



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).

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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

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 Jbilet, 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.

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

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

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