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Original Investigation

Absence of heterothermy in the European red squirrel (*Sciurus vulgaris*)

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ABSTRACT

The European red squirrel *Sciurus vulgaris* inhabits areas which undergo profound seasonal declines in food availability and ambient temperature. We measured the body temperature (T_b) of free-ranging *S. vulgaris* over the course of one year to examine its thermoregulatory strategies and found no evidence of heterothermy, with T_b never dropping below 36.7 °C. A lower average T_b and a reduced active phase are likely to have resulted in some energetic savings, sufficient for survival during the particularly mild winter with unhindered access to food stores. We cannot exclude that a different T_b pattern may be seen in energetically more demanding years, but we can confirm that heterothermy is not an obligatory behaviour in this species to counter energetic bottlenecks. Either *S. vulgaris* is indeed a strict homeotherm, or the need for torpor is flexibly adjusted.

Introduction

Of all fundamental principles in biology, energy expenditure is perhaps the single-most important as it is a prerequisite for life itself (Fletcher et al., 2012). However, maintaining the equilibrium between energy intake and energetic costs is made difficult by the variable nature of both the biotic and abiotic characteristics of native habitats. Most animal species are specialised in the sense that they have relatively narrow environmental niches, therefore environmental instability can prove challenging. For example, climatic conditions change not only on a day-to-day basis but also seasonally (and due to global warming), and can do so in an unpredictable manner. Therefore, flexibility in physiology can contribute to the success and persistence of species (e.g. Schleucher et al., 2008; Kobbe et al., 2011). In particular, the ability to modify thermal biology via seasonal adjustments in physiological processes can be vitally important. This is especially critical during winter when food resources are low for many species and ambient temperature (T_a) decreases.

Small mammals in particular are strongly affected by environmental conditions. To cope with environmental energetic bottlenecks many small mammal species use torpor or hibernation, temporary and controlled physiological states of reduction in metabolic rate and body temperature (T_b). Their relatively large surface area to volume ratio results in high heat loss, and consequently they generally have high metabolic rates relative to their body size, making energetic savings through hypometabolic strategies most profitable for small bodied species (Heldmaier and Neuweiler, 2004). For example, many members of the tribe Marmotini of the family Sciuridae (ground squirrels, chipmunks, prairie dogs and marmots) are heterothermic (i.e. show periods of active reduction of metabolic rate, which leads to a decrease of T_b beyond the regular fluctuations of the euthermic sleep-wake-cycle) and undergo long periods of hibernation (Bakko et al., 1988; Harlow, 1995; Pereira et al., 2002). Interestingly, members of the subfamily Sciurinae (tree and flying squirrels) are thought to remain homeothermic, that is they maintain high T_b year-round and do not enter torpor regardless of environmental conditions (e.g. Pereira et al., 2002; Brigham and Geiser, 2012). This is remarkable given their small size, close phylogenetic proximity to species which readily employ torpor, and only medium insulation capacities of their dreys (nests; Pulliainen, 1973). However, most species of this subfamily occur in tropical and subtropical climates, and small reductions in T_b have been found in others, e.g. American red squirrel (*Tamiasciurus hudsonicus*; Pauls, 1978), Abert's squirrel (*Sciurus aberti*; Golightly and Ohmart, 1978) and eastern grey squirrel (*Sciurus carolinensis*; Pereira et al., 2002). On the other hand, food might not be as limited during winter for tree seed predators: tree seeds are only slowly depleted over winter when food trees have produced good seed-crops. In fact, for these species it is rather the spring and early summer that are periods of shortage of high-energy food resources (Wauters and Dhondt, 1987; Wauters et al., 1992). Nevertheless, Cade (1964) suggested that rodents with a strong tendency to hoard food might be prime candidates for developing the propensity of seasonal heterothermy.

The European red squirrel (*Sciurus vulgaris*; 200–400 g) is the only tree squirrel species native to Europe and its distribution spreads from the European Atlantic shores to the Pacific coastline of Asia. It is active throughout the year and assumed homeothermic (Tonkin, 1983; Reynolds, 1985; Wauters et al., 1992). Therefore,

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the study of its thermal biology is of interest as it may provide insight into how small mammals avoid an energy deficit during unfavourable environmental conditions. The high costs of thermoregulation during winter are thought to be fuelled by food cached in anticipation of seasonal decline in resource availability (hazelnuts, walnuts, beechnuts, etc.), as well as perennially available food (coniferous cones; Wauters et al., 1992). However, continuous measurements of T_b for free-ranging individuals are not available. If we are to fully understand a species' ecology and physiological abilities, we must gain information from wild individuals in their natural habitat. For example, recent studies on free-ranging animals have identified heterothermic phases in species that had previously been studied for decades in the laboratory without any indication of heterothermy (Kobbe and Dausmann, 2009; Schmid and Ganzhorn, 2009; Nowack et al., 2010). Accordingly, evidence shows that the thermal biology of captive animals can differ substantially from their wild conspecifics both for heterotherms (Geiser et al., 2000, 2007) and homeotherms (Warnecke et al., 2007). In light of this, it is conceivable that *S. vulgaris* might show (short) heterothermic phases in the wild to economize their energy resources during energetic bottlenecks that have so far remained undetected due to a lack of field studies of T_b.

