Heterothermy and seasonal patterns of metabolic rate in the southern African hedgehog (*Atelerix frontalis*)

by

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Declaration:
In accordance with Rule G4.6.3, I hereby declare that the above-mentioned treatise/dissertation/thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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Date: 31 March 2011
The work described in this dissertation was carried out on a private farm (Plaatfontein) in the Northern Cape Province, South Africa. All equipment used in this field-based study is the property of the Zoology department at the Nelson Mandela Metropolitan University, Port Elizabeth. The study was carried out under the supervision of Dr Nomakwezi Mzilikazi.

The content of this dissertation is original work by the author and has not been previously been submitted for assessment to another University or for another qualification. Where use has been made of the work of others it is duly acknowledged in the text.

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All procedures adhered to the Code of Animal Experimentation adopted by the Nelson Mandela Metropolitan University (NMMU). Animal ethics clearance was granted by the NMMU ethics committee (A08 – SCI – ZOO – 003). Permits were issued by the Northern Cape Department of Tourism, Environment and Conservation (FLORA 036/2009).

Some of the work described in this dissertation has been accepted for publication in an international journal, Journal of Comparative Physiology B (the abstract is attached as Appendix 3).
ABSTRACT

Animals that inhabit unfavourable habitats and experience seasons where the cost of maintenance exceeds the available energy resources have over time developed behavioural and physiological mechanisms to survive. These adaptations include changes in activity, improvement of cold tolerance by using nonshivering thermogenesis (NST), improvement of thermal conductance, reduction of body mass, or acclimation to colder temperatures (reduction of metabolic requirement). In addition some species exhibit heterothermy, in the form of either daily torpor or longer-term hibernation. The southern African hedgehog (*Atelerix frontalis*) is an excellent candidate to investigate the phenomenon of heterothermy because it is a small insectivore (summer body mass ca. 300 to 400g), burrows, inhabits harsh habitats and is not easy to find during the winter months.

In this study I aimed to investigate whether *A. frontalis* exhibits seasonal differences in metabolic rate and furthermore if this species exhibits heterothermy. The study was carried out in the Northern Cape Province, South Africa. Hedgehogs were hand captured and their metabolic rates were measured using indirect calorimetry. Individuals were implanted with temperature dataloggers for a summer period (November 2009-January 2010) and a winter period (May-August 2009).

The summer BMR of adult *A. frontalis* (0.448 ±0.035 mlO$_2$/g/h, n=4) was significantly lower than their winter BMR (0.811 ±0.073 mlO$_2$/g/h, n=4) and statistical analyses revealed that this was an affect caused by seasonal changes in the ambient environment. Individuals spent up to 84% of time during the measurement period torpid (-8°C <T$_a$<21°C). Body mass appears to be an important factor in determining the pattern of heterothermy (daily torpor versus hibernation) used in this species.

To my knowledge the extremely low body temperature (T$_{b,\text{min}}$) of 1.0°C recorded for *A. frontalis* is the lowest T$_{b,\text{min}}$ recorded for a mainland Afrotropical mammal. This species displays classic up-regulation in metabolic rate during winter, resulting in an increase in the energetic requirements of the species. As a result, heterothermy appears to play a significant role in the energy balance of this species during winter, contributing to energy saving. Heterothermy may enable this species to survive in the face of global climate change.
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INTRODUCTION

Survival of an individual animal is dependant on the adequate intake of energy (food) from its surrounding environment, in order for it to not only meet its maintenance requirements, but also to have excess energy to allocate to procreation (Fig 1) (Brown et al. 1993; Lovegrove 2000; Lovegrove 2003). Any surplus energy can then be utilised for reproduction, and thus an animal’s fitness is achieved (Brown et al. 1993; Lovegrove 2000; Lovegrove 2003). The amount of energy required for body maintenance, reproduction and production, varies according to various physical and environmental factors, such as the quality of the ingested food items, the efficiency of the digestive system, life history strategies, the amount of effort allocated to reproduction and even the type of locomotion (Lovegrove 2000, Lovegrove & Haines 2004; McKechnie et al. 2007).

![Energy Cascade Diagram](image)

**Fig. 1** The Energy Cascade (adapted from Lovegrove, 2006). Ingested energy gets digested and metabolised before it can be used for maintenance mechanisms such as locomotion, basal metabolism and thermoregulation. Any excess is then used for production and reproduction.

An endothermic animal has advantages; such as, a higher and more stable body temperature, which allows for increased physiological efficiency (Hayes & Garland 1995; McNab 1978). Additionally, endotherms can be active at any time of the day and at a wider range of environmental temperatures, which leads to increased niche availability (Hayes & Garland 1995; McNab 1978). Small endotherms have higher metabolic requirements gram per gram, than larger endotherms, because of their high surface area to volume ratio, since they lose more heat to the environment and therefore have to allocate more energy to
thermoregulation (Heldmaier 1989; Willmer et al. 2005). One of the most common ways of measuring the energy use of an animal is the measurement of metabolic rate (Willmer et al. 2005).

Previous studies on thermoregulation and energetics extended our understanding of how animals are able to survive in their environments and how they are able to cope with changing or challenging environmental conditions (Geiser 2004; McKechnie & Lovegrove 2002; Mzilikazi & Lovegrove 2004). Some animals inhabit harsh environments characterised by extreme environmental temperatures, seasonally low productivity, as well as daily fluctuations in ambient temperature, for example the desert and karoo biomes of Southern Africa (Mucina & Rutherford 2006). These conditions are seemingly unfavourable, however animals that inhabit those areas are able to adapt and thrive. Therefore, the question arises; how are these animals able to survive in unfavourable habitats?

Animals exhibit different adaptations to survive temperature extremes and low food availability, either in combination with, or in the absence of, torpor and hibernation. Some species exhibit changes in activity; some are able to improve their cold tolerance by using nonshivering thermogenesis (NST), by improving their thermal conductance, by reducing their body mass or by becoming acclimated to colder temperatures, through reduction of metabolic requirements during the colder months (Heldmaier et al. 1986; Heldmaier 1989). Many factors have been found to influence metabolic rate, such as body mass, habitat, phylogeny, food source, climatic changes (Hochachka et al. 2003; Lovegrove 2000). Interestingly, Lovegrove (2001) found that animals with body armour had lower basal metabolic rates than nonarmoured animals of the same size. Of these factors body mass and climate have been extensively studied and are very important in the context of this study.

Many studies have shown that small mammals tend to up-regulate their metabolic rates during winter, as can be expected when the decrease in ambient temperature increases the energetic requirements for thermoregulation (Heldmaier 1989; Lovegrove 2005; McNab 1980). However, this is not always the case and there is often a difference in up-regulation depending on zoogeography for example differences have been observed between the northern and southern hemisphere (Lovegrove 2000; Smit & McKechnie 2010). Smit and McKechnie (2010) studied birds in a subtropical desert and observed the down-regulation of basal metabolic rate during winter, instead of up-regulation. This implies the greater need for
subtropical animals to conserve energy in winter, rather than being cold tolerant (Smit & McKechnie 2010).

Responses to adverse environmental conditions are not limited to changes in metabolic rate; animals often display heterothermy as one adaptation that enables them to survive when the cost of body maintenance exceeds the available energy sources. Heterothermy in endothermic species manifests itself as daily torpor or hibernation (Geiser & Ruf 1995; Lovegrove 2000; Lyman et al. 1982). Torpor is defined as a state of nearly complete inactivity accompanied by a reduction in metabolic rate, a reduction in body temperature, and a change in many other body functions (Lawrence 2000; Schmidt-Nielson 2004). Torpor may occur in short daily bouts (of less than 24 hours) or if a reduction in body temperature occurs on a seasonal scale it is known as hibernation (can last several days) (Geiser & Ruf 1995; Lawrence 2000; Wilz & Heldmaier 2000). Hibernators exhibit obligatory behaviours, whereas animals utilising daily torpor exhibit facultative behaviours either linked to change in photoperiod or season. For example hibernators will hoard or store food and build up fat reserves before they go into hibernation for example the European ground squirrel (Millesi et al. 1999). There is a lot of controversy around the definitions of hibernation and daily torpor, as a result of exceptions where overlapping values confound defining what state the animal is in (Geiser & Ruf 1995).

