INTEGRATED PHYSIOLOGY AND BEHAVIOUR OF *Thallomys nigricauda* ALONG AN ARIDITY GRADIENT

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PREFACE

The fieldwork described in this dissertation was carried out in Weenen Game Reserve (KwaZulu-Natal Province), Molopo Nature Reserve (North-West Province) and Haina Game Farm (Botswana) from February 2006 to December 2008, under the supervision of Professor Colleen T. Downs.

This dissertation, submitted for the degree of Doctorate of Philosophy in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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I certify that the above statement is correct …………………………..

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Abstract

Climate change predictions suggest that the continent most vulnerable to climate change is Africa. The impacts of potential changes which include increases in air temperatures and rainfall variability are negative with potential species extinctions projected throughout southern Africa. A number of climate models have been applied to examine the consequences of climate change for ranges of South African animal species. One such model frequently predicted range shifts from west to east, which is realistic considering the marked aridity gradient in an east-west direction across the country, but the authors suggested that these shifts may not be as marked if species are able to use physiological and behavioural methods to adapt to an increase in aridity. Information on the degree to which behavioural and physiological flexibility affect species range in southern Africa is scant which is surprising given its importance with regard to climate change.

Thallomys nigricauda occurs along an east-west aridity gradient in southern Africa, inhabiting mesic, semi-xeric and xeric regions. One would expect phenotypic flexibility in physiological and behavioural traits in response to the diverse environmental conditions to be related to the success and range of the species. The wide distribution and arboreal habits, suggesting that *T. nigricauda* is exposed to greater extremes of temperature than fossorial rodents, makes *T. nigricauda* an ideal species to test this assumption. Hence I expected that *T. nigricauda* would exhibit variation in physiological and behavioural traits measured along an aridity gradient. This has important implications in predicting the survival of small mammal species in the light of climate change in southern Africa.

Thallomys nigricauda were live-trapped in winter 2006 and 2007 and summer 2007 using Elliot traps in three sites: mesic site Weenen Game Reserve (KwaZulu-

Natal Province, South Africa); semi-xeric site Haina Game Farm (Botswana) on the northern boundary of the Central Kalahari Desert and xeric site Molopo Nature Reserve (southern Kalahari savannah, North-West Province, South Africa).

I studied the home-range size of *T. nigricauda* by radiotracking 12 males and 16 females in winter 2006, 2007 and summer 2007. Home ranges were estimated using 100% and 95% minimum convex polygons and 95% and 50% fixed kernels. Home ranges varied widely, from 166 to 80199m^2 for males and from 46 to 8810m^2 for females. Males had larger home ranges than females, which supports a promiscuous mating system reported for the species. Although range size was reduced in both sexes in winter, this was not significant. I found no significant difference in home range size along the aridity gradient. It is suggested that a combination of precipitation, habitat productivity and breeding system influences the size of home range of the species, and that this species displays phenotypic flexibility in terms of its behavioural responses to these factors.

I measured the urine concentrating ability (UCA), as indicated by urine osmolality and relative medullary thickness (RMT), and water turnover rate (WTR) of *T. nigricauda*. There was no significant difference in RMT between sites or sex and no difference in osmolalities when site, season and sex were taken into account. In addition, specific WTR was not significantly influenced by season. Lack of significant differences could be the result of the high degree of individual variation in the traits measured, an indication of the flexibility in UCA and WTR. However, higher urine osmolality and lower WTR's were recorded in the dry winter months.

I quantified the thermal environment perceived by a small, arboreal, mammalian endotherm using a number of methods at three study sites in winter and summer. Our area of interest was how well these methods accurately portrayed the

actual temperatures that small mammals are exposed to. Temperature differences between the methods were largest during the midday, when temperatures were highest. All methods recorded a greater range of temperatures during photophase than during scotophase. Black-bulb and model temperatures produced more accurate, rapid measurements when compared to measurements produced by direct temperature recording devices, particularly during photophase, when solar radiation is the major influence of heating. Other methods lagged behind black-bulb measurements. Although the mean temperatures of some of the methods were significantly different, there was a high degree of correlation between all methods, even after randomization and generation of 25% and 10% subsamples. Computed thermal indices and black-bulb temperatures produced similar thermal profiles. In studies requiring accurate time series measurements, it is suggested that black-bulb or copper models be employed rather than direct temperature recording devices. Simpler measurement devices would suffice for studies requiring an estimate of the temperature variation and trends in the microclimate of small mammalian endotherms, particularly arboreal or cavity dwelling species.

In the wild, across an aridity gradient, I measured abdominal body temperarture (T_b) of *T. nigricauda* using implanted iButtons®. All but three *T. nigricauda* displayed significant 24 h T_b rhythmicity. The T_b range for free-living *T. nigricauda* was 32.33-40.63 ^{o}C (n = 13) and 32.69-40.15 ^{o}C (n = 17) in winter and summer respectively. Although there was variation in T_b profiles, *T. nigricauda* generally displayed a bimodal distribution of T_b, with high and low T_b values during scotophase and photopase respectively. Body temperature range was significantly greater in winter, when *T. nigricauda* reduced its minimum T_b. It was shown that the maximum amplitude of circadian rhythms of body temperature was on average

259.6% of expected values. To determine the extent to which the microclimate of *T. nigricauda* cavities assists in the maintenance of T_b, I measured the temperatures of cavities across the gradient, providing an indication of the degree of buffering provided by refugia. I measured the temperatures of shallow and deep regions of cavities using iButtons® in summer and winter and recorded operative and shade temperatures for comparison. Compared with operative temperature, cavities had stable microclimates, displaying smaller ranges in temperature. Mean minimum and maximum cavity temperatures differed significantly to operative temperature and between seasons, whereas there was no significant difference between shallow and deep measurements in cavities. Differences in the buffering capacities of the cavities between seasons were not significant. To determine whether *T. nigricauda* alter its length of exposure in response to lower ambient temperatures in winter as a means of maintaining T_b, I measured the activity of *T. nigricauda*, defined as the proportion of fixes outside the home cavity of the individual. Males spent a greater proportion of the active phase away from their home cavity in summer, and significantly in winter when compared with females, but there were no differences between seasons. It is suggested that *T. nigricauda* realize energy savings by lowering its T_b during their rest phase during the day, allowing them to maintain nocturnal activity and overall energy balance.

Thus, besides the larger male home range, a result of the reproductive pattern, the physiological and behavioural traits of *T. nigricauda* measured in this study did not differ between aridity sites or seasons. The results of this study, in highlighting the variation in physiological and behavioural responses of subpopulations of *T. nigricauda* to diverse conditions, suggest that this variation is due to phenotypic flexibility. Understanding the extent and nature of this flexibility is critical to our comprehension of the consequences climate change. By defining the presence and extent of intraspecific variation in physiology and behaviour, this study resolved the necessary first step towards this understanding for the widely distributed *T. nigricauda* in southern Africa.

Keywords: Activity, aridity gradient, body temperature, cavity temperature, home range, operative temperature, osmolality, relative medullary thickness, season, *Thallomys nigricauda*, water turnover rate.

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CHAPTER 1

INTRODUCTION

Climate change predictions suggest that the continent most vulnerable to climate change is Africa (Lovett *et al.* 2005). In addition to increased temperature, changes in precipitation are expected (Hulme 2005), the most critical climate variable for African ecosystems and although precipitation predictions for African regions are variable, dry woodlands and savannahs in semi-arid and subhumid areas are expected to become more arid in the next century (Hely *et al.* 2006). The impacts of potential changes which include increases in air temperatures and rainfall variability are negative with potential species extinctions projected throughout southern Africa. Little is known about the response of African flora and fauna to projected climate changes. A number of climate models have been applied to examine the consequences of climate change for ranges of South African animal species and preliminary results indicate substantial range shifts by wild species (Lovett *et al.* 2005).

Erasmus and collegues (2002) applied a climate model to examine the consequences of climate change for ranges of South African animal species. Range shifts from west to east were a frequent prediction of the model, which is realistic considering the marked aridity gradient in an east-west direction across the country (Rutherford & Westfall 1994; Schulze *et al.* 1997), but suggested that these shifts may not be as marked if species are able to use physiological and behavioural methods to adapt to conditions. Information on the degree to which behavioural and physiological flexibility affect species range in southern Africa is scant which is surprising given its importance with regard to climate change.

The limits to geographic distribution are an ultimate expression of the limitation in the responses of organisms to challenges from the environment (McNab 2002). Since adapting to current climate extremes should be consistent with adapting to future climate change (Hulme 2005), the physiology of free-ranging animals can be viewed within the functional range of responses that have been established under controlled conditions and this will allow us to understand the susceptibility of animals to physiological stress (Goldstein & Pinshow 2006). This mechanistic perspective provides an alternative approach to modeling distributions by incorporating data on species' physiology (Hulme 2005).

Ecophysiological studies are suited to examining the role of behavioural and physiological flexibility on species range distributions, since this field of study combines the physiological, morphological and behavioural adaptations as well as the natural history of organisms in order to examine how the adaptations allow it to succeed in its natural environment (Degen 1997). The fitness of an animal depends on its ability to divide time and energy among competing behavioural and physiological demands to optimise benefits relative to costs (McNab 2002). Spatial and temporal variations in the activities of animals are centered on how to obtain, allocate and conserve energy (Bozinovic *et al.* 2004). The balance between the acquisition and expenditure of energy is fundamental to the ecological success and survival of vertebrates and this balance depends on the interaction among energy intake, digestive processing, allocation to alternative functions such as thermoregulation, growth, reproduction and others (Karasov 1986; Bozinovic 1992; Bacigalupe & Bozinovic 2002; Bozinovic *et al.* 2004).

Diversity

One of the primary objectives of modern physiology is the understanding of physiological diversity in organisms (Feder 1987) and the importance of this diversity is central to physiological ecology (McNab 2002). Although the study of adaptation is a major focus within vertebrate environmental physiology, studies of geographic variation in physiological traits are relatively rare (Garland & Adolph 1991). The traits and behaviours of organisms are moulded by their phylogenetic histories and by evolutionary forces. However, several traits may exhibit evolutionary plasticity and thus differ between closely related organisms, reflecting selective forces (Roll *et al.* 2006).

The study of geographic variation of metabolic traits in animals that are subject to different degrees of abiotic stress may provide indications of adaptations to stressful environments since metabolic processes regulate the energy of an organism and thus contribute to the ecological and physiological efficiency of an animal. Adaptation can be inferred by observing geographical phenotypic variance and correlating this variation with aspects in the environment that also vary geographically. Intraspecific differences are more related to the environment in which the organism occurs. The chance that these differences are due to changes in characteristics which occurred in the past and which have little relation to the population's present environment is small (whereas this is always a possibility with interspecific comparisons) (Feder 1987).

Studies looking for the adaptive nature of physiological traits have compared traits between species (Willmer *et al.* 2005) and have generated species specific mean values for each trait as the unit of analysis. These studies assume that traits are fixed for a species and pay no attention to variation between individuals (Bennett 1987). In traits which have high within species variation, this variation represents biological significance (Nespolo *et al.* 2003) and since this variation is the raw material upon which natural selection acts (Bozinovic & Gallardo 2006), intraspecific variation or population variability is the best way of measuring environmental effects on animals (Garland & Adolph 1991). Intraspecfic analysis of physiological traits is a useful approach which, unlike interspecific studies, can evaluate hypotheses regarding mechanisms and adaptations to environments (Bozinovic & Gallardo 2006). The recent focus on the effects of global climate change has seen an increase in the consideration of the importance of intraspecific variation and attention is being given to the flexibility in stress tolerance within species.

Phenotypic flexibility

Individual plasticity has been increasingly accepted as a major source of phenotypic variation in natural populations (Sultan & Spencer 2002). Phenotypic plasticity is a general term that includes al types of environmentally induced phenotypic variation (Stearns 1989) and has been defined as the potential for an organism to produce a range of fit phenotypes in multiple environments (De Witt *et al.* 1998). Phenotypic flexibility as a category of phenotypic plasticity involves reversible behavioural, physiological or morphological variations within an individual to changes in environmental conditions (Piersma & Drent 2003). When the environments within the range of a species differ, a single phenotype would be unlikely to confer fitness in all situations, and in such cases, a change in the phenotype that depends on the environment could provide increased environmental tolerance (Via *et al.* 1995). Individual plasticity has been recognized as an important source of phenotypic variation in natural populations, allowing individual genotypes and phenotypes to maintain fitness in diverse environmental conditions (Sultan 1995), the degree of plasticity is expected to increase with environmental variability (Morse 1980).

Aridity gradient

Aridity has been defined in a variety of ways and because deserts differ in climate, I use the term “xeric” to include all arid regions. Environments form a continuum in terms of meteorological parameters (Tieleman *et al*. 2003), dependent on a number of variables, including precipitation and temperature (Thornthwaite 1948; Meigs 1953). Emberger (1955) developed an aridity index that has been widely used. This index is low in hot, dry deserts and high in cool, wet areas (Tieleman *et al.* 2003). The index increases rapidly when environments become more mesic. According to the aridity index, I emphasised the continuum of aridity by categorizing study sites as mesic, semi-xeric and xeric. This is in accordance with the marked aridity gradient in an east-west direction across southern Africa (Rutherford & Westfall 1994, Schulze *et al.* 1997). The xeric and semi-xeric sites form part of the Kalahari desert system of southern Africa, caused by the presence of high pressures which result in dry, stable air masses (Degen 1997).

Xeric regions

The suite of physiological, behavioural and morphological attributes which enable small mammals to thrive in deserts has been intensively studied (Withers *et al*. 1980). It might be expected that animals that live in xeric areas possess behavioural an physiological adaptations that would enable them to cope with the lack of free water, high ambient temperatures (T_a), low food resources, the main features of these environments (Tieleman *et al*. 2002) and that they have established a balance between their requirements and the problems presented by the extreme conditions in these environments (McNab & Morrison 1963).

The environmental variables in xeric regions are not constant, but fluctuate at both daily and seasonal scales (Degen 1997; Kronfeld-Schor *et al.* 2000). Differences in aridity not only affect the availability of drinking water, but also primary productivity, an indirect correlate of food supply. Precipitation thus plays the dominant role in controlling biological productivity in the desert ecosystem (Noy-Meir 1973). The lack of water is combined with seasonal periods of high temperatures and this combination produces a physiological challenge for mammals (Schmidt-Nielsen 1975; Walsberg 2000). These conditions favour the loss of water and heat loading and this has the potential to elevate body temperature (T_b) making thermal and water relations of critical importance to vertebrates (Lillywhite & Navas 2006).

Willmer (2005) split xeric fauna into three strategic categories based on their size, with rodents dominating the small endotherm evaders. Features shared by this group include a fossorial lifestyle, rapid, darting modes of locomotion from a central place, reduced metabolic rate, lower resting metabolic rate, higher rates of nonshivering thermogenesis, changes in coat colour, long loops of Henle in proportion to their size, high urine osmolalities and low rates of water loss. Comparisons show that a particular capacity is greater among organisms exposed to more extreme conditions (Withers 1992). The dominance of rodents in desert regions indicates that they can either avoid the stresses or that they have employed effective physiological counter measures (Schmidt-Nielsen 1975).

Water

Water is the driving force of desert ecosystems (Noy-Meir 1973) its scarcity being the main challenge to survival of desert animals (Nagy 1988) and the mechanisms which xeric rodents use in obtaining and conserving water from dry environments have been the subject of many studies (Reaka & Armitage 1976). The major climatic determinant of water regulation in terrestrial organisms should be precipitation since it correlates positively with water availability and primary productivity (Leith 1975), and therefore with food quality and quantity (MacMillen 1983). The water balance of a species depends on the free water available in the environment as well as on temperature and humidity (Reaka & Armitage 1976). Water metabolism is a function of water intake and water loss (Yousef 1973) and thus for an animal to remain in water balance, total water intake must equal total water loss (Schmidt-Nielsen 1975).

Factors determining the availability to and loss of water from a mammal vary between environments. Such variation is matched by physiological and behavioural adaptations by the mammals and influences the distribution and abundance of mammals (Chew 1951). Water loss is influenced by an animals heat production plus heat gained from the environment and accumulated heat must be dissipated to prevent an intolerable rise in T_b (Yousef 1973). Terrestrial vertebrates expend energy to carry out processes to sustain life, and constantly lose water through respiration, cutaneous evaporation and excretion (Tieleman *et al.* 2002), yet it is doubtful whether small mammals drink water in the field (MacMillen 1983) relying rather on oxidative and preformed water from their food (Schmidt-Nielsen 1975; Downs & Perrin 1990).

Patterns displayed by small desert mammals which contribute to the maintenance of a positive water balance include nocturnality, fossoriality, urine concentrating ability and minimization of respiratory water loss (Withers *et al.* 1980).

Evaluations of states of water balance, renal performance and rates of water turnover under natural conditions allow us to determine the extent to which the physiological capacities for water economy are employed (MacMillen 1972).

Measurements of rates of water turnover (WTR) allow the assessment of the extent to which species are buffered from the effects of aridity by the efficiency of their homeostatic regulatory systems (Bradshaw *et al.* 2001). Factors influencing body water turnover rates in rodents include metabolic rate, body size, water availability, environmental heat load, species and water content of the food (Yousef 1973; Holleman & Dieterich 1973). It has been shown that xeric mammals have lower WTR's than those inhabiting mesic zones (Degen *et al.* 1981) and that WTR's vary seasonally in xeric rodents (Nagy 1988; Grenot & Buscarlet 1988). Tritiated water (TOH) turnover, an estimate of body water turnover, is a measure of the overall state of water economy of the animal. The magnitude of TOH flux reflects the daily water input and output and the approach an animal takes to supply its water needs. The change of flux with season and reproductive activity for example, reflects the impact of biological and environmental factors on water economy (Grubbs 1980).

Energy

One of the primary means by which the environment influences animals is through the exchange of energy, and over an extended period of time, an animal must be in energy balance with its environment (Porter & Gates 1969). The energy balance of small mammals is tightly coupled to environmental conditions, owing to high surface-to-volume ratio, limited insulation, and a relatively shallow boundary layer (Chappell *et al.* 1978). Food availability and climatic conditions influence the rate at which animals can acquire and expend energy (Bozinovic *et al.* 2004) and thus have a direct effect on the structure of an animal's energy budget (Corp *et al*. 1999). The rate at which an animal uses resources is determined by its metabolic requirements, thus feeding rates are determined by daily energy needs (Nagy *et al.* 1999). For non-hibernating small mammals in cooler climates, winter is often the most energetically challenging since low T_a's require increased energy intake (Speakman 2000).

A second feature characteristic of desert rodents linked to low WTR is a lower rate of energy expenditure (Weissenberg & Shkolnik 1994; Scantlebury *et al.* 2004). A low rate of energy metabolism implies a low rate of heat production, thereby conserving water that would be used to dissipate this heat, and this should be advantageous to xeric life. A low rate of energy metabolism also implies a reduced demand for food. Xeric rodents have resting metabolic rates which are lower than predicted for their body mass (Schmidt-Nielsen 1964) and this is likely to help an animal cope with the shortage of food that like the shortage of water, characterizes the desert environment (Rubal *et al.* 1995). Most desert evaders have reduced metabolic rates and the data strongly suggest that lowering metabolic rate is an adaptive feature (Willmer 2005).