Given their seasonal habitat and phylogenetic proximity to a group of torpor prone species, the aim of this study therefore was to investigate whether free-ranging red squirrels indeed remain homeothermic throughout the year, regardless of environmental conditions, small size, and relatively poor insulation capacities of their resting sites during winter.

Material and methods

Red squirrels were caught in Ohlsdorf cemetery, Hamburg, one of the largest park cemeteries in the world. The 400 ha grounds consist of mixed woods and open areas overgrown with hedges and shrubs. Sherman squirrel traps (15 cm × 15 cm × 45 cm) were baited with hazelnuts and placed in spots known to be frequented by squirrels. 6 trapped males were transported to the Zoological Institute, individually marked with subcutaneously injected passive identification transponders (ID100 Trovan, EURO I.D. Usling GmbH, Weilerswist, Germany), and weighed with a spring balance (weight 305 ± 45 g; mean ± SD). The animals were implanted subcutaneously at the abdomen with iButton temperature loggers (0.5 °C increments; model DS1922L, Maxim Integrated Products, Dallas, USA), which had been calibrated in a water bath and coated with medical silicon. The loggers were programmed to log T_b once an hour. During implantation the animals were anaesthetised with 11 mg/kg Xylazin and 100 mg/kg Ketamin. Squirrels were released either 2 or 3 days after implantation at their capture locations. Of the 6 implanted individuals, 1 was found dead of unknown causes after 3 months, and 3 were predated upon, presumably by beech martens (*Martes foina*). The remaining 2 individuals were recaptured after the winter season and the temperature loggers recovered by the same procedure as for implantation. One T_b-logger logged from 22 April 2007 to 28 March 2008 (the mass of the animal was 273 g and 264 g at release and recapture) and the other one from 27 September 2007 to 14 March 2008 (365 g and 350 g). All procedures used in this study were approved by the federal and institutional animal care and use committee.

T_a was recorded once an hour within the study area with iButton temperature loggers placed in the shade at a height of 2 m on a tree.

Results

The 2 squirrels remained homeothermic throughout the year and T_b patterns of the two individuals were very similar (data are given separately for the 2 individuals): T_b never dropped below 36.7 °C (Fig. 1a). As is typical for diurnal mammals, T_b decreased slightly during the nocturnal resting phase (Fig. 1b and c).

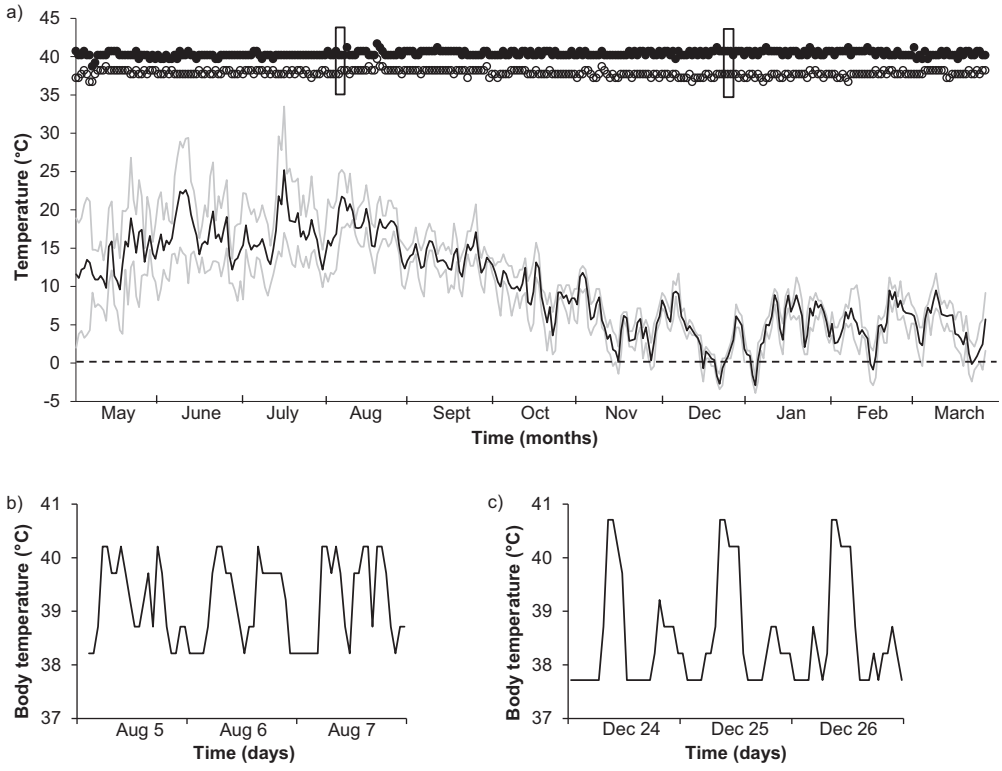

Fig. 1. Body temperature of *Sciurus vulgaris* (a) over the course of the year. Dark and light circles give maximal and minimal daily body temperature. The black line shows average, grey lines show minimal and maximal daily ambient temperature. Boxes show the positions of the inserts, (b) for 3 days during summer (05–07 August 2007) and (c) for 3 days during winter (24–26 December 2007).