Seasonal patterns in body temperature and behaviour in Cape ground squirrels, *Xerus inauris*, living in a semi-arid environment

by

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Declaration

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The work contained in this thesis describes original research undertaken towards a Master of Science degree at the Zoology Department, University of Cape Town. None of this work has been submitted in any form towards a degree at any other university. It is submitted as my own endeavour, and all assistance received has been duly acknowledged. I hereby empower the University to reproduce for the purpose of research the whole or any part of the dissertation.

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Abstract

Miniature temperature-sensitive data loggers were implanted into the abdominal cavities of 16 free-ranging Cape ground squirrels, *Xerus inauris*, to investigate seasonal body temperature patterns. Data loggers recorded body temperature at 5-min intervals while microclimate variables were recorded *in situ* at 15 minute intervals. The behaviour of the study animals was recorded using 5-min scan samples throughout the day. These data were collected for eight Cape ground squirrels for 27 and 28 days during the austral winter and summer respectively.

During winter, despite a marked variation in globe temperature (-7 to 37°C), Cape ground squirrels maintained a relatively stable body temperature of 37.0 ± 0.2°C (range 33.4 to 40.2°C). Lactating females consistently had a significantly higher body temperature (0.7°C) than did non-lactating females and males. There was a pronounced nychthemeral rhythm with a mean active phase body temperature of 38.1 ± 0.1°C and a mean inactive phase body temperature of 36.3 ± 0.3°C for non-lactating individuals. Mean daily amplitude of body temperature rhythm was 3.8 ± 0.2°C. Body temperature during the active phase closely followed globe temperature and mean active phase body temperature was significantly correlated with mean active phase globe temperature ($r^2 = 0.3 - 0.9$; $P < 0.01$). There was no evidence for daily torpor or pronounced hypothermia during the inactive phase and mean minimum inactive phase body temperature was 35.7 ± 0.3°C for non-lactating individuals.

During summer mean daily body temperature was 37.0 ± 0.2°C (range 32.3 to 40.6°C), with an active phase body temperature of 37.6 ± 0.2°C and an inactive phase body temperature of 36.3 ± 0.3°C. Mean daily amplitude of body temperature rhythm was 3.9 ± 0.2°C. High rainfall occasionally kept the squirrels in their burrows during the active phase which resulted in body temperatures not attaining normal active phase levels. As in winter, body temperature during the active phase closely followed globe temperature and mean active phase body temperature was significantly correlated with mean active phase globe temperature ($r^2 = 0.5 - 0.7$; $P < 0.01$).

Cape ground squirrels maintained a mean body temperature of 37.0°C in summer and winter, with a mean inactive phase body temperature of 36.3°C. However, mean active phase body temperature was lower in summer (37.6°C) than in winter (38.1°C), most likely as a result of body temperatures not reaching active phase levels when rainfall during summer kept the ground squirrels in their burrows during their normal active phase. The endogenous T_b rhythm of Cape ground squirrels appears to be variable and can be modulated based on prevailing environmental conditions.

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Chapter 1 - General Introduction

Endothermic homeothermy

Endothermy is the maintenance of a high and constant body temperature (T_b) by metabolic means (Bennett and Ruben 1979) and is one of the most significant evolutionary alterations involving the relationship between an animal and its environment (Hayes and Garland 1995; Wooden and Walsberg 2002). The advantages of endothermy are numerous and include providing a steady state for physiological and biochemical functions (e.g. locomotion, enzymatic activity, membrane and action potentials, digestion, growth, excretion), independence of daily activity patterns over a wide range of temperatures and habitats, and resistance to freezing (Bennett and Ruben 1979; McNab 1979; Barnes 1989; Song and Geiser 1997; Wooden and Walsberg 2004).

Many endotherms precisely regulate metabolic heat production and heat loss to maintain a high (35 – 42°C) and stable (± 1.0°C) core T_b regardless of environmental conditions (Wooden and Walsberg 2002). For species that practice strict homeothermy, hypothermia of more than 2°C results in loss of coordinated locomotory performance, impairment of physiological function and loss of consciousness (Clark and Edholm 1985; Reinertsen 1996). Hypothermia of more than 5°C is usually fatal unless T_b is rapidly returned to normal. At the other extreme, terrestrial vertebrates, with few exceptions, exhibit an upper lethal T_b limit of 42 – 43°C, with most humans collapsing from heat stress at 39 – 40°C (Louw and Seely 1982).

The "thermodynamic freedom" provided by endothermic homeothermy, however, places a significant burden on the animal in the form of increased energy expenditure and water loss (Song and Geiser 1997; Wooden and Walsberg 2002). An endotherm requires a basal metabolic rate four to ten times greater per gram of tissue than that of most ectotherms (Bennett and Ruben 1979; Louw 1993). To maintain a constant T_b when exposed to air temperatures below the thermoneutral zone, endotherms need to increase their metabolic rate, often as much as eightfold that of basal metabolic rate (Hinds et al. 1993).

Basal metabolic rate is defined as the minimal metabolic rate measured for an endothermic animal when it is quiet, inactive, not digesting a meal, and not experiencing stress (Withers 1992). It thus describes the minimum amount of energy required to support life processes, e.g. heart function, respiration, muscle tonus, in a thermally neutral environment (Louw 1993). The range of temperatures at which basal metabolic rate remains constant is known as the thermoneutral zone and metabolic rate increases above and below the upper and lower critical temperatures respectively (Withers 1992). The width of the thermoneutral zone depends largely on the body size and conductance of the animal involved.

Thermoregulation in arid environments

Arid regions have been classified from extremely arid (mean annual precipitation less than 100 mm) to semi-arid with a mean annual precipitation less than 500 mm (McGinnies 1968 in Louw and Seely 1982). The effect of aridity on biological productivity is however more complex and regions defined as arid are better described by precipitation that is not only low, but also infrequent and variable (Noy-Meir 1973). Although aridity is usually associated with extremely high ambient temperatures (T_a), arid-adapted animals are often faced with cold stress especially at night (Louw and Seely 1982).

The high temperatures and intense solar radiation associated with arid environments produce conditions in which environmental temperatures may substantially exceed T_b and effective thermoregulation relies on the animal's ability to move heat out of the body against a temperature gradient (Walsberg 2000). The only mechanism known to do this is water evaporation, which depends on differences between water vapor pressure at the animal's surface and in the surrounding atmosphere. The fundamental difficulty of this is obvious: animals must use the resource whose scarcity defines the habitat they live in.

Despite this apparent limitation, arid environments support a wide diversity of life with remarkable and extensively researched thermoregulatory adaptations (Louw and Seely 1982; Louw 1993; Walsberg 2000). These adaptations are both physiological and behavioural, although at the level of the physics and physiology of the cell, are indistinguishable. Physiological thermoregulation is described as the use of endogenous metabolic heat production, cardiovascular adjustment and evaporation. Adaptive physiological responses to minimize water loss include adaptive heterothermy, efficient reabsorption of water from faecal material in the rectum, production of highly concentrated urine, a low metabolic rate, and high thermal conductance. Specialized pelages are a morphological adaptation and are usually a compromise between thermal shielding and the facilitation of heat loss via radiation and convective cooling.

Behavioural adaptations include the use of site selection, position and posture (Louw and Seely 1982; Louw 1993) and are comparatively rapid, less costly and more flexible than physiological adaptations (Simeone et al. 2004). Small mammals rely almost exclusively on escape to a thermally buffered microclimate (refer: Importance of burrows / refuges). Solar load can be significantly reduced by orientating the long axis of the body relative to the sun's rays thus reducing the surface area exposed to radiation. Postural adaptation includes the use of appendages to either maximize convective cooling (e.g. ostrich's wings) or shield the body from solar radiation (e.g. ground squirrel's tail).

Endothermic heterothermy

The limits of variability traditionally associated with homeothermy are ± 2°C (Cabanac and Simon 1987). However, research on small endotherms has shown the presence of larger variations around a mean T_b for many species particularly in response to stressful conditions e.g. heat and cold stress and limited food and water availability (e.g. Chappell and Bartholomew 1981a; McKechnie and Lovegrove 2002; Wooden and Walsberg 2002; Mzilikazi and Lovegrove 2004; Hwang et al. 2007). The heterothermy thought to be adaptive in the thermoregulatory capabilities of large mammals living in warm, arid environments has recently come under dispute with recent research on free-ranging large mammals indicating that their T_b is far more stable than previously thought (Mitchell et al. 2002; Fuller et al. 2005).

Mitchell et al. (2002) argue that for heterothermy (in particular hyperthermia) to qualify as adaptive, "excursions from core T_b should be large enough to account for appreciable heat storage, be in phase with circadian changes in environmental heat load, increase when ambient heat stress increases and be linked demonstrably to conserving body water". The hypothermic morning T_b observed in captive water-deprived camels, *Camelus dromedarius* (Schmidt-Nielsen et al. 1957) and free-ranging kangaroos, *Macropus spp.* (Maloney et al. 2004) is thought to be a pre-emptive strategy when high environmental heat loads are expected.

Maintaining strict homeothermy becomes more costly with decreasing body size (Buffenstein and Yahav 1991; Wooden and Walsberg 2002). Many small endotherms have thus abandoned tight thermoregulatory control as a survival mechanism. The most extreme example of facultative hypothermia in small endotherms is torpor - a mechanism to survive northern hemisphere winters and to reduce energy expenditure in unpredictable environments (refer: Torpor and Hibernation). However, many non-torpid individuals employ temporary hypothermia in response to low T_a's and some species have been shown to maintain normal function even at T_b's as low as 30°C, e.g. Puerto Rican Tody, *Todus mexicanus* (Merola-Zwartjes and Ligon 2000) and round-tailed ground squirrel, *Spermophilus tereticaudus* (Wooden and Walsberg 2004).

By depressing T_b at low T_a's endotherms can reduce the energy expenditure otherwise needed to maintain strict homeothermy and may also conserve water which would be of critical importance in arid environments (Walsberg 2000; Wooden and Walsberg 2002). Body water can be conserved in two ways: firstly ventilation rate and respiratory water loss decrease as oxygen requirements for metabolic heat production are reduced, and secondly as T_b is lowered, exhaled air becomes cooler (i.e. carries less water vapor per unit volume) and transcutaneous water loss may thus decrease as a result of a lower skin temperature.

Hyperthermia in response to high T_a's would also be advantageous. Allowing T_b to rise above T_a would maintain the driving force (T_b - T_a) for non-evaporative heat loss and would conserve body water by eliminating the need for evaporative cooling (Wooden and Walsberg 2002). Similarly, a rise in T_b when T_a exceeds T_b would reduce the rate of heat influx ($T_a - T_b$) and conserve water and energy needed to eliminate incoming heat through evaporative cooling. Small endotherms that maintain normal function at T_b's as high as 41°C include the Puerto Rican Tody (Merola-Zwartjes and Ligon 2000), the round-tailed ground squirrel (Wooden and Walsberg

2004) and the antelope ground squirrel, *Ammospermophilus leucerus* (Chappell and Bartholomew 1981b).

Conductance

Thermal conductance is "a measure of the ease with which heat enters or leaves a body" (McNab 1980), and includes the flow of heat from deeper parts of the body to the skin surface and from the skin surface to the environment (Schmidt-Nielsen 1983). Heat is transferred between the body and its environment by means of radiation, conduction, convection and evaporation and is the reciprocal of insulation (Bradley and Deavers 1980). It has been described as a physiological composite of fur thickness, piloerection, subcutaneous fat deposits, vasomotor changes and evaporative cooling (Hudson and Deavers 1973). An animal has the ability to change conductance within limits either physiologically (e.g. circulation, respiration) or behaviourally (e.g. body posture, huddling, piloerection), (Aschoff 1982).

Heat transfer from or to the environment is retarded by insulation on the body. Smaller mammals, of necessity, have relatively shorter and lighter fur (and therefore lower insulation values) than large animals and hence they need to employ alternative thermoregulation strategies when faced with cold environments (Schmidt-Nielsen 1983). Conversely, in warm arid environments, high conductance values will facilitate heat loss without necessitating the loss of water (Aschoff 1981).

Pelage properties and skin colour in thermoregulation

The relationship between pelage properties and skin colour and their respective roles in thermoregulation has been broadly investigated and almost unanimously agreed to involve complex interactions (Louw and Seely 1982; Walsberg 1988; Walsberg and Schmidt 1989; Louw 1993; Maloney and Dawson 1995). Solar radiation is potentially critical in determining an animal's energy budget (Walsberg 1988). Under clear skies, solar radiation often exceeds 1000 W/m^2 on a plane perpendicular to the solar beam which is approximately 10 – 20 times the area- specific basal metabolic heat production of typical endotherms. Solar heat gain (which can be quantified as the decrease in metabolic heat production caused by an animal's exposure to simulated solar radiation) is further affected by wind speed and decreases as wind speed increases (Walsberg and Wolf 1995). In particular, solar heat gain has the potential to be of vital importance in the energy budget of diurnal animals inhabiting arid environments characterized by intense irradiation (Walsberg 1988; Wooden and Walsburg 2000), but predicting its effects on the heat balance of animals is extremely difficult (Walsberg et al. 1997a).

The adaptive role of pelage colour in thermoregulation is complicated in that it serves other functions, e.g. camouflage, mimicry and communication between animals (Louw and Seely 1982). Early empirical evidence appeared to confirm the belief that dark coloured animals absorb more radiation and experience higher radiative heat loads than lighter coloured animals. Dark coloured animals in deserts (e.g. black ravens, black bedouin goats, emus), and light coloured animals in Polar Regions (e.g. polar bears and arctic foxes), would therefore appear to be thermally maladapted.

Presuming that because black absorbs more radiation, the dark pelage of emus, *Dromaius novaehollandiae*, would be disadvantageous on hot summer days is naïve. Research on emus has revealed that there is nothing remarkable about the bird's ability to remain active on hot days (Maloney and Dawson 1995). The morphological adaptations of a dark coat with low penetrance and a high insulation value to protect the body from absorbed radiation are sufficient to minimize heat gain without excessive evaporative water loss in the emu. The black skin in both the antelope squirrel and the round-tailed ground squirrel has been shown to have minimal thermal effects and is possibly more important in blocking the transmission of ultraviolet radiation to minimize subepidermal tissue damage (Walsberg 1988).

The heat gain from solar radiation is also not purely a product of the animal's colour – i.e. the amount of radiation reflected or absorbed by the coat. Rather solar heat gain depends on a complex suite of properties including coat optical, structural, and insulative characteristics, as well as skin colour and the optical properties of individual hairs (Walsberg 1988). The rock squirrel, *S. variegates*, has been shown to increase solar heat gain in winter by 20% without changing coat colour (Walsberg and Schmidt 1989). This difference was assigned to changes in hair optics and coat structure. This is further confirmed by Walsberg and Wolf (1995) who found that solar heat loads did not differ between two species of ground squirrel, *S. lateralis* and *S. saturatus*, with light and dark coats respectively.

Subcutaneous properties of the animal, independent of pelage properties, will also affect the significance of solar heat gain to the animal (Walsberg et al. 1997b). Alterations in blood flow through peripheral tissues and tissue thermal resistance between the skin and the core of the animal will affect heat gain from insolation. These effects are still poorly understood but should not be discounted (Wooden and Walsberg 2000). However, it is known that solar radiation can significantly reduce metabolic heat production in T_a's below an animal's thermoneutral zone. Thus solar radiation may be an important component of the daily energy balance of animals which may ultimately affect their long term fitness and survival (Walsberg and Wolf 1995; Walsberg et al. 1997a; Geiser and Drury 2003).

Huddling

Huddling is an extremely important behavioural mechanism to reduce heat loss and allow survival at low T_a's, especially in small mammals with a large surface-to-volume ratio and a limited capacity for increasing pelage insulation (Vogt and Lynch 1982; Bazin and MacArthur 1992). The energy savings are through reductions in mass-specific thermal conductance, resting metabolic rate and/or evaporative water loss (Withers and Jarvis 1980; Vogt and Lynch 1982; Bazin and MacArthur 1992). If the huddling occurs in a refuge (e.g. nest, tree cavity, burrow), an individual's energy expenditure is further reduced by warming within the refuge through the combined metabolic heat production of the huddle (Bazin and MacArthur 1992; Du Plessis and Williams 1994; Du Plessis et al. 1994).

The benefits of huddling may be further increased by the use of torpor (Vogt and Lynch 1982) or may even preclude the necessity to undergo torpor where this would be disadvantageous (Hwang et al. 2007). Torpid white-footed mice *Peromyscus leucopus* that were huddling in a nest were shown to have a 74% daily energy saving versus non-torpid, individual mice without a nest at a low T_a (Vogt and Lynch 1982). The ability to forego torpor by employing huddling during winter in the normally solitary male striped skunk, *Mephitis mephitis*, may give normothermic skunks a physiological breeding advantage upon emergence in spring (Hwang et al. 2007).

Importance of burrows / refuges

To avoid temperature extremes, small and medium sized mammals rely almost exclusively on escape to the thermally stable microclimate of subterranean refuges or crevices and nests (e.g. Buffenstein 1984a; Jackson et al. 2002; Anderson and Richardson 2005). This behaviour may be permanent (e.g. mole rats), diurnal (e.g. kangaroo rats and gerbils), for a few hours over midday (e.g. hyrax, suricates), or periodically throughout the day to relieve transient periods of hyperthermia (e.g. ground squirrels) (Louw 1993). Besides thermoregulation benefits, burrows also offer protection from predators.

Burrow temperatures have been extensively studied and show marked diurnal and seasonal constancy (even at a depth of only 25 cm) compared to above ground temperatures (e.g. Lynch 1980; Lovegrove and Knight-Eloff 1988; Walsberg 2000). Burrows used by Cape ground squirrel, *Xerus inauris*, yellow mongoose, *Cynictus penicillata*, and suricates, *Suricata suricatta*, in southern Africa have diurnal temperature fluctuations at a depth of approximately 500 mm of less than 1 °C in both winter and summer (Lynch 1980). A microclimate thus provides an escape from extreme diurnal summer heat and nocturnal winter cold.

Different temperature gradients exist at different depths and are slightly variable with the texture of the substrate (Lynch 1980). Both Lynch (1980) and Lovegrove and Knight-Eloff (1988) concluded that animals aid thermoregulation by moving up and down the soil column (i.e. using burrows at different depths) seeking burrow temperatures that are closest to their thermoneutral zone. Temperature is not the only variable influencing the microclimate provided by burrows, and humidity needs to be taken into account (Walsberg 2000). Measurement of humidity is complex, relying on the geometry and ventilation of the burrow system, evaporative water loss from the animal and soil properties affecting vapor diffusion. Measuring humidity is probably less difficult when studying arid-adapted animals as they of necessity minimize evaporative water loss and arid soils are normally dry.

Torpor and hibernation

The most powerful measures available to endotherms to reduce energy expenditure are hibernation in winter, aestivation during hot, dry summers and daily torpor in both seasons (Wilz and Heldmaier 2000; Heldmaier et al. 2004). These adaptations, especially the latter, are widely used by small mammals (< 10 kg) in nine mammalian and six avian orders, to overcome adverse environmental conditions (Geiser and Ruf 1995; Geiser 1998).