Kidney function

Adaptive radiation into different environments may involve structural and functional variation of the kidney, since it is the major organ in maintaining the internal environment at constant osmolality (Nevo *et al.* 1989). Mammalian kidneys play an important role in controlling the concentration and volume of body fluids, the morphological and vascular organizations of the nephrons enabling the organism to produce urine that is more concentrated than body plasma (Al-Kahtani *et al.* 2004). Physiological adaptations of small rodents to arid conditions are achieved mainly through concentrating ability of their kidneys (Beuchat 1996) and producing hyperosmotic urine is the single physiological means of reducing water loss characteristic of nocturnal, xeric-dwelling rodents (MacMillen 1972).

Sperber (1944) proposed relative medullary thickness (RMT) as a structural index for quantifying the relative length of the longest loops of Henle and found that species from arid environments had higher values than mammals from mesic habitats. "Long looped nephrons" can be distinguished by an extended renal papilla (Bankir & de Rouffignac 1985) and the maximum length of the loop of Henle is directly proportional to medullary thickness (Beuchat 1990; 1993; 1996). RMT has been correlated with the ability to concentrate urine (UCA) and studies demonstrate a trend for xeric and semi-xeric species to have high UCA and high RMT (Heisinger & Breitenbach 1969; Heisinger *et al.* 1973; Greegor 1975; Blake 1977; Geluso 1978).

Urine osmolality could be used as an index of the extent to which rodents encounter water stress as adjustments of renal output represent a major physiological response a mammal may make to remain in water balance (Grubbs 1980). Urine osmolality is the most widely studied renal function in relation to adaptation to a xeric environment, the greater the osmolality of the urine to that of the plasma, the greater the advantage to the animal that needs to conserve water (Dantzler 1982). Animals that survive xeric conditions form urine of high solute concentration, the highest concentrations being found in rodents that do not depend on a high water intake (Schmidt-Nielsen 1975).

Temperature

Temperature is the most pervasive physical parameter affecting biological functions and organisms in thermally heterogenous environments must cope with varying physiological performance unless regulation is implemented. Extreme environments place severe demands on the thermoregulation of the smallest birds and mammals (Schmidt-Nielsen 1964; Porter & Gates 1969) and the influence of temperature on energy exchange and behaviour is large, thermoregulation representing the largest component of an animal's energy budget (Bennett 1987).

Body temperature in most mammals, regulated by the combined action of the thermoregulatory system and the circadian system (Refinetti & Menaker 1992), is maintained independent of moderate changes in environmental temperature. These temperatures are not fixed, but vary within a range of values (McNab & Morrison 1963; Refinetti 1995) controlled by an internal circadian clock (Refinetti & Menaker 1992; Weinert & Waterhouse 1998). The variation is influenced by several factors (Gebczynski & Taylor 2004) other than T_a, most variations in an animal's temperature reflecting the state of activity (McNab & Morrison 1963). Body temperature of mammals may undergo short term (daily) fluctuations as well as seasonal ones (Rodriguez-Girones 2002). The amplitude of the daily rhythm of T_b is important in determining a mammal's ability to regulate $\mathrm{T_b}$ in the maximum range of $\mathrm{T_a}$'s experienced in its environment (Refinetti & Menaker 1992; Lovegrove & Heldmaier 1994).

Tolerance of a wide range of T_a's allows animals to survive in energetically and thermally stressful environments. When challenged energetically under conditions of low T_a or decreased food supply, some mammals may allow T_b to fluctuate with ambient conditions (Lehmer *et al.* 2006), by lowering T_b, for example (Pereira *et al.* 2002). Numerous small mammals decrease their T_b during the rest phase (Jones *et al.* 1997; Cooper & Withers 2004) thereby reducing the cost of euthermy (Barclay *et al.* 2001).

In addition to endogenous thermoregulatory responses, some mammals make use of behavioural responses to ambient temperatures, such as nocturnalism (Fielden *et al.* 1990), suggesting that behavioural thermoregulation also plays a role in the fluctuation of T_b of an animal in its environment (Refinetti 1995; 1996; 1997; Refinetti & Menaker 1992). The majority of studies of animals living in hot, dry environments have concentrated on mechanisms employed to counteract stresses imposed by the harsh conditions, particularly high ambient temperatures and scarcity of water (Schmidt-Nielsen 1964; Degen 1997). Nocturnal animals avoid the problems of high temperature stress (MacMillan 1983), and this may be a reason for nocturnal rodents being largely ignored (Goodfriend *et al.* 1991). These authors concur with Hadley (1979) that the study of adaptations to low T_a's is a neglected aspect of the physiology of desert organisms.

For many nocturnal rodents which occupy deserts with low ambient night temperatures, the principal thermoregulatory problem is not coping with high temperatures during summer, but coping with very low nighttime temperatures during the winter (Bartholomew & Dawson 1974). The capacity for thermogenesis and energy intake are important for the survival of small winter active nocturnal mammals (Song & Wang 2006) since the seasonal decline in T_a increases the cost of both thermoregulation and foraging (Kronfeld-Schor *et al.* 2001; Song & Wang 2006).

Behaviourally, in cold environments, rodents often choose microhabitats that reduce the need for physiological thermoregulation and choose to be active during times that are least thermally stressful (Sears *et al.* 2006) being active closer to sunset than later in the night (Seabloom *et al.* 1994). In addition, social huddling reduces exposure and thus heat loss during cold weather (Madison *et al.* 1984). In addition, buffered refugia provide thermal environments which may result in energetic benefits for the inhabitants (Stains 1961; Robb *et al.* 1996)

Ambient temperature is not the actual thermal condition experienced by the animal in its natural environment (Chappell & Bartholomew 1981). The factors of the environment which are primarily responsible for energy flow to an animal include radiation, air temperature, wind and humidity (Porter & Gates 1969). In order to estimate the energetic effects of the thermal regime an animal experiences in the field, it is convenient to integrate the effects of these parameters into an index value that can be directly compared to the animal's physiological performance (Chappell 1981). A useful index of the thermal potential driving heat flow between animals and their thermal environments is the operative temperature (T_e) (Byman 1985). Operative temperature is considered to be the temperature of an inanimate object of zero heat capacity that is of the same size, shape, and has the same radiative properties as the animal exposed to the same microclimate (Bakken & Gates 1975). This thermal index thus gives an indication of the thermal conditions experienced by an animal in its natural surroundings (Chappell & Bartholomew 1981). Operative temperatures (Bakken & Gates 1975; Bakken 1976) have become a tool for studying the thermal effects of ectotherms and endotherms (Bakken 1992). However, relatively few studies have been undertaken on the T_e of small mammals and none to date on nocturnal arboreal endotherms.

Previous attempts to calculate 'perceived' temperature have resulted in a number of indices. The primary function of these indices is to produce estimates of thermal load, rather than absolute perceived temperatures. As an alternative, basic composite measures of the indices should produce workable estimates of the perceived thermoregulatory loads experienced by animals in their natural habitats.

The method chosen which provides a biologically relevant thermal index, 'perceived environmental temperature' incorporates the temperature-humidity index or heat index based upon the black bulb solar radiation temperature and relative humidity and the wind chill index based upon the actual temperature and wind speed (Hill *et al.* 2004).

Activity and home range

Behaviour is primary and sometimes the crucial means by which an animal copes with an environmental challenge (Bennett 1987). One circumstance in which the behaviour of an animal becomes critical is when environmental conditions exceed the capacities of physiological systems to achieve homeostasis (Goldstein & Pinshow 2006).

The 24 h rhythms displayed by animals in the field are a result of the interaction between endogenous physiological and environmental factors (Aschoff 1966; Ashby 1972; Rezende *et al.* 2003), with most animals having rest and activity states. The seasonal pattern of activity of rodents is influenced by changes in photoperiod and temperature (Lockard & Owings 1974; Lockard 1978; Hanski *et al.* 2000; Waulters *et al.* 2000). The capacity for thermogenesis and energy intake are important for the survival of small winter active nocturnal mammals (Song & Wang 2006) since the seasonal decline in T_a increases the cost of both thermoregulation and foraging (Kronfeld-Schor *et al.* 2001; Song & Wang 2006). The problem is especially acute for non-hibernating small mammals because they lose heat rapidly and need to consume large amounts of food relative to their body mass (Bozinovic *et al.* 1997; Schwaibold & Pillay 2006). In such cases, in addition to physiological mechanisms discussed, additional behavioural mechanisms to maintain body mass and temperature and to conserve energy can be expected to occur (Contreras 1984; Vickery & Millar 1984). Animals may make use of buffered refugia which provide a thermal environment resulting in energetic benefits to the inhabitants (Stains 1961; Robb *et al.* 1996) in addition to reducing the cost of foraging (Ashby 1972; Bozinovic *et al.* 2000). Moreover, animals may huddle in refugia thereby reducing heat loss (Madison *et al.* 1984; Kaufman *et al*. 2003).

Variations in activity should be reflected by corresponding differences in ranging behaviour. One might expect changes in physiological states and energetic requirements to be reflected in the movements of the animals, since home range size is related to the energetic requirements and reserves of the animal (Hawes 1977). Home range was first defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). The size of home range has been shown to be correlated with body mass, food type, the way that food is obtained (McNab 1963), mating system (Ostfeld 1990), energy requirements, habitat productivity (Swihart *et al.* 1988), population density and season (Mares *et al*. 1976). Although nocturnal desert rodents, owing to their small size and tendency to restrict activity to finite home ranges, are not highly mobile (MacMillen 1972)), directed seasonal movements can be expected in small mammals living in seasonal environments (Schradin & Pillay 2006).

Present study

The study was multifaceted and investigated various traits of the Black-tailed Tree Rat, *Thallomys nigricauda* to differing environments along an aridity gradient in southern Africa. The three study sites, which lie in a summer rainfall area (Schulze *et al*. 1997), were Weenen Game Reserve, Haina Game Farm and Molopo Nature

Reserve. These localities were chosen to represent an aridity gradient from west to east (Rutherford & Westfall 1994; Schulze *et al.* 1997). Field studies were conducted in winter (May-July) in 2006 and 2007 and summer (January-February) in 2007.

Thallomys nigricauda is a small (32-116g), arboreal, nocturnal, murid rodent, occurring in mesic to xeric regions of South Africa, Botswana, Swaziland, Zimbabwe and Namibia (Skinner and Chimimba 2005). They are folivores, feeding on young *Acacia erioloba* leave and fine twigs and the outer green coating of seed pods, but may supplement their diets with insects and gum (de Graaff 1981; Skinner and Chimimba 2005). This is in contrast with the majority of xeric rodents, which are predominantly granivorous or opportunistically insectivorous. It was suggested that the water yield of their food is sufficient to permit *T. nigricauda* to survive without drinking water (Bradfield in Shortridge 1934). While the vast majority of rodent species evade the harsh conditions by burrowing, the *T. nigricauda* is one of a few species in arid environments to have adopted an arboreal lifestyle with nests composed of sticks and leaves situated in forks and hollows of trees (mainly *Acacia erioloba*) (Skinner and Chimimba 2005). Being arboreal, *T. nigricauda* is exposed to greater daily temperature fluctuations and lower humidities in their nests compared to most other southern African xeric rodents which use subterranean microhabitats with stable milieux to escape daytime heat (de Graaff 1981; Lovegrove & Knight-Eloff 1988; Downs & Perrin 1989; Skinner & Chimimba 2005). Thus, there are possibly thermal costs resulting from an arboreal lifestyle compared with the thermal refuge of a burrow.

Data on the physiology of *T. nigricauda* are from laboratory studies. Past research has concentrated on thermal energetic profiles (Lovegrove *et al.* 1991), T_b daily rhythms and activity (Lovegrove & Heldmaier 1994), urine concentrating ability

(Frean *et al*. 1998) and the effects of andrenergic blockade on rhythms of T_b and oxygen consumption (Haim *et al*. 2001). Recent ecological studies in the field have focused on activity and space use (Eccard *et al*. 2004), tree use (Eccard *et al*. 2006), density (Meyer *et al.* 2007) and diet (Meyer *et al.* 2008).

Given the negative climate change predictions for southern Africa and the paucity of research on the degree to which behavioural and physiological flexibility affect species range in the region, this study was poised to address these concerns. Since *T. nigricauda* occurs along an east-west aridity gradient in southern Africa (Skinner & Chimimba 2005), one would expect phenotypic flexibility in physiological and behavioural traits in response to the diverse environmental conditions to be related to the success and range of the species. The wide distribution and arboreal habits, suggesting that *T. nigricauda* is exposed to greater extremes of temperature than fossorial rodents, makes *T. nigricauda* an ideal species to test the assumption of Erasmus and colleagues (2002). In general this study undertakes to explain the physiological and behavioural patterns of *T. nigricauda* along an aridity gradient. Seasonal data will facilitate the understanding of the temporal variation in environmental effects on the species. The study of intraspecific variation in physiological and behavioural traits will facilitate understanding about the extent of phenotypic flexibility of the species along the aridity gradient. I hypothesised that *T. nigricauda* exhibit variation in physiological and behavioural traits along an aridity gradient. This has important implications in predicting the survival of small mammal species in the light of climate change in southern Africa.

The aims of this study were multifaceted, incorporating ecological, physiological and behavioural aspects as follows:

The first objective was to determine whether there were differences in the home range size of *T. nigricauda* between seasons and along an aridity gradient. It was predicted that home-range size would differ significantly between summer and winter, and along an aridity gradient. I predicted that the home-range size of males would be significantly larger than that of females.

The second objective was to determine whether there were differences in urine osmolality and specific WTR of free-living *T. nigricauda* between seasons, and in urine osmolality and kidney RMT along an aridity gradient. I predicted that osmolalities and specific WTR would not differ significantly between summer and winter, and that urine osmolalities and kidney RMT would not differ significantly along an aridity gradient. I predicted that *T. nigricauda* would have a renal structure indicative of efficient UCA.

The third objective was to quantify the degree to which temperature data derived using copper models, black-bulb and more direct temperature measurement devices accurately predict the actual temperatures perceived by small, endothermic mammals. I predicted that black-bulb and copper model temperatures would more accurately and precisely predict T_e during the day when compared to other direct measurement devices and that black-bulb would record the greatest variation in temperatures.

The fourth objective was to measure and describe T_b daily rhythms of free-living *T. nigricauda* and to determine whether these rhythms differed along an aridity gradient and between seasons. In addition, I compared cavity temperatures with T_e, and determined and compared activity patterns between sexes and seasons. I predicted that *T. nigricauda* would display a T_b daily rhythm typical of an endotherm T_b daily pattern and that T_b would be maintained, irrespective of season or aridity site. In addition, I expected that cavity temperatures would buffer T_a and that maintenance of T_b would influence activity patterns.

This thesis is presented in four main chapters that cover the above four broad subject areas. Chapter 6 is a conclusion that integrates the conclusions of the entire study. This thesis has been written in the form of papers for publication, and has followed the format of the relevant journal. There is unavoidable repetition of aspects of the introduction in subsequent chapters based on the manuscript style of presentation of the thesis. The chapters prepared for submission are as follows:

Chapter 2: Does home range of the Black-tailed Tree Rat (*Thallomys nigricauda*) along an aridity gradient change with season? Formatted for Journal of Mammalogy.

Chapter 3: Seasonal changes in urine concentrating ability and water balance of the Black-tailed Tree Rat *Thallomys nigricauda*, along an aridity gradient. Formatted for Comparative Biochemistry and Physiology Part A.

Chapter 4: Characterising the thermal environment of small mammalian endotherms: what should we be measuring, and how? Formatted for Functional Ecology.

Chapter 5: Daily rhythms of body temperature and activity in free-living Black-tailed Tree Rats (*Thallomys nigricauda*) along an aridity gradient. Formatted for Physiology and Behavior.

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Chapter 2

DOES HOME RANGE OF THE BLACK-TAILED TREE RAT (*THALLOMYS NIGRICAUDA*) ALONG AN ARIDITY GRADIENT CHANGE WITH SEASON?

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Home range size may reflect the physiological state and energetic requirements of an individual. In the Black-tailed Tree Rat (*Thallomys nigricauda*), which occurs along an aridity gradient, we expected seasonal variations in the home range size. We studied the variations in home-range size of *T. nigricauda* by radiotracking 12 males and 16 females in winter 2006, 2007 and summer 2007 at 3 study sites along an aridity gradient in southern Africa. Home ranges were estimated using 100% and 95% minimum convex polygons (MCP) and 95% and 50% fixed kernels. Home ranges varied widely, from 166 to 80199m^2 for males and from 46 to 8810m^2 for females. Males had larger home ranges than females, which supports a promiscuous mating system reported for the species. Although range size was reduced in both sexes in winter, this was not significant. We found no significant difference in home range size along the aridity gradient. It is suggested that a combination of precipitation, habitat productivity and breeding system influences the size of home range and that this species displays phenotypic flexibility in terms of its behavioural responses to these factors.

Key words: aridity gradient, home range, nocturnal, phenotypic flexibility, radiotelemetry, season, sex, *Thallomys nigricauda*

Home-range size is an ecological parameter regularly described for a given species, and attention has been focused on the analysis of factors influencing its size (Harestad and Bunnell 1979; McLoughlin and Ferguson 2000; Kelt and van Vuuren 2001). Home-range size varies with body size and is influenced by energetic requirements (McNab 1963; Harestad and Bunnell 1979; Lindstedt et al., 1986, Swihart et al., 1988), mating system (Ostfeld 1990), habitat productivity (Swihart et al. 1988), population density and season (Mares et al. 1976), and predation (Swihart et al. 1988). Home-range size may differ between seasons, between sexes and also due to reproductive status (Clutton-Brock et al. 1982). Home-range has been defined as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943). One might expect changes in physiological states and energetic requirements to be reflected in the movements of the animals, since home-range size is related to the energetic requirements and reserves of the animal (Hawes 1977).

Since food is usually more abundant in summer than in winter, animals may employ physiological and/or behavioural mechanisms to cope with seasonal stress. Thus directed seasonal movements can be expected in small mammals living in seasonal environments (Schradin and Pillay 2006). In winter, animals either forage widely to obtain enough food to offset maintenance costs or reduce metabolic requirements by reducing movements and drawing on stored energy reserves (Slade and Swihart 1983). In some herbivores, winter home-range is smaller than summer home range (Harestad and Bunnell 1979).

Differences in the size of home-range between sexes may be attributed to sex-related differences in weight (Harestad and Bunnell 1979). As larger animals expend more energy, they would require more food and thus have larger home-ranges than smaller animals (McNab 1963). Numerous studies of space-use patterns of small mammals have reported differences in home-range size between sexes, male home-ranges being typically larger than female home-ranges. A common interpretation of this difference is that males cover a large range to gain access to receptive females, whereas the range of a female reflects the size needed to obtain resources to raise offspring (Madison 1980; Ostfeld 1985; Gaulin and Fitzgerald 1988). Moreover, sex-specific evolutionary pressures may cause differences in behaviour and space use between sexes (Ostfeld 1990). In polygynous and promiscuous species, males usually have larger home-ranges than females (Clutton-Brock 1989; Fisher and Lara 1999).