According to Geiser and Ruf (1995) the most distinctive factor separating hibernation and daily torpor is bout duration, i.e. how long the animal stays in a state of inactivity with a reduced metabolic rate. However, Wilz and Heldmaier (2000) argue that there is no clear definition between daily torpor and hibernation and there is instead a physiological continuum whereby bout length is determined by the timing of the entrance into dormancy. Some species can exhibit daily torpor most of the time and will not arouse from torpor for four or more days, for example in dormice (Gliridae) (Wilz & Heldmaier 2000).

Although traditionally associated with the cold northern climates, daily torpor and hibernation have been recorded in species inhabiting the southern hemisphere, where the average winter temperatures tend to be higher and snowfall is uncommon, except at high altitudes (Bozinovic et al. 2004; Dausmann et al. 2004; Geiser 2007; Geiser and Broome 1991; Lovegrove & Génin 2008; Stawski et al. 2009). In the tropics hibernation is associated with both low and high extreme temperatures, as well as low food availability (Dausmann et al. 2004; Lawrence 2000; Schmid 2000). It
has been demonstrated that in the tropics, hibernation is not necessarily coupled with low body temperature (Dausmann et al. 2004). The effect of nest characteristics on body temperature has shown that animals that hibernate in poorly insulated nests tend to allow their body temperature to fluctuate with the environment, whereas if they hibernate in well-insulated nests their body temperatures are more stable (Dausmann et al. 2004).

Hibernation and daily torpor have been found to occur in both mammals and birds (Geiser 1998). Heterothermy has been reported in various mammalian taxa, including monotremes (Grigg et al. 2003), marsupials (Körntner & Geiser 2000), some members of the Afrotheria (Mzilikazi & Lovegrove 2004; Lovegrove et al. 1999), rodents (Mzilikazi et al. 2002; Bozinovic et al. 2004) and primates (Dausmann et al. 2004; Schmid 2000; Nowack et al. 2010), as well as Xenarthra (Superina & Boily 2007), Pholidota, Eulipotyphla (Mouhoub-Sayah et al. 2008) and Chiroptera (Willis & Brigham 2003).

Studies focusing on mammals in the Afrotropics have mainly concentrated on rodents, presumably because of the ease with which they can be maintained in the laboratory (Lovegrove & Raman 1998; Mzilikazi & Lovegrove 2004; Perrin & Richardson 2004), Afrotherians, because of their intriguing phylogenetic placement (Jackson et al. 2009; Lovegrove & Génin 2008; Mzilikazi & Lovegrove 2004; Scantlebury et al. 2008) and primates, because of the interest that torpor in primates holds for medical applications (Dausmann et al. 2004; Nowack et al. 2010). Research into mammalian heterothermic responses has in the past been biased towards laboratory studies, even though their use under laboratory conditions may not be truly reflective of how these responses are expressed by animals in their natural environment (Geiser et al. 2000).

Amongst animals that subsist primarily on insects the seasonal variation in their prey availability leads to physiological challenges, which are often overcome by adaptations such as daily torpor and hibernation (Mzilikazi & Lovegrove 2004). Insectivores live in a range of habitats and have many different life histories and as a result their metabolic rates vary between families and between species. For example, within the Family Erinaceidae, three species of hedgehogs were compared, all had a normothermic body temperatures of 34°C but differing metabolic rates (Shkolnik & Schmidt-Nielsen 1976). Erinaceus europaeus (obtained from France and Israel) represented a temperate environment, Hemiechinus auritus (Egypt) was from a semi-
arid climate and from the desert, Paraechinus aethiopicus (Ethiopia/North Africa). *E. europaeus* had a body weight of approximately 749g and basal metabolic rate of 40.3kcal/day, *H. auritus* had a body weight of approximately 397g and basal metabolic rate of 18.0kcal/day and *P. aethiopicus* had a body weight of approximately 453g and basal metabolic rate of 14.0kcal/day (Shkolnik & Schmidt-Nielsen 1976). Malaysian moon rats (*Echinosorex gymnurus*) are also insectivorous (625<body mass (M_b) <788g) and have metabolic rates that vary between 0.65 and 0.79 mlO_2/g/h (measured at ambient temperatures (T_a) between 28.9 and 30.6°C) (Whittow *et al.* 1977). These animals have a much lower metabolic rate gram per gram than the smallest desert shrew (*Notiosorex crawfordi*) from the Arizona desert, whose standard metabolic rate is 2.95 mlO_2/g/h and its approximate mass is 4g (Lindstedt 1980).
The study animal

The Southern African Hedgehog or krimpvarkie (*Atelerix frontalis*) belongs to the Family Erinaceidae and Order Eulipotyphla (Skinner & Chimimba 2005). *Atelerix frontalis* is one of six species of hedgehogs endemic to Africa, and it is the only species occurring in southern Africa (Skinner & Chimimba 2005; Smithers 1992). *A. frontalis* can be distinguished from other species of hedgehog by the characteristic white band extending across its forehead to below both ears (Burger 2004; Skinner & Chimimba 2005; Smithers 1992). *A. frontalis* has a body mass of between 236 and 480 grams and its lifespan is approximately 3 years (Burger 2004; Skinner & Chimimba 2005; Smithers 1992).

*A. frontalis* feeds mainly on insects but also supplements its diet with lizards, small mice, birds’ eggs, chicks, earthworms and even carrion (Burger 2004; Skinner & Chimimba 2005; Smithers 1992). *A. frontalis* is nocturnal and inhabits burrows, or nests under leaves and twigs, dense grass or bushes during the day (Burger 2004; Skinner & Chimimba 2005; Smithers 1992). However, after heavy rain they are often seen out during the day (Burger 2004; Skinner & Chimimba 2005; Smithers 1992; also confirmed by anecdotal reports). Lion (*Panthera leo*), leopard (*Panthera pardus*), caracal (*Caracal caracal*) and the giant eagle owl (*Bubo lacteus*) are known to prey on hedgehogs (Burger 2004; Skinner & Chimimba 2005; Smithers 1992; Stuart & Stuart 2001).

*A. frontalis* has a wide distribution from Namibia to Zimbabwe, Botswana and South Africa (Fig 2.) (Skinner & Chimimba 2005; Smithers 1992). In South Africa, they occur throughout the Free State, Gauteng and the North West Province, and in parts of the Limpopo Province, Mpumulanga and the Eastern Cape (Skinner & Chimimba 2005). In South Africa, this species inhabits a variety of arid habitats, including the Karoo regions, where temperatures are extreme, both in winter and summer, often dropping to below freezing in winter and easily reaching 37°C in summer (Mucina & Rutherford 2006, SAWS). Frequent and extended droughts in this area also pose energetic and water bottlenecks for the species living in this region (Skinner & Chimimba 2005).
A number of ecological and behavioural factors render *A. frontalis* an interesting model for investigating the potential use of heterothermy; it is a relatively small insectivore (summer body mass ca. 300 to 400g), is known to burrow, inhabits harsh habitats and cannot be found during winter (Skinner & Chimimba 2005). The Order Eulipotyphla has a number of species that exhibit dormancy, this is believed to be as a result of the insect availability fluctuating seasonally (Schmidt-Nielson 2004). Within the Order Eulipotyphla there are approximately 16 species of hedgehogs (Skinner & Chimimba 2005). However, some scientists believe that there could be more species, since this subfamily (Erinaceinae) is currently understudied. Southern African hedgehogs are extremely vulnerable for a variety of reasons; there are increased incidences of road mortalities, predation by humans, capture for use in traditional medicines and as pets, some farming practices and climatic changes such as the increased incidence of lengthy droughts (Skinner & Chimimba 2005).

Although, there is a large body of literature available on the European Hedgehog (*Erinaceus europaeus*), there is currently very little information available on other species of hedgehogs and most of the information has been from animals in captivity. Indeed people in Southern Africa are often confused between a hedgehog (*Atelerix frontalis*) and a porcupine (*Hystrix africaeaustralis*) (SLH, personal)
observation). Only a few studies have been published about *Atelerix frontalis* and they were in captivity (Gillies *et al.* 1991; Kok & van Ee 1989). Previous laboratory based studies suggest that this animal might be capable of hibernation in the wild (Gillies *et al.* 1991; Kok & van Ee 1989).

One of the criticisms of laboratory work on a species is that it cannot be related directly back to the wild. Geiser *et al.* (2000) studied the differences between free-ranging animal data and data obtained in captivity, for some species of birds, monotremes, marsupials, bats and rodents. They found that animals in the laboratory did not enter hibernation and torpor as readily as in the field, and when they went into hibernation or torpor in the field, heterothermic bouts were longer, deeper and more frequent (Geiser *et al.* 2000). They argue that the main reason for these differences is due to the disturbances in laboratory, such as noise and possible entrainment to feeding times (Geiser *et al.* 2000).