During torpid states metabolic rate is decreased to well below euthermic levels with reductions in T_b, ventilation and heart rate (Geiser 1998; Heldmaier et al. 2004). Although it is thought that torpor may be pleisiomorphic in mammals, it is not necessarily functionally primitive, and is widely regarded as a sophisticated adaptation of particular endotherms to a hostile environment (Geiser 1998). Unlike ectotherms, "heterothermic endotherms" are able to regulate their T_b at, or above, a species-specific set point during torpor by increasing metabolic rate, and they are able to rewarm themselves to normothermia by using endogenous heat production (Geiser 1998).

Traditionally hibernation and daily torpor have been considered to be two distinct patterns of heterothermy, often characterized as "deep" and "shallow" or "seasonal" and "daily" respectively. In an attempt to classify the differences, Geiser and Ruf (1995) tested the frequency distributions of the variables involved including mean minimum T_b, minimum metabolic rates, metabolic rate reduction expressed as a percentage of basal metabolic rate, mean body weights, and maximum torpor bout duration, across 104 avian and mammalian species. Although all the variables differed significantly, the only frequency distribution that showed a clear gap between daily heterotherms and hibernators was maximum torpor bout duration (1.5 – 22 hours for daily torpor and 96 – 1080 hours for hibernation). The other variables showed an overlap between daily heterotherms and hibernators and it was thus concluded that they were not suitable for classifying torpor patterns.

This conclusion is supported by Wilz and Heldmaier (2000) who studied the physiological differences between hibernation, aestivation and daily torpor in the edible dormouse, *Glis glis*, which is capable of using all three forms of torpor. Their results suggest that all three forms are based on the same physiological mechanism of thermal and metabolic regulation and that bout duration was the only distinguishing variable.

Because daily torpor and hibernation substantially reduce energy expenditure, they have been widely associated with endothermic species that have adapted to cold Northern temperate zones with low food availability and cold exposure during winter (Lyman et al. 1982; Coburn and Geiser 1998). Recent studies, however, are showing that daily heterothermy in small endotherms may be equally common, if not more so, in the southern hemisphere (Geiser and Drury 2003). In continents of Gondwana origin (mostly tropical or subtropical), rainfall is highly variable (Lovegrove 2003). This unpredictability is associated with summer rainfall anomalies related to the El Niño Southern Oscillations (Philander 1983; Stone et al. 1996). Associated decreases in productivity (Tyson 1986) result in food resources that are spatially and temporally unpredictable.

Studies on Australian (e.g. Song and Geiser 1997; Bartels et al. 1998; Coburn and Geiser 1998), Afrotropical (e.g. Lovegrove and Raman 1998; Lovegrove et al. 1999; Mzilikazi and Lovegrove 2004) and Neotropical (e.g. Bozinovic and Rosenmann 1988; Bozinovic and Marquet 1991) small endotherms suggest that although cool temperatures may facilitate torpor, it is not exclusively an adaptation to the cold and may be employed by species that have a limited ability to store fat and/or have to withstand unpredictable spatial and temporal food resources (Bartels et al. 1998).

A major disadvantage of torpor from an energetic point of view is the high cost of endothermic arousals at the end of a torpor bout (Geiser and Drury 2003). The cost of arousal may comprise as much as 75% of the total energy used during a torpor bout (Tucker 1965). Despite this high cost, and even with the shortest possible torpor bout, i.e. entry followed by immediate arousal, small mammals have been shown to conserve at least a component of their normothermic daily energy expenditure (Schmidt-Nielsen 1983). Recent studies are, however, showing that the cost of arousals from torpor may have been greatly overestimated in the past as laboratory studies conducted under constant ambient temperatures do not take into account the possibility of passive re-warming either by the increase of ambient temperature or by basking in the sun (Lovegrove et al. 1999; Mzilikazi et al. 2002; Geiser and Drury 2003).

Detailed studies on the stripe-faced dunnart, *Sminthopsis macroura*, have shown that the overall energetic cost during active re-warming was 6.3-times greater than that during passive, radiant heat-assisted re-warming (Geiser and Drury 2003). This energy saving confers a significant benefit to small endotherms living in sunny regions and provides an alternative explanation to the prevalence of daily heterothermy in these areas.

Circadian rhythms of body temperature

Circadian rhythmicity is a persistent property of mammalian physiology (Refinetti and Piccione 2005). A daily (nycthemeral) rhythm is a process that consistently repeats itself every 24 hours, and if this rhythm persists with approximately the same period in the absence of external time cues it is called a circadian rhythm (Refinetti and Menaker 1992). A circadian rhythm is therefore endogenously generated and is controlled by a circadian pacemaker located in the suprachiasmatic nuclei of the hypothalamus (Reppert and Weaver 2002).

After exposure to an environment without time cues for several weeks or months the circadian rhythm gradually disappears and it is not yet clear why the circadian pacemaker needs occasional priming by an external "zeitgeber" to maintain its rhythmicity (Refinetti and Menaker 1992). This entrainment of the circadian rhythm is usually by cycles of photoperiod and T_a (Enright 1970; Haim and Levi 1990), although these variables would not explain the circadian T_b rhythm found in subterranean naked mole-rats living in a dark and constant T_a environment (Riccio and Goldman 2000). In contrast to this, root voles *Microtus oeconomus* lack circadian T_b variation which is thought to be linked to long photoperiods in their natural habitat (Gębczyński and Taylor 2004).

The T_b of mammals is characterized by a stable long-term mean with circadian variations around that mean (Aschoff 1982). It was previously thought that this oscillation was weight dependent with amplitude decreasing with increasing body weight, but this has since been disputed (Refinetti and Menaker 1992; Refinetti 1999). The amplitude of the circadian rhythm of T_b varies between 1 – 3°C but in some species has been reported to be as large as 5°C (Lee et al. 1990; Refinetti and

Menaker 1992; Refinetti 1996). This is greater than the limits of variability (± 2°C) traditionally associated with homeothermy (Cabanac and Simon 1987).

The circadian rhythm of activity level and metabolic heat production run in phase with that of T_b (Refinetti and Menaker 1992; Riccio and Goldman 2000; Refinetti 2003; Gębczyński and Taylor 2004). Although changes in activity can affect T_b, circadian rhythm of T_b is not a side-effect of activity (Refinetti and Menaker 1992; Gębczyński and Taylor 2004), rather its relationship with metabolic heat production is more complex (Refinetti 2003). The increment in heat production between day and night is much greater than that needed to account for the variation in T_b and circadian rhythm of T_b is a result of two separate processes: heat production and heat dissipation (Haim and Levi 1990; Refinetti 2003).

Thermoregulation and water balance in arid-adapted small mammals

Small mammals face numerous obstacles in arid environments. They need to overcome a low thermal inertia due to a greater surface area to body mass ratio, a relatively high thermal conductance, and the inability to migrate or move between few and widely spaced sources of surface water (Louw and Seely 1982). Rodents are probably the most successful mammals in adapting to arid conditions and research on their survival mechanisms is extensive (Buffenstein 1985; Lovegrove et al. 1991; Louw 1993; Walsberg 2000; Haim et al. 2006). As previously discussed, these animals would be highly unlikely to survive without behavioural adaptations such as huddling and escaping to thermal refugia. In addition, most rodents in arid areas are nocturnal and are thus able to escape the twin pressures of high incident solar radiation and high T_a's.

Small mammals, irrespective of their habitat, do not sweat because of the danger of dehydration, and only in an emergency will cover their body surfaces with saliva (Louw 1993). Well known methods to conserve water in arid-adapted small mammals are the production of highly concentrated urine and relatively dry faeces (Schmidt-Nielsen and Schmidt-Nielsen 1951; Buffenstein 1984b; Louw 1993; Walsberg 2000; Haim et al. 2006). Increased kidney efficiency, as a result of a high relative medullary thickness, is a common physiological adaptation (Haim et al. 2006), while respiratory water loss is ameliorated by the presence of a nasal counter flow system. Walsberg

(2000) argued that, even with these remarkable abilities to conserve water, animals exposed to T_a's commonly experienced in arid environments would not be able to achieve water balance (i.e. balance metabolic water production, the major source of water on a dry diet, with evaporation, the major avenue of water loss) without some preformed water in their diet.

Low basal metabolic rate and high thermal conductance (relative to their respective allometric equation) have long been considered important to conserving both energy and water in unpredictable arid environments (McNab 1979; Müller and Lojewski 1986; Haim and Izhaki 1993). Within arid-adapted rodents, diurnal species have lower metabolic rates than nocturnal species (Haim and Izhaki 1993). The advantages of a low basal metabolic rate are a reduced need for food intake, a lower endogenous heat production (which would allow them to forage for longer at higher T_a's) and diminished water loss through respiratory pathways. Another possible advantage of a low basal metabolic rate for small arid-adapted mammals is an increased life span which would enhance long term reproductive success in an unpredictable environment where breeding might not be possible every year (Haim et al. 2006).

McNab (1979) concluded that there is a complex interaction between body mass, basal metabolic rate, thermal conductance, the temperature differential maintained by an endotherm with its environment, the animal's diet and its use of thermal refugia. For example, most studies on nocturnal arid-adapted rodents show that they have lower than expected basal metabolic rates and conductances (e.g. McNab 1979; Buffenstein 1984a; Haim 1984; Lovegrove et al 1991). Whether the low basal metabolic rate compensates for a low thermal conductance or visa versa depends largely on the author (the endothermic range hypothesis proposed by Lovegrove et al. (1991) versus the water-economy hypothesis proposed by previous authors e.g. Buffenstein (1984a)). Small arid-adapted rodents may also undergo a "metabolic switch" when food deprived (Merkt and Taylor 1994). Golden spiny mice, *Acomys russatus*, significantly lower their metabolic rate when food is limited without decreasing T_b or activity, and can maintain their weight indefinitely on these rations (Merkt and Taylor 1994).

Besides the obligatory thermogenesis (i.e. basal metabolic rate) required to maintain a high T_b, endotherms are able to increase heat production in response to T_a or diet, through a process known as adaptive or facultative thermogenesis (Louw 1993; Bicego et al. 2007). One of these mechanisms, which is of particular importance to small mammals, is non-shivering thermogenesis where heat is produced by the uncoupling of oxidative phosphorylation in brown adipose tissue (Haim and Izhaki 1993; Gębczyński 2005). Non-shivering thermogenesis is vital to the survival of temperate zone small mammals and for arousal from torpor or hibernation (Louw 1993; Liu et al. 2006; Zao and Wang 2006). Winter-acclimated animals in some rodent species have a higher non-shivering thermogenesis capacity relative to summer-acclimated animals (Haim et al. 1991), but this is not necessarily so for all species (Haim and Izhaki 1993). Results from a study by Haim and Izhaki (1993) found that non-shivering thermogenesis capacity in arid, as well as diurnal rodent species, was higher than that in mesic and nocturnal species, respectively, from the same habitat. It was concluded that for arid and diurnal species which are characterized by a low basal metabolic rate, high non-shivering thermogenesis is a crucial compensation. High non-shivering thermogenesis would allow heat production to be kept at a low rate under resting conditions, and when necessary, an increase in heat production could be achieved in a very short period by increasing non-shivering thermogenesis.

Thermoregulation in ground squirrels

There are 95 species of ground squirrels grouped into nine genera living in Eurasia, North America and Africa (Mercer and Roth 2003). Research into their thermoregulatory abilities has been extensive, especially in North America. They show remarkable adaptations to a wide range of habitats and are among the few strictly diurnal small mammals. Their habitats range from hot, dry deserts to arctic tundra (Hudson and Deavers 1973). A comprehensive laboratory study on eight species of North American ground squirrels revealed that desert species are able to tolerate far higher T_a's than montane species (Hudson and Deavers 1973). In the laboratory environment, all species of ground squirrel rub saliva over themselves when severely heat stressed. All species have a lower basal metabolic rate than expected and arid-adapted species have the highest levels of conductance. This conductance can vary by as much as 50% and this is attributed to the control of peripheral blood flow. The ability to adjust peripheral heat loss together with the ability to increase heat production despite a low basal metabolic rate is advantageous, not only for hibernators but also for a diurnal homeotherm which periodically moves between a thermally buffered burrow and its thermally labile above-ground niche.

Research on ground squirrels in the more northern latitudes of North America and in Europe has focused on both their ability to survive a long harsh winter by hibernating and to make full use of a short active season (frequently not more than four months) within which to breed successfully and gain sufficient reserves to survive hibernation (e.g. Morhardt and Gates 1974; Michener 1977; Kenagy et al. 1989; Vispo and Bakken 1993; Sharpe and Horne 1999; Hut et al. 2002; Long et al. 2005). These squirrels vary widely in their use of thermoregulatory mechanisms during the active season in accordance with the microclimates they experience. The Belding's ground squirrel, *S. beldingi*, allows its T_b to fluctuate over a range of 3 – 4°C which would reduce the metabolic costs of maintaining a constant temperature, but it does not appear necessary for it to make use of microclimates such as burrows, for thermoregulatory purposes (Morhardt and Gates 1974). Other studies on ground squirrels, e.g. Wyoming ground squirrel, *S. elegans*, (Byman 1985), thirteen-lined ground squirrel, *S. tridecemlineatus*, (Vispo and Bakken 1993), European ground squirrel, *S. citellus*, (Váczi et al. 2006), indicate the importance of burrow use to avoid lethal hyperthermia during hot weather with a bimodal activity pattern when midday temperatures increase above the thermoneutral zone.

The Arctic ground squirrel, *S. parryii*, has one of the longest hibernating periods (eight to ten months) for hibernators and frequently faces hibernaculum temperatures below freezing (Barnes 1989). It was the first hibernator identified to adopt a regular, prolonged and spontaneously reversible core T_b of below 0°C. The metabolic savings of not maintaining a higher T_b in burrow temperatures that can reach -18°C is presumably of enormous advantage in the short but frenetic breeding season. During this active season, Arctic ground squirrels often experience temperatures outside the critical limits of their thermoneutral zone (Chappell 1981; Long et al. 2005). Mean T_b's over this season are relatively stable at 38.5°C but can fluctuate rapidly. The typical daily fluctuation is between 3 – 5°C but can vary as much as 10.5°C within a single day. Long et al. (2005) concluded that Arctic ground squirrels respond to the potential costs of physiological thermoregulation, at T_a's outside the thermoneutral zone, by behavioural use of burrows to maximize foraging time on hot days and minimize energy expenditure for thermoregulation on cold days.

At the opposing extreme to the Arctic habitat are the Sonoran and Mohave Deserts inhabited by the round-tailed ground squirrel (Wooden and Walsberg 2002). This species is faced with both temperature extremes (daytime T_a's that range from less than 5°C in winter to 50°C in summer) and limited food availability. The round-tailed ground squirrels' basal metabolic rate is 60% of that predicted by body mass and its thermal conductance is 45% higher than that predicted by Aschoff's (1981) allometric equation. This species has the ability to both aestivate and enter torpor under conditions that do not permit the maintenance of a positive energy balance. Despite these abilities they are typically active above ground throughout the year (Hudson 1964). Although its' sparse coat would appear maladaptive in an environment with high levels of irradiance, it has a remarkably low rate of solar heat gain which apparently results from changes in thermal resistance at the tissue level (Wooden and Walsberg 2000). By employing heterothermy the round-tailed ground squirrel is able to lower its energy expenditure by up to 50% (Wooden and Walsberg 2002). It is one of the few endotherms that remain active, alert and responsive over a wide range of T_b's (30 – 42°C) with full locomotory capacity at T_b's ranging from 31 – 41°C (Wooden and Walsberg 2004).

The antelope ground squirrel lives in the deserts of southwestern North America and faces extreme heat and aridity in summer and often sub-freezing temperatures in winter (Kramm 1972). It neither hibernates nor aestivates, but can enter a torpid state as a last resort in response to cold stress. However, in this state it is unable to reduce posterior blood flow by differential vasoconstriction as is typical of hibernating species during arousal from torpor, and consequently it cannot arouse unless it is exposed to high T_a's (Lyman 1964). In contrast to this, the Mohave ground squirrel, *A. mohavensis*, which is sympatric with the antelope ground squirrel, is dormant for over half of the year during the winter months (Bartholomew and Hudson 1961).

The most researched adaptation of the antelope ground squirrel to its environment is its ability to tolerate extreme hyperthermia, an often quoted adaptation in both text books and reviews (Kavanau and Rischer 1972; Chappell and Bartholomew 1981a and 1981b; Hainsworth 1995). These ground squirrels have extremely labile T_b's which fluctuate rapidly throughout the day by as much as 7.5°C. They appear to maximize their foraging time by shuttling between the hot desert surface and their relatively cool burrows where heat can be rapidly lost through convection (Chappell and Bartholomew 1981b; Hainsworth 1995). There appears to be a set physiological upper and lower limit to T_b during the hottest period of the day with an upper extreme of 43.6°C having been recorded in the field (Hainsworth 1995). Maximum T_b's are lower over this period and are probably related to the high heating rates and the risk of overheating. Minimum T_b's are also lower over this period (i.e. on exiting the burrow) and probably relate to maximizing net energy gain from the shuttling cycle. The antelope ground squirrel also decreases heat load by holding its wide, flat tail over its back (Chappell and Bartholomew 1981a).

In winter, the antelope ground squirrel's thermal balance is similar to that of the majority of smaller animals in that it must increase its metabolic heat production to maintain T_b in the face of continuous heat loss (Chappell and Bartholomew 1981a). However, daily energy expenditure studies on free-living ground squirrels indicate that less energy is expended in winter than in summer which appears paradoxical especially in the face of a wintertime "energy crisis" (Karasov 1981). This is explained by the fact that antelope ground squirrel huddle at night during winter and lower their nocturnal T_b's by up to 6°C (Chappell and Bartholomew 1981b; Karasov 1983). Night time burrow sharing only occurs during winter and is suggested to save up to 40% of the daily energy expenditure (Karasov 1983). The nocturnal hypothermia observed in winter could reduce metabolic rate by 35% which represents a significant energy saving (Chappell and Bartholomew 1981b).

The study animal: Cape ground squirrel, Xerus inauris

Cape ground squirrels belong to the subfamily Sciurinae (Family Sciuridea) which is characterized by long, bushy tails (Skinners and Smithers 1990). All four species of the genus *Xerus* live in Africa, and although they are closer phylogenetically to the African tree squirrels, they are ecologically more similar to temperate ground squirrels (tribe Marmotini), (Moore, 1959; Waterman 1995). The Cape ground squirrel is a relatively large (average mass = 600 g), diurnally active, semi-fossorial rodent that lives in semi-arid to arid regions of Southern Africa (Zumpt 1970; Straschil 1975; Marsh et al. 1978; Waterman 1995). They are common in central South Africa, especially in the Free State and Northern Province, Namibia and southern Botswana.

Social structure

Cape ground squirrels are highly social with males and females living in separate social units that are both highly cohesive and persist throughout the year despite dramatic changes in resource abundance (Waterman 1997; Waterman and Fenton 2002). Female groups are typically comprised of two to three related females with their subadult young of either sex (Waterman 1995). These groups are characterized by female philopatry and male-biased dispersal. A social group shares sleeping burrows and feeding ranges. These feeding ranges are large with a core area usually encompassing the area within the burrow cluster. Interactions within these groups are amicable and there is no apparent dominance hierarchy. Feeding ranges are not cooperatively defended from adjacent groups. Male groups of up to 19 individuals are largely amicable with a stable, linear dominance hierarchy with older males being more dominant than younger males (Waterman 1995). Male groups have larger feeding ranges than female groups and within this area they may travel from one female group to another. Although predicted, high rates of aggression amongst males for breeding opportunities are not observed and competition is manifested by competitive searching, repeated copulations and disruptions of copulations (Waterman 1998). Dominant males have more copulations with more females.