Within a trophic class, it is expected that animals in high productivity habitats will have smaller home-ranges than animals in areas of lower productivity and if primary production is directly proportional to precipitation, sizes of home-ranges for a species should be larger in areas of low precipitation (Harestad and Bunnell 1979). Precipitation correlates with the productivity of the habitat (Leith 1975) and larger home-ranges should be found in arid habitats than in habitats with high precipitation (Mares et al. 1976). There is great intraspecific variation in home range size (Gompper and Gittleman 1991) and one of the factors shown to influence this variation is resource availability (Oehler et al. 2003). Many studies combine populations from very different geographical or ecological areas to yield a single value for a species, but variability of home range sizes of local populations within a species can be extensive (Gompper and Gittleman 1991).

Phenotypic flexibility as a category of phenotypic plasticity involves reversible behavioural, physiological or morphological variations within an individual to changes in environmental conditions (Piersma & Drent, 2003). When the environments within the range of a species differ, a single phenotype would be unlikely to confer fitness in all situations, and in such cases, a change in the phenotype that depends on the environment could provide increased environmental tolerance (Via et al., 1995). Individual plasticity has been recognized as an important source of phenotypic variation in natural populations, allowing individual genotypes to maintain fitness in diverse environmental conditions (Sultan, 1995), the degree of plasticity being expected to increase with environmental variability (Morse, 1980).

Thallomys nigricauda, the Black-tailed Tree Rat, is an arboreal, nocturnal, murid rodent, occurring in mesic to xeric regions of South Africa, Botswana, Swaziland, Zimbabwe and Namibia (Skinner and Chimimba 2005). They are folivores, feeding on young *Acacia erioloba* leaves and fine twigs and the outer green coating of seed pods, but may supplement their diets with insects and gum (de Graaff 1981; Skinner and Chimimba 2005). This is in contrast with the majority of xeric rodents, which are predominantly granivorous or opportunistically insectivorous. It was suggested that the water yield is sufficient to permit *T. nigricauda* to survive without drinking water (Bradfield in Shortridge 1934). While the vast majority of rodent species evade the harsh conditions by burrowing, *T. nigricauda* is one of a few species in arid environments to have adopted an arboreal lifestyle with nests composed of sticks and leaves situated in forks and hollows of trees (mainly *Acacia erioloba*) (Skinner and Chimimba 2005).

Information on the degree to which behavioural flexibility affects species range in southern Africa is lacking, which is surprising considering its importance with regard to climate change. Since *T. nigricauda* occurs in mesic, semi-xeric and xeric regions of southern Africa, one would expect phenotypic flexibility in its behaviour in response to the diverse environmental conditions to which it is exposed to play a role in the success and range of the species. The aim of this study was to determine whether there were differences in the home-range size between seasons and along an aridity gradient. More specifically, we predicted that home-range size would differ significantly between summer and winter, and along an aridity gradient. We predicted the home-ranges of males to be significantly larger than those of females.

MATERIALS AND METHODS

Study sites.- The study was conducted at three sites along an east-west aridity gradient (Rutherford and Westfall 1994; Schulze et al. 1997) (Fig. 1): mesic locality Weenen Game Reserve (KwaZulu-Natal Province, South Africa, 28°50’43”S; 29°59’12”E); semi-xeric site Haina Game Farm (Botswana 20˚56’56”S; 23˚40’40”E) on the northern boundary of the Central Kalahari Desert, and xeric site Molopo Nature Reserve (southern Kalahari savannah, North-West Province, South Africa 25˚50’52”S; 22˚55’37”E). Aridity index data for the three sites are detailed elsewhere (Chapter 3). Degree locations were plotted using a Magellan GPS 4000 XL.

Vegetation of Weenen Game Reserve is a mosaic of three vegetation units (Mucina and Rutherford 2006). The KwaZulu-Natal Highland Thornveld, is a hilly undulating landscape supporting grassland dominated by *Hyparrhenia hirta* and occasional savanoid woodlands, with scattered *Acacia* spp. The steeper slopes are comprised of Thukela Valley Bushveld, with deciduous trees, including *Acacia* spp. and *Boschia albitrunca,* large shrubs and succulents. Thukela Thornveld featuring valley slopes to undulating hills, is dominated by *Acacia* bushveld with dense grassy undergrowth. Mean annual rainfall for the 3 units ranges from 682 mm to 752 mm and the mean annual temperature ranges from 16.5 ºC to 17.9 ºC. Vegetation of Molopo Nature Reserve is classified as Molopo Bushveld and comprises open woodland to closed shrubland with trees (*Acacia erioloba* and *Boschia albitrunca*), shrubs and an open grass layer. Mean annual rainfall is 333 mm and the mean annual temperature is 19.1 ºC (Mucina and Rutherford 2006). Haina Game Farm forms part of the Savannah biome (Rutherford and Westfall, 1994) and the dominant tree species are the Blue thorn (*A. erubescens*), Black thorn (*A. mellifera*), Trumpet thorn (*Catophractes alexandri*) and Raisin bushes (*Grewia flava, and G. monticolor*). The three most dominant grass covers, which vary between seasons and years, are *Urochloa mosambicensis, Aristida mendionalis and Eragrostis curvula* (CJ Spykerman pers. comm.). Mean annual rainfall is approximately 400 mm and the mean annual temperature is between 20 - 22 ºC (Schulze and McGee, 1978).

Telemetry procedures.-Thallomys nigricauda were live trapped at each study site during winter (May – July) in 2006 and 2007, and in summer (January – February 2007) using Elliot traps. Nests and resting places of *T. nigricauda* were identified by searching the stems and bases of trees with potential cavities for faeces and the distinctive smell of excreta. Traps were also placed at sites where study animals had been previously seen and/or trapped. Traps were placed on the branches and at the base of potential trees and baited with oats and peanut butter. Traps were set in the late afternoon, checked shortly after sunrise and removed from trap sites. *T. nigricauda* were transported to a veterinarian within 36 h of capture.

Thallomys nigricauda were sexed, weighed, ear clipped and reproductive status was noted. *Thallomys nigricauda* (>40g) were anaethesized using isoflorthane (2%) or Anakel – V (100mg/ml) and Chanazine (20 mg/ml). A total of 60 *T. nigricauda*, 28 in winter and 32 in summer, were fitted with radio-transmitters (C. Dearden, Pietermaritzburg) and released back into their natural environment at the point of capture after a 4-12 h recovery period. Transmitters were two-stage radio-transmitters encased in epoxy resin and attached to a cable-tie collar with a 15 cm vertical whip aerial. Radio-transmitters were powered by a single silver oxide 1.5V watch battery and weighed 3.0g, which was less than 5% of the average animal's body mass (2-4% of body mass). Transmitters had 60 days of battery life and an average range of 1 km.

Tracking was conducted on foot with a hand held three element aerial and an Alinco DJX10 (Osaka, Japan) receiver. Fixes (the location of an animal at one point in time) were recorded by their grid coordinates using a handheld GPS (Magellan GPS 4000 XL). Locations of *T. nigricauda* were obtained from direct sightings/homing in (White and Garrott 1990) and activity, where possible, was recorded with each fix. Use of homing techniques had no effect on diurnal locations. In addition, there was no evidence that nocturnal locations were affected by homing techniques since our close proximity to *T. nigricauda* rarely appeared to affect their behaviour or movement patterns (pers. obs.). At the end of the study, all animals were recaptured and radio-transmitters removed.

In winter, nights from 17:00 to 07:00 were divided into 14 hourly intervals, whereas in summer from 19:00 to 06:00 into 11 hourly intervals. Similarly in winter, days were divided from 07:00 to 17:00 into 10 hourly intervals, whereas in summer from 06:00 to 19:00 into 13 hourly intervals.

Home-range estimation/Data analyses.-We estimated home-range sizes for *T. nigricauda* using the Home Range Extension (HRE; Rodgers and Carr 1998) for ArcView 3x (ESRI, Redlands, California, USA). We selected animals with > 34 fixes for home-range calculations.

A problem using any area estimation is that they assume that the location data are statistically independent. It has been suggested that data needs only to be biologically independent (de Solla et al. 1999), as defined by ‘a sampling interval long enough for an animal to move from any point in its home range to any other point’ (Lair 1987) and a growing number of researchers are defining independence biologically rather than statistically (Andersen and Rongstad 1989; Reynolds and Laundre 1990; McNay et al. 1994). Data with independent sampling intervals have been found to underestimate home range size and produced less accurate estimates than autocorrelated fixes (Reynolds and Laundre 1990; de Solla et al. 1999). In addition, current methods used to detect autocorrelation are not necessarily suitable for all organisms (Andersen and Rongstad 1989). Therefore, using a sampling methodology that captures biologically independent data, which is species specific, is perhaps more important than the elimination of autocorrelation when using utilization distribution estimation techniques. Home-range areas with autocorrelated observations are often associated with important resources (e.g. Swihart and Slade 1985; Lair 1987) and can reflect features of an animal’s use of space (Swihart et al. 1988). If the criteria for biological independence are determined prior to the collection of data, and the appropriate sampling interval is then used during the study, it could be argued that statistical measures of autocorrelation are irrelevant (de Solla et al.

1999). In this study it was appropriate to substitute statistical independence with biological time to independence, that is, the time needed for an animal to transverse its home range.

We used all fixes for each animal to calculate the size of the home-range since kernel estimators are robust to violations of independence (Swihart and Slade 1997) and estimates should incorporate the entire activity cycle of the animal (Harris et al. 1990). Prior to the study, we evaluated independence biologically for this species guided by the definition in Lair (1987). We ensured that each *T. nigricauda* was radio-tracked every hour of the day during the study period and to confirm nesting sites. During the night we attempted to radio-tracked each individual hourly. At night we allowed at least one hour to elapse between locations on individual mice which was sufficient to allow an individual to move across its home range, thereby ensuring independence of data points, avoiding problems of autocorrelation (Kenward 1987; Swihardt and Slade 1985), while optimizing the number of locations.

We conducted minimum convex polygon (MCP) analyses using both 100% of the locations (100% MCP) and 95% of the locations (95% MCP) with a floating mean approach (Rodgers and Carr 1998) for each *T. nigricauda*. Minimum convex polygons were calculated because it is the most commonly reported method in the literature (Harris et al. 1990) and thus allows for comparison with other studies. 100% of fixes were included to determine the maximal area used and 95% MCPs were calculated to exclude the occasional excursion.

We also conducted 95% fixed-kernel analyses (Worton 1989). All were conducted with a 95% volume and default resolution (70 x 70 cell grid) options in HRE (Rodgers and Carr 1998). We also used the fixed kernel method as it is less sensitive to autocorrelated data (Millspaugh and Marzluff 2001), has been shown to produce a less biased home-range size calculation and better surface fit than the adaptive kernel method (Worton 1989; Seaman and Powell 1996; Seaman et. al. 1999) providing a more reliable estimate of the outer contours and centers of activity (Kernohan et al. 2001). Kernel estimates are less likely to be biased than MCP estimates, given the problems concerning autocorrelated data (Swihart and Slade 1997).

We used the smoothing parameter calculated by ArcView (h_{ref}) except in the cases where a reduced h value (e.g. 0.9 h_{ref}, 0.8 h_{ref}, 0.7 h_{ref} ….0.1 h_{ref}) resulted in a smaller, non-fragmented home range. In such cases, we chose the smallest increment of h_{ref} that resulted in a contiguous rather than disjoint 95% kernel home-range polygon, referred to as h_{user}. This was used in 8 out of 28 analyses. Probability contours of 50% were calculated which represented an individual's core area of greatest use. To determine uniformity of use of *T. nigricauda* home ranges, we calculated the ratio of core home-range size to total home-range size (50% home-range contour/95% home-range contour).

We compared male and female home range size to that expected on the basis of body sizes. We estimated home-range size (A) from body mass with the formula for herbivorous mammals (Swihart et al. 1988):

$$A = 4.90M^{1.56} \qquad \text{(Equation 1)}$$

where M was body mass (kg).

All mean values are presented as mean ± SE. The distribution of home range data was not distributed normally, thus non-parametric analyses were used. Statistical analyses were performed using the Statistica 7 package (Statsoft Inc., USA).

RESULTS

Several *T. nigricauda* died during the study, mainly due to predation and veterinary procedure. Consequently, telemetry data for 13 and 15 Tree Rats were used for home range analysis in winter and summer respectively (Table 1). Mean mass of female and male Tree Rats was 63.41 ± 4.41g (n = 16) and 71.47 ± 4.46g (n = 12) respectively. There was no significant difference in body mass when site, season and sex was taken into account (ANOVA, $F_{(2, 16)} = 1.31$, $p = 0.30$), or between sexes (ANOVA, $F_{(1, 26)} = 1.16$, $p = 0.22$).

A total of 1274 fixes were recorded. Nocturnal fixes accounted for 65.1% of the fixes recorded, 34.9% were diurnal fixes. An average of 45.5 (± 1.53) fixes was recorded for each *T. nigricauda*. An average of 53.1 fixes was recorded for each hourly interval. Average number of night fixes for each animal was 29.6 whereas average number of day fixes was 15.9. An average of 2.1 night fixes was recorded for each animal for each hourly interval, whereas an average of 1.6 day fixes was recorded for each animal for each hourly interval.

Locations of 20 animals were autocorrelated according to Schoener's index (Rodgers and Carr 1988). We expected our data to be autocorrelated as study animals sometimes did not move between relocations and often returned to previously used portions of their home-ranges (Hansteen et al. 1997), resulting in a nonrandom use of their home-range. In addition to returning to common feeding or resting sites, a common pattern among terrestrial mammals is the use of well-known "runways" to travel to and from familiar feeding spots or nesting sites. This further contradicts the assumption of random temporal use of home-range area and thus statistical independence of locations (Samuel et. al. 1985; Samuel and Garton 1987). As expected, due to the fact that they make use of cavities, some *T. nigricauda* had nonstationary home-ranges. This resulted from shifts in centers of activity and marked expansion of its home-range, which violates the assumption of a stationary home range in tests of independence (Swihart and Slade 1997).

Home-range estimates, irrespective of season and site and using different methods, for female *T. nigricauda* are summarized in Table 2. Mean 95% kernel (2030.08 ± 620.46 m^2) was larger than mean 100% MCP (1341.54 ± 405.81 m^2) and mean 95% MCP (743.44 ± 262.78), and females used an average core area (50% kernel) of 300.96 ± 100.46 m^2. On average, core areas represented 14.82% of the 95% kernel estimation. Home-range size of females varied from 4.67 to 5248.85 m^2 (100% MCP), from 96.95 to 3834.30 m^2 (95% MCP) and from 46.23 to 8806.83 m^2 (95% kernel). Female 50% core size ranged from 5.97 to 1499.13m^2. Females had significantly smaller home-ranges for all home range estimates than males (Table 5).

Home-range estimates, irrespective of season and site and using different methods, for male *T. nigricauda* are summarized in Table 2. Male mean 95% kernel (20976.57 ± 7227.49 m^2) was larger than mean 100% MCP (8739.69 ± 3016.31 m^2) and mean 95% MCP (6860.62 ± 2261.27), and males used an average core area (50% kernel) of 3959.92 ± 1448.71 m^2. On average, core areas represented 18.9% of the 95% kernel estimation. Home-range size of males varied from 181.20 to 28721.36 m^2 (100% MCP), from 197.40 to 23211.02 m^2 (95% MCP) and from 165.68 to 80199.35 m^2 (95% kernel). Male 50% core size ranged from 22.90 to 16365.91 m^2.

Home-range estimates of *T. nigricauda* for the three study sites, irrespective of sex and season, are summarized in Table 3. Although mean home-range size for all estimates was largest in Molopo than the other two sites, we found no significant difference in any home-range estimate between sites (Table 5). The non-significant results were due to variability in home-range sizes (Figure 2). On average, cores represented 18.15% in Weenen, 17.53% in Molopo and 21.13% in Haina of the 95% kernel estimation.

Home-range estimates of *T. nigricauda* for summer and winter, irrespective of site and sex, are summarized in Table 4. Season did not explain range variability since we found no significant difference in any home-range estimate between seasons (Table 5). Mean 95% MCP was larger in summer, while all other estimates were greater in winter. On average, cores represented 18.87% in summer and 18.03% in winter of the 95% kernel estimation.

Thallomys nigricauda showed wide variation in their home-ranges based on the different methods (Tables 2, 3, 4). There was a significant difference between 100% MCP and 95% MCP estimates (Friedman ANOVA$_{(1,24)}$, $p = 0.00$). Similarly, there was a significant difference between 95% MCP and 95% kernel estimates (Friedman ANOVA$_{(1,24)}$, $p = 0.00$), and again between 100% MCP and 95% kernel estimates (Friedman ANOVA$_{(1,27)}$, $p = 0.00$), as well as between 95% MCP and 50% kernel estimates (Friedman ANOVA$_{(1,27)}$, $p = 0.00$). There was no significant difference in the ratio of 50%:95% kernel estimates when site, season and sex were taken into account (ANOVA, $F_{(2, 15)} = 0.55$, $p = 0.59$).

It has been suggested that home-range scales with body size in mammals (Swihart et al. 1988) and using their model, predicted home-range size for males was 0.08ha. Predicted area for females was 0.07ha. In males, observed 95% MCP and 95% kernel estimates were 8.58 and 26.25 times larger, respectively, than the predicted values. In females, observed 95% MCP and 95% kernel estimates were 1.12 and 3.06 times greater, respectively, than predicted values

In winter, all *T. nigricauda* had one core area except for one male which had three core areas. In summer, all *T. nigricauda* had between one and two core areas in their range.

DISCUSSION

Home-range size of *T. nigricauda* varied intraspecifically in relation to sex as predicted. For all methods of estimating home-range size, male *T. nigricauda* occupied significantly larger home ranges than females. One reason might be that males are larger than females and thus require a larger range for increased energy demands (McNab 1963). In this study there was no significant difference in body mass between males and females and thus differences in body mass alone could not explain the significantly larger home-ranges of males.