In this study I aimed to investigate the seasonal daily energy expenditure and basal metabolic rate, to ascertain whether this species exhibited any seasonal changes in energetics to cope with the adverse environmental conditions. I also investigated whether the southern African hedgehog uses heterothermy in its natural habitat and the parameters associated with heterothermy, focusing on the depth of heterothermic bouts, bout length and frequency of arousal. These data should show how the hedgehog copes with extreme temperatures characteristic of their habitat, as well as the cost of living in harsh conditions. If the Southern African hedgehog readily uses hibernation in the wild, this could be an important adaptation that has helped this species persist through increasingly challenging environmental conditions (Geiser & Turbill 2009).
The study site

The study was conducted on a private game farm, ‘Jules of the Karoo’ which is situated on Plaatfontein farm (S31°01.693’, E023° 45.993’) in the Karoo, Northern Cape Province, South Africa (Fig 3). The area is primarily farmland with a few private game farms and hunting lodges. The hedgehogs were hand caught on the farms and roads both within and surrounding Jules of the Karoo. The exact capture locations were recorded with a geographic positioning system (GPS) to enable the release of the hedgehogs to their original location once the study was completed.

The study area is located in the Nama-Karoo biome. The typical vegetation in this area is dwarf karoo shrubs and grasses, and occasional low trees (Mucina & Rutherford 2006; SLH, personal observation). The soil comprises a rocky shale (Mucina & Rutherford 2006; SLH, personal observation). The landscape is dominated by flat or gently sloping terrain with small isolated hills (Mucina & Rutherford 2006; SLH, personal observation). The study area was bordered by very large hills on two sides of its expanse (SLH, personal observation). The rainfall in this part of the karoo is low, between 50 and 500 mm per annum, during the summer temperatures frequently exceed 37 °C and in the winter the temperature can drop to below 0 °C (Mucina & Rutherford 2006; SAWS; SLH, personal observation).
Fig. 3 A map showing the location and size of the area used for collecting study animals relative to the location of the enclosure site (Garmap 2010).
MATERIALS AND METHODS

Trapping techniques

In previous studies on hedgehogs, a number of methods have been used to capture study animals and obtain information. Information about their distribution and abundance in New Zealand, was obtained using questionnaires distributed among rangers, field officers, veterinarians, farmers, hunters etcetera (Brockie 1975). One study collected injured hedgehogs along the roads (Özen 2006) and other studies collected hedgehogs that were hand caught by people in the communities (Mouhoub-Sayah et al. 2008; Raymond & Garner 2001; Warwick et al. 2006). Studies using the African pygmy hedgehog (*Atelerix albiventris*) obtained their samples from pet owners and hedgehog breeders (Allison et al. 2002; Juanes-Sallés et al. 2006; Graesser et al. 2006; Heatley et al. 2005).

At the start of this project, walk-in live traps baited with dog food were set to trap hedgehogs. Since this species is classified as ‘of least concern’ in the IUCN red data book, I expected this species to occur in reasonably high densities and therefore live trapping seemed plausible. However, the walk-in live traps proved unsuccessful and therefore an alternative trapping technique was attempted, which comprised of pit-fall traps connected with drift fences. Yet again, this trapping technique proved unsuccessful after repeated attempts and trapping methods were re-examined. Previous studies on *A. frontalis* had success hand capturing individuals (Gillies et al. 1991; Kok & Van Ee 1989) and therefore the individuals used in this study were hand captured from roads and in areas surrounding farm houses. A total of ten individuals were captured over a two year period (details in Table 1 of Appendix 1). After capture each individual was tagged, using a Trovan identification transponder, to keep track of their identities. Throughout the study, details of individuals were observed and recorded, such as body mass, reproductive status and behaviour.

This study was initially conducted on completely free-ranging individuals. The first three individuals were released into the wild, but the combination of apparent low animal densities and a recapture rate of 0% after three months, necessitated a modification of the study design. Study animals were subsequently kept under semi-captive conditions, where they were exposed to natural temperatures and photoperiod. The enclosures were built in the Karoo veld, away from people. The enclosures were 5m long, 5m wide, 1.5m high and 0.5m below ground level, and the
fencing was constructed using chicken mesh (mesh hole diameter approximately 2cm) (Lovegrove and Génin 2008). The fences were buried down to 0.5m to prevent escape under fencing and digging out. The enclosures contained natural vegetation and leaf litter. The males and females were kept in separate enclosures to prevent breeding during the study.

The hedgehogs were supplied with canned dog food and ad libitum water throughout the duration of the study. Food was placed in the enclosure once a day to minimise disturbance and contact with the animals was avoided. The animals were also supplied with nesting boxes, made from thin plywood (Fig 4). The nest boxes were 54cm long, 31cm high and 29cm deep, with a tunnel 20cm wide, 17cm high and 32cm long leading into the entrance (Fig 5 drawn to scale using Autodesk inventor version 10). The nest boxes had a small hole in the back panel for ventilation and this hole was fitted with a small piece of pipe angled downwards and outwards (to prevent rain from entering), and covered in mesh on the end (to prevent other animals from entering through the tube and blocking it).

![Fig. 4 The nest boxes, set up in the enclosure. A hedgehog can be seen in the entrance of the nest box in the centre.](image-url)
Despite having taken care with the enclosure construction, a total of 3 individuals escaped (one of which was subsequently and luckily recaptured by a farmer’s dog). One individual managed to use one of the nest boxes to climb the fence and the other two individuals managed to squeeze through a hole in the fence that was so small, only their skull would have fitted through comfortably.
**Metabolic rate measurements**

During metabolism, the food an animal consumes is converted into usable energy (adenosine triphosphate (ATP)) by a process that requires oxygen (Schmidt-Nielson 2004). Metabolic rate can thus be measured indirectly by measuring the volume of oxygen consumed ($V_{O_2}$). Once caught, the animal's body mass was measured and it was housed in a cage until metabolic rate measurements could begin. Animals were caught during their active phase and most metabolic rate measurements occurred in their rest phase. Care was taken to ensure the animals were postabsorptive before measurement. It was placed in a metabolic chamber, that was constructed using an 8.3L plastic container, holes were drilled in 2 sides of the container to enable air flow through the container. The metabolic chamber was then placed into a temperature controlled cabinet. In the field a modified, insulated box attached to a water bath was used as a temperature cabinet. The temperature cabinet was used to control the temperature that the metabolic rate measurements were performed at.

Atmospheric air was first drawn from the metabolic chamber through a Whatman filter to remove any debris, and then through a scrubber containing silica gel to remove water vapour, after which it entered the FoxBox (Sable systems, Las Vegas), which is a Field Oxygen analyser in a Box, that incorporates a pump, flow meter, carbon dioxide and oxygen analyser. The flow rate was chosen so as to maintain <1% oxygen depletion between incurrent and excurrent air. The air was analysed for carbon dioxide content. The air was then pumped through another scrubber that contains both silica gel and soda lime, to remove any excess water vapour and all carbon dioxide. The air was subsequently analysed for oxygen content before being released back into the atmosphere. Measurements were cycled between the animal and an empty reference channel (‘control’ channel). The FoxBox corrects the data for standard temperature and pressure.

Since an extra water scrubber was used during measurement, there was no need to correct the flow rate during analyses. To convert the output data from the FoxBox into a measurement of the volume of oxygen consumed by the animal ($V_{O_2}$), the program ExpeData (Sable systems, Las Vegas) was used. The oxygen content data is first corrected for drift (changes in the environment around the FoxBox can
cause the readings to drift). The data can then be corrected for flow rate and converted to ml/min, using the formula \(((\text{O}_2/100)\times 100-1)\times \text{FR})/(1-0.209)\).

**Thermoneutral zone**

Before basal metabolic rate measurements could begin, the thermoneutral zone of the species had to be determined, to ensure that the right temperature was used during measurements. The thermoneutral zone (TNZ) is the range of environmental temperatures \((T_a)\) where metabolic rate is at its lowest and a change in \(T_a\) does not cause a change in \(\text{VO}_2\). To determine the TNZ of the species the animals were exposed to various temperatures (15, 20, 23, 25, 28, 30, 32, 35, and 37°C) during their rest phase, under postabsorptive conditions (this was achieved by preventing access to food for a minimum of 3 hours prior to measurements). \(\text{VO}_2\) was measured for 3 hours with manual switching of channels, between the animal and control every 15 minutes. The thermoneutral zone of the species was measured in 4 adult individuals in summer (3 males and 1 female).