Reproduction

Breeding occurs throughout the year and is highly asynchronous within and between female groups (Waterman 1996). Sub-adult females reach sexual maturity by eight months of age. Gestation and lactation periods average 48 and 52 days respectively, with one to three litters per year of one to two young. However, most females rear only one litter per year and in years of drought will cease breeding altogether (Waterman and Fenton 2000). Females usually give birth in a burrow away from their burrow cluster and will remain there until after weaning or losing their litter (Waterman 1996). If the litter is successful the female will return to her social group with her young after weaning. Compared to North American ground squirrels, Cape ground squirrels have early reproductive activity, small litter sizes, and long periods of gestation and lactation (Waterman 1996). This strategy appears to facilitate reproductive success in an unpredictable environment with year-round activity.

Diet

Cape ground squirrels are mainly herbivorous, although remnants of insects have been found in their diet and they have been observed to feed on termites (Zumpt 1970; Marsh et al. 1978; Knight 1991). They are entirely dependent on preformed water in their diet (Zumpt 1970) and have not been observed to drink water even when it is freely available (Van Heerden and Dauth 1987; personal observations). As is typical of an exclusively herbivorous animal, the stomach is capable of enlargement to accommodate the intake of large volumes of plant matter and the caecum is greatly enlarged to facilitate the digestion of cellulose (Marsh et al. 1978).

Although the range of plant foods eaten is diverse, green grass blades, underground storage organs, seeds and berries, which are nutritionally superior, predominate in the diet (Marsh et al. 1978; Knight 1991). Despite the presence of dry grass during the winter dry season, dietary emphasis switches to underground storage organs (Marsh et al. 1978) and more digging behaviour during foraging is observed (Knight 1991). The Cape ground squirrel does not hoard food (Knight 1991).

Physiological and behavioural adaptations to temperature extremes in arid environments

Cape ground squirrel show remarkable behavioural, physiological and morphological adaptations to arid environments with extremes in temperature (Marsh et al. 1978; Bennett et al. 1984; Haim et al. 1987; Van Heerden and Dauth 1987). Physiological adaptations include the ability to produce highly concentrated urine and very dry faeces (Marsh et al. 1978; Van Heerden and Dauth 1987). Water loss is further prevented by skin structure (well-developed epidermis and prominent keratin layer) which probably allows for minimal transcutaneous water loss. The skin has no sweat glands and salivation has only been noted in laboratory experiments when animals were exposed to high temperatures from which they could not escape (Knight 1991).

The thermoneutral zone is high and lies between 29 and 35°C (Haim et al. 1987). Metabolic rate is low and VO_2 in the thermoneutral zone is 0.602 ± 0.08 ml O_2/g.h^{-1}. This is 20% less than predicted for a rodent of the same mass according to Kleiber's (1961) equation. Overall thermal conductance calculated at $T_a = 26°C$ is 0.071 ± 0.003 ml O_2/g.h.°C which is high and of benefit in heat dissipation and water conservation.

Behavioural adaptations include the use of the bushy tail as a portable parasol to reduce environmental head load, sun-orientation behaviour, and the use of burrows to escape extreme temperatures (Bennett et al. 1984). At high temperatures, ground squirrels turn their backs towards the sun thus minimizing exposure of the body to direct ultraviolet radiation while at lower temperatures body orientation is random (Van Heerden and Dauth 1987).

It is widely believed that the parasol tail lowers the T_b of the foraging ground squirrel and that this prolongs its foraging time at high temperatures (Marsh et al. 1978; Bennett et al. 1984; Van Heerden and Dauth 1987). Bennett et al. (1984) used pelt covered taxidermic mannequins to report that tail elevation decreased environmental heat load by an average of 5.6°C during the hottest part of the day. However, a recent study by Fick et al. (in press) has confirmed the importance of simultaneously monitoring both the behaviour and T_b of free-ranging animals. Their study on free-ranging ground squirrels reported that T_b continued increasing while the tail was raised and only decreased upon entry into a burrow. Fick et al. (in press) thus concluded that tail use was more for "thermal comfort" than actual lowering of T_b.

Burrow use is perhaps much more important than a parasol tail to Cape ground squirrel thermoregulation and is vital as a thermal refuge (from both high and low temperatures) and to escape from predators (Bennett et al. 1984; Knight 1991; Fick et al. in press). At high temperatures foraging squirrels shuttle in and out of their burrows and Fick et al. (in press) concluded that this was the main tactic to dissipate heat load. Low ambient temperatures are avoided by spending the night in burrows, with activity time above ground beginning well after sunrise and ending at or before sunset.

Motivation for this study

To improve the understanding of the interrelationships between animal behaviour, physiology, and ecology, consistent and simultaneous collection of short-interval data on behaviour, micro- and macroclimate conditions, and T_b over long time periods in free-ranging animals, especially between seasons, is important (Fuller et al. 2005; Brown and Downs 2006; Long et al. 2005). To date only a two week study incorporating these variables has been done on Cape ground squirrels (Fick et al. in press). Miniature temperature data loggers with high sampling rates and large memories have revolutionized research into continuous T_b measurement of free-ranging animals, including small animals of less than 100 g (e.g. Kamerman 2001; Mzilikazi and Lovegrove 2004; Brown and Downs 2006).

Measurement of microclimate variables is however more complex. Detailed studies of thermal conditions and their affect on the thermal energetics of animals require a more intricate measurement of these variables than standard T_a (e.g. Bakken 1980; Chappell 1981; Chappell and Bartholomew 1981a; Byman 1985; Vispo and Bakken 1993). The operative, or effective environmental temperature is the temperature at which an animal will equilibrate if it lacked metabolic heat production and evaporative water loss and is commonly measured using thermocouples inserted into pelt covered, hollow copper models of the animal. Operative environmental temperature is a better index of the thermal potential which drives heat flow than T_a, but it does not incorporate the effects of changes in thermal conductance. Standard operative temperature is an index that takes the animal's conductance into account and is calculated using operative environmental temperature and laboratory studies of the animal's conductance.

This study focuses on the T_b variation of free-ranging Cape ground squirrels and its variation between seasons rather than the full extent of microclimate variables on its thermal energetics (e.g. Mzilikazi et al 2002; Brown and Downs 2006; Warnecke et al. 2007). Black globe temperature (T_g) which provides an integrated measure of T_a, solar radiation and wind speed, although not as accurate as operative environmental temperature or standard operative temperature, was therefore deemed adequate for this study (Hey 1968; Kuehn et al. 1970; Bakken 1992; Dzialowsky 2005).

The general aims of this study were to determine abdominal T_b's of free-ranging Cape ground squirrels during winter and summer in a semi-arid, summer rainfall area, together with simultaneous behavioural observations and measurement of microclimate variables. These would be used to determine seasonal and daily patterns of thermoregulation and the possible use of daily torpor.

Chapter 2 - Winter body temperature patterns in free-ranging Cape ground squirrel, Xerus inauris: no evidence for torpor

Abstract

I measured abdominal T_b of eight free-ranging Cape ground squirrels (*Xerus inauris*, Sciuridae) over 27 days during the austral winter. Mean daily T_b was relatively stable at 37.0 ± 0.2°C (range 33.4 to 40.2°C), despite a marked variation in T_g (-7 to 37°C). Lactating females ($n = 2$) consistently had a significantly higher mean T_b (0.7°C) than did non-lactating females ($n = 3$) and males. There was a pronounced nychthemeral rhythm with a mean active phase T_b of 38.1 ± 0.1°C and a mean inactive phase T_b of 36.3 ± 0.3°C for non-lactating individuals. Mean daily amplitude of T_b rhythm was 3.8 ± 0.2°C. T_b during the active phase closely followed T_g and mean active phase T_b was significantly correlated with mean active phase T_g ($r^2 = 0.3 - 0.9$; $P < 0.01$). There was no evidence for daily torpor or pronounced hypothermia during the inactive phase and mean minimum inactive phase T_b was 35.7 ± 0.3°C for non-lactating individuals. Several alternatives (including nocturnal huddling, an aseasonal breeding pattern and abundant winter food resources) as to why Cape ground squirrels do not employ nocturnal hypothermia are discussed.

Introduction

Endotherms, in particular small mammals, face a potential energy crisis in winter (Karasov 1983) when both primary production and ambient temperatures are at their lowest. The low thermal inertia and relatively high thermal conductance typical of small endotherms translates into substantial losses of internally produced body heat when ambient temperatures are low (Louw and Seely 1982; Geiser 2004). To ensure survival, many small mammals exhibit various energy-saving strategies which rely mainly on thermoregulatory processes, involving both behavioural and physiological mechanisms. Behavioural strategies include basking (Brown and Downs 2007), changing the timing of daily activity (Kenagy et al. 2002), and periodic use of burrows to escape inclement weather (Long et al. 2005). The physiological strategies employed to reduce energy expenditure during adverse conditions include daily torpor and hibernation, both of which include a controlled reduction of T_b and metabolic rate (Aujard et al. 1998; Mzilikazi and Lovegrove 2004; Geiser 2004). Daily torpor in contrast to hibernation lasts only for several hours, usually during the daily rest phase, and the animal attempts to forage during its active phase (Geiser 2004).

Ground squirrels (Sciuridae) inhabit a diverse range of habitats across a broad latitudinal range in both hemispheres. As such they are a useful group of small mammals with which to investigate thermoregulatory adaptations to low winter temperatures. All ground dwelling sciurids in North America with distributional ranges that extend north of 40°N are spontaneous hibernators (Lehmer et al. 2001). The only exception is the black-tailed prairie dog, *Cynomys ludovicianus*, which is active throughout winter but employs facultative torpor for varying periods, apparently in response to local environmental conditions (Lehmer et al. 2006). The use of torpor in ground squirrels that inhabit arid areas in southern North America, which are characterized by extremes of high and low temperatures, is more variable. During winter these squirrels may hibernate (Bartholomew and Hudson 1961), employ daily torpor (Hudson 1964), or lower T_b during the inactive phase compared to summer (Chappell and Bartholomew 1981b; Lehmer et al. 2003). The distinction between rest-phase hypothermia and daily torpor is not clearly defined, but in small mammals daily torpor is generally regarded as a sustained drop in T_b below 30 – 32°C

(Lovegrove and Raman 1998; Mzilikazi et al. 2002; Lehmer et al. 2003; Kelm and von Helversen 2007).

To date only a handful of studies have provided evidence for daily torpor in small mammals in Southern Africa (Lovegrove and Raman 1998; Lovegrove et al. 1999; Mzilikazi et al. 2002; Perrin and Richardson 2004; Scantlebury et al. 2008). Nevertheless, daily torpor may be more common in southern hemisphere small mammals than previously thought (Geiser and Drury 2003; Geiser 2004), particularly in those species that have a limited ability to store fat or have to withstand unpredictable spatial and temporal food resources (Bartels et al. 1998).

The Cape ground squirrel may represent one such species, as it has a wide distributional range in Southern Africa characterised by hot wet summers and cold dry winters with low productivity. Currently we know that Cape ground squirrels do not hibernate (Waterman 1995), but to date no study has investigated whether they engage in daily torpor. I implanted temperature-sensitive data loggers into the abdominal cavities of Cape ground squirrels to investigate their nychthemeral rhythm of T_b and whether they employ nocturnal hypothermia or daily torpor to mitigate a potential energy crisis during winter. In addition, I recorded certain aspects of behaviour to investigate the use of behavioural thermoregulation.

Material and methods

Study site and animals

The study was conducted between 25 July and 19 August 2005 at Moolmanshoek Private Game Reserve in the Eastern Free State, South Africa (28°38'S, 28°01'E). The reserve extends over 3500 ha and is situated in a valley surrounded on three sides by the Witteberg Mountain Range. The area has been a private game reserve for over 15 years and is stocked with plains game (e.g. blesbok, zebra, springbok and black wildebeest) indigenous to the area. Vegetation at the study site is consistent with the grassland biome of central and eastern South Africa (van Oudsthoorn 1992). Natural water springs that originate in the mountains provide water throughout the year. The average yearly rainfall for the region over the preceding 12 year period (1993 – 2004) was 529 ± 133 mm. Rainfall is highest between November and March and the coldest months of the year are June and July.

The Cape ground squirrels in my study inhabited a grass plain of approximately 500 m^2 at an elevation of 1763 m surrounded on three sides by natural boundaries. The boundaries are to the north, a sandstone ridge, to the south, a ravine with a perennial supply of water supporting a natural forest of ouhout, *Leucosidea sericea*, and to the east, Visierskerf, a 2407 m peak of the Witteberg Mountain Range. The position of Visierskerf delayed the arrival of sunlight to the occupied burrows by approximately one hour after sunrise.

Five female squirrels (body mass 464 – 724 g) and four male squirrels (724 – 806 g) were captured from two distinct burrow 'clusters' (*sensu* Waterman 1995) approximately 200 m apart. The larger cluster was comprised of females, varying in number from 15 - 20 individuals at any one time, living in multiple burrows. The smaller burrow cluster was occupied by a social group of males comprising approximately five individuals.

Capture and surgical procedure

The squirrels were captured using carnivore trap cages (1.0 x 0.4 x 0.4 m) which were placed around the entrances of well-used burrows. The traps were baited using peanut butter (Crunchy Peanut Butter, Pick 'n Pay, South Africa) and were triggered by a footplate mechanism. Most of the squirrels were caught, operated on and released on the same day. Those that were caught in the evening or operated on late in the day were held overnight. Capturing and surgery appeared to cause little impediment as, on several occasions, squirrels captured and operated on in the mornings and released at midday were recaptured on the same afternoon. Recapture was highly successful with eight (five females and three males) out of nine squirrels being recaptured at the end of the study period.

Once captured the squirrels were transferred from the trap cages to mesh wire holding cages lined with a towel and covered by another towel to reduce stress to the animal. They were then transported to a nearby (a drive of ~ 20 min) temporary surgical theatre with a veterinary surgeon in attendance. Each animal was placed in an anaesthetic tank, and anaesthetised with 8% halothane (Fluothane, Astra Zeneca, Johannesburg, South Africa) in oxygen. Induction lasted approximately four min. Anaesthesia was maintained with 1.5 – 4% halothane in oxygen via a face mask. Anaesthesia lasted approximately 30 min when implanting the miniature data loggers and processing the animals (e.g. weighing and marking the fur with hair dye) and only 15 min when removing the data loggers. Respiratory rate, heart rate, blood oxygen saturation and rectal temperature were monitored continuously during surgery.

An area of ~ 30 x 40 mm on the ventral abdominal surface of each squirrel was shaved and sterilized with chlorhexidine gluconate (Hibitane, Zeneca, Johannesburg, South Africa) in alcohol. An incision of not more than 30 mm was made through the abdominal muscle, along the mid-ventral line 20 mm anterior to the anal opening (slightly more anterior for males due to the positioning of their genitals) and extended anteriorly. The data loggers were implanted or removed through this incision. The incision was sutured closed and the wound sprayed with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa). Each squirrel was injected with a non-steroidal anti-inflammatory drug (1 mg carprofen, Rimadyl®, Pfizer, South Africa) and a long-acting antibiotic (0.05 ml procaine benzylpenicillin 150 mg/ml and benzathine benzylpenicillin 126 mg/ml, Peni LA, Virbac Animal Health, South Africa).

During anaesthesia individually identifiable markings were made with permanent hair dye (Rich Brown, Viva, Wella AG, Darmstadt, Germany) on each squirrel. After surgery the animals were placed in a wire cage and kept warm until full recovery, which took less than one hour. If the animals had recovered by early afternoon they were released back at their point of capture. All animals recovered completely from implant surgery and their behaviour appeared normal. The smallest ground squirrel (464 g) died from postoperative bleeding into the abdominal cavity after removal of the data loggers. Post-mortem results revealed that the animal's liver was heavily infested with *Capillaria hepaticum*, a liver parasite common in rodents, which inhibits production of coagulating factors and causes mortality in the wild.

Data loggers and measurement of body temperature

T_b was measured by miniature temperature-sensitive data loggers (DS1921 Thermochron iButtons®, Dallas Semiconductor, Texas, USA). These loggers have a range of measurement from –40 to 85°C and can store 4096 data points at a resolution of 0.0625°C. The loggers were set to record the animals' T_b every five minutes which equated to a maximum of 14 days of continuous data. To obtain data for 27 days, two loggers were implanted into each ground squirrel. One logger was set to start measuring temperature two weeks after surgery (to allow for complete recovery of the animal from surgery) and the second was set to start approximately four weeks after surgery, thus allowing for 27 days of continuous T_b recording. The two loggers were taped together and coated in inert wax (Sasolwax Exp987, Sasol, South Africa) for added waterproofing.

The final weight of the two loggers when covered in wax was ~ 10 g and measured ~ 20 x 21 x 22 mm. The smallest ground squirrel used in this research weighed 464 g and thus the weight of the implants was no more than 2% of body mass, which is within acceptable limits (Kamerman et al. 2001). Before surgery, the loggers were calibrated against a high-accuracy thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath to an accuracy of at least one sampling step (0.06°C) of the logger within the physiological range of T_b. The wax-covered loggers were dry-sterilised by formaldehyde vapour and rinsed in sterile water before implantation.

Behavioural observations

Squirrels were observed through binoculars (10 x 50 Bushnell, USA) from a stationary vehicle parked near the burrow clusters. Detailed observations could be made from as little as 10 to 30 m from the vehicle without appearing to influence the squirrels' behaviour.

Observers were present before the squirrels exited their burrows in the morning. The time of exit was recorded after which scan sampling began. It was not logistically possible to continuously record every marked squirrel's behaviour for the full duration of the study. Observations were thus made opportunistically on marked squirrels that were foraging on the burrow cluster or within sight of it. In the late afternoon or early evening the time that the squirrels entered their burrows for the night was recorded.

Focal sampling of individual squirrels was done at five minute intervals (Altmann 1974) to coincide with the temperature readings recorded by the loggers. Behaviours recorded were resting, foraging, locomotion, social, and below the surface. These behaviours were selected based on descriptions of the activity budgets of squirrels observed by Knight (1991) and Waterman (1995) with slight modifications to make them more suitable for a thermoregulation study. The behaviours were defined as follows:

- *Resting:* all activities not involving movement e.g. basking in the sun after rising in the morning and alert (i.e. surveying the surroundings for predators etc).
- *Foraging:* searching and scratching for food, eating and shuffling short distances while feeding.
- *Locomotion:* anything faster than a slow shuffle e.g. walking or running.
- *Social:* the squirrel grooming itself or another squirrel and all other behavioural interactions with another squirrel(s).
- *Below the surface:* the squirrel was out of sight in a burrow (on several occasions the squirrels retreated to the burrows due to initial movement of the observation vehicle; these recordings were not included in the analysis).

In addition, orientation to the sun (either parallel or perpendicular) and tail position (either up or down) were recorded with each behavioural observation. Tail use was only recorded with respect to thermoregulation (i.e. the tail held above the body to shield it from solar radiation), and makes no reference to tail use for social interactions, e.g. communication of predator presence, fighting or playing.

Because of possible differences in the behaviour of the two lactating females their data was not included in behaviour analyses. Behavioural data collected for the male ground squirrel that was not recaptured at the end of the study period were included, thus behavioural data were analysed for seven animals.