Since home-range size can often be determined by the mating system of a species (Ostfeld 1990), the observed differences in home range size of males and females may reflect differences in parental investment of the sexes (Safi et al. 2007). The larger home-range of male *T. nigricauda* may result from increased ranging by males during the breeding season, although no significant difference was found in summer and winter when sex was taken into account. Male and female *T. nigricauda* 100% MCP home-range size in the breeding season (summer) in Molopo fall within the range reported in a previous study in the same Reserve (Eccard et al. 2004). However, the lack of significant differences between seasons contrasts with that found in the previous study. Sizes of the 100% MCP estimate in both male and female *T. nigricauda* in the non-breeding season (winter) were smaller than the range given in the previous study. Eccard and colleagues (2004) found that male *T. nigricauda* in Molopo had significantly larger home-ranges than females during the breeding season, suggesting a promiscuous mating system. In promiscuous mating systems, there may be significant selection for traits that increase male exposure to prospecting mates. Expanded home-range may be one such trait, by which male *T. nigricauda* increase their home-range size to increase the rate of encounters with females. Thus the large home-ranges of the male *T. nigricauda* may be a response to the distribution of the females. This is supported by our study. Generally, *T. nigricauda* had a summer breeding season (Skinner and Chimimba 2005). However, it appears that *T. nigricauda* exhibit reproductive flexibility and reproduce opportunistically as a lactating female with new-born offspring were found in July 2006 in Molopo Nature Reserve (pers. obs.). Rodents display flexible social systems that vary in response to changing climatic conditions (Schradin and Pillay 2005). It has been suggested that flexible behaviour in desert rodents may be a response to the unpredictable conditions of an arid environment (Randall et al. 2005; Schradin and Pillay 2006; Cooper and Randall 2007). Opportunistic reproduction has been reported in other rodents and is probably an adaptation to the unpredictability of the climate, allowing reproduction at varying times of the year, for example during winter, if conditions are suitable (Jackson and Bernard 2005). This would have implications for seasonal differences in home range size.

Unlike that predicted, home-range size of *T. nigricauda* did not differ as a function of season. Seasonality did not explain the wide home-range variation for *T. nigricauda*. Both male and female *T. nigricauda* did enlarge their home-ranges in summer, but this was not significant. This suggests that they reduced their movements in winter, thereby reducing metabolic requirements (Slade and Swihart 1983). An increase in home range size in summer is expected for herbivores (Harestad and Bunnell 1979). The cost of movement in winter is high, when temperatures and food availability are low. In winters with low primary productivity, it would be beneficial for *T. nigricauda* to contract its home-ranges and reduce the size to that required to maintain energetic needs only.

Variations in individual movements of *T. nigricauda* may represent dynamic responses to fluctuating food resources. When food resources are a determinant of spatial distributions of individuals within a population, one alternative would be to possess a dynamic home-range, movement patterns being rapidly adjusted to short term fluctuations in food resources (Mares et al. 1982). Species that were opportunistic and adaptable in their food and shelter requirements would be better able to exploit available resources than habitat specialists (Haythornwaite and Dickman 2006). In an unpredictable environment, such as the semi-xeric and xeric sites in this study, it would be beneficial for male *T. nigricauda* to expand its home-range in winter after high summer rainfall and thus high primary productivity. However, a winter with high primary productivity would provide metabolic requirements needed for enlarged home-ranges for males in search of receptive females and for gestation and lactation in females in rodents that display opportunistic breeding. Reproductive flexibility, as demonstrated in Molopo in winter (see above), could explain the lack of significant differences in home-range size between seasons. Male *T. nigricauda* breeding opportunistically out of the expected breeding season would be expected to have similar home-range sizes to those in the breeding season. Male *T. nigricauda* appear to be flexible in this regard, exhibiting seasonally labile movements. Confounding effects exist between season and reproductive activity (Slade and Swihart 1983). Most studies have shown domain change with season, but it is generally not possible to remove the effects of breeding behaviour (Don 1983).

Unlike predicted, home-range size of *T. nigricauda* did not differ as a function of site. Site did not explain the wide home-range variation for *T. nigricauda.* In general, animals in productive habitats tend to have smaller home-ranges than those in less productive habitats. Patterns can be evaluated by relating home-range size to variables for productivity, such as latitude and precipitation. Fisher and Owens (2000) used rainfall as an index of environmental productivity in macropod marsupials and found that annual rainfall explained most variation in home-range size, suggesting a strong link between climate and social organization. If primary production is assumed directly proportional to precipitation (Leith 1975), one would expect the sizes of home-ranges for a given species to be inversely related to precipitation (Mares et al. 1976; Harestad and Bunnell 1979). We would then expect the home-ranges in Molopo, the most arid site, to have the largest size and Weenen, the mesic site, to have the smallest size. In fact, Molopo did have the largest home-range size for all estimates and Weenen did have the smallest size for all estimates with the exception of the 100% MCP estimate. We found no significant differences between home-range size measured across an aridity gradient. The aridity index is calculated over a number of years and thus does not take into consideration rainfall and primary productivity in a particular year. This might mask the effects of a higher than average summer rainfall in xeric and semi-xeric sites in one particular year on home range size. We suggest that opportunistic rodents respond to the proximate prevailing microclimatic conditions that they are exposed to and to the existing resources available in order to maximize individual success.

An alternative suggestion is that home-range of *T. nigricauda* may vary due to ecological differences (precipitation) between study sites, but such differences may be masked by the variation in home-range size at each site. The largest amount of variation in home range size was observed in Molopo, the most xeric.

Estimates of individual home-range size exhibited a trend of high intraspecific variation, home-ranges of males being significantly more variable than females. This variation needs to be considered concerning the lack of significant differences between seasons and sites. Intraspecific variation in home-range size in different areas has been reported (Nevo et al. 1982) and has been related to a number of factors, including variation in environmental productivity. Most of the variability resulted from extraordinarily long-distance movements of particular males. Two male *T. nigricauda* moved out of the reception range during the study and were found later at a distant location, one 744m away in winter 2006 and the other 254m away in summer 2007. These high-risk movements into unfamiliar areas were made within 2h and were considerably further than expected excursions. The individuals had reached their final known locations without evidence of exploratory movements to these locations. Females, unlike males, made few exploratory movements. There was uniformity of use of *T. nigricauda* home ranges as indicated by 50% kernel: 95% kernel ratios.

Home-ranges of both male and female *T. nigricauda* were larger than predicted using the model of Swihart et al. (1988). In a previous study, home-range sizes of males were larger and those of females smaller than predicted (Eccard et al. 2004). Home-range size of other mammals exceeded the prediction of the model (Hanski et. al. 2000; Shibata et. al. 2004), suggesting that other factors, including the sex of an animal and the mating system may be more important than body size in determining home-range size.

In summary, it is suggested that a combination of precipitation, habitat productivity and breeding system influences home range size in *T. nigricauda.* The fact that neither aridity site nor season influenced the home range site of *T. nigricauda* suggests that *T. nigricauda* has sufficient behavioural flexibility allowing opportunistic responses to prevailing conditions in an unpredictable climate as evidenced by intraspecific variability in home range size. During a winter of unusually high primary productivity, male *T. nigricauda* expanded home range size, resulting in similar home range sizes between aridity sites and seasons. Knowledge of space use in these subpopulations of *T. nigricauda* may help in understanding how small mammals are able to cope with environmental change. Adapting to current climate extremes should be consistent with adapting to future climate change (Hulme 2005). Studies which pay attention to geographical variation in responses of populations in different environments enable one to establish the extent to which variation is due to phenotypic flexibility (Chown and Storey 2006). This has consequences for the conservation of small mammal species in the light of climate change in southern Africa.

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FIGURE LEGENDS

Figure 1: Location of the 3 study sites of *T. nigricauda* in southern Africa.

Figure 2.-Box-plots of mean home-range size of *T. nigricauda* at the 3 study sites using estimates a) 100% MCP, b) 95% MCP, c) 95% kernels and d) 50% cores, irrespective of season or sex.

Figure 3.-Box-plots of mean home-range size of male and female *T. nigricauda* using estimates a) 100% MCP, b) 95% MCP, c) 95% kernels and d) 50% cores, irrespective of season or site.

Table 1.-Summary of *T. nigricauda* deaths and numbers for telemetry data at the 3 study sites in winter and summer.

			Deaths					
Season	Site	Number implanted	Unknown cause	Veterinary procedure	Predation	Unable to locate	Faulty transmitter	n
	M	7	1	1				5
Winter	H	6		1	1			4
	W	15		2	5	2	2	4
	M	8	1	2	1		1	3
Summer	H	7		1				6
	W	17		3	5	1	2	6

M = Molopo; H = Haina; W = Weenen.

Table 2.-Mean home-range sizes of male and female *T. nigricauda* irrespective of season or site, using different methods.

Estimate	Male (m^2)	Female (m^2)
100% MCP	8739.69 ± 3016.31	1341.54 ± 405.81
95% MCP	6860.62 ± 2261.27	743.44 ± 262.78
95% kernel	20976.57 ± 7227.49	2030.08 ± 620.46
50% kernel	3959.92 ± 1448.71	300.96 ± 100.46

Table 3.-Mean home-range sizes for *T. nigricauda* at the three study sites irrespective of sex or season, using different methods.

Estimate	Weenen (m^2)	Molopo (m^2)	Haina (m^2)
100% MCP	2175.69 ± 650.12	10907.71 ± 4364.12	1732.24 ± 760.87
95% MCP	1558.25 ± 583.41	6454.84 ± 3024.32	1907.35 ± 897.63
95% kernel	3852.34 ± 1429.99	22382.00 ± 10155.96	7176.72 ± 4913.75
50% kernel	699.36 ± 311.88	3924.38 ± 1984.98	1516.09 ± 1121.14

Table 4.-Mean seasonal home-range sizes for *T. nigricauda* irrespective of site or sex, using different methods.

Estimate	Summer (m^2)	Winter (m^2)
100% MCP	4105.02 ± 1646.15	4981.97 ± 2583.70
95% MCP	3818.87 ± 1707.12	2669.92 ± 1441.48
95% kernel	9842.59 ± 3797.34	11105.67 ± 6570.17
50% kernel	1857.29 ± 772.40	2002.41 ± 1290.22

Table 5.-Summary of H and p values of statistical analyses (Kruskal-Wallis) of home range size estimates of male and female *T. nigricauda* at the 3 study sites in winter and summer. An asterisk (*) represents significance.

Estimate		H value	p value
100% MCP	Site	6.02	0.05
	Season	1.27	0.26
	Sex*	5.61	0.02
95% MCP	Site	1.89	0.39
	Season	1.55	0.21
	Sex*	9.63	0
95% kernel	Site	1.9	0.39
	Season	2.26	0.13
	Sex*	5.04	0.02
50% kernel	Site	1.43	0.49
	Season	2.56	0.11
	Sex*	4.82	0.03

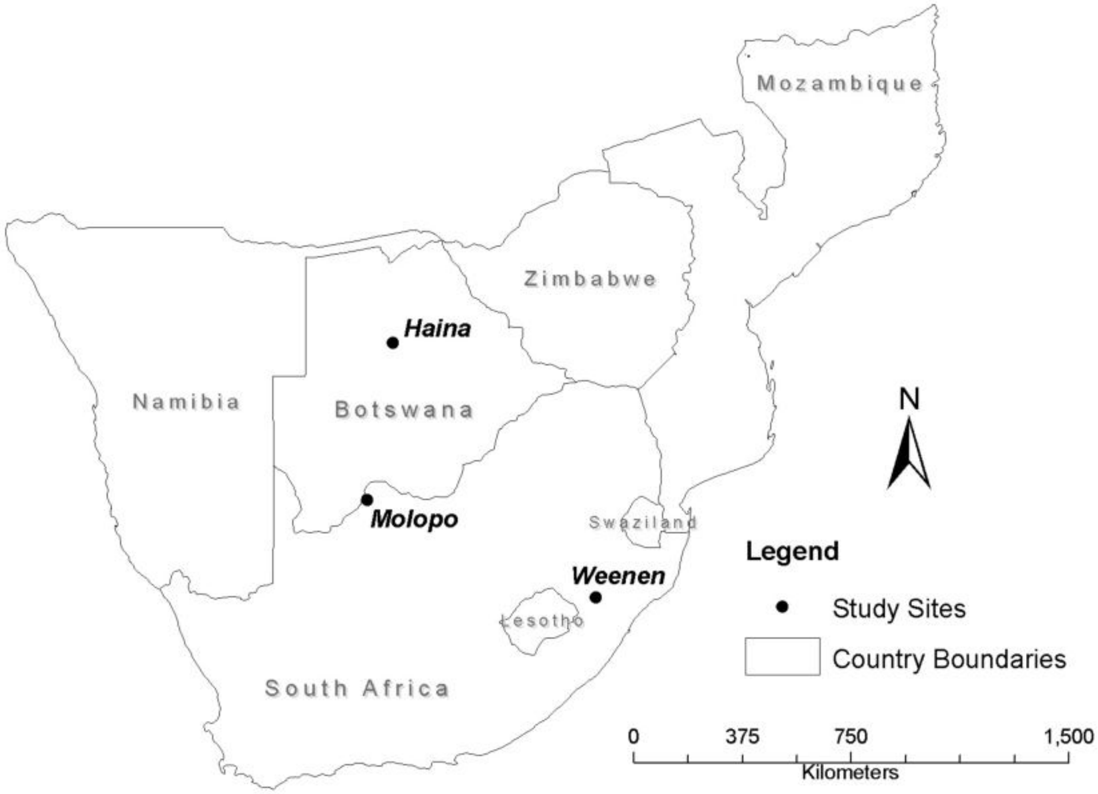
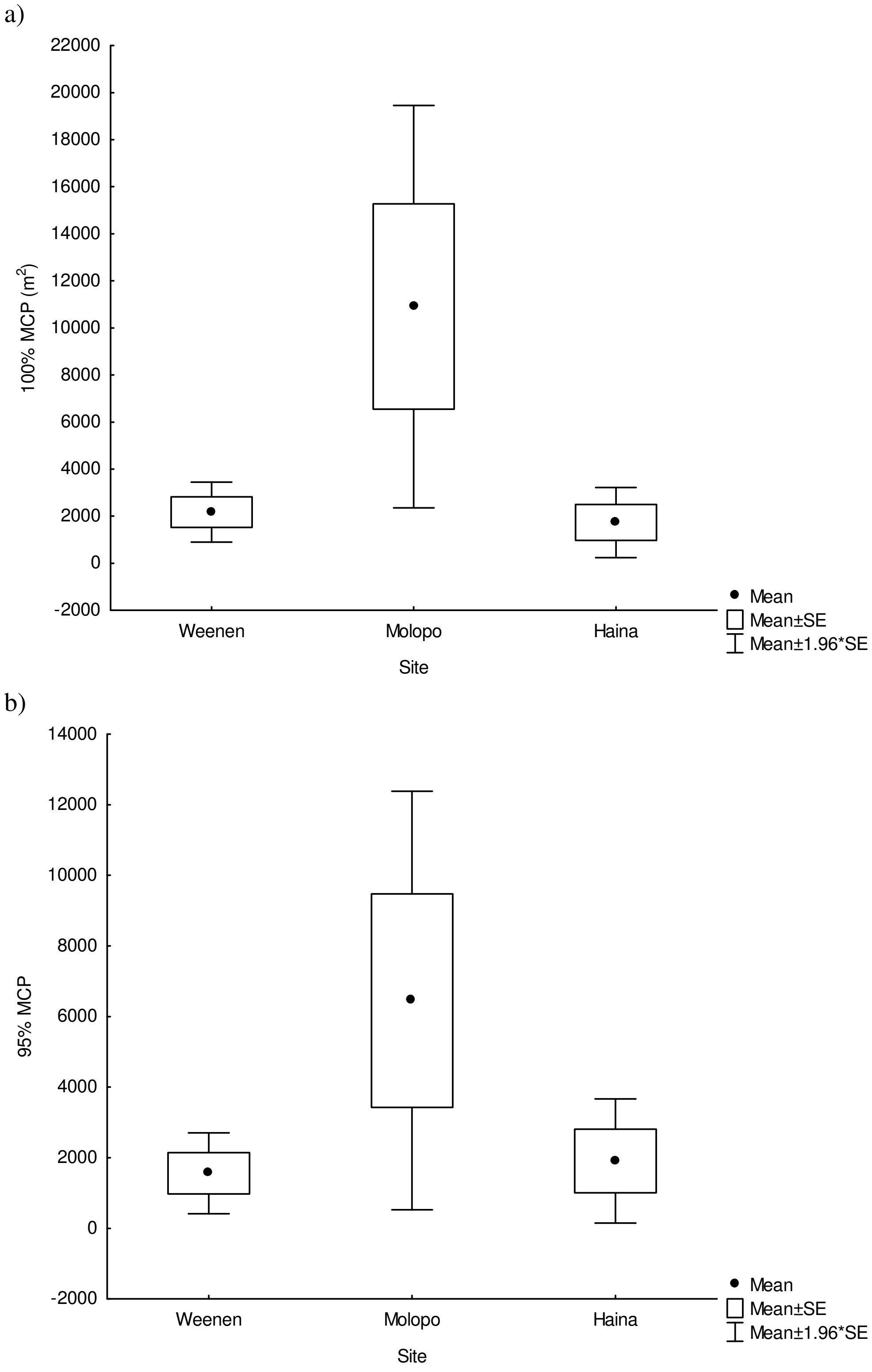


Fig. 1.-Location of the 3 study sites of *T. nigricauda* in southern Africa.


a)
22000
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
-2000
100% MCP (m^2)
Weenen
Molopo
Haina
Site
● Mean
☐ Mean±SE
Ⅰ Mean±1.96*SE
b)
14000
12000
10000
8000
6000
4000
2000
0
-2000
95% MCP
Weenen
Molopo
Haina
Site
● Mean
☐ Mean±SE
Ⅰ Mean±1.96*SE