**Daily rhythm of metabolic rate**

The \(\text{VO}_2\) of individuals was measured at 25°C for a continuous 24-hour period, with manual changing of channels every 15 minutes. 25°C was chosen for comparison with previous studies (Gillies *et al.* 1991). From these measurements the daily rhythm of the animals was inferred and plotted, by calculating the average \(\text{VO}_2\) consumed per hour. Average \(\text{VO}_2\) consumed per hour was calculated by finding the mean of two values for \(\text{VO}_2\) per hour, the first value was calculated by averaging 20 data points recorded in the first half the hour and the second value was the average of 20 data points recorded in the second half of the hour. The daily rhythms of four adult individuals were measured in both summer (November, 2 males and 2 females) and winter (July, 3 males and 1 female). In summer (February) four juveniles were also measured (3 males and 1 female).

**Daily energy expenditure**

The average hourly \(\text{VO}_2\) values were used to calculate resting metabolic rate (RMR), active phase metabolic rate (AMR) and average daily metabolic rate (ADMR). RMR is the mean of all the hourly mean \(\text{VO}_2\) values during the rest phase of the animal’s daily rhythm, and AMR is the mean of all the hourly mean \(\text{VO}_2\) values during the active phase of the animal’s daily rhythm. ADMR is the mean of all the hourly
mean VO\(_2\) values over the course of the 24 hours. ADMR can be converted into daily energy expenditure (DEE) by using the conversion factor of 20.083kJ/L of O\(_2\) (Schmidt-Nielson 2004).

*Basal metabolic rate*

For basal metabolic rate measurements each individual was measured at 27\(^\circ\)C (which is within their thermoneutral zone), during their rest phase, and while postabsorptive. BMR measurements were recorded for 3 hours and manual changing of channels occurred every 15 minutes with samples being taken every 30 seconds. BMR for each individual was calculated from the VO\(_2\) values by calculating the mean of the lowest VO\(_2\) values measured during the 3 hour period. During each 3 hour period there was a total of 1\(\frac{1}{2}\) hours of measurements on the animal channel separated into six 15 minute time slots by the control channel. For every 15 minute time slot for the animal, there was a total of 30 data points. The lowest 20 data points for VO\(_2\) were averaged per 15 minute time slot. Thus a total of 120 data points (60 minutes) constituted a single animal’s BMR value.

The temperature of 27\(^\circ\)C was chosen for the BMR measurements because when some of the animals were exposed to temperatures higher than 27\(^\circ\)C, they were extremely stressed. The animals started sweating profusely and flattened themselves out on the bottom of the chamber, in one case the animal was so stressed that it had to be removed from the chamber and re-measured after a period of rest. BMR was measured in four adult individuals in summer (November, 2 males and 2 females) and winter (July, 3 males and 1 female). In addition four juveniles (3 males and 1 female) were also measured in summer (February), under the same parameters as the adults’ BMR. I have referred to these measurements in the results as resting metabolic rate measured within the adult thermoneutral zone (RMR in TNZ).
Body temperature measurements

Individuals were surgically implanted with temperature dataloggers (Thermocron iButtons DS1922L, calibrated against a mercury thermometer from 2 – 50°C; accuracy 0.5°C) that were coated in surgical wax (to prevent leaking). While the animals were under anaesthesia (isoflorane in oxygen; induction, 4% and maintenance, 3%; flow rate, ca 1.0 ℓ.min⁻¹), the iButtons were programmed and then placed into the peritoneal cavities of the animals. All surgical procedures were performed by Dr Nomakwezi Mzilikazi who is licensed by the South African veterinary council (Authorisation number: ART 02/5508). The dataloggers weighed approximately 3g, did not exceed 1% of the animals’ body mass and therefore did not inhibit the animals in any way. The hedgehogs were released into the enclosures 24 hours after the surgical procedure. Thermocron iButtons were placed in the enclosure to measure ambient temperatures during the study periods. These were placed in the nest box, under a bush, in a black bulb in the shade and in a black bulb in the sun. The black bulbs were used to measure the radiant heat absorbed by a body during the day and the black bulb is a standard used in many physiology studies.

For the winter component of the data body temperature measurements of five individuals were recorded continuously every 40 minutes between the 30th of April and the 22nd of August 2009. However, one individual escaped and the sample size was therefore N=4 for winter temperature data. For measurement of summer body temperature, four individuals were surgically implanted with Thermocron iButtons set to take measurements every 27 minutes between the 1st of November 2009 and the 17th of January 2010. An escapee resulted in a decrease in sample size to three (N=3) for summer measurements.
Data and statistical analyses

Metabolic rate

Differences in body mass ($M_b$) between seasons and, between adults and juveniles were analysed using t-tests. Differences in metabolic rate between seasons and, between adults and juveniles were analysed using, firstly the homogeneity of slopes model, followed by Analysis of co-variance (ANCOVA). For the seasonal data $N=1$ for winter and $N=1$ summer, from a statistical point of view this was problematic. In order to study the seasonal effects and show that the data measured were representative of what happens seasonally on a year to year basis, climate data were obtained from the South African weather service (SAWS). The climatic data was analysed using an Analysis of variance (ANOVA). All statistical tests were performed in Statistica 7.0 and graphs were plotted in Sigma Plot 10.0. Analysis of differences in data between sexes was not statistically possible due to sample size.

Body temperature

Winter temperature data were obtained from four individuals (one female; three males). Summer body temperature ($T_b$) data were obtained from three individuals (one female; two males). Animals were presumed to be torpid when their $T_b$ decreased below 33°C (Mouhoub-Sayah et al. 2008). Minimum body temperature ($T_{b\,\text{min}}$) was taken as the lowest body temperature ($T_b$) per 24 hours in both torpid and normothermic animals. Bout length was taken as the amount of time that $T_b$ was below 33°C. The expression “torpor” was used to refer to both heterothermic bouts that lasted for < 24hr as well as multiday bouts lasting for longer than 24hr. The time of entrance into torpor, start of arousal and end of arousal were determined for each torpor bout. The heating rates were calculated from $T_{b\,\text{min}}$ to $T_{a\,\text{max}}$ because $T_a$ did not fluctuate over the same range of temperatures as $T_b$ ($T_a$ rarely exceeded 25°C and $T_b$ rarely decreased below 5°C) (Fig 6). This method ensured that heating rates were only calculated for periods where the ambient temperature and body temperature were coupled. The environmental heating rates were approximated using the same time periods as the animal heating rates.
Fig. 6 To calculate the heating rates only the values at $T_{b\text{ min}}$ and $T_{a\text{ max}}$ were used. This is because (as seen in the graph) there are no values for $T_b$ below $T_{b\text{ min}}$, and no values for $T_a$ above $T_{a\text{ max}}$.

Due to the small sample size no comparisons between the sexes could be made for both metabolic parameters and body temperature measurements. In addition, animals did not enter torpor on the same days and also displayed torpor at different ambient temperatures. Linear effects mixed models were used to investigate relationships between different parameters (bout length, $T_{b\text{ min}}$ and $T_a$), using the animal ID as the categorical predictor, to allow for repeated measures. All mean values in the text are reported ± one standard deviation. All statistical analyses were performed using Statistica 7.0 and graphs were plotted in Sigma Plot 10.0.
RESULTS

Metabolic rate measurements

Resting metabolic rate (RMR) of *A. frontalis* was lowest at ca. 27°C. Therefore, measurements of basal metabolic rate were performed at 27°C; which is at the lower end of their thermoneutral zone. At 32°C and above, some of the animals were extremely stressed and this is reflected in Fig 7 by the increase in metabolic rate at 32°C. Although there was no significant difference between RMR at 30°C and 32°C, it was assumed that 30°C was at the upper end of the TNZ, due to observations in the animals’ behaviour.