Delaying emergence: the effect on T_b

To investigate whether the T_b increase that occurred at the start of the active phase was an endogenous rhythm, an implanted squirrel was prevented from exiting its burrow for ~ two hours in the morning. The experiment began immediately after the squirrel first emerged from its burrow in the early morning. The experimental squirrel was forced below ground by the approach of a human observer on foot who then sat within three metres of the burrow entrance to keep the squirrel below ground for the remainder of the experiment. A randomly selected squirrel with a logger implant that was not prevented from emerging acted as the control. This experiment was carried out on six squirrels on six randomly selected mornings. The exact time of initial emergence of the experimental and control individuals was recorded. At the end of the two-hour experimental period the observer retreated back to the observational vehicle and the experimental animal was allowed to emerge.

Environmental conditions

Microclimate variables (black globe, dry bulb, burrow and ground temperatures, relative humidity, wind speed and solar radiation) were recorded every 15 min for the duration of the study. All microclimate variables, except for burrow temperature, were measured and recorded by a portable weather station (HOBO Weather Station, Onset Computer Corporation, Pocasset, MA, USA) situated ~ 50 m from the "female burrow cluster", a position deemed to be representative of the microclimate variables experienced by all study animals. The temperature and relative humidity probes were housed in a vane which was painted white to reflect solar radiation and which moved in response to wind to allow ventilation of the probe. A temperature probe, situated in the centre of a 150 mm copper globe that was painted matt black and mounted one metre above the ground facing north, integrated air temperature, solar radiation and wind speed, and is hereforth referred to as globe temperature (T_g).

Ground temperature was measured using a thermocouple that was buried about 10 mm below the ground and recorded by a data logger (HOBO Data Logger, Onset Computer Corporation, Pocasset, MA, USA). Burrow temperature was recorded by placing a data logger, in a small plastic container (50 x 20 x10 mm) which had perforations to ensure adequate air flow, into a burrow at a slant depth of ~ 1 m. The burrow was located near the middle of the burrow cluster used by the female ground squirrels. A wire was attached to the container to facilitate its insertion into and subsequent removal from the burrow. According to Lynch (1980) a slant depth of 1 m corresponds to a vertical depth of approximately 500 mm. Environmental temperature data were collected for 26 continuous days, and analyzed with corresponding days of T_b measurements.

Data analysis

T_b and environmental data were divided into two categories: active and inactive, which corresponded to the active and inactive phases of the ground squirrels' activity. The start of the active phase did not correspond with sunrise but was taken as the arrival of sunlight at the study site, which was delayed by approximately one hour because of the position of the mountain, and usually corresponded with the squirrels' emergence from the burrows. The active phase ended at sunset and the inactive phase was thus taken from sunset to the start of the next active phase.

For each successive 24-h period (calculated from 0:00 to 0:00), I calculated mean T_b for each individual. In addition, I calculated mean, minimum and maximum T_b for each individual during their active and inactive phase. I averaged these parameters for each individual for the full study period. Due to the start time of the data loggers (6:00), 24-h means were calculated for 25 days, while active and inactive phase means could be calculated for 27 days. The amplitude of nychthemeral rhythm for each individual was calculated as the difference between the maximum and the minimum T_b reached within a 24-h period. An independent Student *t*-test was used to compare mean T_b between the experimental and control animals for the two-hour experimental period. One-way analysis of variance (ANOVA) was used to compare amplitude of nychthemeral rhythm and mean 24-hour T_b, for the 25 days, between individuals (*sensu* Lehmer et al. 2003). Tukey HSD post hoc tests were used to discern differences between individual squirrels when the overall test statistic was significant. During the active phase, mean hourly T_b per individual per day, was correlated against corresponding mean hourly T_g, using Pearson's linear correlations. I also correlated mean active phase T_b for each individual squirrel against mean active phase T_g. The slopes calculated from regression lines for this correlation were then correlated against the body mass of the corresponding squirrel. The amplitude of nychthemeral rhythm for each individual was correlated with its body mass. All statistical analyses were performed using STATISTICA 8 ©, Statsoft Inc. Values of $P < 0.05$ are considered significant. All means are reported ± standard deviation. The Animal Ethics Committee of the University of Cape Town (approval 2002/V09/JOR) approved all experimental procedures.

Results

Environmental conditions

Burrow temperature over the study period was remarkably stable (10.6 ± 1.0°C) with minimal daily fluctuation compared to large daily fluctuations in T_g (Table 1; Fig. 1). Mean T_g during the active phase was 24.7 ± 4.6°C with a mean maximum of 30.0 ± 4.7°C. Mean T_g during the inactive phase was 4.7 ± 4.3°C with a mean minimum of 1.0 ± 4.2°C. Mean burrow temperatures were always higher than mean T_g at night and lower than mean T_g during the day (Table 1).

Table 1. Average (mean ± SD) environmental conditions and absolute minimum and maximum values for the winter study period.

Variable measured	Active period	Inactive period	Minimum	Maximum
Globe temperature (°C)	24.7 ± 4.6	4.7 ± 4.3	-7.2	37.5
Ground temperature (°C)	26.1 ± 5.5	7.6 ± 4.1	-4.0	44.9
Ambient temperature (°C)	17.8 ± 2.8	5.5 ± 4.1	-6.3	26.3
Burrow temperature (°C)	10.6 ± 1.0	10.6 ± 0.9	8.1	14.0
Solar radiation ($W.m^{-2}$)	429 ± 74	-	1	893
Wind speed ($km.h^{-1}$)	9.0 ± 6.0	5.5 ± 5.7	0.0	41.1
Relative humidity (%)	28.9 ± 15.9	51.1 ± 15.3	4.8	97.8

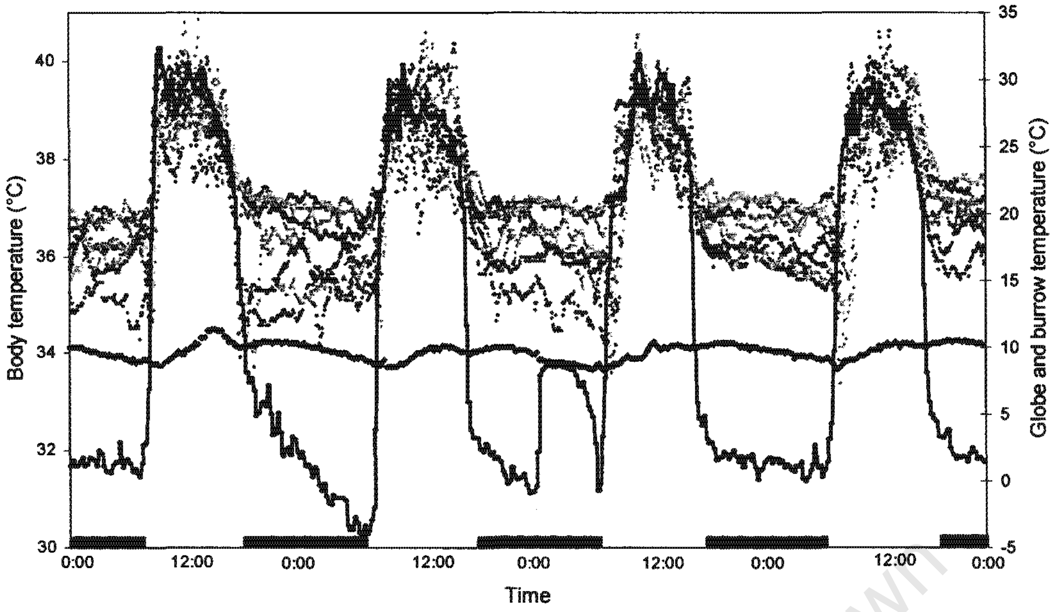

Figure 1. Body temperature (upper lines) of eight free-ranging Cape ground squirrels over four consecutive days with the corresponding globe (black line) and burrow temperatures (dark grey line). The dark bars above the x-axis indicate the inactive phase.

Behavioural observations

I recorded 83 hours (994 scan samples) of behavioural observations on seven implanted ground squirrels. Mean emergence time from the burrow in the morning was 08:13 ± 5 min (range 08:00 to 08:41) and mean entrance time into the burrow in the afternoon was 17:01 ± 6 min (range 16:33 to 17:27). Sunlight reached and left the burrow area by ~ 08:00 and 17:30 respectively during the study period. Mean T_g at time of emergence of the squirrels in the morning was 12.4 ± 2.6°C (range 4.5 to 21.7°C) and at time of entrance in the afternoon was 22.4 ± 1.3°C (range 17.2 to 25.6°C). The emergence of the squirrels in the morning appeared to be strongly influenced by solar radiation and coincided with the rapid increase in T_g (Fig. 1). Squirrels were never above ground after sunlight had left the site and their entrance into the burrow coincided with the rapid drop in T_g in the late afternoon.

Ground squirrels spent the majority of their day above ground foraging (74 ± 8%), followed by resting (17 ± 5%). Most of the resting period involved basking in the morning after emergence and resting on return to the burrow after foraging further afield. Ground squirrels spent an average of 20.4 ± 11.4 min (range 5 to 40 min) basking in the morning but were, on occasion, observed to forage immediately after emergence. During the active period, minimal time was spent below ground in the burrow (3 ± 2%), socializing (3 ± 3%), and engaged in locomotion (3 ± 3%). Time spent in the burrow during the active period appeared to coincide with squirrels carrying nesting material below ground and males investigating the females' burrows.

During the active phase perpendicular orientation of ground squirrels to incident solar radiation showed a clear bimodal pattern with most perpendicular orientation occurring in the early morning and late evening (Fig. 2). Parallel orientation occurred less frequently during these periods and peaked during the middle of the day. The parasol tails were observed to shield the body in only 3.7% of all observations (37 out of 994 scan samples).

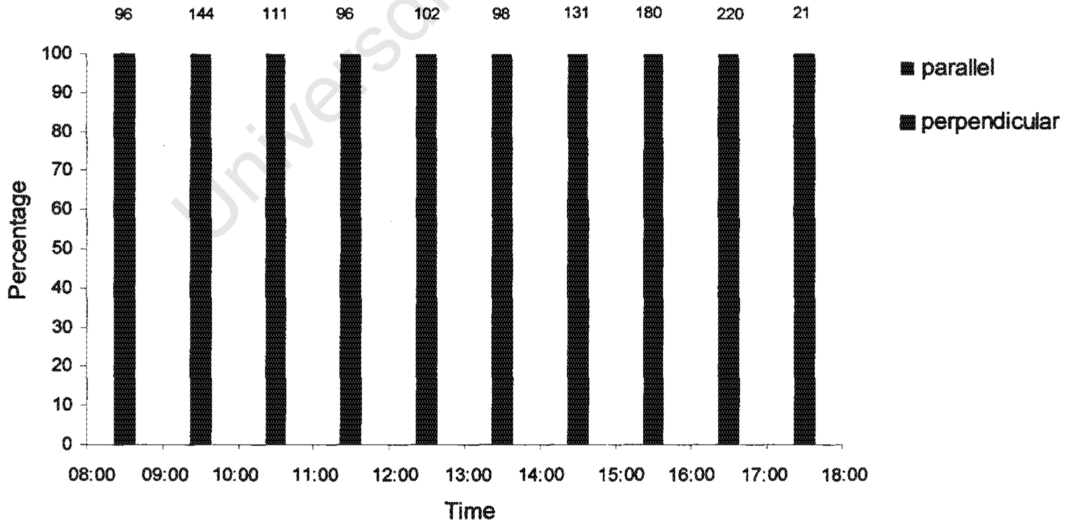

Figure 2: Frequency distribution of orientation of Cape ground squirrels to solar radiation during the active phase in winter. Orientation perpendicular to solar radiation shows a clear bimodal pattern. Numbers above columns represent the number of observations within the hourly period.

Body temperature patterns

T_b of the ground squirrels showed a pronounced and consistent amplitude pf nychthemeral rhythm with a high T_b during the day and a low T_b during the night (Fig. 1). The mean amplitude of nychthemeral rhythm was 3.8 ± 0.2°C. The nychthemeral rhythm of one female (female 4) was significantly lower than that of two females (females 1 and 5), (ANOVA, $F_{7,198} = 2.65$, $P = 0.01$, post hoc Tukey HSD test; Table 2). There was no correlation between the nychthemeral rhythm and body mass of the squirrel ($r^2 = 0.02$; $P = 0.72$; $n = 8$). Upon emergence from the burrow in the morning T_b rose rapidly and in parallel with T_g. T_b oscillated around what appeared to be a diurnal setpoint T_b of 38.2 ± 0.1°C between 11:00 and 16:00 before the onset of a rapid decrease in the late afternoon (~ 17:00) and prior to the ground squirrels going below for the night. T_b continued to decrease after the study animals had gone below ground until it stabilized around the mean inactive phase T_b of 36.3 ± 0.3°C in the early evening (~ 20:00).

Mean active phase T_b correlated positively with mean active phase T_g for each ground squirrel ($r^2 = 0.3 – 0.9$; $P < 0.01$; $n = 27$; female 1 shown in Fig. 3a). There was a significant negative correlation between the slope calculated from the above regression and the body mass of each squirrel ($r^2 = 0.6$; $P < 0.05$; $n = 8$; Fig. 3b). There also was a significant correlation between hourly T_b and hourly T_g for each squirrel during the active phase for each day of the study (e.g. 1st August; $r^2 = 0.6 – 0.9$; $P \leq 0.01$), with the exception of one day (15th August) in which there was atypical light rainfall.

During the study I found that two of the females were lactating. Their mean 24-h T_b (37.7 ± 0.1°C, $n = 2$) averaged over 25 days was significantly higher (ANOVA, $F_{(7,191)} = 42.5$, $P < 0.001$, post hoc Tukey HSD test), than that of the six non-lactating squirrels (37.0 ± 0.2°C; Table 2; Fig. 4). For the six non-lactating ground squirrels T_b rarely rose above 40°C (0.2% of all active phase T_b recordings) and the highest T_b

Table 2. Comparison of mean, minimum and maximum daily body temperatures (T_b) in °C, of eight free-ranging Cape ground squirrels during the austral winter. The two lactating females are indicated with *. Highest and lowest values reached during each phase across all individuals are indicated with **.

	Female 1	**Female 2**	**Female 3**	**Female 4 ***	**Female 5 ***	**Male 1**	**Male 2**	**Male 3**	**Mean (non-lactating)** $N = 6$	**Mean (lactating)** $N = 2$
Body Mass (g)	464	580	504	704	724	806	740	724	636 ± 140	714
Mean T_b	37.1 ± 0.5	37.4 ± 0.3	37.1 ± 0.3	37.8 ± 0.2	37.7 ± 0.2	37.0 ± 0.3	36.6 ± 0.4	37.0 ± 0.2	37.0 ± 0.2	37.7
Active phase										
Mean T_b	38.1 ± 0.7	38.1 ± 0.3	38.1 ± 0.4	38.9 ± 0.4	38.7 ± 0.3	38.1 ± 0.3	37.9 ± 0.4	38.2 ± 0.4	38.1 ± 0.1	38.8
Mean min T_b	35.2 ± 0.7	35.7 ± 0.9	35.6 ± 0.8	36.6 ± 1.0	35.8 ± 0.9	35.7 ± 0.7	35.5 ± 0.8	35.8 ± 0.9	35.6 ± 0.3	36.2
Mean max T_b	39.5 ± 0.5	39.4 ± 0.3	39.4 ± 0.5	40.1 ± 0.4	40.4 ± 0.5	39.4 ± 0.3	39.3 ± 0.3	39.6 ± 0.4	39.5 ± 0.1	40.3
Absolute min T_b	34.2	33.4	34.1	35.9	35.0	34.2	34.2	33.6	33.6**	35.0**
Absolute max T_b	40.2	40.2	40.2	40.8	41.3	39.9	40.1	40.1	40.2**	41.3**
Inactive phase										
Mean T_b	36.3 ± 0.5	36.9 ± 0.3	36.4 ± 0.4	37.1 ± 0.2	37.0 ± 0.3	36.2 ± 0.4	35.8 ± 0.5	36.3 ± 0.3	36.3 ± 0.3	37.1
Mean min T_b	35.5 ± 0.5	36.2 ± 0.4	35.7 ± 0.5	36.5 ± 0.3	36.5 ± 0.3	35.6 ± 0.6	35.2 ± 0.7	35.7 ± 0.5	35.7 ± 0.3	36.5
Mean max T_b	37.3 ± 0.5	37.5 ± 0.3	37.4 ± 0.5	37.9 ± 0.3	37.8 ± 0.5	37.1 ± 0.5	37.1 ± 0.7	37.3 ± 0.5	37.3 ± 0.2	37.9
Absolute min T_b	34.7	35.2	34.7	35.8	35.8	33.7	33.9	34.4	33.4**	35.2**
Absolute max T_b	38.3	38.6	38.9	38.5	39.5	37.8	38.9	38.3	38.9**	39.2**
Nychthemeral amplitude	4.0 ± 0.6	3.4 ± 0.4	3.7 ± 0.7	3.6 ± 0.4	3.9 ± 0.6	3.8 ± 0.6	4.1 ± 0.6	3.8 ± 0.5	3.8 ± 0.3	3.8

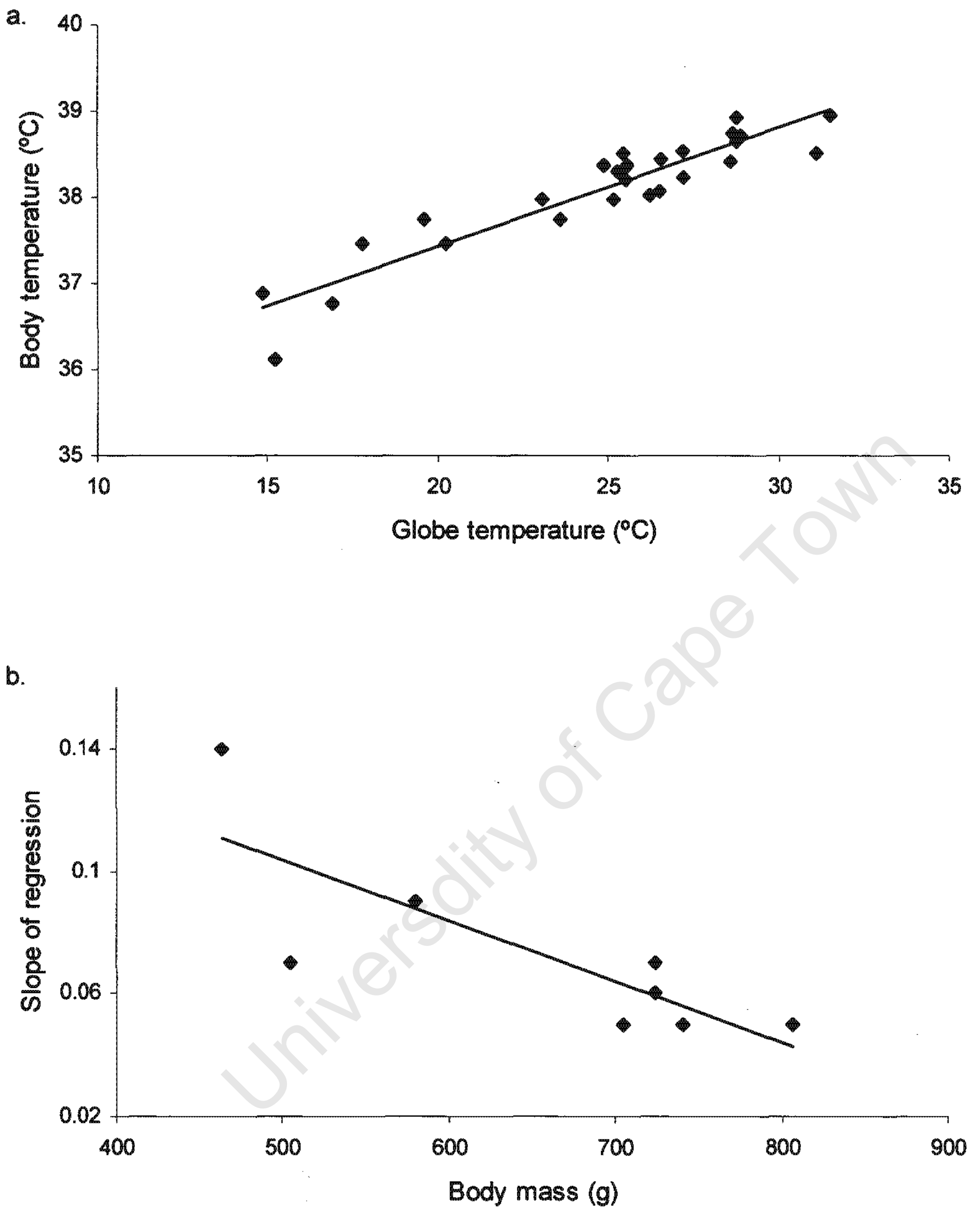

Figure 3. Mean active phase body temperature plotted against mean active phase globe temperature (a), for one female (female 1, 26 days data), with linear regression line ($r^2 = 0.90$, $P < 0.01$). The slope of this regression for all eight Cape ground squirrels was correlated with body mass (b), with linear regression line ($r^2 = 0.60$, $P < 0.05$).

recorded for a non-lactating individual during the study was 40.2°C. The T_b of the two lactating females rose above 40°C for 7% of all active phase T_b recordings and their mean maximum active phase T_b (40.3 ± 0.2°C) was 0.8°C higher (ANOVA, $F_{(7,208)} = 27.1$, $P < 0.001$, post hoc Tukey HSD test), than that for non-lactating individuals (39.5 ± 0.1°C, $n = 6$). The mean minimum inactive phase T_b for the two lactating females was 36.5 ± 0.0°C, which was significantly higher (ANOVA, $F_{(7,208)} = 28.3$, $P < 0.001$, post hoc Tukey HSD test) than that of all but one (female 2) of the non-lactating squirrels (35.5 ± 0.3°C, $n = 6$). No ground squirrel dropped its T_b below 33.4°C during the inactive phase (Table 2).