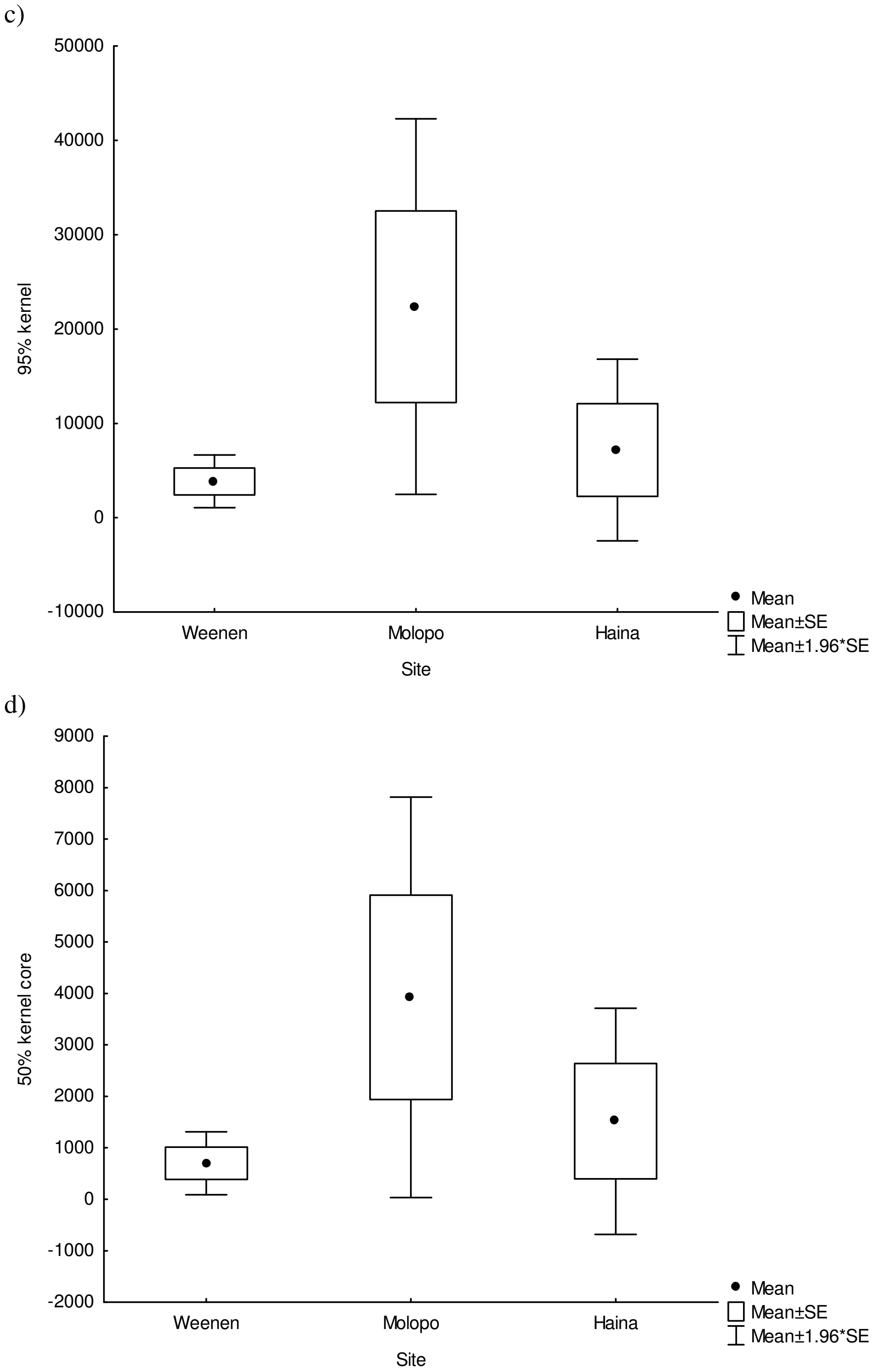
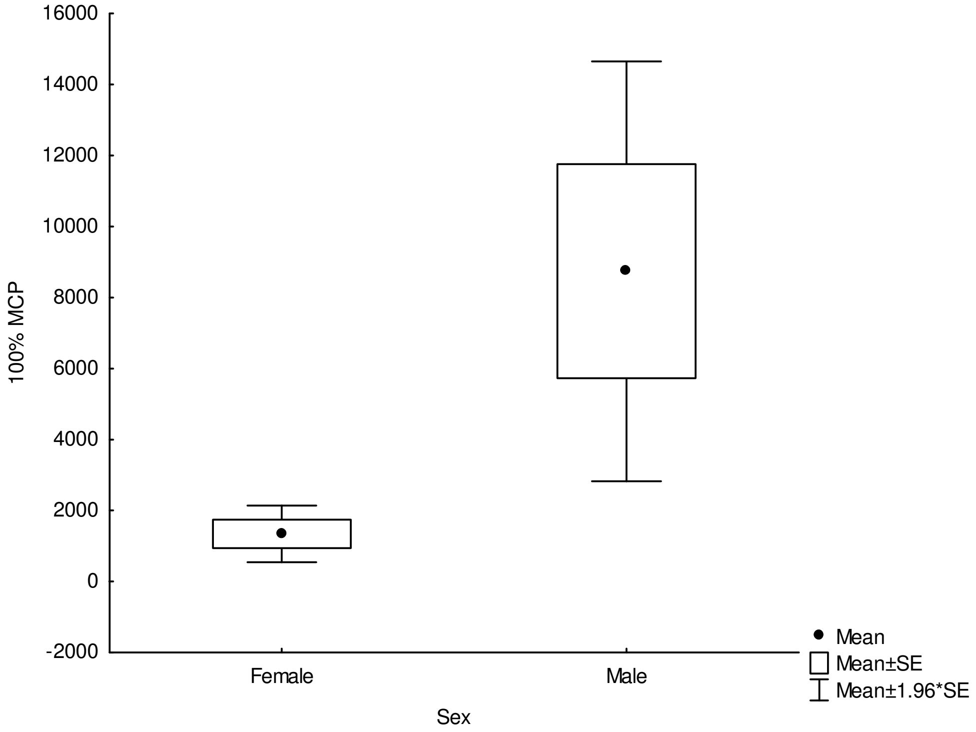


Fig. 2.-Box-plots of mean home-range size of *T. nigricauda* at the 3 study sites using estimates a) 100% MCP, b) 95% MCP, c) 95% kernels and d) 50% cores, irrespective of season or sex.

a)


16000
14000
12000
10000
8000
6000
4000
2000
0
-2000
100% MCP
Female
Male
Sex
Mean
Mean±SE
Mean±1.96*SE

b)


12000
10000
8000
6000
4000
2000
0
-2000
95% MCP
Female
Male
Sex
Mean
Mean±SE
Mean±1.96*SE

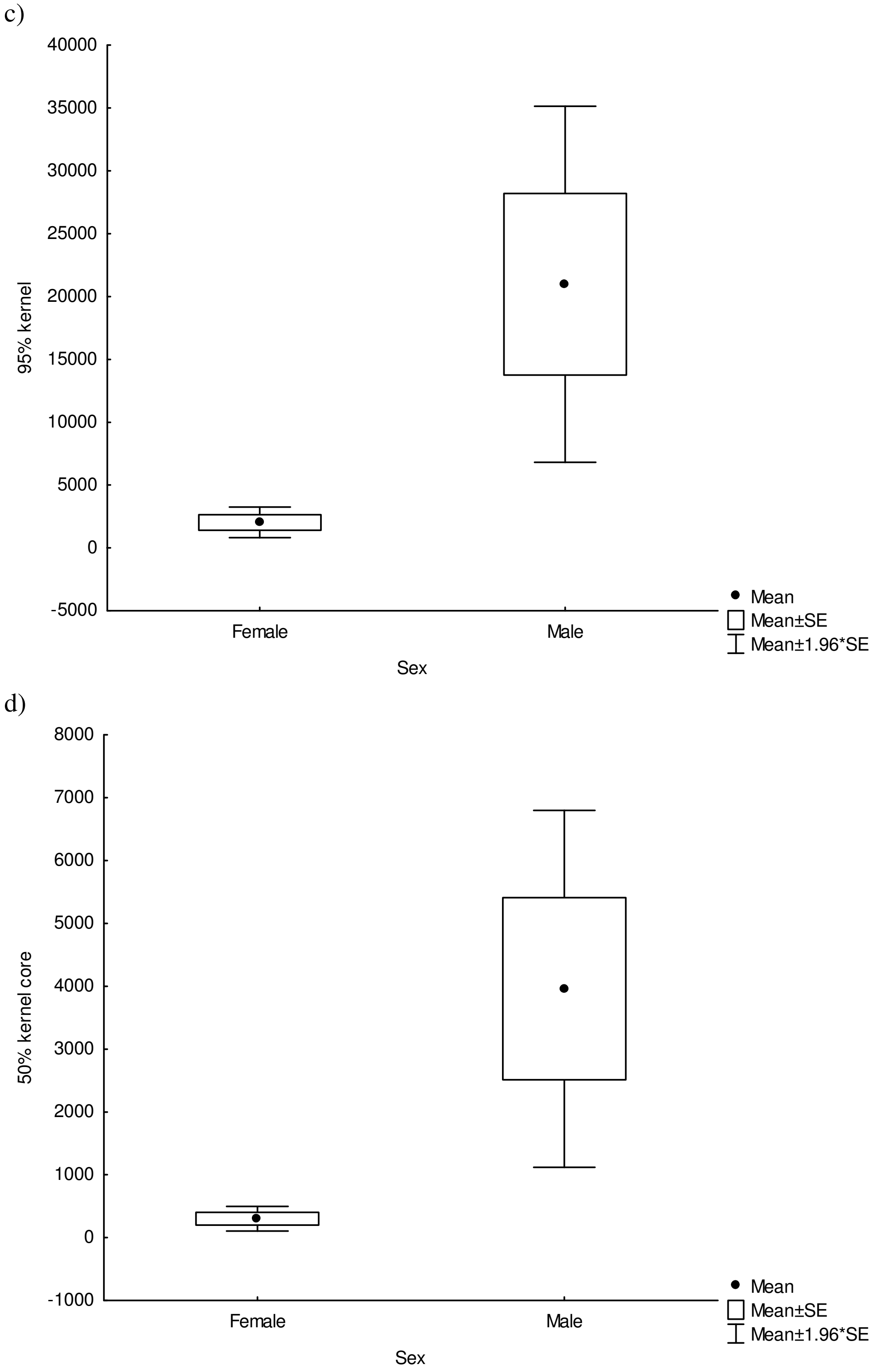


Fig. 3.-Box-plots of mean home-range size of male and female *T. nigricauda* using estimates a) 100% MCP, b) 95% MCP, c) 95% kernels and d) 50% cores, irrespective of season or site.

Chapter 3

Seasonal changes in urine concentrating ability and water balance of the Black-tailed Tree Rat *Thallomys nigricauda*, along an aridity gradient

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Formatted for Comparative Biochemistry and Physiology, Part A (note Journal allows abbreviated species Latin names at the beginning of a sentence).

Abstract

The ability of mammals to concentrate urine has been seen as an adaptation to xeric environments. Urine osmolality and relative medullary thickness (RMT) are two indices which indicate urine concentrating powers. In addition, mammals living in xeric regions have lower water turnover rates than their mesic counterparts. The urine concentrating ability (UCA) and water turnover rate of the Black-tailed Tree Rat, *Thallomys nigricauda*, were investigated at three study sites along an aridity gradient. *T. nigricauda* is a good model to evaluate the degree of phenotypic flexibility in these traits since they occur in mesic, semi-xeric and xeric regions in southern Africa. The aim of this study was to determine whether there were differences in urine osmolality and water turnover rate (WTR) between seasons, and in urine osmolality and RMT along an aridity gradient. There was no significant difference in RMT between sites or sex, and no difference in osmolalities when site, season and sex were taken into account. In addition, specific water turnover rate was not significantly influenced by season. Lack of significant differences could be the result of the high degree of individual variation in the traits measured, an indication of the flexibility in urine concentrating ability and water turnover rates. However, higher urine osmolality and lower water turnover rates were recorded in the dry winter months. It is suggested that *T. nigricauda* employs a suite of physiological and behavioural mechanisms to meet its water requirements and that it has sufficient phenotypic flexibility in these traits to allow it to colonise mesic, semi-xeric and xeric regions of southern Africa.

Keywords: Aridity gradient; Osmolality; Phenotypic flexibility; Relative medullary thickness; Specific water turnover rate; Tritiated water; Urine concentrating ability

1. Introduction

Climate change predictions suggest that the continent most vulnerable to climate change is Africa (Lovett et al., 2005) and the impacts of potential changes which include increases in air temperatures and rainfall variability are negative with potential species extinctions predicted throughout southern Africa. Projected species range shifts, in accordance with the aridity gradient in an east-west direction across the country (Rutherford & Westfall, 1994; Schulze et al., 1997), may not be as marked if species are able to use physiological and behavioural methods to adapt to conditions (Erasmus et al., 2002). Environments form a continuum based on the interactions between a number of variables, for example precipitation and temperature (Thornthwaite, 1948; Meigs, 1953). Thus aridity provides a substitute for the selection pressures that animals face, for example with increasing aridity there is decreasing water availability and increasing daytime air temperatures (Tieleman et al., 2003).

Factors determining the availability to and loss of water from a mammal vary between environments and such a variation is matched by physiological and behavioural adaptations by the mammals influencing the distribution and abundance of mammals (Chew, 1951). The major climatic determinant of water regulation in terrestrial organisms should be precipitation since it correlates positively with water availability and primary productivity (Rosenzweig, 1968), and therefore with food quality and quantity (MacMillen, 1983). Terrestrial vertebrates lose water through respiration, cutaneous evaporation and excretion (Tieleman et al., 2002), yet it is doubtful whether small mammals drink water in the field (MacMillen, 1983) relying rather on oxidative and preformed water from their food (Schmidt-Nielsen, 1975; Downs and Perrin, 1990).

Specifically, environmental variables within a xeric environment fluctuate at both daily and seasonal scales (Degen, 1997; Kronfeld-Schor et al., 2000). Water scarcity is the main survival challenge for desert animals (Nagy, 1988) and when combined with seasonal periods of high temperatures, produces a physiological challenge for mammals (Schmidt-Nielsen, 1975; Walsberg, 2000). The dominance of rodents in xeric regions indicates that they can either avoid the stresses or that they have employed effective physiological counter-measures (Schmidt-Nielsen, 1975). Attributes of small desert mammals which contribute to the maintenance of a positive water balance include nocturnality, fossoriality, urine concentrating ability (UCA), minimization of respiratory water loss (Withers et al., 1980), and gaining preformed water from their diet (Pienke and Brown, 1999).

Mammalian kidneys play an important role in controlling the volume and concentration of body fluids, the morphological and vascular organizations of the nephrons enabling the organism to produce urine that is more concentrated than body plasma (Al-Kahtani et al., 2004). Adaptive radiation into different environments may involve structural and functional variation of the kidney, since it is the major organ in maintaining the internal environment at constant osmolality (Nevo et al., 1989). Physiological adaptations of small rodents to arid conditions are achieved mainly through concentrating ability of their kidneys (Beuchat, 1996) and producing hyperosmotic urine is the single physiological means of reducing water loss characteristic of nocturnal, xeric-dwelling rodents (MacMillen, 1972).

Sperber (1944) proposed relative medullary thickness (RMT) as a structural index for quantifying the relative length of the longest loops of Henle and found that species from arid environments had higher values than mammals from mesic habitats. "Long looped nephrons" can be distinguished by an extended renal papilla (Bankir and de Rouffignac, 1985) and the maximum length of the loop of Henle is directly proportional to medullary thickness (Beuchat, 1990, 1993, 1996). Schmidt-Nielsen and O'Dell (1961) revealed a correlation between the relative length of the longest loops of Henle (reflected by RMT) and the maximum urine concentration. Various studies demonstrate a trend for arid and semi-arid species to have high UCA and high RMT (Heisinger and Breitenbach, 1969; Heisinger et al., 1973; Greegor, 1975; Blake, 1977; Geluso, 1978). Other indices have been proposed to estimate renal performance, RMT being the most commonly cited (Beuchat, 1996).

Urine osmolality is the most widely studied renal function in relation to adaptation to a desert environment, the greater the osmolality of the urine to that of the plasma, the greater the advantage to the animal that needs to conserve water (Dantzler, 1982). Urine osmolality could be used as an index of the extent to which rodents encounter water stress as adjustments of renal output represent a major physiological response a mammal may make to remain in water balance (Grubbs, 1980). Animals that survive xeric conditions form urine of high solute concentration, the highest concentrations being found in rodents that do not depend on a high water intake (Schmidt-Nielsen, 1975).

Measurements of water turnover rates (WTR) allow the assessment of the extent to which species are buffered from the effects of drought by the efficiency of their homeostatic regulatory systems (Bradshaw et al., 2001). Factors influencing body WTR in rodents include metabolic rate, body size, water availability, environmental heat load, species and water content of the food (Yousef, 1973; Holleman and Dieterich, 1973; Yousef et al., 1974) and urine concentrating ability (Yousef et al., 1974). It has been shown that mammals inhabiting xeric regions have lower WTR than those inhabiting mesic zones (MacFarlane and Howard, 1972; Yousef et al., 1974; Degen et al., 1981) and that WTRs vary seasonally in desert rodents (Nagy, 1988; Grenot and Buscarlet, 1988).

Tritiated water (TOH) turnover, as an estimation of body water turnover, is a measure of the overall state of water economy of the animal. The tritium-dilution method (Richmond et al., 1962) affords a convenient means for measuring total body water (TBW) and WTR in free-ranging animals (MacFarlane and Howard, 1972; Nagy and Costa, 1980). TBW is determined on the basis of dilution and equilibrium of TOH with body fluids and water turnover rate is calculated from the decline of specific activity of tritium over a known period (Degen et al., 1981). The magnitude of TOH flux reflects the daily water input and output (assuming the animal is in balance) and the approach an animal takes to supply its water needs. Change of flux with season and reproductive activity for example, reflects the impact of biological and environmental factors on water economy (Grubbs, 1980).

Phenotypic flexibility is a category of phenotypic plasticity that involves reversible behavioural, physiological or morphological variations within an individual to changes in environmental conditions (Piersma and Drent, 2003). When the environments within the range of a species differ, a single phenotype would be unlikely to confer fitness in all situations, and a change in the phenotype that depends on the environment could provide increased environmental tolerance (Via et al., 1995). Individual plasticity is an important source of phenotypic variation in natural populations, allowing individual genotypes to maintain fitness in a wide range of environmental conditions (Sultan, 1995), and the degree of plasticity is expected to increase with environmental variability (Morse, 1980).

Evaluations of states of water balance, renal performance and rates of water turnover under natural conditions allow us to determine the extent to which the physiological capacities for water economy are employed (MacMillen, 1972). For an organism that inhabits areas with unpredictable rainfall, renal molecular and physiological flexibility may allow an organism to respond to limited water availability during a dry season and remain in water balance (Gallardo et al., 2005). Information on the degree to which physiological and behavioural flexibility affect species range in southern Africa is scant which is surprising given its importance with regard to climate change.

Thallomys nigricauda, the Black-tailed Tree Rat, is a small (32-116g), arboreal, nocturnal, murid rodent, occurring in mesic to xeric regions of southern Africa (Skinner and Chimimba, 2005). As folivores, they feed on young *Acacia erioloba* leaves and fine twigs and the outer green coating of seed pods, but may supplement their diets with insects and gum (de Graaff, 1981; Skinner and Chimimba, 2005). This is in contrast with the majority of xeric rodents, which are predominantly granivorous or opportunistically insectivorous. It was suggested that the water yield of their food is sufficient to permit the *T. nigricauda* to survive without drinking water (Bradfield in Shortridge, 1934). While the vast majority of rodent species evade the stressful conditions by burrowing, the *T. nigricauda* is one of a few species in xeric environments to have adopted an arboreal lifestyle with nests situated in forks and hollows of trees (mainly *Acacia erioloba*) (Skinner and Chimimba, 2005). Being arboreal, *T. nigricauda* is exposed to greater daily temperature fluctuations and lower humidities in their nests compared to most other southern African xeric rodents which use subterranean microhabitats to escape daytime heat (de Graaff, 1981; Lovegrove and Knight-Eloff, 1988; Downs and Perrin, 1989; Skinner and Chimimba, 2005). Thus there are thermal costs resulting from an arboreal lifestyle which may be reduced in the thermal microhabitat of a burrow.

Since *T. nigricauda* occurs along an east-west aridity gradient in southern Africa, inhabiting mesic, semi-xeric and xeric regions, one would expect phenotypic flexibility in its osmoregulatory capacity in response to the diverse environmental conditions to be related to the success and range of the species. The wide distribution makes *T. nigricauda* an ideal species to test this assumption. The aim of this study was to determine whether there were differences in urine osmolality and specific WTR between seasons, and in urine osmolality and kidney RMT along an aridity gradient. More specifically, we predicted that osmolalities and specific water turnover rate would not differ between summer and winter, and that urine osmolalities and kidney RMT would not differ along an aridity gradient. We predicted that *T. nigricauda* would have a renal structure indicative of efficient UCA.