![Fig. 7](image-url) The thermoneutral zone (TNZ) of *Atelerix frontalis* individuals measured in summer 2008 (N=4).
**Comparison between the metabolic rates of adult and juvenile A. frontalis**

The metabolic rates of adults and juveniles were measured in the summer months. Adult metabolic rates were higher during the known active phase of this species, compared to the rest phase, and a clear daily rhythm in metabolic rate can be seen (Fig 8). This is also reflected in the RMR and AMR measurements (Fig 9). The juveniles also showed a daily rhythm, however their metabolic rate was lower (Fig 8 & Fig 9). Within the rest phase, the metabolic rate of the juveniles showed greater fluctuations, which can be seen as a series of peaks and troughs in Fig 8. These fluctuations were not as pronounced in the adults. Total metabolic rate data are presented in this section due to the large differences in body mass between adults and juveniles. When body mass is considered, the juveniles have a much higher metabolic rate per gram of body weight than the adults.

**Fig. 8** 24 hour patterns of metabolic rate in adult and juvenile *A. frontalis* in summer.
The juveniles had a lower rest phase metabolic rate that was measured within the TNZ of the adults (RMR in TNZ), when compared to the adults (RMR in TNZ is BMR in the adult individuals). In addition the juveniles had a lower average daily metabolic rate (ADMR), resting metabolic rate (RMR), active metabolic rate (AMR) and daily energy expenditure (DEE) than the adults. The juveniles were almost a quarter of the body mass, of the adults and this difference was found to be statistically significant ($t=9.38; \text{df}=6$ and $p<0.001$) and because of the large differences in the variances of the body mass, statistical analyses taking into account the $M_b$ were not possible. The data suggests that the differences in metabolic rates are as a result of body mass differences.
Fig. 9 A A comparison between mean metabolic rates ± standard deviation of adult (N=4) and juvenile (N=4) A. frontalis.

B A comparison between mean daily energy expenditure (DEE) ± standard deviation and mean body mass (M_b) ± standard deviation of adult (N=4) and juvenile (N=4) A. frontalis. The presence of an asterix indicates statistical significance.
Comparison between years using climate data

The SAWS data were used to compare ambient temperatures between years over the last 15 years (i.e. Jan 1996- end of 2010) to establish whether there was a statistical significance between the study period and previous years. There is not much between-year variation in temperature (Fig 10). Fig 10 shows the mean monthly maximum and minimum temperatures in the De Aar region for the last 5 years, which illustrates the large variation in temperature the region experiences on a monthly basis. An ANOVA was used to compare the mean maximum and minimum temperatures for each month, over the last 15 years. No single month over the last 15 years was statistically different from the other years. Therefore, although the data in this study were obtained over a single winter and summer season, the year in which the data were obtained was not significantly different in terms of environmental conditions (temperature). It is therefore reasonable to assume that the data obtained during this study are representative of long-term patterns in metabolic rates and body temperature patterns during the different seasons.
Fig. 10 A A graph of the mean monthly maximum temperatures experienced in the De Aar area over the last 5 years.
B A graph of the mean monthly minimum temperatures experienced in the De Aar area over the last 5 years.
Comparison between summer and winter metabolic rates in adult *A. frontalis*

In summer a clear daily rhythm is found, with higher metabolic rates during the active phase than during the rest phase (Fig 11). In winter a daily rhythm in metabolic rates can still be discerned, however the amplitude is lower (Fig 11). None of the winter metabolic rates were measured in torpid animals.

![Graph showing 24 hour patterns of summer and winter metabolic rate in adult *A. frontalis*.](image)

**Fig. 11** 24 hour patterns of summer and winter metabolic rate in adult *A. frontalis*.

The difference between summer (N=4) and winter BMR (N=4) (Fig 12) was statistically significant ($F=9.394; df=1$ and $p<0.05$) with BMR increasing in the hedgehogs in winter. The differences between summer and winter ADMR ($F=3.090; df=1$ and $p>0.05$) and DEE ($F=3.090; df=1$ and $p>0.05$) were not statistically significant. The difference between summer and winter AMR ($F=10.463; df=1$ and $p<0.05$) was significant. However, the difference between summer and winter RMR at 25°C was not significant ($F=0.126; df=1$ and $p>0.05$). Body masses were significantly different between summer and winter ($t=-3.163; df=6$ and $p<0.05$).
Fig. 12 A A comparison between summer (N=4) and winter (N=4) mean metabolic rates ± standard deviation of adult *A. frontalis*. B A comparison between summer (N=4) and winter (N=4) mean daily energy expenditure (DEE) ± standard deviation and mean body mass (M<sub>b</sub>) ± standard deviation of adult *A. frontalis*. The presence of an asterisk indicates statistical significance.
Summer body temperature measurements

The body temperature of *A. frontalis* remained fairly constant during summer, with a range between 34 and 37°C (Fig 13 & Fig 14) on a daily basis. No bouts of torpor were recorded during the summer measurement period. Each individual occasionally allowed their body temperature to drop below 33°C and one even went as low as 28°C (Fig 14), however these drops were not for extended periods of time i.e. not for longer than 40 minutes. A period of 40 minutes is too short to be considered as a torpor bout.

**Fig. 13** A Daily rhythms of body temperature for an adult female *A. frontalis* (Hog 5) over one month in summer.
B Daily rhythms of body temperature of an adult male *A. frontalis* (Hog 6) over one month in summer.
Fig. 14 The frequency distribution of minimum (n=228) and maximum (n=228) body temperature for normothermic free-ranging *A. frontalis* (N=4), with bin intervals of 0.5°C.
**Winter body mass fluctuations**

Figure 15 shows the body mass of one adult *A. frontalis* and three juvenile *A. frontalis*. The body mass reported in Fig 15 as ‘high body mass’ (Mₐ) individual is for an adult male *A. frontalis*. This individual had a dramatic increase in body mass from 434g to 767g, almost doubling in body mass prior to the winter months. During the cold months there was a steady decline in Mₐ. This individual lost 33.5% of its Mₐ by the end of the cold season and was recorded at 510g in August.

The body masses reported as low Mₐ individuals belong to three juvenile *A. frontalis* (two males and one female) born in the summer preceding the measurement period. These juveniles doubled their body mass prior to winter, however they did not reach the same mass as the adult individual (394.0±20.0g vs 767.0g). Interestingly, there was no decrease in Mₐ during winter in the lower body mass individuals; their mean Mₐ in August was 530.3±23.3g representing a mass gain of 34.6% (Fig 15). At the start of T_b measurements (May 2009) they were sexually mature and of an adult body mass.

![Graph showing body mass fluctuations](image)

**Fig. 15** The body mass fluctuation of semi-captive *A. frontalis* (n=1 high (‘adult’) body mass individual and n=3 low (‘juvenile’) body mass individuals) between April – November 2009. The ‘juveniles’ were born beginning of February.
Winter body temperature measurements

Torpor use and frequency

During the winter period *A. frontalis* showed a high propensity for heterothermy. During the measurement period consisting of 112 days, a total of 323 bouts of torpor were recorded for the four animals. For each of the individuals the percentage time spent torpid was between 80 and 84% of all the days measured. On average each animal went into torpor for 93±1 days out of the total 112 days measured. Torpor bouts were observed between 3 and 8 days after the measurements commenced on the 30th of April 2009. The first torpor bouts were observed when the mean daytime $T_a$ was 12.6±0.7°C and mean night time temperature was 6.4±1.3°C. $T_a$ frequently did not exceed 10°C during the daytime and during this time heterothermy was used daily.

Torpor bout length

Torpor bout length ranged between 40 mins – 116.3 hrs (4.8 days) with the mean torpor bout length being 16.0±0.8 hours. Interestingly, 89% of the total number of torpor bouts, were less than 24 hours long (Fig 16), this could be an artefact of the sample size and the associated ratio of low body mass to high body mass individuals. There was a significant negative relationship between bout length and ambient temperature ($R^2 = 0.236; F = 24.580$ and $P<0.001$; Fig 17). There was also a significant negative relationship between bout length and $T_{b\ min}$ ($R^2 = 0.354; F = 43.596$ and $P<0.001$; Fig 17 inset).
Fig. 16 Frequency distribution of torpor bout (n=312) length in semi-captive *A. frontalis* (N=4). The different grey bars are for visual purposes only.