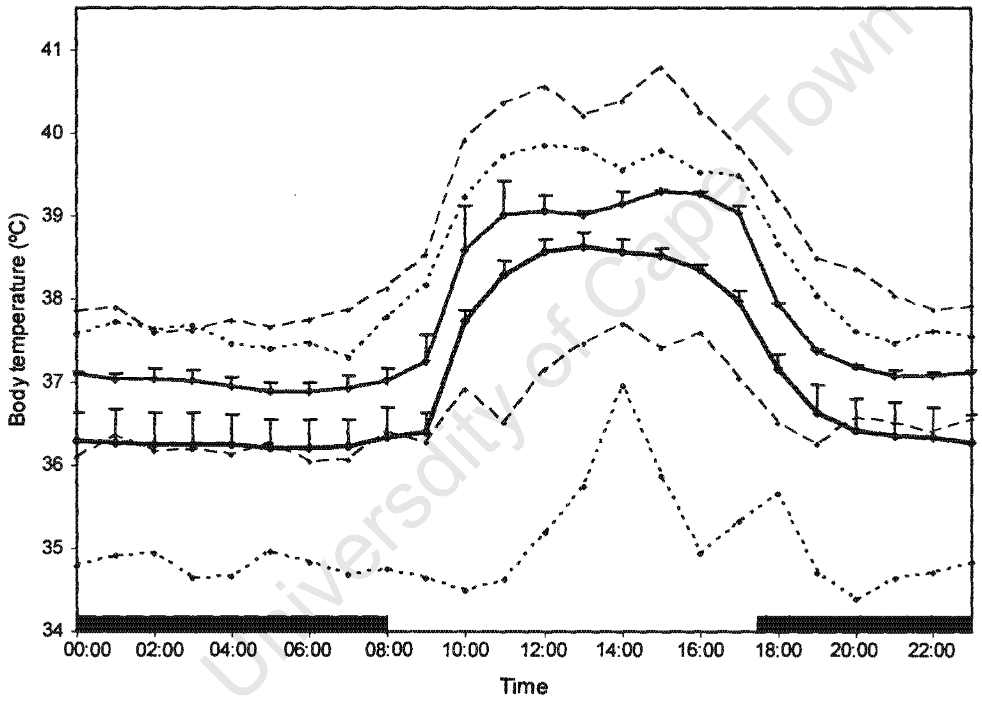

Figure 4. Mean (± SD) hourly body temperature of eight free-ranging Cape ground squirrels (6 non-lactating – black lines; 2 lactating – grey lines). Dotted (non-lactating) and dashed (lactating) lines represent mean hourly minimum and maximum body temperature values. The dark bars above the x-axis indicate the inactive phase.

T_b typically dropped sharply immediately after ground squirrels emerged from their sleeping burrows in the morning (Fig. 5). This drop was evident in 97% of all instances ($n = 28$ observations) in which I could superimpose the exact time of emergence of a squirrel on that same squirrel's T_b profile for that morning. This drop was not consistent within and between individuals or between days. Six out of the eight squirrels (exceptions being female 4 and male 2) experienced the highest frequency of daily minimum T_b's during their active phase between 08:00 and 08:59 as a result of this morning drop.

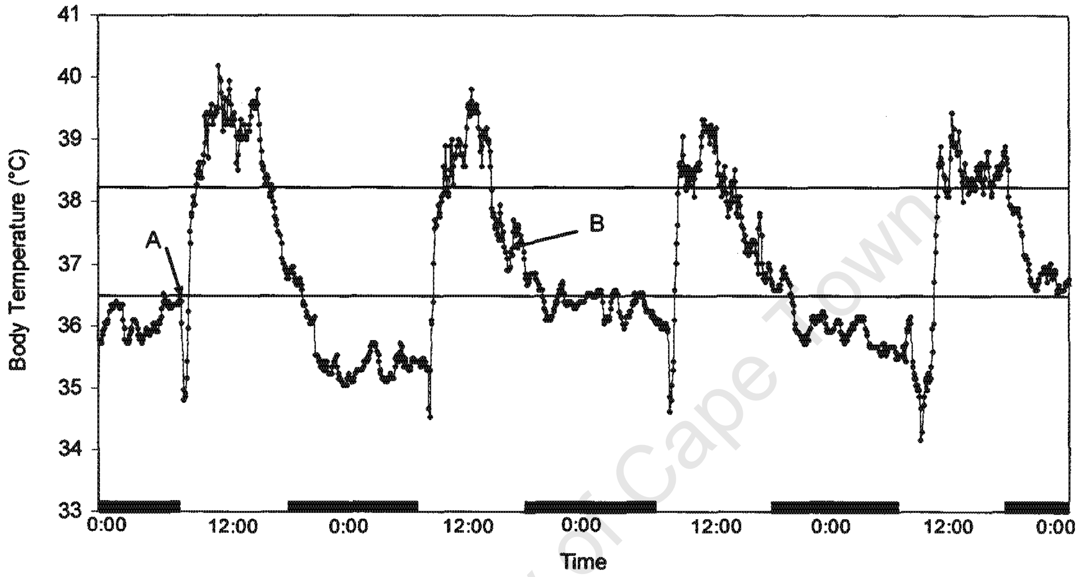

Figure 5. Body temperature of a representative Cape ground squirrel (female 3) over four consecutive days in winter. Arrow A indicates the T_b and time at which the squirrel was observed to emerge from its sleeping burrow on the first day. Arrow B indicates the T_b and time at which the squirrel was observed to go below ground into its burrow on the second day. Solid horizontal lines are the mean active (top line) and inactive (bottom line) phase T_b for this individual averaged over the entire study period. The dark bars above the x-axis indicate the inactive phase.

The six ground squirrels that were experimentally delayed from emerging from their sleeping burrow in the morning had a significantly (*t*-test, $t_{10} = -6.7, P < 0.01$) lower mean T_b (36.1 ± 0.5°C) than the mean T_b of the six control animals (37.9 ± 0.4°C) during the two-hour experimental period. It is evident from Figure 6 that T_b profiles of the experimental and control animals were out of phase. The control animal exhibited the characteristic dip in T_b immediately following emergence from the burrow followed by rapid heating (see similar pattern in Fig. 5). By contrast the experimental animal's T_b declined steadily throughout the experiment. When the experimental animals were subsequently allowed to emerge T_b rapidly increased to that of the control individuals within approximately one hour.

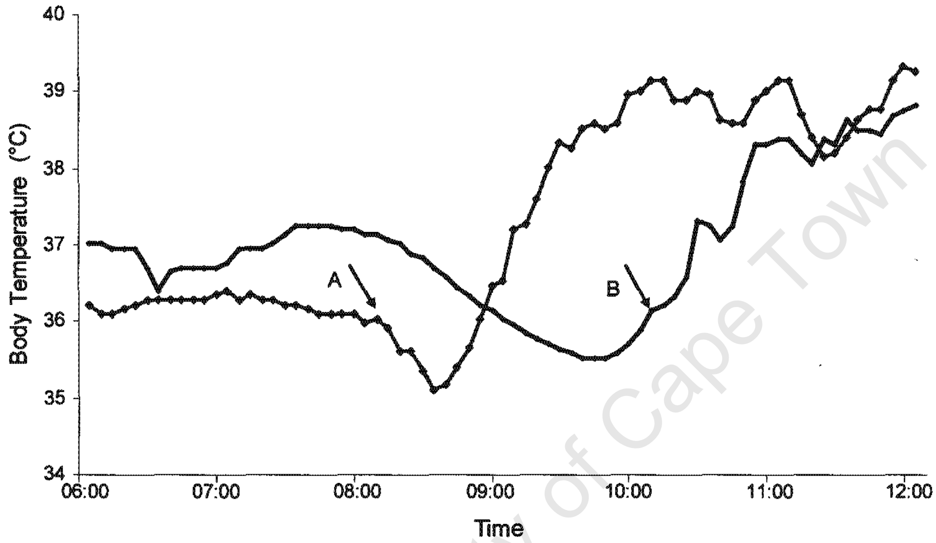

Figure 6. Body temperature of a Cape ground squirrel prevented from emerging from its burrow in the morning (dark line) in comparison to the body temperature of a control ground squirrel (light line) on the same day. Arrow A indicates the T_b and time that the control animal emerged from its burrow and the experimental animal was forced below, while arrow B indicates the delayed time of emergence of the experimental animal.

Discussion

This study provides the first continuous measurement of core T_b in free-ranging Cape ground squirrels living in their natural environment during the austral winter. There was a pronounced nychthemeral rhythm of T_b with two apparent setpoints corresponding to periods of inactivity during the night and activity during the day, which is consistent with the T_b rhythm observed in diurnal small mammals (Refinetti 1999). My free-ranging Cape ground squirrels' core T_b fluctuated daily by ~ 4°C and the largest amplitude on a single day for an individual was 6.2°C. This result is surprising given the large fluctuations of T_b (up to 10°C) reported for other ground squirrels within a single day (Chappell and Bartholomew 1981b; Wooden and Walsberg 2002; Long et al. 2005), and previous research on captive Cape ground squirrels reporting that T_b's can fluctuate between ~ 29 - 42°C (Van Heerden and Dauth 1987; Knight 1991). There was no evidence for torpor or pronounced hypothermia at night with mean nocturnal T_b minima above 35°C.

There are several reasons why Cape ground squirrels may not need to employ daily torpor. These include nocturnal huddling, aseasonal breeding, and abundance of food resources. Huddling results in significant energy savings, especially if it occurs in a buffered refuge with insulation (Withers and Jarvis 1980; Chappell and Bartholomew 1981b; Vogt and Lynch 1982; Bazin and MacArthur 1992). In male antelope ground squirrel, *Ammospermophilus leucerus*, for example, huddling during winter nights lowers daily energy expenditure compared to summer (Chappell and Bartholomew 1981b). Although several small mammals are known to huddle during winter hibernation, for example the black-tailed prairie dog (Gummer 2005) and the yellow-bellied marmots, *Marmota flaviventris* (Arnold 1988), there is evidence in the striped skunk, *Mephitis mephitis,* that huddling precludes the need for torpor which then provides benefits for reproduction on emergence in the spring (Hwang et al. 2007). It has also been suggested that the gregarious sandy inland mouse, *Pseudomys hermannsburgensis,* does not employ torpor in response to food deprivation in winter due to its reliance on social strategies for thermoregulation. By contrast, under similar conditions the solitary house mouse, *Mus musculus*, does employ daily torpor (Tomlinson et al. 2007).

It is probable that five of the non-lactating study animals employed huddling at night. Three of the implanted males regularly descended into a single burrow entrance in the late afternoon with two other males. Similarly, two of the implanted females descended into a single burrow entrance with at least one other individual. So, although it is thought that sociality in Cape ground squirrels (in particular males) is not primarily for thermoregulatory purposes (Waterman 1997), it may nevertheless have thermoregulatory benefits which preclude the necessity for daily torpor despite the low ambient temperatures prevalent during this study.

The aseasonal breeding pattern of Cape ground squirrels may also have precluded the use of daily torpor. Breeding occurs throughout the year and is highly asynchronous within and between female groups (Waterman 1996). Males would, therefore, presumably maintain a state of physiological readiness for reproduction throughout the year. The costs of a low T_b to reproduction (i.e. spermogenesis; Arnold and Dittami 1997; Fietz et al. 2004), may outweigh any benefits associated with daily torpor, as has been suggested for the lesser bushbaby, *Galago moholi* (Mzilikazi et al. 2006).

It is possible that primary reason why the study animals did not employ daily torpor is the relative abundance of food. The realisation that daily torpor in the southern hemisphere is more common than previously thought has been attributed to the spatial and temporal unpredictability of food resources (e.g. Bartels et al. 1998; Lovegrove 2000). Animals that rely on an ephemeral food resource, such as insects (rock elephant shrews, *Elephantulus myurus*; Mzilikazi et al. 2002) or nectar (northern blossom-bats, *Macroglossus minimus*; Bartels et al. 1998), are likely to employ daily torpor. Although Cape ground squirrels feed preferentially on above ground food matter during the wet summer season, they can fall back on the underground storage organs of annuals during the cold, dry season and are observed to employ more digging during this season (Marsh et al. 1978; Knight 1991; this study). Thus, although digging is energetically expensive, ground squirrels have a food source with both a high water and nutritional content available to them during the winter season when primary production is reduced (Knight 1991). Unless there is a prolonged period of drought, Cape ground squirrels thus do not appear to face an energetic bottleneck during the dry winter months, which would otherwise favour the use of torpor (Lovegrove 2000).

The absence of daily torpor does not preclude pronounced nocturnal hypothermia as reported in other non-hibernating ground squirrels during winter (Chappell and Bartholomew 1981b; Lehmer et al. 2003). Free-ranging antelope ground squirrels, which do not employ daily torpor during winter, maintained a lower mean inactive phase T_b (~ 33°C) despite employing huddling and using burrows with a temperature range between 20 - 25°C (Lyman 1964; Chappell and Bartholomew 1981b).

Similarly non-torpid black-tailed prairie dogs had a mean inactive phase T_b of ~ 32°C during winter (Lehmer et al. 2003). By contrast the squirrels in this study had a mean inactive phase T_b of ~ 36°C which is substantially higher than both of the above examples and suggests that Cape ground squirrels do not employ nocturnal hypothermia as an alternative to torpor.

The inactive phase T_b of Cape ground squirrels in this study remained remarkably stable from approximately 20:00 to 08:00 and T_b did not start increasing until the squirrels emerged from their burrows in the morning. This finding is in contrast to reports that small mammals raise their T_b's before the onset of daily activity (Refinetti 1999; Long et al 2005; Brown & Downs 2006). In addition to not raising T_b before the start of the active phase, Cape ground squirrels do not raise their T_b should they be unable to exit the burrow in the morning (i.e. with the presence of a human observer / potential predator), and T_b remained at an inactive level and even decreased. This is in contrast to a report that a wild numbat, *Myrmecobius fasciatus*, increased its T_b at the start of its normal active period in the morning even though it did not exit its burrow due to inclement weather (Cooper & Withers 2004). Thus, unlike the numbat, Cape ground squirrels appear to be able to modulate their endogenous circadian T_b rhythm. The advantage of not raising T_b before emergence from the burrow at the start of the activity period may be an energy saving so that metabolic heat to raise T_b would not be wasted should the ground squirrels be unable to forage because of the presence of a predator or if faced with inclement weather.

Using environmental heat load to increase T_b in the morning would further act to reduce the metabolic costs of thermoregulation (Mzilikazi et al. 2002). It seems likely that such passive heat gain during the morning and heat loss in the late afternoon resulted in the strong correlation between hourly T_b and T_g. In addition, Cape ground squirrel T_b's appear to be strongly influenced by environmental conditions during the active phase with a positive correlation between mean active phase T_b and T_g. This correlation also appears to be influenced by the body mass of the individual squirrel. The mean active phase T_b of smaller individuals appears to be more strongly influenced by mean active phase T_g on a daily basis, and may be due to their lower thermal inertia. Although Haim et al. (2006) do not report T_b of the diurnal fat sand rat, *Psammomys obesus*, their results indicate that heavier individuals spend more time foraging at high environmental temperatures and concluded that this was due to their better ability to thermoregulate. Active phase environmental temperatures in this study were not extreme and more detailed research on activity and T_b of Cape ground squirrels across a broad range of body masses at extreme temperatures is warranted.

The majority of the active phase is spent foraging (74%) with little to no basking behaviour despite low ambient temperatures and high solar radiation in the early morning and late afternoon. It is possible that squirrels have dispensed with basking, a common behaviour in other small mammals (Brown and Downs 2007; Geiser and Pavey 2007), because they can benefit from solar radiation whilst feeding by simply orientating perpendicular to the sun (see Figure 2). In the southern hemisphere the costs of thermoregulating in winter may be mitigated by high solar radiation during the day. Squirrels rarely used their burrows during the active phase in this study, compared to other studies (Golightly and Ohmart 1978; Long et al. 2005), suggesting that the thermal environment did not constrain their daily activity. However, entrance into the burrows in the late afternoon appeared to be influenced by low environmental temperatures and the study animals generally entered their burrows before T_g dropped below 20°C. This finding suggests that the squirrels were minimising the thermoregulatory costs associated with surface activity at low environmental temperatures (Vispo and Bakken 1993).