2. Materials and methods

2.1. Study sites

The study was conducted at three sites along an east-west aridity gradient (Rutherford and Westfall, 1994; Schulze et al., 1997): mesic locality Weenen Game Reserve (KwaZulu-Natal Province, South Africa, 28°50’43”S; 29°59’12”E); semi-xeric site Haina Game Farm (Botswana 20˚56’56”S; 23˚40’40”E) and xeric site Molopo Nature Reserve (southern Kalahari savannah, North-West Province, South Africa 25˚50’52”S; 22˚55’37”E) (Chapter 2). Degree locations were plotted using a Magellan GPS 4000 XL. Vegetation, rainfall and temperature data for the three sites are detailed elsewhere (Chapter 2).

2.2. Aridity gradient

We calculated an aridity index as:

$$Q = P/((T_{\max} + T_{\min})(T_{\max} - T_{\min})) \text{ X } 1000 \qquad \text{(Equation 1)}$$

where P is the average precipitation (mm), $T_{\max}$ is the mean minimum temperature of the hottest month (ºC) and $T_{\min}$ is the mean minimum temperature of the coldest month (ºC) (Emberger, 1955). This index is low in hot, dry deserts and high in cool, wet areas (Tieleman et al., 2003). The index Q increases rapidly when environments become more mesic. We thus used log Q in our analyses to avoid unequal weighting of data for the mesic location (Tieleman et al., 2003). Climatic data were sourced from the management of Molopo Nature Reserve. The South African Weather Service provided data for Weenen Game Reserve from the nearest meteorological station, 10 km from the study site. The national meteorological service in Botswana provided data for Haina Game Farm from the nearest meteorological station, 70 km from the study site.

2.3. Kidney function

T. nigricauda was live trapped at each study site during winter (June – July) in 2006 and 2007 and in summer (January – February 2007) using Elliot live-traps. We identified cavities of *T. nigricauda* were identified by searching trees with potential cavities for faeces and the distinctive smell of excreta. Traps were also placed at sites where study animals had been previously seen and/or trapped. Traps were placed on the branches and at the base of potential trees and baited with peanut butter and oats. Traps were set in the late afternoon, checked shortly after sunrise and removed from trap sites. Individuals were transported to a veterinarian within 36 h of capture.

T. nigricauda was sexed, weighed, ear clipped and reproductive status was noted. When possible, urine from individuals was collected in Eppendorf tubes by placing gentle pressure on the bladder. For specific veterinarian procedures, individuals (>40g) were anaethesized using isoflorthane (2%) or Anakel – V (100mg/ml) and Chanazine (20 mg/ml). In cases where urine could not be obtained using the technique described above, urine was extracted directly from the bladder using a syringe while the abdominal cavity of *T. nigricauda* was open.

Urine samples were collected in winter (June – July) in 2006 and 2007 and in summer (January – February 2007). Urine was stored in sealed Eppendorf tubes below 4°C until analysis. Presence of precipitate was noted. A total of 25 samples were collected during the study periods. No samples were collected from Molopo in summer 2007. Urine osmolality (mosmol/kg) was determined using a Hermann Roebling (Messtechnik) Automatic Micro-Osmometer. Urine was diluted when concentration was out of the range of the osmometer.

Individuals were euthenased after retrapping and kidneys were immediately removed and weighed. Length, width and thickness at midpoint were measured using electronic digital callipers (accurate to 0.01mm). The left kidney from each individual was prepared for light microscopy. Kidneys were approximately halved along the longitudinal mid-saggital plane and placed in Bouin's fixative for 24 h before being stored in 70% ethanol. Mid-sagittal sections were prepared and stained with Erlich's haematoxylin and eosin counter-stain (Culling et al. 1985). Sections were viewed, and the cortex and inner and outer medulla (as measures of thin and thick ascending limb length) thicknesses were determined using a Leica MZ16 Stereo Dissecting Microscope with Auto Montage depth-of-focus enhancement software. Width of cortex was measured from the periphery of the kidney to the cortico-medullary junction. Thickness of the cortex and outer medulla were determined with a line perpendicular to the long axis of the kidney. A line following the curvature of the papilla was used to obtain the inner medullary thickness (Fig. 2). Differential staining of the cortex, outer and inner medulla, and visible structures such as the glomeruli in the cortex enabled identification of the three regions. Measurements, converted to mm were used to calculate RMT (Sperber, 1944):

$$\text{RMT} = 10 \times (\text{medullary thickness}) / \sqrt[3]{(\text{length} \times \text{breadth} \times \text{width})} \quad \text{(Equation 2)}$$

2.4. Water flux

Water flux in seven and ten animals was measured during winter (June-July) and summer (January-February) in 2006–2007 respectively using TOH. During the veterinary procedure (see Chapters 2 and 5), *T. nigricauda* was injected intraperitoneally with 0.5 ml TOH (0.1 mCi/ml). After 1-2 h a 0.3-0.5 ml initial equilibrium blood sample was taken by cardiac puncture. Blood samples were immediately centrifuged at 15000 g for 10 mins. Plasma was collected in cryogenic vials, sealed and stored in a refrigerator at 4°C until assayed. After the veterinarian procedure, animals were given a 4-12 h to recover before being released back at their point of capture. The final blood sample was taken by cardiac puncture when individuals were euthenased at the end of the study after retrapping. In winter and summer, the mean time between initial and final blood sample was 18.99 ± 5.17 days and 10.30 ± 3.15 days respectively. Specific activity of each water sample was determined using 20 µl samples of plasma mixed with 5 ml scintillation cocktail (Beckmann, Ready Value^{TM}) which was then read on a Beckmann liquid scintillation counter (Model LS 6000LL).

Estimated water turnover rates were calculated from specific changes of tritium between initial equilibration and final blood sample collection over time (Lifson and McClintock, 1966). The standard equations for K (the rate constant), total body water and specific WTR were used in calculations (MacFarlane and Howard, 1972; Nagy and Costa, 1980).

2.5. Statistics

In the analysis of correlation between urine osmolality and RMT, only data for *T. nigricauda* with both measurements were included (n = 8). Statistical analyses were performed using the Statistica 7 package (Statsoft Inc., USA). RMT and percentage total body water were analysed non-parametrically. Means are presented ± 1 SE.

3. Results

3.1. Aridity gradient

The mean aridity index for Weenen was 2.9 ± 0.01 (n = 48), 2.51 ± 0.06 (n = 13) for Haina, and 2.43 ± 0.06 (n = 15) for Molopo.

3.2. Kidney function

Body mass of *T. nigricauda* used for the respective analyses of urine osmolality, kidney RMT are shown in Table 1. There were significant differences between the kidney height (dependent *T*-test: $t = -11.51$, df = 21, $p<0.05$) and width (dependent *T*-test: $t = -8.99$, df = 21, $p<0.05$) measured in the field and measured using prepared sections. These differences may be due to shrinkage of tissue from preservative solutions. Field measurements were used to calculate length, breadth and width of kidneys since only field data were available for kidney breadth. This may have been alleviated by performing measurements just prior to sectioning.

All *T. nigricauda* had similar renal anatomical structure. Their kidneys were unilobular with an elongated papilla (Fig. 1). A scatterplot of body mass and kidney mass revealed a correlation of $r = 0.65$ (Fig. 2). There was no significant difference in kidney mass between sites (ANOVA, $F_{(2, 21)} = 1.26$, $p = 0.30$). Kidney RMT of 17 *T. nigricauda* were analysed. Kidney RMT mass data were not normally distributed. A scatterplot of *T. nigricauda* body mass versus kidney RMT determined that the outliers were not juvenile Tree-rats with undeveloped kidneys (Fig. 3). Kidney RMT scaled negatively with body mass ($r = -0.15$) (Fig. 3). Mean kidney RMT of all *T. nigricauda* was 5.98 ± 0.15 units. Although lower mean kidney RMT values were recorded for Weenen individuals (Fig. 4), there was no significant difference in kidney RMT between aridity sites (Kruskal-Wallis, $H_{(2,17)} = 4.69$, $p = 0.10$), or between sexes (Kruskal-Wallis, $H_{(1,17)} = 0.01$, $p = 0.92$). The intraspecific variation coefficient for kidney RMT was low (CV = 0.10).

There was no difference in urine osmolalities when site, season and sex were taken into account (ANOVA, $F_{(1,\ 15)} = 0.09$, $p = 0.77$) (Fig. 5). Overall mean urine osmolality was 1980.16 mosm kg^{-1}. The mean urine osmolality of *T. nigricauda* in winter was 2282.85 ± 216.19 mosm kg^{-1} and the range 803-3216 mosm kg^{-1}. Mean urine osmolality of *T. nigricauda* in summer was 1652.25 ± 180.51 mosm kg^{-1} and the range 648-2604 mosm kg^{-1} (Table 2). A scatterplot revealed that osmolalities scaled negatively with body mass ($r = -0.20$) (Fig. 6). The intraspecific variation coefficient for urine osmolality was 0.10. A scatterplot of urine osmolarities and kidney RMT revealed that there was no relationship between the two variables ($r = 0.23$) (Fig. 7).

3.3. Water balance

Body mass of male and female *T. nigricauda* used for the analysis of WTR are shown in Table 1. Results of percent body water and water flux are shown in Table 3. Water influx and efflux were 6.49 ml day^{-1} and 8.53 ml day^{-1} in winter and summer respectively, or 98.74 ml kg^{-1} day^{-1} and 129.31 ml kg^{-1} day^{-1} in winter and summer respectively. Percent total body water was consistent in summer and winter, resulting in a non-significant difference between seasons (Kruskal-Wallis, $H_{(1,\ 17)} = 0.15$, $p = 0.7$). Although there was an increase in specific water turnover (ml day^{-1} kg^{-1}) (ANOVA, $F_{(1,\ 15)} = 3.57$, $p = 0.08$) in summer, this difference was not significant.

4. Discussion

4.1. Aridity gradient

The computed aridity index for the three sites was in accordance with the west-east aridity index across southern Africa (Rutherford and Westfall, 1994;

Schulze et al., 1997). This emphasises that the distribution range of *T. nigricauda* extends across an aridity gradient.

4.2. Kidney function

Body mass is the main factor determining kidney gross size and morphology (Diaz et al., 2006), after accounting for phylogenetic effects. In the present study body mass and kidney mass were correlated by 0.65. When considering all mammals, least squares linear regression analysis indicated that kidney mass scaled on body mass with a slope of 0.88 (Beuchat, 1996), and there were no large differences in the scaling of kidney mass with body mass among animals from arid and mesic habitats. Body mass was found to have a positive effect on kidney mass in rodents in conventional analyses and with phylogenetically independent contrasts. Habitat had no effect on kidney mass in rodents in conventional analyses, but was significant in the phylogenetic analysis, kidney mass increasing with increasing habitat aridity (Al-Kahtani et al., 2004). However, we found no such influence of aridity on kidney mass.

Kidney RMT is a highly significant predictor of as an indicator of maximum urine concentrating ability in rodents (Al-Kahtani et al., 2004). Mammalian kidney RMT scales negatively with body mass (Beuchat, 1996; Al-Kahtani et al., 2004) and this was supported by the results of the present study. In addition, mammals from arid habitats tend to have greater kidney RMT values than those from mesic habitats (Beuchat, 1996; Al-Kahtani et al., 2004). The lower mean kidney RMT values recorded at our mesic site supports this, although we found no significant influence of aridity on kidney RMT. In a previous study, the mean kidney RMT of captive-born *T. nigricauda* was 5.67 ± 0.39 units (Frean et al., 1998), which was similar to the results found in this study.

Goyal and colleagues (1988) derived an equation for predicting the urine osmolality (as an indication of UCA) using the kidney RMT:

$$y = (306.7 + 524.5x)\ 10^{-3} \qquad \text{(Equation 3)}$$

where y represents urine osmolality (osmol kg^{-1}) and x represents kidney RMT. The mean urine osmolality predicted for *T. nigricauda* from this equation was 3.55 osmol kg^{-1}, which was higher than the observed mean urine osmolality (for kidney RMT and urine osmolality data) of 1.81 osmol kg^{-1}. Based on data for mammals in general, a kidney RMT of 5.98 should be associated with a maximum urine concentration of 3370.4 mosm kg^{-1} (Beuchat, 1990). The observed mean urine osmolality in the present study was 1980.16, 58 mosm kg^{-1} which is 58.75 % of the expected maximum urine concentration. However, there was variation between individuals, and individual *T. nigricauda* did exhibit the capability of concentrating their urine > 3000.00 mosm/kg in winter. Higher urine osmolalities than those in the present study were found in a previous study of captive *T. nigricauda* (Frean et al., 1998) fed a diet of pellets. As urine concentrating ability can increase as a consequence of various factors this supports the expectation of phenotypic flexibility in this trait in the present study.

Although higher mean urine osmolalities were recorded in winter, there was lack of significant differences in osmolalities between seasons which may be explained by high individual variation and hence overlap. Variation in urine osmolalities may also be ascribed to the time since last fed and different times of sampling during the day.

Urine osmolality has been found to scale negatively with body mass (Beuchat, 1996; Al-Kahtani et al., 2004) which is supported by this study. Mammals from xeric habitats tend to have greater urine osmolalities than those from mesic habitats

(Beuchat, 1996). However, we found no significant differences in urine osmolalities between sites.

Beuchat (1996) reported a statistically significant relationship between maximum urine osmolality and kidney RMT, but since both traits scaled negatively with body mass, they could be related since they both are correlated to body mass (Al-Kahtani et al., 2004). Similar results were obtained by Diaz and colleagues (2006) in a study on hystricognath rodents. No relationship between maximum urine osmolality and kidney RMT was observed in the present study. However, there was a high variability of urine osmolalities between individuals and between sites.

The computed correlations which attempt to unravel the adaptive nature of the structural and functional traits of the mammalian kidney in both the Beuchat's review (1996), and in the extension of this review (Al-Kahtani et al., 2004) deal with a species specific mean value for each trait as the unit of analysis. However, comparisons between species assume that a given trait is fixed for a species, with no consideration given to the intraspecific variation (Bennett, 1987), which in some metabolic traits has been shown to be high (Nespolo et al., 2003). This inter-individual variability represents phenotypic flexibility and could ensure survival of species under changing conditions. In addition, as mentioned earlier, urine osmolality may vary with time since last fed and the time of the day when sampled. We suggest that for comparative purposes, a more realistic approach would be to use the range of values of the trait under consideration.

Bozinovic and Gallardo (2006) suggest that kidney indices should be used with caution since some osmolalities do not fit the kidney RMT index and the index does not take into account the organization of tubules and blood vessels inside the medulla. Further, kidney RMT has been positively associated with the proportion of long looped nephrons, which has been positively correlated with urine concentrating ability yet some rodents with high UCA have more short than long looped nephrons.

4.3. Water balance

Regardless of season, *T. nigricauda* kept a constant water balance, as indicated by the % total body water. Although the specific water turnover (ml day^{-1} kg^{-1}) increased in summer, the difference was not significant, due to individual variability in specific water turnover. Yousef and colleagues (1974) found great variability in WTR of a number of species of rodents from xeric regions and attributed this variation to the varied physiological and behavioural adaptations, primarily related to their thermoregulatory capacities (Yousef et al., 1974).

Since WTR is influenced by many factors, the additional amount of water which was turned-over by *T. nigricauda* in summer cannot be ascribed to a single factor. However, all sites experienced summer rainfall which could be correlated with an increase in primary productivity and hence food quality and quantity (MacMillen, 1983). It is suggested that *T. nigricauda* is independent of drinking water (Bradfield in Shortridge, 1934), and are dependant on preformed water from their diet as well as metabolic water to supply their water needs. Thus increased water flux corresponds with increase in preformed water in consumed foliage. The lower specific water turnover was measured in a typically dry season. Considering these conditions, the lower specific water turnover in winter may be partially explained. Increases in water flux, during the rainfall season have been reported in other free-living mammals (Nagy et al., 1976; Richards, 1979; Karasov, 1983; Downs and Perrin, 1990; Degen et al., 1991; Duxberry and Perrin, 1992; Bradshaw et al., 1994; Ellis et al., 1995). Differences in water flux have been suggested to result from differences in preformed water in plant species consumed due to increase in primary productivity after rain (Nagy et al., 1976; Richards, 1979; Karasov, 1983; Degen et al., 1991; Duxberry and Perrin, 1992; Bradshaw et al., 1994; Ellis et al., 1995).

It is unrealistic to compare field and laboratory studies due to difference in diet and behavioural differences. Moreover, it is unrealistic to compare mass specific WTR alone between free-living animals since differences in diet, behaviour and relative ability to reduce water loss causes seasonal variation in water flux (Karasov, 1983). Higher water fluxes are expected in herbivorous mammals due to the high water content of plant tissues coupled with the comparatively low digestibility of plant diets by mammals. (Grubbs, 1980; Nagy and Petersen, 1988). To our knowledge, there have been two studies on water flux in free-ranging rodents in southern Africa, both studies on rodents in the Namib Desert (Withers et al., 1980; Downs and Perrin, 1990). The water flux in the herbivorous Dassie Rat, *Petromus typicus*, of 4.4 ml day^{-1} (Withers et al., 1980) is lower than that found in the present study during summer. However, the present study includes mammals from mesic, semi-xeric and xeric localities and the xeric localities have a higher rainfall than the Namib Desert. Non-desert rodents generally require more water than desert rodent (Richmond et al., 1962; Holleman and Dieterich, 1973).

When taking both seasons into account, the water flux of *T. nigricauda* is 7.69 ml day^{-1}. This is less than that predicted by the equation of Nagy and Peterson (1988) both for eutherian mammals, generally, in the field (75.1% of predicted) and for eutherian herbivores in the field (38.1% of predicted). However, this analysis included individuals from both mesic and xeric locations. The water flux of *T. nigricauda* from Molopo and Haina was 81.1 % of the predicted value, using the equation for desert eutherians. When considering the water flux for Weenen, the more mesic site, using the general field equation, this was 80.3% of the predicted value.

Water turnover rates do not necessarily demonstrate an ability to live in xeric regions, but are rather indicators of water usage (Downs and Perrin, 1990) and may be used as an index of daily water requirements (Yousef et al., 1974). Seasonal changes in *T. nigricauda* water flux does illustrate the flexibility and summed effects of a number of factors associated with water metabolism.