Fig. 17 The relationship between $T_a$ (nest box) and torpor bout length. *Inset graph*: the relationship between $T_{b\text{ min}}$ and torpor bout length. For torpor bouts n=312 and *A. frontalis* individuals N=4.
Torpor entry and arousal

Entry into torpor occurred mostly between 2-14 hrs after sunset, between 20h00 and 08h00 (Fig 18A). This shows the high variation in the timing of entrance into torpor of A. frontalis. The start of arousal usually occurred around 08h40 in the morning (Fig 18B) and arousal usually ended around 14h00 in the afternoon (Fig 18C). The mean heating rate for the hedgehogs was 0.055±0.002ºC/min.
Fig. 18 A The timing frequency of entrance into torpor of semi-captive *A. frontalis*. B The frequency of the time at the start of arousal from torpor in *A. frontalis*. C The frequency of the time when the animal was normothermic (end of arousal). In all graphs, the inner axis represents the frequency of the times and the bin interval is 40 minutes.
**Patterns of torpor**

The overall patterns of torpor differed between the light and heavier animals. The lighter individuals (Fig 19) displayed numerous short torpor bouts whereas the heavier individual had several short torpor bouts leading up to longer torpor bouts (Fig 20). The longest torpor bout in the lighter individuals was observed in Hog 6 (Fig 19B) and lasted 60.0 hrs whereas, the longest observed in the heavier individual was 116.3 hrs, almost double in duration. The mean torpor bout length for lighter individuals was 12.9±0.4 hrs whilst that observed in the individual with a higher $M_b$ was 18.0±3.9 hrs.

**Fig. 19** A Fluctuations in body temperature of a low body mass adult female *A. frontalis* (Hog 5) over one month showing daily, short torpor bouts. B Fluctuations in body temperature of a low body mass adult male *A. frontalis* (Hog 6) over one month showing daily, short torpor bouts.
Fig. 20 Fluctuations in body temperature of an high body mass, adult male *A. frontalis* (Hog 9) over the course of the study showing numerous short torpor bouts leading up to longer torpor bouts.

**Minimum body temperature**

The mean $T_{b\text{min}}$ of animals on the days spent normothermic was $33.9\pm0.1^\circ\text{C}$ ($N=4$ and $n=70$) whereas during the torpid days, the mean $T_{b\text{min}}$ was $12.3\pm0.4^\circ\text{C}$. Most torpor bouts were observed when $T_a \leq 20^\circ\text{C}$ (Fig 21). Torpor $T_{b\text{min}}$ ranged between $1^\circ\text{C}$ and $32^\circ\text{C}$ (Fig 22). The lowest $T_{b\text{min}}$ recorded was $1^\circ\text{C}$ at $T_a = -0.6^\circ\text{C}$ in a low body mass (376g), female *A. frontalis*. In torpid animals there was a significant positive relationship between $T_{b\text{min}}$ and $T_a$ ($R^2 = 0.429$; $F = 59.839$ and $P < 0.001$) whereas in normothermic animals this relationship was a significant negative relationship ($R^2 = 0.240$; $F = 5.221$ and $P < 0.05$).

During the study three out of the four hedgehogs were observed to be torpid under bushes, rather than in the nest boxes. This is presumed to be the reason for a few of the $T_{b\text{min}}$ values being below the $T_{b\text{min}} = T_a$ line. The mean value for $T_{b\text{min}} - T_a$ was $8.2\pm0.5^\circ\text{C}$ (Fig 23). In torpid animals the relationship between $T_{b\text{min}} - T_a$ and
$T_a$ was negative and significant ($R^2 = 0.119; F = 10.721$ and $P < 0.001$) (Fig 23). This relationship was also significant and negative in normothermic animals ($R^2 = 0.995; F = 3473.415$ and $P < 0.001$). This shows that during both torpor and normothermia the body temperature is coupled with the environment.

![Graph showing the relationship between ambient temperature (nest box) and minimum body temperatures for normothermic (n=70) and torpid (n=312) free-ranging $A. frontalis$ (N=4).]

Fig. 21 The relationship between ambient temperature (nest box) and minimum body temperatures for normothermic (n=70) and torpid (n=312) free-ranging $A. frontalis$ (N=4).
Fig. 22 The frequency distribution of minimum body temperature for normothermic (n=70) and torpid (n=312) free-ranging *A. frontalis* (N=4), with bin intervals of 1°C, showing the wide range of $T_{b\ min}$ during torpor.

Fig. 23 The relationship between the $T_{b\ min} - T_a$ gradient and the ambient temperature for normothermic (n=70) and torpid (n=312) free-ranging *A. frontalis* (N=4).
DISCUSSION AND CONCLUSION

Metabolic rate measurements

During the metabolic rate measurements, individuals were observed to be stressed and adopted a flat, stretched out posture at temperatures $\geq 32^\circ$C. This has been observed in other insectivores of similar body mass for example moon rats (Whittow et al. 1977). Since the ambient temperatures in the habitat often exceed the upper limit of their thermoneutrality, these data imply that hedgehogs may employ behavioural mechanisms that enable them to avoid these extreme environmental temperatures. One such method could be the use of microclimates with much muted temperatures during the day to reduce their heat exposure. Hedgehogs were observed beneath bushes, they were also observed beneath broken branches and the nest boxes and one individual (the female) consistently used the inside of the nest boxes. The individuals that nested under either bushes or leaf litter were observed to be creating shallow hollows in the ground, as deep as half an ostrich egg. When the hedgehogs were in these hollows, they filled the hollows with half their body and their other half protruding out, was protected by body armour (quills). No evidence of digging burrows was found. Although burrows were not used, microclimates that were available (in the form of natural vegetation) had more stable temperatures than under direct exposure to the sun. Whether the quality of the soil (large slabs of slate and rocks were fairly close to the surface) in the enclosure was a limiting factor to the hedgehogs burrowing, it is as yet unknown. Further studies are needed to investigate what microclimates are available to free-ranging hedgehogs and whether there is a preference for any from.

The statistical tests suggest that the differences in metabolic rate between adults and juveniles were as a result of the differences between their body masses, these differences have been seen consistently between species (Lovegrove 2000). The juveniles’ mass specific mean resting metabolic rate measured under the same conditions as adult basal metabolic rate (RMR in TNZ) was $0.785 \pm 0.071$ mlO$_2$/g/h, whereas the adults’ mean mass specific BMR was almost half that ($0.448 \pm 0.035$ mlO$_2$/g/h). This is to be expected, as larger animals do tend to have a lower RMR gram per gram due to their larger body weight, however this has not been quantified in this species before. The adults showed a clear daily rhythm of metabolic rate, with
their rest phase metabolic rate being low and their active phase metabolic rate, high. However, the juveniles displayed smaller amplitudes between the rest and the active phase and showed peaks and troughs of activity in both phases. It is highly likely that the bouts of increased active phase metabolism in juveniles coincided with times when the juveniles would have been feeding; because of their age feeding would occur periodically throughout the day.

Most seasonal studies investigating metabolic rate have been performed on daily heterotherms during torpor (Coburn and Geiser 1996; Schmid 2000). During this study, the animals did not stay torpid once disturbed therefore the animals were measured while they were normothermic. This resulted in an inability to quantify the energetic savings made through use of torpor. The summer mass specific BMR (0.448 ±0.035 mlO₂/g/h) was found to be about half of that measured in winter (0.811 ±0.073 mlO₂/g/h), the same pattern was observed when comparing non-mass specific values. Statistical analyses revealed that this difference is attributed to seasonal modification of energy expenditure (metabolic rate). Interestingly, other studies on seasonal differences in BMR have shown that summer BMR is higher than winter BMR, however these measurements were recorded during torpor (Coburn and Geiser 1996; Schmid 2000).

Lovegrove (2005) examined global seasonal changes in metabolic rate in mammals, and found that the principal adjustments of energy saving in small mammals (<100g), was focussed on energy conservation through reducing body mass and consequently reducing the overall energy requirements. Since A. frontalis is larger than 100g and exhibits an increase in winter BMR, they fit into the intermediate mammal group as described in Lovegrove (2005). The intermediate body size group are likely to increase their capacity for thermogenesis by increasing their maintenance power (a measure of MR) and non-shivering thermogenesis (NST) capacity, as well as reducing their conductance (Lovegrove, 2005). When we examine the normothermic metabolic rates in each season, we do see an increase in metabolic rate but whether A. frontalis uses NST still remains to be investigated. This species does have the capacity for heterothermy and with the decrease in metabolic rate during torpor they are able to make significant energy saving despite the up-regulation of their BMR, and this has been described in other species of hedgehogs (Webb & Ellison 1998).
As expected, both summer and winter daily metabolic rate patterns showed a higher MR in the active phase than in the rest phase. However, the amplitude during winter is lower. It appears that the main energy saving during winter takes place during the active phase, as there was a significant difference between the AMRs between seasons. It is likely that the lower AMR in winter can be attributed to behavioural mechanisms such as the animal not foraging in between torpor bouts due to low food availability.