The sharp drop in T_b immediately on emergence from the burrow in the morning is most likely attributable to rapid heat loss to a cold environment as the ground squirrels exit from the relatively warm microenvironment of their nests. This drop was highly variable between squirrels on a given day and within an individual on different days and could vary from no drop to a maximum recorded drop of 2.3°C. It thus appears to be uncontrolled and may be another reason why there is no pre-emptive increase in T_b before emergence and the start of the active phase. This acute drop has not been reported in other diurnal small mammals but, although not as acute, has been noted in the larger herbivores (Schmidt-Nielsen et al. 1957; Brown and Dawson 1977; Fuller et al. 2000; Maloney et al. 2004). Such a drop in morning T_b has been attributed to sudden peripheral vasodilation initiated by direct exposure to solar radiation and is thought to pre-emptively anticipate high environmental heat loads (Maloney et al. 2004). In zebra, *Equus burchelli*, the fall in T_b after dawn has been attributed to sweating (Fuller et al. 2000). Most small mammals do not sweat (Louw and Seely 1982) and, since high environmental heat loads would not be expected in winter, it is unlikely to be a pre-emptive strategy. Rather, the energetic costs of re-warming from this drop would be a disadvantage and further research into this phenomenon is thus warranted.

Although daily torpor has been reported in lactating small mammals, especially when food deprived, it would have a negative effect on pup growth and survival (Kurta 1990; Stamper et al. 1998). As expected the two lactating female Cape ground squirrels did not employ torpor, but consistently maintained T_b's that were approximately 0.7°C higher than those of non-lactating individuals. This finding is consistent with reports that some small mammals such as Sprague-Dawley rats, *Rattus norvegicus,* (Eliason and Fewell 1997) and dwarf hamsters, *Phodopus spp,* (Scribner and Wynne-Edwards 1994) chronically elevate their core T_b by approximately 0.5°C during lactation. This elevation is thought to be due to an increased heat load because of the highly exothermic process of milk production (Eliason and Fewell 1997). The nychthemeral amplitude of T_b of the lactating females did not differ significantly from the other study animals and may indicate that although T_b's are elevated during lactation, there is still thermoregulatory control over T_b. During winter this hyperthermia would be advantageous at night for providing the altricial ground squirrel pups with the warmth essential for their growth (Hill 1972). However, this chronic elevation of T_b during lactation may constrain the breeding season of Cape ground squirrels, as high day-time summer temperatures might increase the possibility of T_b's reaching lethal limits, and would limit the time available for lactating females to forage, an hypothesis that remains to be investigated.

In this study I have characterised the T_b patterns of Cape ground squirrels during winter in their natural environment and shown no evidence for daily torpor. The use of huddling and thermally buffered burrows to escape low environmental temperatures at night and the presence of underground storage organs as a food source throughout winter appear to be sufficient to mitigate a potential energy crisis in winter. My research documents lactational hyperthermia in Cape ground squirrels for the first time. In addition I have demonstrated that Cape ground squirrels appear to be able to modulate their endogenous T_b rhythms, which may be a possible energy saving mechanism should conditions be unfavourable for foraging. Further research on T_b patterns in Cape ground squirrel populations living in the northern arid regions of their distributional range and in the western winter rainfall areas would provide valuable insight into their thermal energetics during winter.

Chapter 3 - Summer body temperature patterns in free-ranging Cape ground squirrel, Xerus inauris, with a seasonal comparison

Abstract

I investigated abdominal T_b's of eight free-ranging Cape ground squirrels, *Xerus inauris*, over 28 days during the austral summer. Mean daily T_b was 37.0 ± 0.2°C (range 32.3 to 40.6°C), with an active phase T_b of 37.6 ± 0.2°C and an inactive phase T_b of 36.3 ± 0.3°C. Mean daily amplitude of T_b rhythm was 3.9 ± 0.2°C. Rainfall occasionally kept the squirrels in their burrows during the active phase, which resulted in T_b's not attaining normal active phase levels. Such a change in T_b pattern as a result of ambient conditions suggests that Cape ground squirrels are able to modulate their endogenous nychthemeral rhythm of T_b. Interestingly, these low T_b's during periods of rain resulted in mean active phase T_b being lower in summer (37.6°C) than in winter (38.1°C). Despite such differences, mean 24-hour T_b (37.0°C) and mean T_b during the inactive phase (36.3°C) did not differ between summer and winter, even though ambient temperatures were up to 10°C warmer in summer than in

winter. There was no evidence for pronounced hyperthermia during the active phase and T_b rarely rose above 40°C (< 1% of all active T_b recordings).

Introduction

Small mammals living in hot, arid and semi-arid environments, are confronted with extreme physical and ecological stresses (Lovegrove et al. 1991) that have resulted in the evolution of a suite of physiological, behavioural and morphological adaptations to conserve both energy and water (for review see Walsberg 2000). Most of these species are nocturnal to avoid exposure to potentially lethal daytime temperatures (Walsberg 2000; Haim et al. 2006). However, a few species, including ground squirrels (Sciuridae), are diurnal and, during summer, may face extreme heat during their active period. One of the strategies to save energy and water is to abandon strict thermoregulatory control (Walsberg 2000).

Displaying a labile T_b is proposed to reduce the metabolic costs of thermoregulation (Morhardt and Gates 1974; Chappell and Bartholomew 1981b; Long et al. 2005). Employing daily torpor, for example, is believed to be of adaptive value in small mammals in the southern hemisphere where food and water resources in summer are frequently unpredictable (Bartels et al.1998; Mzilikazi and Lovegrove 2004; Séguy and Perret 2005). Similarly, tolerating hyperthermia would not only conserve energy and water, but would allow an animal to increase its foraging time. Both the arid-adapted antelope ground squirrel, *Ammospermophilus leucerus* (Chappell and Bartholomew 1981b), and the round-tailed ground squirrel, *Spermophilus tereticaudus* (Wooden and Walsberg 2004), have been shown to increase their foraging time by allowing their T_b's to reach approximately 42°C. Similarly, in the laboratory, Cape ground squirrels have been shown to elevate their T_b's above 42°C at ambient temperatures above their thermoneutral zone. Further evidence that such an increase in T_b is adaptive is that summer acclimated squirrels allowed their T_b's to rise significantly higher than do winter acclimated squirrels (Knight 1991).

This excess heat can then be dissipated, largely through convective heat loss, upon entering a relatively cool burrow. Both the antelope ground squirrel (Chappell and Bartholomew 1981b), and the round-tailed ground squirrel (Wooden and Walsberg

2004) appear to maximize their diurnal foraging time by alternating exposure to the hot desert surface and relatively cool burrows. This shuttling behaviour is common in most ground squirrels, including temperate species, when environmental temperatures exceed their thermoneutral zone (Vispo and Bakken 1993; Long et al. 2005; Váczi et al. 2006). Additional behavioural thermoregulatory strategies to cope with high ambient temperatures include minimizing direct solar radiation by appropriate body positioning and shading the body with the parasol-like tail (van Heerden and Dauth 1987; Bennett et al. 1984; Knight 1991). However, whether such thermoregulatory behaviour influences T_b has recently been questioned. Fick et al (in press) reported that the T_b of Cape ground squirrels continued to increase while the tail was raised and that T_b only decreased rapidly and significantly upon entry into a burrow. Their conclusion was that tail use was more for "thermal comfort" than actual lowering of T_b. It is therefore important to combine behavioural observations with T_b *measurements in the field to improve our understanding.*

In this study, I implanted temperature-sensitive data loggers into the abdominal cavities of Cape ground squirrels to investigate their T_b patterns during summer, in particular to document their use of hyperthermia and/or hypothermia, but also to enable a comparison with winter T_b patterns in the same population (Chapter 2). In addition I recorded certain aspects of behaviour to investigate the use of behavioural thermoregulation, in particular the effect of raising the parasol-like tail on active phase T_b.

Material and methods

Study site and animals

The study was conducted between 8 January and 4 February 2006 at Moolmanshoek Private Game Reserve in the Eastern Free State, South Africa (28°38'S, 28°01'E). The reserve is 3500 ha and is situated in a valley surrounded on three sides by the Witteberg Mountain Range. The area has been a private game reserve for over 15 years and is stocked with plains game (e.g. blesbok, zebra, springbok and black wildebeest) indigenous to the area. Vegetation at the study site is consistent with the grassland biome of central and eastern South Africa (van Oudsthoorn 1992). Natural water springs that originate in the mountains provide water throughout the year. The average yearly rainfall for the region over the preceding 12 year period (1993 – 2004) was 529 ± 133 mm. Rainfall is highest between November and March and the warmest months of the year are January and February.

The Cape ground squirrels in my study inhabited a grass plain of approximately 500 m^2 at an elevation of 1763 m surrounded on three sides by natural boundaries. The boundaries are to the north, a sandstone ridge, to the south, a ravine with a perennial supply of water supporting a natural forest of ouhout, *Leucosidea sericea*, and to the east, Visierskerf, a 2407 m peak of the Witteberg Mountain Range. The position of Visierskerf delayed the arrival of sunlight to the occupied burrows by approximately one hour after sunrise.

Seven female squirrels (body mass 602 – 712 g) and three male squirrels (704 – 864 g) were captured from two distinct burrow 'clusters' (*sensu* Waterman 1995) approximately 200 m apart. The larger cluster was comprised of females and sub-adult young, varying in number from 15 - 20 individuals with multiple burrows. The smaller burrow cluster was occupied by a social group of males comprising approximately five individuals.

Capture and surgical procedure

The squirrels were captured using carnivore trap cages (1.0 x 0.4 x 0.4 m) which were placed around the entrances of well-used burrows. The traps were baited using peanut butter (Crunchy Peanut Butter, Pick 'n Pay, South Africa) and were triggered by a footplate mechanism. Most of the squirrels were caught, operated on and released on the same day. Those that were caught in the evening or operated on late in the day were held overnight. Capture and surgery appeared to cause little impediment as, on several occasions, squirrels captured and operated on in the mornings and released at midday were recaptured on the same afternoon. Recapture was highly successful with eight (five females and three males) out of ten squirrels being recaptured at the end of the study period.

Once captured the squirrels were transferred from the trap cages to mesh wire holding cages lined with a towel and covered by another towel to reduce stress to the animal. They were then transported to a nearby (a drive of ~ 20 min) temporary surgical theatre with a veterinary surgeon in attendance. Each animal was placed in an anaesthetic tank, and anaesthetised with 8% halothane (Fluothane, Astra Zeneca, Johannesburg, South Africa) in oxygen. Induction lasted approximately four min, after which anaesthesia was maintained with 1.5 – 4% halothane in oxygen via a face mask. Anaesthesia lasted approximately 30 min when implanting the miniature data loggers and processing the animals (e.g. weighing and marking the fur with hair dye) and only 15 min when removing the data loggers. Respiratory rate, heart rate, blood oxygen saturation and rectal temperature were monitored continuously during surgery.

An area of ~ 30 x 40 mm on the ventral abdominal surface of each squirrel was shaved and sterilized with chlorhexidine gluconate (Hibitane, Zeneca, Johannesburg, South Africa) in alcohol. An incision of not more than 30 mm was made through the abdominal muscle, along the mid-ventral line 20 mm anterior to the anal opening (slightly more anterior for males due to the positioning of their genitals) and extended anteriorly. The data loggers were implanted or removed through this incision. The incision was sutured closed and the wound sprayed with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa). Each squirrel was injected with a non-steroidal anti-inflammatory drug (1 mg carprofen, Rimadyl®, Pfizer, South Africa) and a long-acting antibiotic (0.05 ml procaine benzylpenicillin 150 mg/ml and benzathine benzylpenicillin 126 mg/ml, Peni LA, Virbac Animal Health, South Africa).

During anaesthesia individually identifiable markings were made with permanent hair dye (Rich Brown, Viva, Wella AG, Darmstadt, Germany) on each squirrel. After surgery the animals were placed in a wire cage and kept warm until full recovery, which took less than one hour. If the animals had recovered by early afternoon they were released back at their point of capture. All animals recovered completely from surgery and their behaviour appeared normal.

Data loggers and measurement of body temperature

T_b was measured by miniature temperature-sensitive data loggers (DS 1921 Thermochron iButtons®, Dallas Semiconductor, Texas, USA). These loggers have a range of measurement from –40 to 85°C and can store 4096 data points at a resolution of 0.0625°C. The loggers were set to record the animals' T_b every five min which equated to a maximum of 14 days of continuous data. To obtain data for 28 days, two loggers were implanted into each ground squirrel. One logger was set to start measuring temperature two weeks after surgery (to allow for complete recovery of the animal from surgery) and the second was set to start approximately four weeks after surgery, thus allowing for 28 days of continuous T_b recording. The two loggers were taped together and coated in inert wax (Sasolwax Exp987, Sasol, South Africa) for added waterproofing.

The final weight of the two loggers when covered in wax was ~ 10 g and measured ~ 20 x 21 x 22 mm. The smallest ground squirrel used in this study weighed 602 g and thus the weight of the implants was no more than 2% of body mass which is within acceptable limits (Kamerman et al. 2001). Before surgery, the loggers were calibrated against a high-accuracy thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath to an accuracy of at least one sampling step (0.06°C) of the logger within the physiological range of T_b. The wax-covered loggers were dry-sterilised by formaldehyde vapour and rinsed in sterile water before implantation.

Behavioural observations

Squirrels were observed through binoculars (10 x 50 Bushnell, USA) from a stationary vehicle parked near the burrow clusters. Detailed observations could be made from as little as 10 to 30 m from the vehicle without appearing to influence the squirrels' behaviour.

Observers were present before the squirrels exited their burrows in the morning. The time of exit was recorded after which scan sampling began. It was not logistically possible to continuously record every marked squirrel's behaviour for the full duration of the study. Observations were thus made opportunistically on marked squirrels that were foraging near the burrow cluster. In the late afternoon or early evening the time that each marked squirrel entered their burrows for the night was recorded.

Focal sampling of individual squirrels was done at five minute intervals (Altmann 1974) to coincide with the temperature readings recorded by the loggers. Behaviours recorded were resting, foraging, locomotion, social, and below the surface. These behaviours were selected based on descriptions of the activity budgets of squirrels observed by Knight (1991) and Waterman (1995) with slight modifications to make them more suitable for a thermoregulation study. The behaviours were defined as follows:

- *Resting:* all activities not involving movement e.g. basking in the sun after rising in the morning and alert (i.e. surveying the surroundings for predators etc).
- *Foraging:* searching and scratching for food, eating and shuffling short distances while feeding.
- *Locomotion:* anything faster than a slow shuffle e.g. walking or running.
- *Social:* the squirrel grooming itself or another squirrel and all other behavioural interactions with another squirrel(s).
- *Below the surface:* the squirrel was out of sight in a burrow (on several occasions the squirrels retreated to the burrows due to initial movement of the observation vehicle; these recordings were not included in the analysis).

In addition, orientation to the sun (either parallel or perpendicular) and tail position (either up or down) were recorded within each time period. Tail use was only recorded with respect to thermoregulation (i.e. the tail held above the body to shield it from solar radiation), and makes no reference to tail use for social interactions, e.g. communication of predator presence, fighting or playing.

Environmental conditions

Microclimate variables (black globe, dry bulb, burrow and ground temperatures, relative humidity, wind speed and solar radiation) were recorded every 15 min for the duration of the study. All microclimate variables, except for burrow temperature, were measured and recorded by a portable weather station (HOBO Weather Station, Onset Computer Corporation, Pocasset, MA, USA) ~ 50 m from the "female burrow cluster", a position deemed to be representative of the microclimate variables experienced by all study animals. The temperature and relative humidity probes were housed in a vane which was painted white to reflect solar radiation and which moved in response to wind to allow ventilation of the probe. A temperature probe, situated in the centre of a 150 mm copper globe that was painted matt black and mounted one metre above the ground facing north, integrated air temperature, solar radiation and wind speed, and is hereforth referred to as globe temperature (T_g).

Ground temperature was measured using a thermocouple that was buried about 10 mm below the ground and recorded by a data logger (HOBO Data Logger, Onset Computer Corporation, Pocasset, MA, USA). Burrow temperature was recorded by placing a data logger in a small plastic container (50 x 20 x10 mm) which had perforations to ensure adequate air flow, into a burrow at a slant depth of ~ 1 m. The burrow was located near the middle of the burrow cluster used by the female ground squirrels. A wire was attached to the container to facilitate its insertion into and subsequent removal from, the burrow. According to Lynch (1980) a slant depth of 1 m corresponds to a vertical depth of approximately 500 mm. Environmental temperature data were collected for 26 continuous days, and analyzed with corresponding days of T_b measurements.

Data analysis

T_b and environmental data were divided into two categories: active and inactive, which corresponded to the active and inactive phases of the ground squirrels' activity. The start of the active phase did not correspond with sunrise but was taken as the arrival of sunlight at the study site, which was delayed by approximately one hour because of the position of the mountain, and usually corresponded with the squirrels' emergence from the burrows. The active phase ended at sunset and the inactive phase was taken from sunset to the start of the next active phase.

For each successive 24-h period, I calculated mean T_b for each individual. In addition, I calculated mean, minimum and maximum T_b for each individual for each day during their active and inactive phase. I averaged these parameters for each individual for the full study period. Because squirrels were forced to remain below ground on two days of heavy rainfall, these days were excluded from these calculations. To analyse the effect of remaining below ground on T_b, I averaged the T_b for all eight ground squirrels separately during the preceding inactive phase, the normal active phase on the day of heavy rainfall, and the following inactive phase. One-way analysis of variance (ANOVA) was used to compare these mean T_b's (*sensu* Lehmer et al. 2003). Tukey HSD post hoc tests were used to discern differences between individual squirrels when the overall test statistic was significant.

The amplitude of nychthemeral rhythm for each individual was calculated as the difference between the maximum and the minimum T_b reached within a 24-h period. During the active phase mean hourly T_b, per individual per day, was correlated against corresponding mean hourly T_g, using Pearson's linear correlations. I also correlated mean active phase T_b for each individual squirrel against mean active phase T_g for each day of the study. Independent Student *t*-tests were used to compare mean daily T_b, variability in T_b (as gauged by the standard deviation of the daily mean T_b's for each ground squirrel), and behaviour variables between summer and winter. The seasonal comparison used T_b data from eight individuals in summer and six in winter, and behavioural data from seven individuals for each season. A non-parametric Mann-Whitney test was used for data that did not meet the assumptions necessary for a parametric two sample test. All statistical analyses were performed using STATISTICA 8 ©, Statsoft Inc. Values of $P < 0.05$ were considered significant. All means are reported as mean ± standard deviation. The Animal Ethics Committee of the University of Cape Town (approval 2002/V09/JOR) approved all experimental procedures.

Results

Environmental conditions

Average environmental conditions prevalent during the study are represented in Table 1. Rainfall during the summer study period was exceptionally high (290 mm) and was over three times the monthly mean rainfall recorded for January over the preceding 12 years. Days were characterised by highly variable cloud cover, consistent with the build up of thunder storms typical of Southern African summer rainfall regions. Both solar radiation and T_g fluctuated rapidly as a result of changes in cloud cover (Fig. 1) and mean maximum T_g and solar radiation during the squirrels' active phase were 39.8 ± 5.3°C and 1092.8 ± 186.0 $W.m^{-2}$ respectively. Burrow temperature over the study period was relatively stable (20.4 ± 1.7°C) with day-time burrow temperatures ~ 1°C higher than at night (Table 1; Fig. 1).