We conclude that the results of the present study highlights the flexibility in the physiological parameters measured, as indicated by the high degree of intraspecific variability and hence overlap in kidney RMT, maximum urine osmolality and specific WTR displayed by subpopulations of *T. nigricauda*. Lack of significant differences in parameters between sites and seasons could be partly explained by this variation and could also be a result of the traits being partly genetically based (Al-Kahtani et al., 2004). Regardless of this variation, the results of this study suggest that the *T. nigricauda* from the three study sites in winter and summer were in similar states of water balance. For small nocturnal herbivorous endotherms in summer rainfall regions, winter poses a greater challenge than summer. During winter, foliage is of an inferior quality, preformed water is limited and to obtain sufficient food requires exposure to very low temperatures. *T. nigricauda* was most water stressed during winter, and responded, as indicated by lower water flux coupled with higher urine osmolalities. These are key factors for water conservation during dry winter months. It is suggested that *T. nigricauda* employs a suite of physiological and behavioural mechanisms in order to meet their water requirements. In addition to the physiological parameters measured in the present study, other mechanisms could contribute to the maintenance of a positive water balance, such as nocturnalism and labile body temperatures (Chapter 5), low thermal conductance and low resting metabolic rates (Lovegrove et al., 1991). These traits and in particular, flexibility in these traits could explain the successful colonization of mesic, semi-xeric and xeric areas of southern Africa which has implications for the survival of the species in the light of climate change.

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Legends for Figures:

Figure 1. Mid-sagittal section of a *T. nigricauda* kidney. (C = cortex, OM = outer medulla, IM = inner medulla). Scale bar represents 1 mm.

Fig. 2. Scatterplot of *T. nigricauda* body mass versus kidney mass at the three sites during winter and summer.

Fig. 3. Scatterplot of *T. nigricauda* body mass versus kidney RMT at the three sites during winter and summer.

Fig. 4. Relative medullary thickness of *T. nigricauda* at the three sites during winter and summer.

Fig. 5. Urine osmolality (mean ± SE) of male and female *T. nigricauda* at the three study sites in winter and summer.

Fig. 6. Scatterplot of *T. nigricauda* body mass versus urine osmolality at the three sites during winter and summer.

Fig. 7. Scatterplot of *T. nigricauda* urine osmolality versus kidney RMT at the three sites during winter and summer.

Table 1
Mean ± SE body mass of male and female *T. nigricauda* used in the study for the three parameters irrespective of season (abbreviations as per text).

Measurement	Sex	n	Mean mass (g)	Minimum (g)	Maximum (g)
Osmolality	Female	15	59.58 ± 3.71	42.30	85.0
	Male	10	63.54 ± 5.01	47.50	95.5
RMT	Female	9	63.06 ± 6.27	42.70	95.9
	Male	8	74.76 ± 5.99	55.00	102.1
WTR	Female	11	64.07 ± 4.68	45.00	95.9
	Male	6	74.15 ± 8.25	55.00	102.1

Table 2
Mean ± SE, minimum and maximum osmolalities of *T. nigricauda* at the three study sites in winter and summer irrespective of sex.

Season	n	Mean osmolality (mosm kg^{-1})	Minimum osmolality (mosm kg^{-1})	Maximum osmolality (mosm kg^{-1})
Winter	13	2282.85 ± 216.19	803.00	3216.00
Summer	12	1652.00 ± 180.51	648.00	2604.00

Table 3
Water turnover parameters of *T. nigricauda* at the three study sites in winter and summer.

						Water flux		
Season	n	BM (g)	K	TBW (ml)	% TBW	ml day^{-1}	ml kg^{-1} day^{-1}	ml $kg^{0.82}$ day^{-1}
Winter	7	66.94 ± 5.92	0.172 ± 0.02	38.47 ± 3.48	57.68 ± 2.44	6.49 ± 0.69	98.74 ± 9.08	60.24 ± 5.05
Summer	10	68.11 ± 6.12	0.223 ± 0.02	39.40 ± 3.44	57.96 ± 0.51	8.53 ± 0.78	129.31 ± 11.89	78.91 ± 6.81

Values are mean ± SE. BM is body mass, K is the water turnover fraction per day, TBW is total body water.

Fig. 1. Mid-sagittal section of a *T. nigricauda* kidney. (C = cortex, OM = outer medulla, IM = inner medulla). Scale bar represents 1 mm.

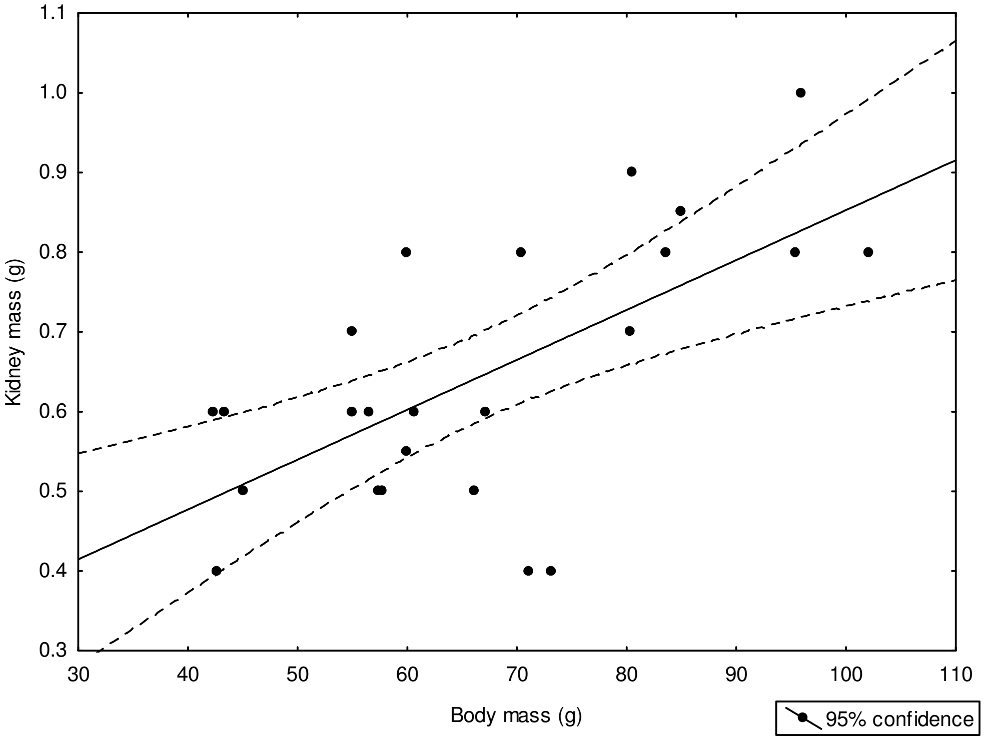

Fig. 2. Scatterplot of *T. nigricauda* body mass versus kidney mass at the three sites during winter and summer.

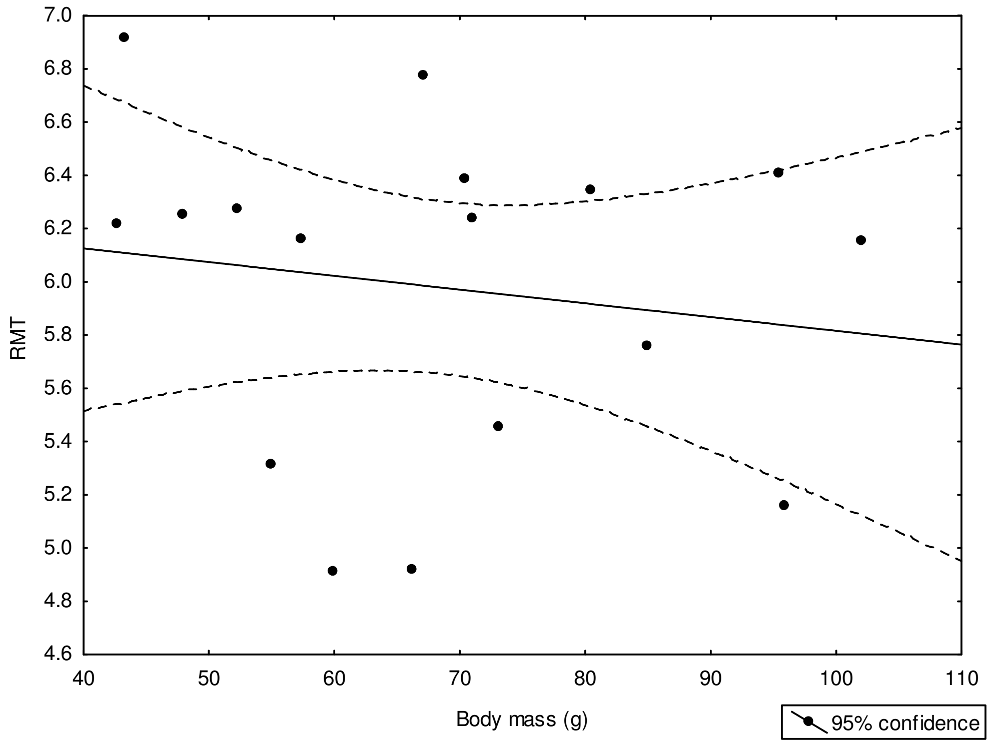

Fig. 3. Scatterplot of *T. nigricauda* body mass versus kidney RMT at the three sites during winter and summer.

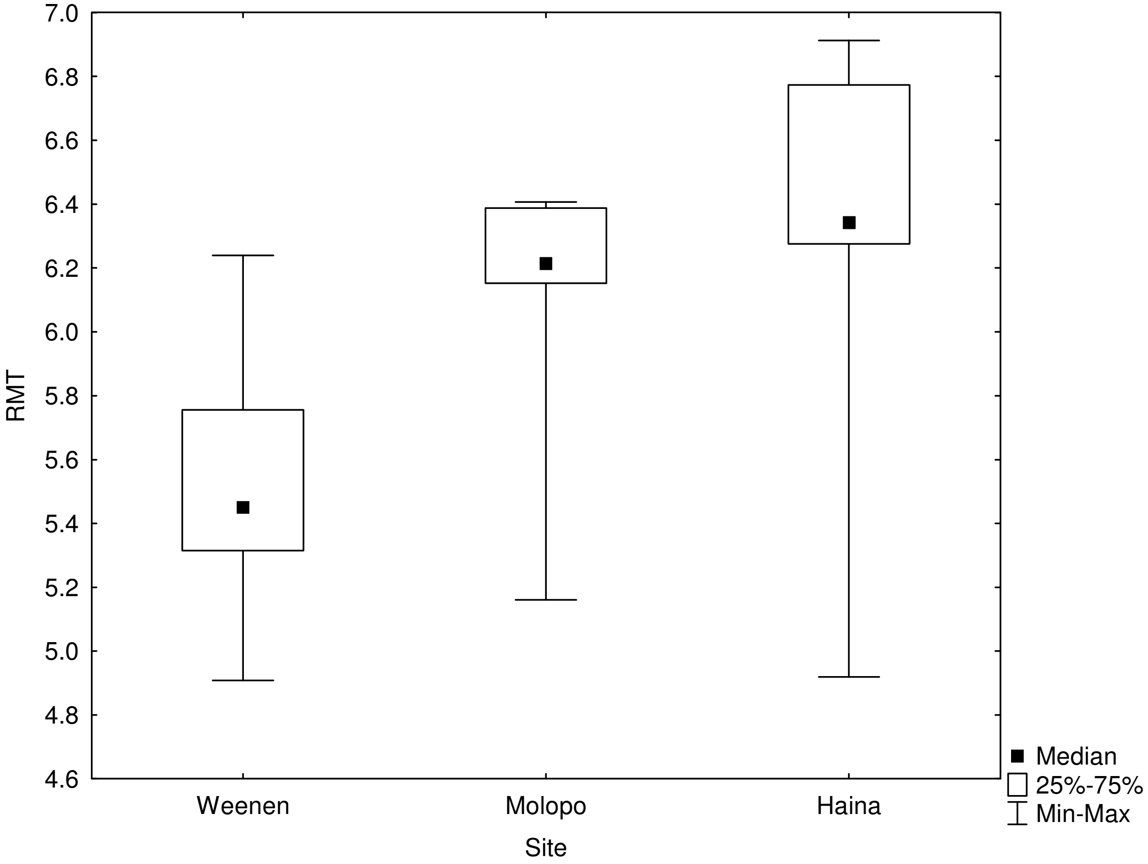

Fig. 4. Relative medullary thickness of *T. nigricauda* at the three sites during winter and summer.

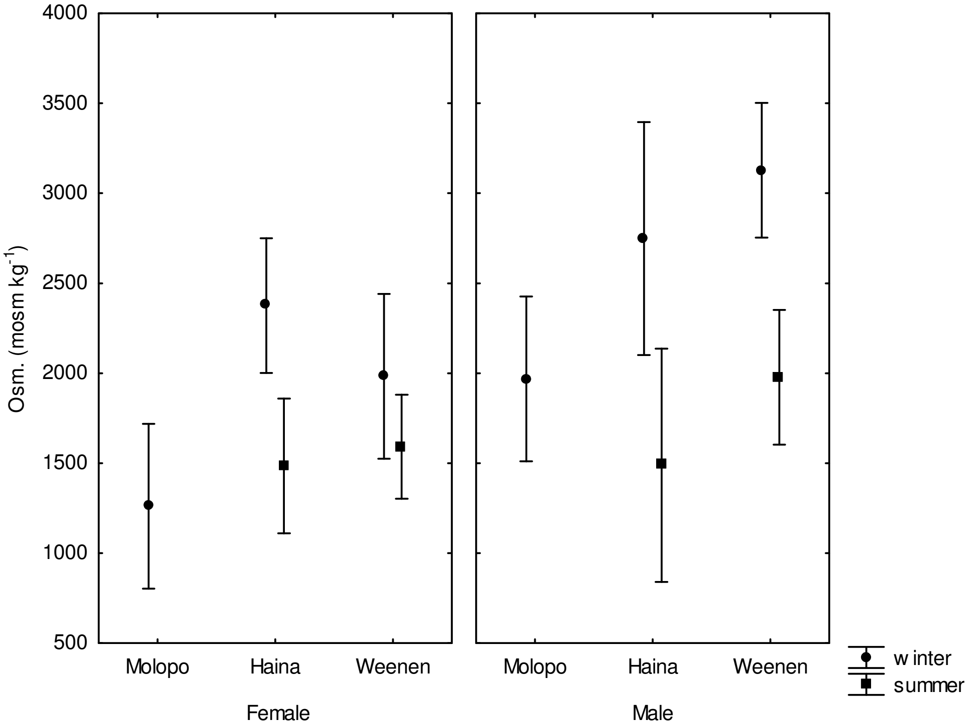

Fig. 5. Urine osmolality (mean ± SE) of male and female *T. nigricauda* at the three study sites in winter and summer.

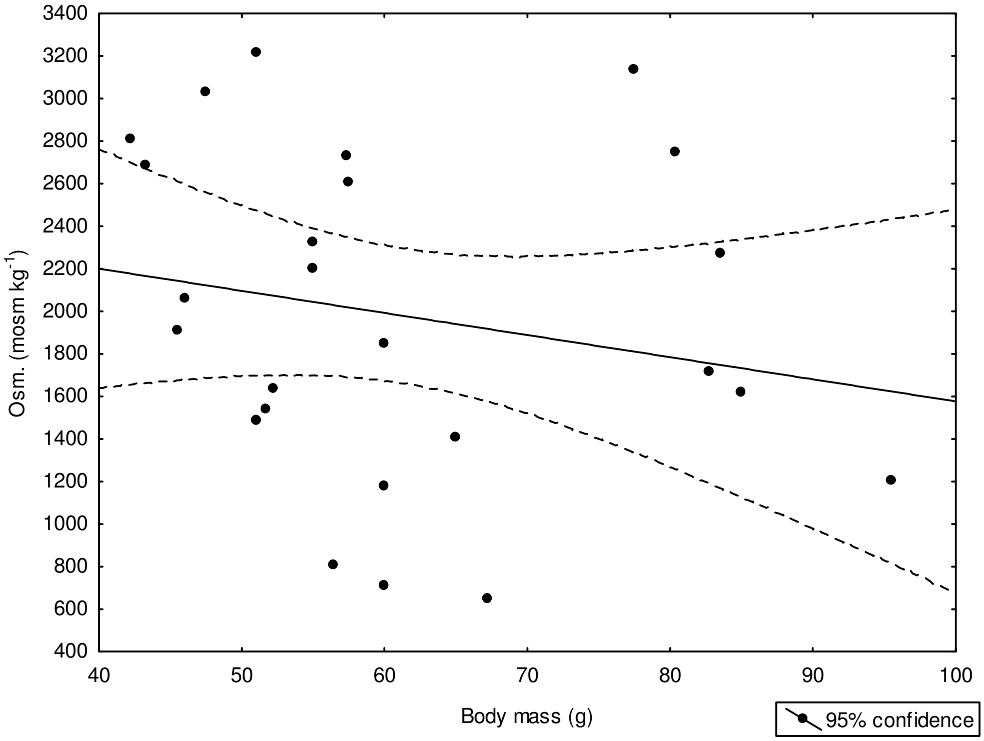

Fig. 6. Scatterplot of *T. nigricauda* body mass versus urine osmolality at the three sites during winter and summer.

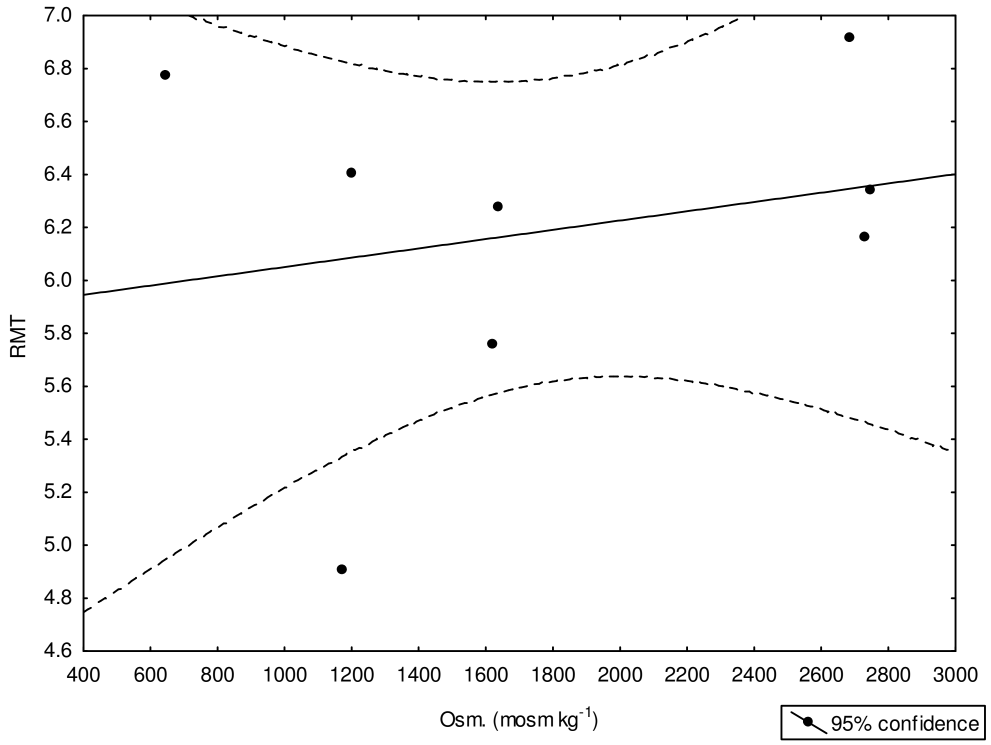

Fig. 7. Scatterplot of *T. nigricauda* urine osmolality versus kidney RMT at the three sites during winter and summer.