The mass specific ADMR for adults during summer was 0.782±0.068 mlO$_2$/g/h was similar to that measured in the laboratory study by Gillies et al. (1991). However, the winter mass specific ADMR in the current study was much higher 0.648±0.041 mlO$_2$/g/h compared to Gillies et al. (1991). This may be attributed to measurements during this study being recorded during normothermia, whereas Gillies et al.’s (1991) measurements were during torpor. It is likely that if measurements of MR during torpor had been made, a large energy saving would have been observed, possibly similar to that observed in the laboratory study (Gillies et al. 1991). Additionally, should individuals of this species use torpor during the summer, an even larger energy saving could be observed. Torpor can hinder reproduction and since summer is when hedgehogs reproduce, it is likely that summer torpor could be observed only under dire circumstances (for example extended periods of drought).

Unfortunately data from only one summer and one winter season were obtained, this meant that for seasonal comparisons N=1 and thus statistically it would not be correct to infer anything from these data. Data were therefore obtained from the South African Weather Service (SAWS). Data from the period 1996 to 2010 were analysed to determine if there was a statistical difference in maximum and minimum temperatures between years. Statistically there was no difference between years and therefore it can be inferred that the data from this study reflect the pattern that this species would exhibit on a seasonal and yearly basis.

**Winter body mass**

During this study, the body masses of each individual, was tracked from the time of capture until the time of release. One individual reached a body mass of almost 800g prior to the onset of winter, this pre-hibernation body mass was also recorded by Kok and Van Ee (1989). Over the winter measurement period this
 individual (with a high body mass at the onset of winter) was recorded to have lost 33.5% of its body mass. This individual adheres to the Dehnel effect, where species are expected to decrease their body mass in response to the colder environment in winter (Heldmaier 1989; Lovegrove 2005). However, it is more likely that the decrease could simply be an artefact of using fat stores during torpor bouts. Indeed, Lovegrove (2005) says that in the intermediate body size group, the Dehnel effect is negligible.

The individuals of lower body mass were caught when they were approximately 4 weeks old and they were observed to be still suckling (as their mother was captured with them). At the onset of winter the body masses of these individuals were only about half (approximately 400g) that of the hedgehog with the high body mass. A possible reason for such a disparity could be related to their age. The lighter individuals in this study were born in February (the middle of summer) as opposed to the beginning of summer in Kok and Van Ee’s study (1989). Thus these individuals did not have as much time before winter to grow and store fat reserves. If juveniles are born too close to the onset of winter, they may not have a sufficient amount of time to attain pre-hibernation mass, as observed in the heavier animal.

The individuals of low body mass continued to increase their body mass before, during and after the winter measurement period. These individuals increased their body mass by 34.6%. Heldmaier (1989) states that juveniles would experience a decrease in growth rate in winter under the Dehnel effect. Table 2 (Appendix 2) shows the growth rates that the individuals of low body mass experienced over the course of winter. They did display a decrease in growth rate during the winter, however since, they were of adult age, it is unclear whether the decrease in growth rate is an artefact of age rather than season.

The resultant increase in body mass during winter in the individuals of low body mass could be attributed to the fact that they were found to use mainly daily torpor, this enabled them to make energy savings during torpor and to wake up to feed at night to replenish their energy (Geiser 2001). The replenishing of energy was possible because of the ad libitum food supply during the study. The supplementation of their food source was needed because hedgehogs have been observed to range widely to obtain enough food and restricting them to enclosures, reduced their opportunity to forage. It may be argued that the daily provision of food could have precluded the use of longer torpor bouts in this species. Laboratory studies have
shown that food restriction usually contributes to entry into torpor entry (Mzilikazi & Lovegrove 2002) and that spontaneous torpor is less common (Geiser & Baudinette 1987).

**Body temperature measurements**

*A. frontalis* is capable of undergoing bouts of torpor during the winter, however whether summer torpor is employed remains unknown as it was not found in this study. Heterothermy appears to play an important role in the energy balance of this species. During the winter, individuals spent a large amount of time torpid (up to 84% of time during the measurement period). The mean $T_{b\min}$ was 12.3±0.4°C and interestingly, *A. frontalis* exhibited an occurrence of extremely low $T_{b\min}$ of 1.0°C for an animal of this body size. This is the lowest $T_{b\min}$ recorded for a mainland Afrotropical mammal and is much lower than that observed in the Algerian hedgehog (*Atelerix algirus*) ($T_{b\min}$ of 9.7°C; Mouhoub-Sayah et al. 2008).

Body temperature tended to track the fluctuations in ambient temperature. Since the ambient temperature in the Karoo tends to plummet below 0°C frequently during winter, it is predicted that the hedgehogs' body temperature would also become extremely low. In some instances the minimum body temperature was observed to drop below the ambient temperature. This did not happen regularly and may simply be a function of the hedgehogs resting in a slightly different place to those that were being measured for the ambient environment.

The small $T_b$-$T_a$ gradients, coupled with the low $T_{b\min}$ and the drastic body mass changes observed in the individual that was larger strongly suggest that *A. frontalis* is a hibernator (Geiser and Ruf 1995). Although the individuals of lower body mass did use daily torpor bouts, the lack of longer bouts of torpor mean that the sample size for long periods of hibernation is one. The individual of larger body mass consistently exhibited longer, deeper torpor bouts than the lighter individuals. Previous studies have shown that bout length is influenced by a variety of factors, namely, dietary lipid composition, body mass and ambient temperature (Geiser 1988; Geiser 1991; Geiser and Broome 1991). However, Malan (2010) argues that there is no effect of body mass on torpor bout duration between species, and bout length is mainly controlled by a daily torpor-arousal clock. However, the emphasis in this study
is on intraspecific differences on bout length and Geiser (1988) has shown that body mass may affect torpor bout duration within a species.

From the data presented in this study, it appears that body mass is an important factor in determining the pattern of heterothermy used in this species, and if sufficient stores of fat reserves are not obtained for hibernation, it is difficult for hedgehogs to remain torpid for extended periods of time. Findings of this study contradict previous studies; which observed smaller individuals of dasyurid marsupials (*Antechinus flavipes* and *A. stuartii*) exhibiting longer and more frequent torpor bouts (Geiser 1988). Even if animals do not exhibit extended bouts of heterothermy, they still make significant energy savings by using shorter torpor bouts on a daily basis. The use of heterothermy albeit characterized by short bouts, therefore ensures survival of this species, especially the juveniles through the winter season.

It is known that the use of daily torpor may decrease energy expenditure in small mammals by up to 60% (Geiser 2001; Heldmaier 1989; Holloway and Geiser 1995). The energy saving obtained by torpid and hibernating individuals remains to be investigated in addition to whether the *ad libitum* food supplementation has an effect on the torpor pattern. No other species has exhibited spontaneous torpor when food was provided *ad libitum* and even at ambient temperatures as low as 10°C (*Macroscelides proboscideus*, Lovegrove *et al.* 1999). Since both, the individual of larger body mass and the lower Mₚ individuals were exposed to feeding, it would be expected that they all would be entrained to feeding times, or at least that the larger individual would exhibit short torpor bouts similar to those prevalent in the smaller individuals. It therefore remains highly possible that body mass and condition of the animal at the onset of winter are major determinants for the torpor patterns employed in this species. More research is required to clarify the role of food availability on heterothermic patterns in the natural habitats as well as whether *A. frontalis* are obligate or facultative heterotherms.

The patterns of heating observed in *A. frontalis* suggest the utilization of a limited amount of passive heating, but because the environmental temperatures remain low, they do not solely utilise passive rewarming to reach normothermic temperatures, as observed for example in hibernating fat-tailed lemurs (Dausmann *et al.* 2004). Instead they probably utilise a two-step rewarming process where they initially use passive heating and then endogenous heat production, as has been
observed previously in other heterotherms such as the elephant shrew (Mzilikazi et al. 2002; Schmid 2000; Ortmann et al. 1996). During rewarming, the heating rates of *A. frontalis* were lower (majority being <0.1°C/min) than would be predicted for an insectivore of this size (body mass > 200g; Geiser and Baudinette 1990). Since calculating thermal conductance requires that metabolic rate is measured simultaneously with $T_b$ (and this was not done in this study), no reference can be made to conductance of this species during torpor.