Table 1. Average (mean ± SD) environmental conditions and absolute minimum and maximum values for the summer study period

Variable measured	Active phase	Inactive phase	Minimum	Maximum
Globe temperature (°C)	29.3 ± 4.5	16.1 ± 1.6	9.2	46.5
Ground temperature (°C)	26.9 ±3.7	19.2 ± 1.6	14.6	45.8
Ambient temperature (°C)	22.4 ± 2.4	16.4 ± 1.6	10.2	31.5
Burrow temperature (°C)	20.7 ± 0.9	19.6 ± 2.7	16.6	22.6
Solar radiation ($W.m^{-2}$)	416.5 ± 129.8	-	1.0	1277.0
Wind speed ($km.h^{-1}$)	6.6 ± 3.5	11.4 ± 8.9	0.0	35.6
Relative humidity (%)	66.7 ± 11.3	82.9 ± 8.4	28.8	99.3

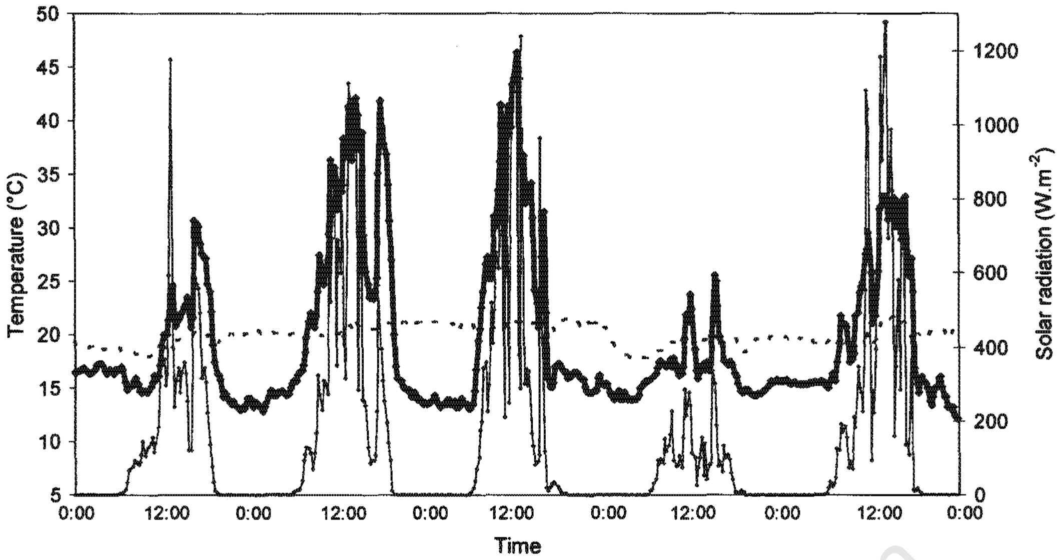

Figure 1: Globe temperature (black line), burrow temperature (dashed grey line) and solar radiation (grey line) over five consecutive days during the study period. The fourth day represents a day of continuous rain.

Behavioural observations

I recorded 265 hours (3184 scan samples) of behavioural observations on seven implanted ground squirrels. The majority of the ground squirrels (five of the eight) did not emerge above ground during the two days of continuous rain, and on seven days their emergence from the burrows in the morning was delayed by several hours (emergence times between 10:30 – 13:45) due to inclement weather. Mean emergence time on relatively clear days was 08:06 ± 5 min (range 07:19 to 08:45). Mean time for going below ground, on both the clear days and after morning rainfall, was 18:01 ± 5 min (range 17:00 to 18:58). Ground squirrels were not observed to bask upon emergence in the mornings and began foraging almost immediately. The majority of the active phase was spent foraging (55 ± 14 %) with 29 ± 9 % of their time spent below ground in the burrow. A large proportion (82 ± 6 %) of all below ground activity was as a direct result of rainfall. Only 12 ± 7 % of the total time was spent resting, with socialising (3 ± 1 %) and locomotion (1 ± 0 %) being performed the least often throughout the study period.

Body orientation to the sun was not analysed due to the exceptionally high frequency of cloud cover (38% of all observations) and the fact that the sun was directly overhead for at least three hours during midday. The tail was raised for 25% of all above ground observations. However, tail use was frequently transient and only on 32 occasions was it observed to shield ground squirrels for longer than 20 min. On most of these occasions (78%), T_b continued to rise, but there was no clear or consistent pattern. In addition, the response of T_b to tail use in the morning and afternoon could be confounded by the typical rise and fall of the nycthemeral rhythm of T_b during the active phase.

Body temperature patterns

T_b of the ground squirrels showed a pronounced nychthemeral rhythm with a high T_b during the active phase and a low T_b during the inactive phase (Fig. 2). The mean nychthemeral amplitude was 3.9 ± 0.2°C. Behavioural observations confirmed that T_b of the ground squirrels did not start increasing from the inactive phase T_b level until they had emerged from their burrows in the morning. Upon emergence T_b rose rapidly reaching a peak after 14:00 before the onset of a rapid decrease in the late afternoon (~ 17:00) and prior to the ground squirrels going below for the night. T_b continued to decrease after the study animals had gone below ground until it stabilized around the mean nocturnal T_b in the late evening (~ 22:00).

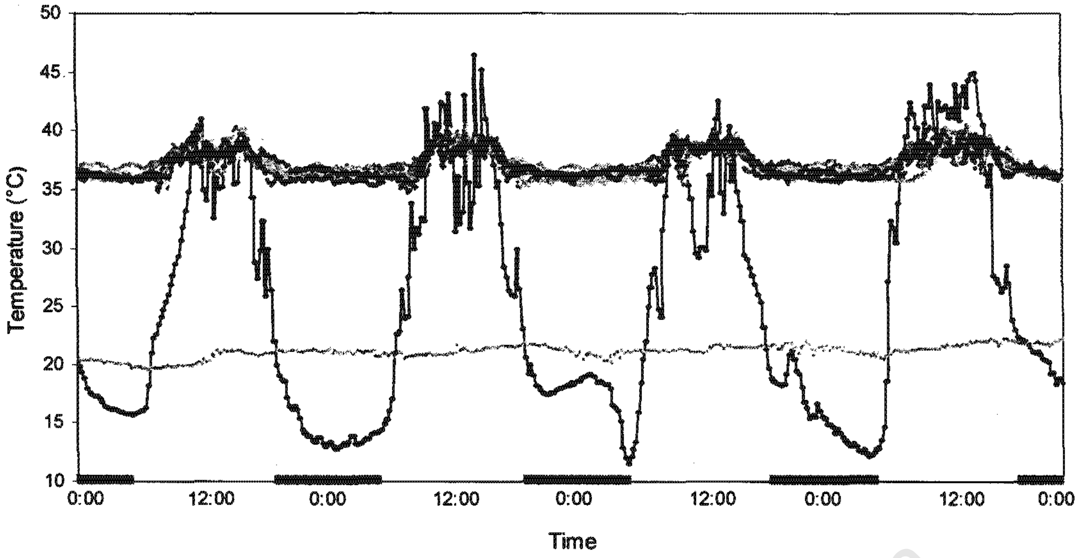

Figure 2: Body temperature (grey lines) of eight free-ranging Cape ground squirrels over four consecutive days with the corresponding globe (black line) and burrow (dashed line) temperatures. The dark bars above the x-axis indicate the inactive phase.

The mean summer T_b for all eight ground squirrels averaged over the 26 days was 37.0 ± 0.1°C. The mean inactive and active phase T_b's were 36.3 ± 0.1°C and 37.6 ± 0.2°C, respectively (Table 2). The mean minimum inactive T_b for the squirrels was 35.6 ± 0.2°C and no ground squirrel dropped its T_b below 32.9°C during the inactive phase (Table 2). The mean maximum active phase T_b for the squirrels was 39.6 ± 0.2°C and T_b rarely rose above 40°C (< 1% of all active T_b recordings). A sharp drop in T_b immediately after emergence from the burrows in the morning was evident on some mornings but was obscured on the vast majority of days because of the cloud induced variability in T_b during the active phase.

Table 2. Comparison of mean, minimum and maximum daily body temperatures (T_b) in °C, for eight free-ranging Cape ground squirrels during the austral summer. Highest and lowest values reached during each phase across all individuals are indicated with *.

	Female					Male			
	Female 1	**Female 2**	**Female 3**	**Female 4**	**Female 5**	**Male 1**	**Male 2**	**Male 3**	**Mean**
Body Mass (g)	712	694	652	624	650	864	818	704	715 ± 84
Mean T_b	36.9 ± 0.5	37.0 ± 0.4	37.1 ± 0.4	37.2 ± 0.4	36.9 ± 0.5	36.9 ± 0.5	36.7 ± 0.4	37.1 ± 0.4	37.0 ± 0.2
Active phase									
Mean T_b	37.5 ± 0.6	37.5 ± 0.5	37.7 ± 0.5	37.8 ± 0.5	37.5 ± 0.6	37.5 ± 0.5	37.4 ± 0.5	37.9 ± 0.5	37.6 ± 0.2
Mean min T_b	35.3 ± 0.9	35.6 ± 0.7	35.6 ± 0.8	35.8 ± 0.6	34.9 ± 1.0	35.4 ± 0.7	35.3 ± 0.8	35.9 ± 0.6	35.5 ± 0.3
Mean max T_b	39.7 ± 0.5	39.5 ± 0.4	39.8 ± 0.34	39.8 ± 0.4	39.6 ± 0.5	39.3 ± 0.5	39.6 ± 0.5	39.6 ± 0.4	39.6 ± 0.2
Absolute min T_b	33.4	34.2	33.2	34.0	32.3	33.8	33.4	34.6	32.3*
Absolute max T_b	40.6	40.0	40.5	40.5	40.3	40.4	40.5	40.6	40.6*
Inactive phase									
Mean T_b	36.2 ± 0.6	36.4 ± 0.5	36.3 ± 0.5	36.5 ± 0.5	36.2 ± 0.8	36.2 ± 0.7	36.0 ± 0.7	36.3 ± 0.4	36.3 ± 0.2
Mean min T_b	35.5 ± 0.8	35.8 ± 0.5	35.6 ± 0.6	35.8 ± 0.6	35.5 ± 0.8	35.5 ± 0.7	35.4 ± 0.7	35.8 ± 0.5	35.6 ± 0.2
Mean max T_b	37.0 ± 0.7	37.1 ± 0.6	37.2 ± 0.6	37.3 ± 0.6	37.1 ± 0.8	37.0 ± 0.8	36.8 ± 0.8	36.9 ± 0.6	37.0 ± 0.2
Absolute min T_b	33.9	34.7	34.4	34.1	33.7	33.3	32.9	34.4	32.9*
Absolute max T_b	38.1	38.0	38.3	38.9	38.2	38.1	37.9	38.4	38.9*
Nychthemeral amplitude	4.1 ± 0.7	3.6 ± 0.5	4.1 ± 0.6	3.9 ± 0.6	3.9 ± 0.7	3.6 ± 0.7	4.1 ± 0.5	3.8 ± 0.6	3.9 ± 0.2

On the two rainy days when ground squirrels were not observed to forage above ground (except for the three animals indicated in Fig. 3), T_b's did not rise to normal active phase levels. There was a stepwise lowering of T_b from the preceding inactive phase, to the usual active phase on the rainy day, to the following inactive phase (Fig. 4; ANOVA, $F_{2,21} = 16.8$, $P < 0.01$; post hoc Tukey HSD test). The T_b's of the three ground squirrels that emerged to forage for one hour when the rain stopped, rose rapidly on emergence and started to decrease again when they re-entered their burrows following further rainfall (Fig. 3).

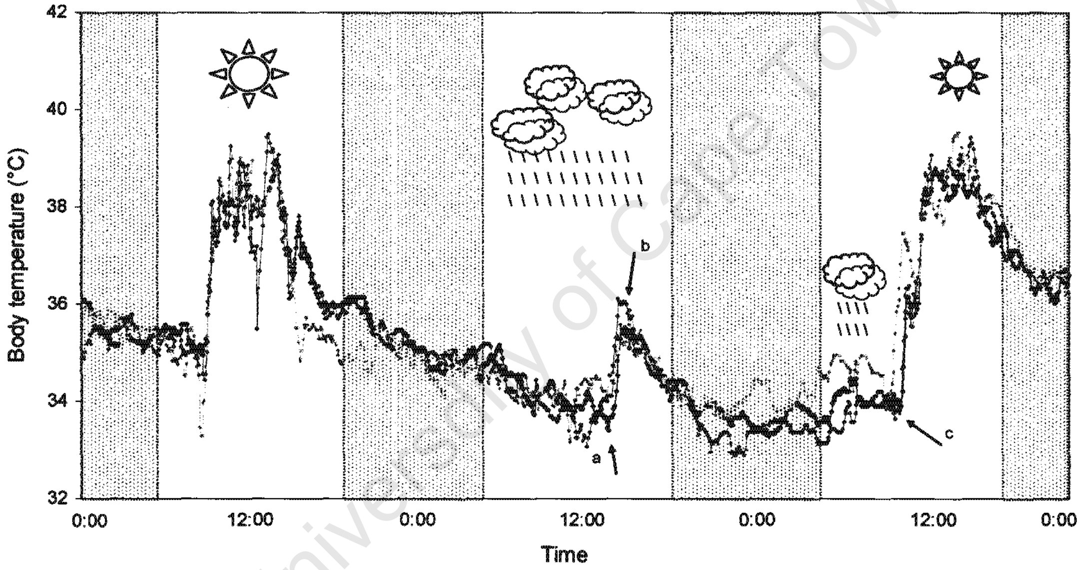

Figure 3: Body temperature of three Cape ground squirrels over three days in summer showing lowered body temperature during a day of continuous rain. Arrow a) and b) indicate a period of an hour when it stopped raining and the ground squirrels came above ground to forage. Arrow c) indicates delayed emergence from the burrow in the morning due to rain. The shaded areas indicate the inactive phase.

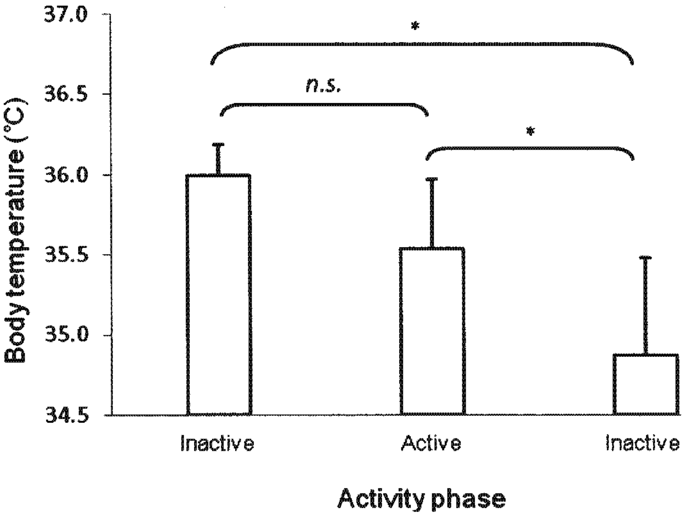

Figure 4: Bar chart showing the effect of continuous rain during the active phase on body temperatures of Cape ground squirrels. Mean body temperatures (± SD) of eight Cape ground squirrels are plotted on the activity phase (preceding inactive, rainy day active, following inactive). Significant differences at $P < 0.05$ are indicated with *; n.s. = not significant.

Mean active phase T_b correlated positively with mean active phase T_g for each ground squirrel ($r^2 = 0.5 - 0.7$; $P < 0.01$; $n = 25$; female 4 shown in Fig. 5). There was also a significant correlation between hourly T_b and hourly T_g for each squirrel during the active phase for most days of the study (e.g. 11th January; $r^2 = 0.6 - 0.9$; $P \leq 0.01$).

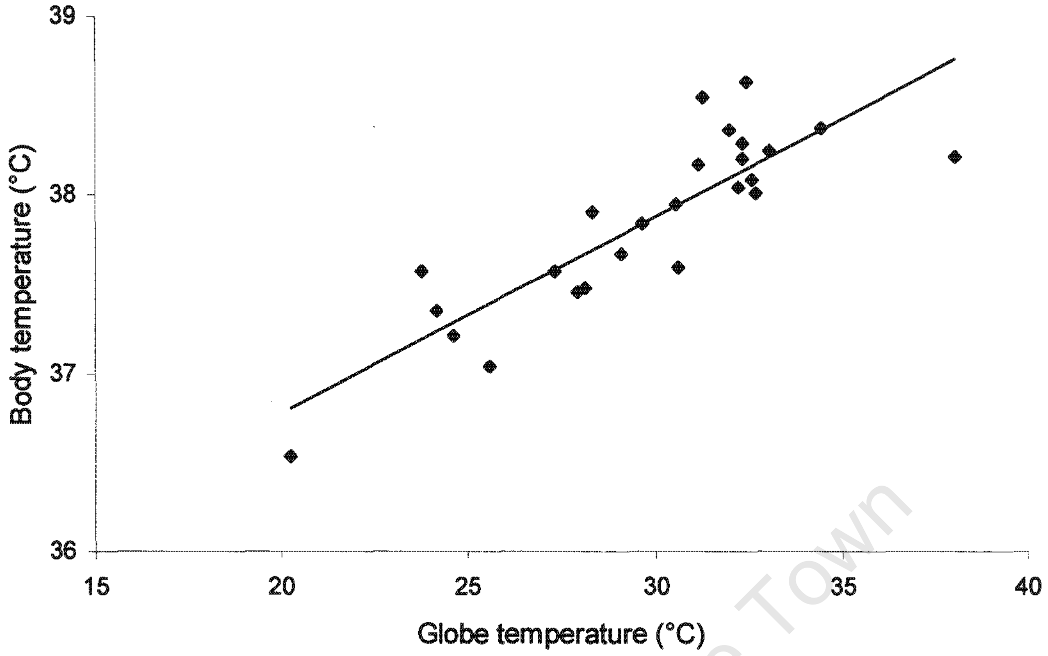

Figure 5: Mean active phase body temperature plotted against mean active phase globe temperature for an adult female (female 4, n = 26 days data), with fitted linear regression line ($r^2 = 0.7$, $P < 0.01$).

Seasonal comparison

Burrow temperature was ~ 10°C higher during summer (20.4 ± 1.7°C) than during winter (10.6 ± 1.0°C). Mean active phase T_g was ~ 5°C higher during summer (29.3 ± 4.5°C) than winter (24.7 ± 4.6°C), even though mean maximum active phase T_g was ~ 10°C higher during summer (39.8 ± 5.3°C) than winter (30.0 ± 4.7°C). Mean inactive phase T_g was ~ 11°C higher during summer (16.2 ± 1.6°C) than winter (4.7 ± 4.3°C).

There were no significant differences in mean daily T_b between summer and winter, despite mean active phase T_b being lower during summer than during winter (Table 3). Nychthemeral amplitude of T_b and mean inactive T_b did not differ significantly between the seasons. Variability in T_b, was higher during the active phase in summer than in winter but there was no difference between the inactive phase variability between the seasons (Table 3). The lower mean active phase T_b and the greater variability of T_b during the active phase in summer, than winter, was likely the result of inclement weather. Such inclement weather also influenced the pattern of the T_b rhythm. The delayed emergence times as a result of rainfall resulted in a phase delay in T_b increase (Fig. 6). The hourly mean minimum T_b's during the active phase in summer were generally lower than during winter due to the low T_b's of squirrels that remained in their burrows during periods of high rainfall (Fig. 6).

