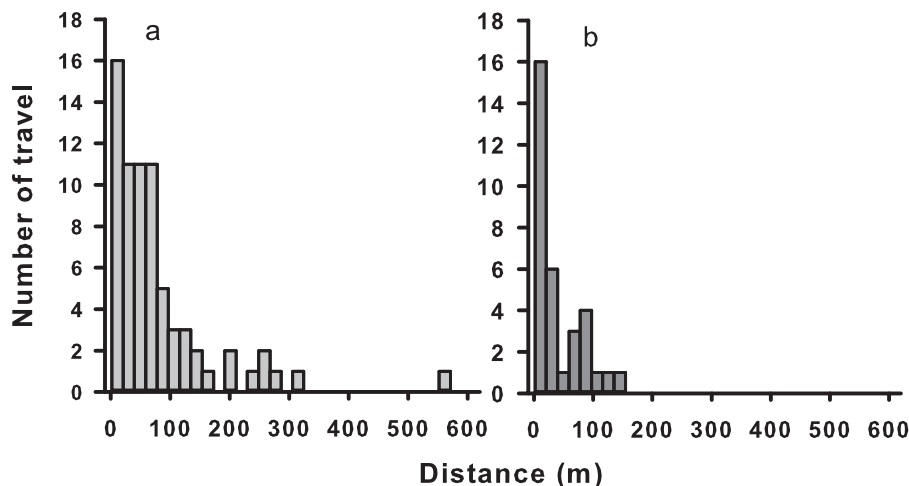

Fig. 5. Distribution of the daily distances travelled by thirteen radio-tracked Moorish tortoises (six males and seven females) in the Jbilet central (Morocco) monitored during twelve days in April 2008. Females (a) move more often and farther than males (b).

reinforces the notion that a 40 °C threshold should be considered as a critical value.

The main limit of our approach is also methodological. We selected hot periods to assess overheating risks during movements. However, the tortoises may remain sheltered and wait for favourable thermal conditions to undertake movements; rendering our selection of sunny-days inappropriate. This might be true if the tortoises could navigate in an unchanging environment with respect to refuge availability, in familiar habitats and perfectly predictable thermal condition. If all these conditions were met, individuals could then safely travel several kilometres during a cool day, navigating between refuges. This is very unlikely for several reasons. First, the tortoises are diurnal and active almost only during sunny days; they remain motionless under cool conditions (Hailey & Coulson 1996b; Lagarde et al. 2003, 2008; Nussear et al. 2007). This temperature dependence of activity is likely explained by the link between physiological performance and body temperature (e.g. movements are precluded under cool conditions) (Angiletta et al. 2002; Hailey & Coulson 1996b; Lagarde et al. 2003, 2008; McMaster & Downs 2006). Second, the habitat is changing rapidly (e.g. across seasons), especially in the arid Mediterranean areas. Relying purely on previous experience, a tortoise may not find the expected shelters in the course of a long and thus potentially perilous trip, especially under unfavourable cool conditions that considerably slow down walking capacities. Third, dispersal is a vital process for the persistence of populations; most dispersing individuals are supposed to be naïve, and thus strong selection to avoid overheating must favour prudency, especially in long-lived species.

In an arid landscape, individuals navigate between refuges (e.g. thick shrubs for the Moorish tortoise, burrows for the gopher tortoise) to escape lethal conditions. Thermal characteristics of available microhabitats suggest that only large bushes are thermally suitable refuges (Lagarde et al. 2012). The difference between the theoretical maximal distance that can be safely traversed by adult tortoises (~1 km) and the actual shorter values (~0.5 km) recorded in free-ranging tortoises suggests that individuals may be minimising the risk of overheating. The tortoises may be avoiding body temperatures greater than 35 °C (by sheltering under large bushes), a value markedly below the 40 °C threshold, by limiting trip duration and distance. The sex difference we observed, with the body size advantage for large females, in limiting overheating was expected as larger body mass confers thermal buffering (O'Connor et al. 2000). We acknowledge that we did not study the most vulnerable age cohorts: the neonates and the juveniles. Incorporating the high thermal sensitivity and low velocity of such small individuals would automatically suggest that a 0.5 km distance between refuges is already excessive. In addition our estimates may not be appropriate for females during the egg laying season as females can move distances greater than 5 km (>5 km week^{-1}, unpublished radio-tracking data).

Thus, connectivity between refuges could be maintained by the females and to a lesser extent by the males (Lagarde et al. 2002, 2008). Our results suggest that the management for arid species should consider the distances between refuges and the potential threat for overheating when assessing or protecting steppe tortoise habitats. A maximum distance of 0.5 km or less should be maintained between refuges. To the best of our knowledge, such a precise field recommendation has never been proposed to promote the conservation of reptiles living in superficially homogeneous arid zones. Our simple albeit precise approach might usefully contribute to habitat protection/restoration of a wide range of organisms that face strong overheating constraints during movements.

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