**Final Conclusions**

Although the difficulties experienced with animal capture necessitated that the data were obtained under semi-captive conditions, this study and the data obtained yielded some insights into seasonal changes in energy use and heterothermic responses in this species. Additional efforts were made to ensure that the semi-captive conditions were as close to the natural habitat and conditions as possible. By constructing the enclosures in the natural environment, they contained natural vegetation and individuals were exposed to natural environmental conditions.

The difficulties faced during the study have highlighted the possible reasons why this species (in addition other species of the Order Eulipotyphla) is so understudied. Not only are *A. frontalis* individuals very cryptic but they also occur in very low population densities that make conventional trapping methods unproductive. Over the course of this study a total of 10 individuals were hand caught and yet only data from four individuals from each of the seasons were obtained.

This study adds to the growing body of literature showing that heterothermic responses are important for survival not only in cold northern hemisphere environments but in the Afrotropics as well. *Atelerix frontalis* is thought to be particularly vulnerable because of increased incidences of road mortalities, predation by humans, some farming practices and climatic changes (Skinner and Chimimba 2005). In addition, sightings of hedgehogs by locals have declined over the last few decades and it is unclear whether this perceived decline is due to a distributional shift (possibly as a response to global climate change) or whether the species is in decline.
Use of heterothermy in this species is therefore interesting in this context because Geiser and Turbill (2009) have suggested heterothermy may be an important response that allows animal species to survive extinction events. They further suggested that heterothermic species might fare better with the challenges imposed by global climate change. If these observations are a reasonable reflection of what happens in the natural habitat then this has implications for the survival of free-ranging hedgehogs.
REFERENCES


## Appendix 1

**Table 1** Capture location and identification information for all the *Atelerix frontalis* individuals used in this study.

<table>
<thead>
<tr>
<th>DATE FOUND</th>
<th>ID #</th>
<th>MICROCHIP</th>
<th>GPS (release location)</th>
<th>BODY MASS (g) when found</th>
<th>SEX</th>
<th>ADDITIONAL NOTES</th>
</tr>
</thead>
<tbody>
<tr>
<td>24/11/2008</td>
<td>HOG 1</td>
<td>00 06 8B 50 4AT</td>
<td>S31° 01.693’ E023° 45.993’ Elev:1353m</td>
<td>355</td>
<td>M</td>
<td>Large amount of ticks and a broken left incisor</td>
</tr>
<tr>
<td>30/11/2008</td>
<td>HOG 2</td>
<td>00 06 8A AB 06T</td>
<td>S31° 05.898’ E023° 48.727’ Elev:1347m</td>
<td>380</td>
<td>M</td>
<td>The animal had a large amount of ticks and fleas</td>
</tr>
<tr>
<td>08/12/2008</td>
<td>HOG 3</td>
<td>00 06 8B 98 89T</td>
<td>S31° 00.560’ E023° 46.861’ Elev: 1364m</td>
<td>440</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>20/02/2009</td>
<td>HOG 5</td>
<td>00 06 8A 45 87T Old number: 00 06 8A 9D 6AT</td>
<td>S31° 19.539’ E023° 19.096’ Elev:1255m</td>
<td>130</td>
<td>F</td>
<td>Immature approximately: 4 weeks old</td>
</tr>
<tr>
<td>20/02/2009</td>
<td>HOG 6</td>
<td>00 06 8B 07 82T</td>
<td>S31° 19.539’ E023° 19.096’ Elev:1255m</td>
<td>140</td>
<td>M</td>
<td>Immature approximately: 4 weeks old</td>
</tr>
<tr>
<td>20/02/2009</td>
<td>HOG 7</td>
<td>00 06 8A F2 88T</td>
<td>S31° 19.539’ E023° 19.096’ Elev:1255m</td>
<td>110</td>
<td>M</td>
<td>Immature approximately: 4 weeks old</td>
</tr>
<tr>
<td>20/02/2009</td>
<td>HOG 8</td>
<td>00 06 8A B2 FBT</td>
<td>S31° 19.539’ E023° 19.096’ Elev:1255m</td>
<td>120</td>
<td>M</td>
<td>Immature approximately: 4 weeks old</td>
</tr>
<tr>
<td>01/05/2009</td>
<td>HOG 9</td>
<td>00 06 8B 4C SAT</td>
<td>S31° 00.560’ E023° 46.861’ Elev: 1364m</td>
<td>767</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>20/01/2010</td>
<td>HOG 10</td>
<td>Not microchipped</td>
<td>S31° 01.693’ E023° 45.993’ Elev:1353m</td>
<td>427</td>
<td>M</td>
<td>Young adult approximately the same age as HOGS 5-8</td>
</tr>
</tbody>
</table>
**APPENDIX 2**

**Table 2** Growth rates calculated from the body mass of four *Atelerix frontalis* individuals.

<table>
<thead>
<tr>
<th></th>
<th>Growth Rates (g/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>30/03-01/05/2009</td>
</tr>
<tr>
<td>Hog 5</td>
<td>3.51</td>
</tr>
<tr>
<td>Hog 6</td>
<td>4.27</td>
</tr>
<tr>
<td>Hog 7</td>
<td>3.29</td>
</tr>
<tr>
<td>Hog 8</td>
<td>4.30</td>
</tr>
<tr>
<td>Mean</td>
<td>3.84</td>
</tr>
<tr>
<td>SD</td>
<td>0.26</td>
</tr>
</tbody>
</table>
Appendix 3

Abstract Most research on mammalian heterothermic responses in southern Africa tends to be laboratory based and biased towards rodents and smaller members of the Afrotheria. In this study, we continuously monitored body temperature of southern African hedgehogs (Atelerix frontalis) between April and August 2009 (−10°C < T<sub>b</sub> < 4°C), kept under semi-captive conditions. A. frontalis showed a high propensity for torpor with animals spending up to 84% of the measurement period torpid. During this study, A. frontalis displayed the lowest T<sub>b min</sub> (ca 1°C) yet recorded in an Afrotropical placental heterotherm. But lengths of between 0.7 h (40 min) and 116.3 h (4.8 days) were recorded. Differences in bout length were observed between lighter individuals compared with an individual exhibiting a higher body mass at the onset of winter, with low M<sub>b</sub> individuals exhibiting daily torpor whereas heavier individuals exhibited torpor bouts that were indicative of hibernation. Our results suggest that heterothermic responses are an important feature in the energy balance of this species and that body mass at the onset of winter may determine the patterns of heterothermy utilised in this species.

Keywords Heterothermy · Torpor · Atelerix frontalis · Body temperature

Introduction Hibernation and daily torpor (heterothermy) are physiological mechanisms that have evolved in some endothermic animals, to enable them to survive adverse environmental conditions (Geiser and Ruf 1995; Lovegrove 2000; Lyman et al. 1982). Heterothermy occurs in various mammalian groups, including monotremes (Grigg et al. 2005), marsupials (Körner and Geiser 2000), some members of the Afrotheria (Mzilikazi and Lovegrove 2004; Lovegrove et al. 1999), rodents (Mzilikazi et al. 2002; Bozinovic et al. 2004) and primates (Dausmann et al. 2003; Schmid 2000; Nowack et al. 2010), as well as Xenarthra (Superina and Bolly 2007), Pholidota, Eulipotyphla, Chiroptera and Carnivora (Geiser and Turbill 2009). Although traditionally associated with the cold northern climates, daily torpor and hibernation have been recorded in species inhabiting the southern hemisphere, where the average winter temperatures tend to be higher and snowfall is uncommon, except at high altitudes (Bozinovic et al. 2004; Dausmann et al. 2004; Geiser 2007; Geiser and Broome 1991; Lovegrove and Génin 2008; Stawski et al. 2009).

In the Afrotropics, research into mammalian heterothermic responses has in the past been biased towards laboratory studies, even though their use under laboratory conditions may not be truly reflective of how the animals utilise these responses in their natural environment (Geiser et al. 2000). Additionally, studies focusing on mammals in the Afrotropics have mainly concentrated on rodents (Lovegrove and Raman 1998; Mzilikazi and Lovegrove 2002; Perrin and Richardson 2006), Afrotherians (Jackson et al. 2005; Lovegrove and Génin 2008; Mzilikazi and Lovegrove 2004; Suttlebury et al. 2008) and primates (Dausmann et al. 2004; Nowack et al. 2010). This is presumably because of the ease with which rodents can be...