Table 3. Comparison of body temperature (T_b), (°C) means, variability and nychthemeral amplitude of free-ranging Cape ground squirrels during winter and summer

Variable measured	Summer	Winter	*df*	*t*	*P*
Mean T_b	37.0 ± 0.2	37.0 ± 0.3	12	-0.68	0.5
Mean active phase T_b	37.6 ± 0.2	38.1 ± 0.1	12	-6.39	< 0.01
Mean inactive phase T_b	36.3 ± 0.2	36.3 ± 0.3	12	-0.54	0.6
Mean maximum active phase T_b	39.6 ± 0.2	39.5 ± 0.1	12	1.70	0.12
Mean minimum inactive phase T_b	35.6 ± 0.2	35.7 ± 0.3	12	-0.46	0.65
Active phase T_b variability	1.1 ± 0.1	0.9 ± 0.1	12	3.45	< 0.01
Inactive phase T_b variability	0.3 ± 0.0	0.3 ± 0.0	12	0.10	0.92
Nychthemeral amplitude	3.9 ± 0.2	3.8 ± 0.3	12	0.75	0.47

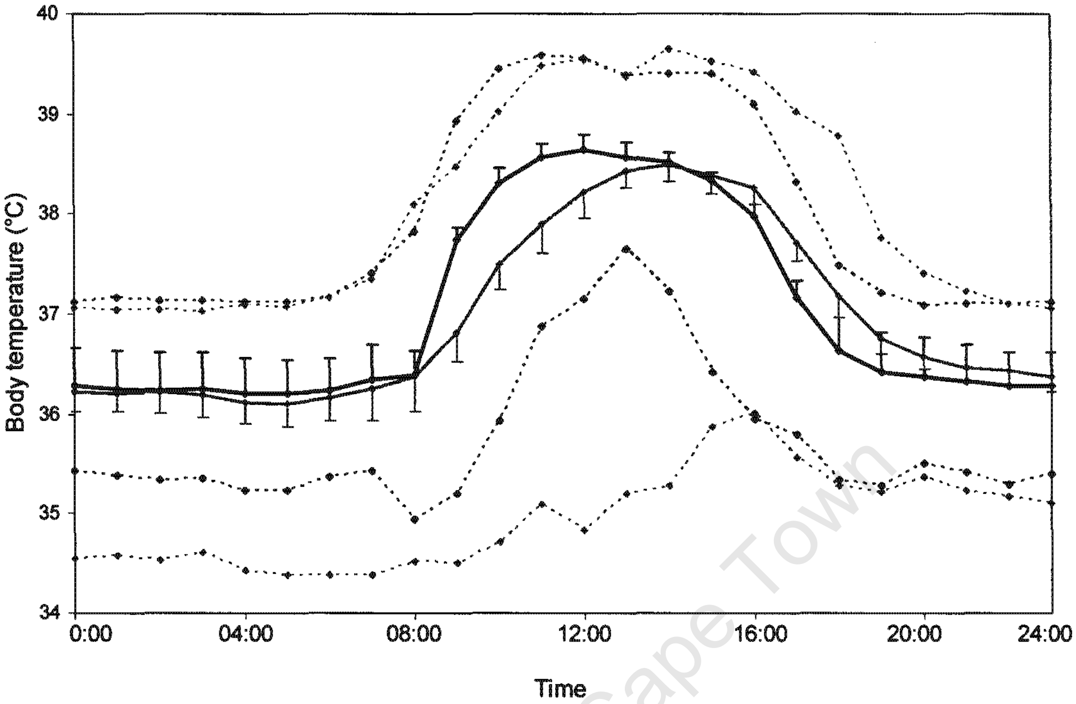

Figure 6: Mean (± SD) hourly body temperature of free-ranging Cape ground squirrels during summer (grey line) and winter (black line). Dotted lines (grey for summer; black for winter) represent mean hourly minimum and maximum body temperature values for each season.

During the active phase in summer the ground squirrels spent significantly less time foraging (55 ± 14 %) than during winter (74 ± 8%), (*t*-test, t_{12} = -3.12, $P < 0.01$). Significantly more time (Mann-Whitney, $P < 0.01$) was spent below ground in burrows during the summer active phase (29 ± 9 %) than during winter (3 ± 2%),.

Discussion

Although mean maximum T_g during the active phase was approximately 40°C, T_g fluctuated rapidly with cloud cover and contrary to my predictions, the above-ground activity of the study animals was largely constrained by rain rather than by high temperatures. The study animals exhibited a nychthemeral rhythm of Tb similar to that observed during winter (Chapter 2) and similar to other diurnal small mammals (Refinetti 1999). However, on mornings when squirrels displayed a delayed emergence as a result of rain, T_b's did not reach mean active phase T_b levels. Such findings confirm my suggestion from the winter study (Chapter 2) that Cape ground squirrels are able to modulate their endogenous circadian T_b rhythm. Responding to a circadian T_b rhythm with a spontaneous increase in T_b before or at the start of the active phase has been observed in other small mammals (Refinetti 1999; Cooper and Withers 2004; Long et al. 2005; Brown and Downs 2006) but may be maladaptive in a small mammal faced with an unpredictable environment.

Remaining below ground during inclement weather has also been observed in the Arctic ground squirrel, *S. paryii* (Long et al. 2005). While the latter maintained a relatively high T_b when forced below by bad weather the Cape ground squirrels in this study maintained T_b at ~ 2°C lower than normal active phase T_b's and similar to that of the inactive phase. Presumably Arctic ground squirrels can maintain high T_b's with basal levels of metabolic heat production because of their well insulated burrows (Chappell 1981). The Cape ground squirrels apparently further reduced metabolic costs by maintaining lower T_b's when deprived of foraging time. In addition, there appears to be a step-wise lowering of T_b from the nights preceding the rainy days to the following nights. This pattern is similar to that observed in captive nectar-feeding bats, *Glossophaga soricina*, that were food-deprived for two days and showed a step-wise lowering of T_b over this period before entering torpor (Kelm and von Helversen 2007). Whether Cape ground squirrels would further lower their T_b and enter torpor after a sustained period of enforced food deprivation requires further research.

The Cape ground squirrels in this study maintained a mean T_b of 37.0°C in both summer and winter. Such findings are in contrast to numerous studies that report that mammals that are active year-round maintain higher T_b's in summer than in winter (Golightly and Ohmart 1978; Muchlinski et al. 1998; Pereira et al. 2002; Fuller et al. 2005; Brown and Downs 2006; Nieminen and Mustonen 2008). A higher T_b during summer has been hypothesised to reduce the thermal radiation gradient between the animal and its environment and facilitates passive heat loss, whereas lower T_b's during winter minimize heat loss to the environment and save thermoregulatory energy (Hayes 1976; Jefimow 2007). There was no difference in the nychthemeral amplitude of T_b in the study animals between the seasons. Research into seasonal changes in the nychthemeral amplitude of T_b of small mammals has yielded variable results. Some researchers have reported no changes in the amplitude between seasons

(Heldmaier et al. 1989; Fuller et al. 2005), others reported a higher amplitude during winter compared to summer (Muchlinski et al. 1998; Pereira et al. 2002; Lehmer et al. 2003; Nieminen and Mustonen 2008), while others have reported a lower amplitude during winter than summer (Haim and Zisapel 1995; Haim et al. 1997; Jefimow 2007).

A decrease in the nychthemeral amplitude of T_b during summer is usually the result of an increase in the inactive phase T_b with a relatively minimal increase in the active phase T_b (Muchlinski et al. 1998; Pereira et al. 2002; Lehmer et al. 2003). The Cape ground squirrels in this study maintained a constant inactive phase T_b (36.3°C) between the seasons. Experimental research has indicated that decreases in inactive phase T_b can be attributed to both a decrease in ambient temperatures (Refinetti 1997; Aujard et al. 1998; Aujard and Vasseur 2001) and to food deprivation (Pereira et al. 2002). Although burrow temperatures were ~10°C lower during winter in this study, Cape ground squirrel may behaviourally modify the thermal environment of the burrow in which they spend the inactive phase by choosing burrows at different depths (Lynch 1980; Lovegrove and Knight-Eloff 1988), using nesting material within a chamber, and huddling (Knight 1991; Chapter 2). T_b during the summer inactive phase was significantly lower only on the two nights following days of heavy rainfall (i.e. the squirrels were food deprived) compared to nights following normal activity and foraging. The ability to maintain a stable T_b during the inactive phase during both winter and summer following days of normal foraging presumably indicates that, although squirrels forage for longer during winter, food resources were not limited in either season.

The mean inactive phase T_b (36.3°C) of the Cape ground squirrels during summer is lower than that reported for northern temperate ground squirrels that are spontaneous hibernators during winter. Arctic ground squirrels, Richardson's ground squirrels, *S. richardsoni*, and the Uinta ground squirrels, *S. armatus*, maintain mean inactive phase T_b's of 38.4°C (Chappell 1981), 37.9°C (Wang 1972), and 38.7°C (Gessaman 1980), respectively. These ground squirrels forage for up to 16 hours per day during their short active season and it is thought that they are unable to cycle their T_b rapidly enough for nocturnal hypothermia to provide an energy saving (Chappell 1981). The Cape ground squirrels in this study were inactive at night for a minimum of 12 hours and even a moderate nocturnal hypothermia (~ 1°C) may provide energetic savings (Golightly and Ohmart 1978; Pereira et al. 2002; Brown and Downs 2006; Warnecke et al. 2007). This moderate hypothermia is similar to that of the black-tailed prairie dog, *Cynomys lucodicianus*, which is active year-round, and maintains a mean summer inactive phase T_b of 36.8°C (Lehmer et al. 2003). Maintaining a lower inactive phase T_b may thus be an energy saving strategy for small mammals that are active year-round.

The finding that mean active phase T_b during summer (37.6°C) was lower than during winter (38.1°C) despite higher summer T_g's was unexpected. I attribute this difference to the large amount of time that the study animals were forced below ground due to high summer rainfall. T_b's of captive Cape ground squirrel rise above 40°C when exposed to high ambient temperatures (Van Heerden and Dauth 1987; Knight 1991). However, the free-living ground squirrels in this study maintained similar mean maximum T_b's of ~ 39.5°C during both summer and winter. Thus it appears that in their natural environment, Cape ground squirrel preferentially maintain T_b's below 40°C and can use a variety of behavioural thermoregulatory adaptations to achieve this. Captive animals do not have access to the full range of thermoregulatory behaviours, and my study emphasises the importance of measuring physiological variables in the field as suggested by Mitchell et al. (2002).

As observed in my winter study (Chapter 2), Cape ground squirrel summer T_b's appeared to be strongly influenced by environmental conditions during the active phase with a positive correlation between mean active phase T_b and T_g. The strong positive correlation between active phase hourly T_b and T_g ($r^2 = 0.5 – 0.7$) is higher than that reported by Fick et al. ($r^2 < 0.2$; in press). As I concluded in my winter study (Chapter 2), the strong correlation observed between hourly T_b and T_g is most likely as a result of passive heat gain during the morning and heat loss in the late afternoon, as a strategy to reduce the metabolic costs of thermoregulation.

Cape ground squirrels in my study spent significantly less time foraging in summer than in winter. Reduced summer foraging may be attributed to high quality forage in conjunction with a reduction in the total time spent active due to inclement weather. By contrast winters were characterised by low primary productivity with a percentage of time spent foraging for high quality below ground food items. Thus during a summer of high rainfall, when the thermoregulatory costs of being active above ground outweigh the benefits gained from foraging, ground squirrels can potentially maximize their energy intake over periods of days, rather than daily, as has been suggested for the thirteen-lined ground squirrels, *S. tridecemlineatus* (Vispo and Bakken 1993) and the Arctic ground squirrels (Long et al. 2005).

A lack of sustained high ambient temperatures prevented us from elucidating the role of the parasol-like tail in thermoregulation. Similar to Fick et al. (in press), I did note that T_b typically continued to rise while the tail was raised. In only one instance did T_b of a study animal rise above 40°C with sustained tail use. Bennett et al. (1984) reported that shade from the tail decreased the heat load on pelt-covered mannequins of Cape ground squirrel by 6 – 8°C. Raising the tail may thus decrease the rate of heat gain and extend the foraging time available to the ground squirrels rather than allowing them to maintain lower T_b's.

It is well known that ground squirrels, including the Cape ground squirrel, use burrows to escape extreme heat and that T_b's drop while in the burrow (Chappell and Bartholomew 1981b; Byman 1985; Vispo and Bakken 1993; Long et al. 2005; Fick et al. in press). My study revealed that burrow use during summer was largely a response to high rainfall. It is possible that the long grass, in which the squirrels foraged, in comparison to exposed areas, provided a cooler microclimate during summer (Morhardt and Gates 1974; McCafferty et al. 2003) and together with the cloud cover negated the need for frequent burrow use during the summer active period.

I have characterised the T_b patterns of Cape ground squirrels in their natural environment during a summer of exceptionally high rainfall. I provide further evidence that Cape ground squirrels apparently have the ability to modulate their endogenous circadian T_b rhythm and that they maintain low T_b's when unable to exit their burrows during their normal active phase. I have suggested that lowered T_b represents an adaptation to save energy when access to food is limited. I have provided evidence that Cape ground squirrels maintain a seasonal mean T_b with moderate inactive phase hypothermia that would provide moderate energy savings to a small mammal that is active year-round. In addition, I have reported that active phase T_b's are influenced by environmental conditions. Tolerance of Cape ground squirrels to hyperthermia of > 40°C in their natural environment requires further investigation.

Synthesis

The advent of miniature temperature-sensitive data loggers that are able to record the T_b's of free-ranging animals has established the importance of determining the thermoregulatory strategies employed by animals living in their natural environment, rather than those determined in the laboratory or in captivity. In the latter cases, animals are not exposed to the complex stressors imposed by their natural environments, and in addition may be inhibited from employing the full suite of behavioural thermoregulatory strategies available to free-ranging animals. In this study I set out to determine T_b patterns of free-ranging Cape ground squirrels living in a semi-arid environment during the austral winter and summer, in addition to simultaneously recording certain microclimate and behavioural variables. More specifically I investigated: 1) whether this small mammal employs nocturnal hypothermia or daily torpor to mitigate a potential energy crisis and low ambient temperatures during winter; 2) whether high ambient temperatures in summer result in the relaxation of strict thermoregulatory control.

Although Cape ground squirrel T_b's in this study ranged between 32.3 and 40.6°C they maintained a mean T_b of 37.0°C in both winter and summer. In addition, the nychthemeral amplitude of T_b of ~ 3.9°C did not vary between seasons. These results were unexpected as mammals that are active year-round are reported to maintain higher T_b's during summer than winter, presumably as a thermoregulatory strategy to save energy. Cape ground squirrels in this study apparently were not exposed to environmental extremes and escaped to thermally buffered burrows during inclement weather and cold winter nights. Seasonal differences in ambient temperature at the study site were dampened by high solar radiation in winter and high cloud cover with rainfall in summer.

I found no evidence of torpor or even marked hypothermia during winter with inactive phase T_b's maintained at ~ 36.3°C during both seasons and mean minimum inactive phase T_b's being consistently above 35°C. Cape ground squirrels appear to employ a moderate nocturnal hypothermia that may be an energy saving strategy for a small mammal that is active year-round. The most likely reason for not employing torpor during the dry and cold winter months is that these ground squirrels have access to abundant food (the underground storage organs of plants) that is both energy and water rich (Marsh et al. 1978; Knight 1991). Lowering of inactive phase T_b's is typically explained by food shortage and/or decreased ambient temperatures. Presumably the constant inactive phase T_b's maintained across seasons in this study indicates that food was not limiting and that although burrow temperatures were ~ 10°C lower during winter than summer, ground squirrels can modify the thermal environment of the burrow by choosing nests at different depths, incorporating nesting material, and huddling with conspecifics.

Surprisingly, winter mean active phase T_b (38.1°C) was higher than summer mean active phase T_b (37.6°C). This is most likely a consequence of the exceptionally high summer rainfall which forced the squirrels to remain below ground for substantial portions of their normal active phase. These periods of forced food deprivation were associated with lower mean T_b's compared with the mean active phase T_b over the whole study period. Active phase T_b's were shown to correlate significantly with ambient temperatures during both winter and summer suggesting that a more typical summer with limited cloud cover and rainfall may result in a higher mean active phase T_b than was reported here.

Cape ground squirrels appear to preferentially maintain T_b's below 40°C with mean active phase maximum T_b's not exceeding 39.6°C during either winter or summer. Unfortunately, ambient temperatures during summer were seldom high enough for me to determine the ability of Cape ground squirrels to tolerate hyperthermia as a thermoregulatory strategy to increase foraging time. I was also unable to elucidate the effect of the parasol-like tail as a behavioural mechanism to extend foraging time because of generally low summer ambient temperatures. Similar to Fick et al. (in press), it was apparent that T_b continued to increase while the tail was raised. I propose that further research into the use of the parasol-like tail, both as a solar radiation shield during summer, as well as a possible insulative blanket at night during winter should be conducted. A novel approach to the adaptive role of the Cape ground squirrel's tail would be to partially and completely shave the tail-hair and to compare both the T_b and behaviour of these experimental individuals with control individuals matched as closely for size and reproductive state as possible.

My research suggests that Cape ground squirrels are able to modulate their endogenous T_b rhythm. Although behavioural observations indicated that T_b's started to rise when ground squirrels exited their burrows in the morning, this increase did not occur when ground squirrels were unable to exit their burrows to begin their normal active phase due to the presence of a potential predator (winter experiment) or inclement weather (rainfall during summer). Responding to an endogenous T_b rhythm with a spontaneous increase in T_b, before or at the start of the active phase, may be maladaptive in a small mammal faced with an unpredictable environment. To further our understanding of the endogenous T_b rhythm of Cape ground squirrels, it is suggested that "free-running" experiments in the absence of external "Zeitgebers" (i.e. under laboratory conditions) be performed.

I report the first example of lactational hyperthermia in Cape ground squirrels. The mean T_b of two lactating females was ~ 0.7°C higher than non-lactating individuals. This elevation is thought to be due to the increased heat load as a result of the highly exothermic process of milk production. The nychthemeral amplitude of T_b for the lactating females did not differ significantly from the other study animals, and may indicate that although T_b's are elevated during lactation, there is still thermoregulatory control over T_b. The hypothesis that this chronic elevation of T_b during lactation may constrain the breeding season of Cape ground squirrels to the cooler months, as high day-time temperatures may increase the risk of T_b's reaching lethal limits, remains to be tested. Furthermore, it remains to be determined whether Cape ground squirrel exhibit gestational hypothermia, as has been documented in other small mammals (Kozak 1997; Cairns et al. 2005).

This thesis documents T_b's in free-ranging Cape ground squirrels during winter for the first time, and provides the first seasonal comparison of T_b's between individuals from the same population within one calendar year. The study site is characterised by a semi-arid, summer rainfall region and will provide a basis for comparisons with Cape ground squirrels living in the northern, arid regions of their distribution as well as in the winter rainfall regions of the west coast of South Africa. Such comparisons will provide further insight into the full extent of the thermoregulatory strategies employed by Cape ground squirrels. I hypothesise that inactive phase T_b's will be lower only if food is limited, as this study has shown that the squirrels are capable of escaping from extreme cold by entering their thermally buffered burrows. I also propose that the nychthemeral amplitude of T_b of Cape ground squirrels will increase in comparison to those reported here if the ground squirrels are faced with food shortage after a prolonged period of drought or when they are faced with higher active phase temperatures than those reached in this study.

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