Chapter 4

Characterising the thermal environment of small mammalian endotherms: what should we be measuring, and how?

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Summary

1. Operative temperature and standard operative temperature have been proposed as providing an estimate of the thermal load experienced by endotherms and ectotherms. Common techniques of measuring operative temperature include black-bulb temperatures or simplified unheated metal models, typically made of copper.
2. We quantified the thermal environment perceived by a small, arboreal, mammalian endotherm using a number of methods at three study sites in winter and summer. Our area of interest was how well these methods accurately portrayed the actual temperatures that small mammals are exposed to. We predicted that black-bulb and copper model temperatures would more accurately predict operative temperature during photophase when compared to

other direct measurements/devices and that black-bulb temperature would record the greatest variation in temperatures.

3. Temperature differences between the methods were largest during the midday, when temperatures were highest.
4. All methods recorded a greater range of temperatures during photophase than during scotophase.
5. Black-bulb and model temperatures produced more accurate, rapid measurements when compared to measurements produced by direct temperature recording devices, particularly during photophase, when solar radiation is the major influence of heating. Other methods lagged behind black-bulb measurements.
6. Although mean temperatures of some of the methods were significantly different, there was a high degree of correlation between all methods, even after randomization and generation of 25% and 10% subsamples.
7. Computed thermal indices and black-bulb temperatures produced similar thermal profiles.
8. In studies requiring accurate time series measurements, it is suggested that black-bulb or copper models be employed rather than direct temperature recording devices. Simpler measurement devices would suffice for studies requiring an estimate of the temperature variation and trends in the microclimate of small mammalian endotherms, particularly arboreal or cavity dwelling species.

Key-words: Ambient temperature, operative temperature, black-bulb, model, perceived environmental temperature

Introduction

For an extended period, the importance of characterizing the thermal environment of ectotherms and endotherms has been documented, resulting in a range of physical model representations of study animals. However, few studies have discussed the applicability and/or relevance of these models to the particular research question. Moreover, recent advances in technology have resulted in a range of small temperature recording devices which may substitute for models (Vitt & Sartorius 1999) depending on the type of data required. Such devices may lower both the cost and time consumed in producing T_e models, by providing accurate thermal indices at a scale relative to the study animal.

Ambient temperature (T_a) is not the actual thermal condition experienced by the animal in its natural environment (Chappell & Bartholomew 1981; Bakken 1992). The factors of the environment which are primarily responsible for energy flow to an animal include radiation, air temperature, wind and humidity (Porter & Gates 1969). In order to estimate the energetic effects of the thermal regime an animal experiences in the field, it is convenient to integrate the effects of these parameters into an index value that can be directly compared to the animal's physiological performance (Chappell 1981). A useful index of the thermal potential driving heat flow between animals and their thermal environments is the operative temperature (T_e) (Byman 1985). This thermal index thus gives an indication of the thermal conditions experienced by an animal in its natural surroundings (Chappell & Bartholomew 1981).

Operative temperature is considered to be the temperature of an inanimate object of zero heat capacity that is of the same size, shape, and has the same radiative properties as the animal exposed to the same microclimate (Bakken & Gates 1975).

Operative temperature would be the body temperature (T_b) of an animal if it were in thermal equilibrium with the environment in the absence of metabolic heating or evaporative cooling (Dzialowski 2005). The difference between T_e and T_b equals the net thermal gradient acting on the animal, and the net effect of a homeotherm's heat production and evaporative water loss is to maintain T_b different from T_e (Walsberg & Weathers 1986). Once the T_e has been determined for the particular natural microclimate in which one is interested, one may estimate the value of physiological and/or ecological variables of the animal which may have been expressed as a function of T_e (Morhardt & Gates 1974).

Operative temperature can be distinguished from standard operative temperature (T_{es}), which by including T_b in its definition, is a direct index of sensible heat flux. Unlike T_e, T_{es} accommodates wind-induced changes in resistance to heat flow by normalization to standard (e.g. metabolism chamber) convective conditions (Bakken 1980), thus avoiding the limitation of one convection condition. Standard operative temperature models have been used with less frequency than T_e models (Dzialowski 2005) as they are more difficult and time consuming to construct and their reliability has been called into question (Walsberg & Wolf 1996). In the present study, we used only T_e.

Operative temperatures (Bakken & Gates 1975; Bakken 1976) have become a tool for studying the thermal effects of ectotherms and endotherms (Bakken 1992). Numerous physical model representations of animals have been used to measure T_e, and when used correctly, T_e models have the potential to be an effective tool for examining the relationship between an animal's thermal environment and its physiology and ecology (Dzialowski 2005). The use of models is now expected in studies of field thermal physiology (Goldstein & Pinshow 2006). Sphere thermometers may provide a reasonably accurate thermal index of an animal's environment (Walsberg and Weathers 1986), copper casts being the most accurate T_e models available (Dzialowski 2005). Wall thickness and the size of both the model and the internal cavity of the model are important considerations for accuracy of readings. Rapid time response to varying thermal conditions can be obtained by using hollow copper bodies, when the walls are of sufficient thickness (1-2 mm for animals up to 100g) to conduct heat and internal gradients are minor in small (<3 cm diameter) models (Bakken 1992). A comparative study by Walsberg and Weathers (1986) indicated that painted metal spheres or cylinders are acceptable T_e thermometers when multiple measurements over long time scales (several hours) are taken.

'Perceived environmental temperature' (PET) is a relatively recent approach used to estimate the thermal load in Chacma Baboons (*Papio hamadryas*). Three indices of the PET were produced to account for the combined effects of temperature, solar radiation, humidity and wind speed on perceived air temperature, suggesting that all three indices were an improvement over shade temperatures in quantifying the thermal environment. Primates respond to 'perceived' rather than 'actual' air temperature, thus all these factors need to be taken into account to understand the role of temperature in primate behavioural ecology (Hill *et al.* 2004).

Of the three indices, PET2, computed as the mean of the heating and cooling thermal elements, could be incorporated into models with behaviour variables, thus providing a biologically relevant thermal index in terms of baboon behaviour. Since solar radiation appeared to be the most important factor underlying the relationships with PET2, black-bulb temperatures represent a simple alternative of the thermal environment if climate records cannot be obtained (Hill *et al.* 2004). Interestingly, to our knowledge, no other studies have either made use of or referred to these indices, which calls into question the utility of these indices. Although these indices were designed for use on larger endotherms, they were computed in the present study to compare resultant temperatures with measurements recorded using black-bulb, models and direct measurement devices.

Thus, although a variety of physical model representations of animals have been used to measure T_e (see Review: Dzialowski 2005), few studies have been designed to question whether the T_e's measured account for the range of temperatures to which the study animal is exposed in its multiple microhabitats. Many small endotherms avoid the hours of the day when solar radiation is at its greatest by sheltering in burrows or by adopting nocturnal activity patterns (Nowak 1999). In such cases, it would be less appropriate to use metal models or black-bulbs placed in the sun and more relevant to use multiple temperature recording devices which would provide accurate thermal indices of the microclimate of the study animal. In addition, few studies have compared measurements obtained using different temperature measuring devices, now available in the market, in the field. In an attempt to determine the utility of electronic devices versus models in field studies, Vitt & Sartorius (1999) found that electronic devices produced sets of T_e's almost identical to lizard models, suggesting that the devices can be substituted for models in certain applications.

The objective of this study was to quantify the degree to which temperature data derived using 1) copper models, 2) black-bulb and 3) direct measurement devices accurately predict the actual temperatures perceived by small, endothermic mammals, using the Black-tailed Tree Rat, *Thallomys nigricauda* as a model species. This species was chosen since it inhabits a wide range of habitats from mesic to xeric localities, this distribution resulting in a wide range of temperatures to which it is exposed. In addition, being arboreal, *T. nigricauda* is exposed to greater temperature fluctuations than burrowing small mammals in southern Africa (de Graaff 1981; Lovegrove & Knight-Eloff, 1988; Downs & Perrin 1989; Skinner & Chimimba 2005). We predicted that black-bulb and copper model temperatures would more accurately and precisely predict T_e during the day when compared to other direct measurement devices and that black-bulb would record the greatest variation in temperatures.

Materials and methods

STUDY SITES

The study was conducted at three study sites in southern Africa during winter (June-July) 2006 and 2007 and summer (January-February) 2007. These were Weenen Game Reserve in the KwaZulu-Natal Province, South Africa (28°50’43”S; 29°59’12”E), Molopo Nature Reserve in the North-West Province, South Africa (25°50’52”S; 22°55’37”E) and Haina Game Farm in Botswana (20°56’56”S; 23°40’40”E). Altitude and degree location were plotted using a Magellan GPS 4000 XL. These study sites were chosen as part of a broader study on aspects of physiology and behaviour of *T. nigricauda* along an aridity gradient. Data were recorded at each site for an average of three days in winter and five days in summer. All climatic instruments were placed at a single location at each study site known to be occupied by study animals.

WIND SPEED AND RELATIVE HUMIDITY

Wind speed, relative humidity and ambient temperature were measured using a pre-calibrated Kestrel 4000 Pocket Weather Tracker (Nielsen Kellerman, Pennsylvania, USA). This instrument was secured on to a tree at a height of 1.5m in such a way as to ensure exposure to wind. The instrument was programmed to record temperatures at four intervals each hour. In all Figures, this measurement is referred to as ‘Kestrel’.

AMBIENT TEMPERATURES

Ambient temperature was measured at each site in three ways. Firstly using a calibrated DS 1921 Thermocron iButton® placed in a Stevenson’s screen (temperature shield). The shields were placed at a height of 1.25 – 2 m, recording shade temperature. (In all Figures, this measurement is referred to as ‘shade’). Secondly, a single, exposed iButton® was also placed on the top of a tree branch at a height of 1.5m. The iButtons® were programmed to record temperatures every 15 mins. (In all Figures, this measurement is referred to as ‘iButton’). Thirdly the Kestrel measurement of T_a was used as a measure of T_a.

OPERATIVE ENVIRONMENTAL TEMPERATURE MEASUREMENTS

We measured T_e using black-bulb solar radiation temperatures (abbreviated as ‘Bbulb’ in all Figures) and unheated models. Black-bulb solar radiation temperatures were recorded using an iButton® placed in a black copper ball (1mm thickness,10cm diameter) that was exposed to direct sunlight throughout the day at a height of 1m.

Heated mounts (required for T_{es}) cannot be used when the operative temperature of the environment exceeds body temperature (Bakken *et al.* 1983). Physical models of the Black-tailed Tree Rat were constructed from hollow, copper pipes (cylinders). The proportions of the model approximated those of an average adult Tree Rat (length: 13cm, diameter: 3.2cm). O’Connor *et al.* (2000) provide a guide for the minimum wall thickness to reduce thermal heterogeneity of model temperatures. Models had a wall thickness of 2mm and were painted black as virtually all animals and flat paints are effectively black (Bakken 1976).

Internal temperatures of the copper models were measured using calibrated DS1921 Thermocron iButtons® (Dallas Semiconductor) suspended in the centre of each model using cotton. Temperature resolution of iButtons® was 0.5˚C. iButtons® were programmed to record operative temperature every 15 min. Before moving the models to their sites, they were lined up on the ground and allowed to equilibrate 15-20 min (equilibration under full solar exposure takes ± 10 min) and since all models were in place at the sites for the entire course of the study they had invariably equilibrated well over the required 10 min before every temperature measurement (Salzman 1982).

Two copper models were placed in permanent positions at each study site. One was placed in a tree at a height of 1.5m (referred to as 'model (elevated)' in all Figures). The second was placed at the base of the tree and referred to as 'model (base)' in all Figures. Copper models in trees were attached in two places, to the top of a branch using copper wire.

PERCEIVED ENVIRONMENTAL TEMPERATURE (PET) INDICES

The indices PET1, PET2 and PET3 were computed using the following equations (Hill *et. a*l., 2004):

PET1 = HI(WC(sr)) (Equation 1)

where WC(sr) was the wind chill equivalent temperature based upon the black-bulb solar radiation temperature in ºC, and HI is the heat index based upon the WC(sr) value.

$$PET2 = \frac{HI(sr) + T(wc)}{2} \qquad \text{(Equation 2)}$$

where HI(sr) was the heat index based upon the black-bulb solar radiation temperature in ˚C and T(wc) is the wind chill equivalent using shade temperatures.

$$PET3 = = \frac{T(sr) + T(wc) + T(hi)}{3} \qquad \text{(Equation 3)}$$

where T(sr) was the black-bulb solar radiation, while both T(wc) and T(hi) were calculated using shade temperatures.

DATA ANALYSES

Kestrel data were downloaded using the Kestrel Interface Communication Software Version 1.12. iButton data were downloaded using the DS1921 Thermochron iButton® Software Download Programme (Dallas). Statistical analyses including descriptive statistics, regressions and randomisation were performed using the Statistica 7 package (Statsoft Inc., USA). As the data represented a time series of values, adjacent values were possibly autocorrelated. To reduce the effect of the lack of independence, samples were randomized. We then performed 1000 replicates on 25% and 10% sub-samples from the randomized dataset for statistical analysis. Since PET indices were computed using data measured by several methods under consideration, these indices were excluded from further analyses.

Results

Temperatures measured using all methods revealed five important patterns. Firstly, temperature differences between the methods were largest during the midday, when temperatures were high, resulting in significant differences between most methods during photophase but lack of significant differences between most methods during scotophase, (Figs 1 and 2). Secondly, all methods recorded a greater range of temperatures during photophase than during scotophase (Figs 1 and 2). Thirdly, most methods had slower heating and cooling rates (indicated by the slope of increase in temperature pet unit time) when compared with the black-bulb (Figs 1 and 2). The fourth pattern apparent was that although the mean temperatures of some of the methods were significantly different, there was a high degree of correlation between all methods (Table 2, Figs 3 and 4). The final pattern was the high degree of similarity between computed thermal indices and black-bulb temperatures. In general, measures of the various temperatures using the respective methods showed similar accuracy. However, black-bulb and models showed greater precision and accuracy than direct measurement devices at short time-scales during photophase.

Mean winter temperatures for all climatic variables at the three study sites showed that there were no significant differences between most methods during the night, while differences were significant for most methods during the day (Fig. 1). PET1 and black-bulb accounted for the highest mean, highest maximum, lowest minimum and greatest range, with the exception of Weenen, where shade temperature recorded the lowest minimum temperature (Table 1). Temperature ranges of all variables were greater during photophase than scotophase at all sites, although this difference was less apparent at Weenen (Fig. 1). In winter black-bulb had a greater temperature range at all sites when compared with models (Table 1a).

When considering PET indices, PET 1 had the highest mean value and the greatest temperature range at all three study sites followed by PET2. During photophase, PET1 was the greatest, followed by PET2. During the scotophase, this situation was reversed, with PET1 recording the lowest value (Table 1a; Fig. 1).

Similar to winter, mean summer temperatures for all climatic variables at the three study sites showed lack of significant differences between most methods during the night, while differences were significant for most methods during photophase (Fig. 2). PET1 accounted for the highest mean, highest maximum temperatures and the greatest temperature range, with the exception of Haina, where PET2 accounted for the greatest temperature range. Lowest minimum temperatures were recorded by Kestrel at both Molopo and Weenen, while PET2 recorded the lowest minimum temperature at Haina (Table 1b). Similarly to winter, temperature ranges of all variables were greater during photophase than scotophase at all sites (Fig. 2). In summer, black-bulb had a greater temperature range at all sites when compared to models, with the exception of Haina, where model (elevated) recorded a greater temperature range than black-bulb (Table 1b).

Similar to winter, when considering summer PET indices, PET1 had the highest mean value at all three sites as well as the greatest temperature range, with the exception of Haina, where PET2 had the greatest temperature range. PET1 had the highest mean value at all sites during both photophase and scotophase, with the exception of Molopo, where PET3 recorded the highest mean temperature at night (Table 1b; Fig. 2)

Mean temperatures for randomized data for 25% and 10% sub-samples of all methods for winter (Fig. 3) and summer (Fig. 4) showed that there was little difference between the means of the 25% and 10% sub-samples for each method, as shown by the overlap of the 95% confidence intervals in the respective figures. Moreover, there was little difference between the means of the sub-samples and the means calculated from the full dataset (Table 1; Fig 3 and 4). Although there were significant differences between the temperature means of different methods (Fig. 3 and 4), there were no noticeable trends.

Even after randomization and generation of 25% and 10% sub-samples, all methods showed a high correlation (Table 2). In addition, there was little difference between the 25% and 10% sub-samples of correlations between methods (Table 2), which indicated that there was similarity in response of direct measurement devices and models to changing temperature.

Discussion

Significant differences during photophase and the lack of significant differences during the scotophase can be attributed to the influence of solar radiation on methods used. Changes in black-bulb and models had a high dependence on solar radiation and thus these heated up to higher temperatures during the photophase when compared with other direct devices. During scotophase, these methods measure similar temperatures to direct temperature recording devices, due to the lack of solar radiation. This accounted for the greater range of temperatures measured during photophase compared with scotophase. However, the position of models has an influence on temperatures measured. The influence of solar radiation can induce variation of 5ºC or more in temperatures measured in thin-walled T_e models depending on how the sun strikes the model (O'Connor *et al.* 2000). Models placed below or in a tree received shade at least for part of the day and thus did not reach the maximum temperatures reached by the black-bulb. For small endotherms, like *T. nigricauda*, which avoids the hours of the day when solar radiation is at its greatest by sheltering in burrows or by adopting nocturnal activity patterns, it would be less appropriate to use metal models or black-bulbs placed in the sun and more relevant to use multiple temperature recording devices which would provide accurate thermal indices of the microclimate of study animals. Similarly, other studies have shown that habitat-level measurements do not always correspond to niche-level measurements (Helmuth 1998; Gilman *et al.* 2006).

The slower rates of heating and cooling in all methods when compared with black-bulb temperature changes were likely due to the position of the measuring devices and/or as they are less affected by solar radiation. The direct devices in this study did produce temperature profiles similar to those of the black-bulb and models. However, direct measurements appeared to change temperature more slowly than the black-bulb and models and reached different equilibrium temperatures. Although this violates one of the classical requirements for physical T_e models (Bakken & Gates 1975; Bakken 1992) and would clearly be a problem when one's research question demands accurate time series measurements, animal T_b would always lag behind model T_e in the field (Dzialowski 2005). This is thus a consideration for studies using T_e against which to compare animal T_b.

All methods show similarity in response to temperature, as indicated by the high correlations, but differ in the maximum and minimum temperatures attained as well as in the heating and cooling rates, as indicated by the means of the full dataset as well as the randomized dataset. We expected mean temperatures between methods to differ since each method differs with respect to the dependence on solar radiation, as well as the positioning in the field.

The lack of usage of PET indices in the literature raises the question of its validity in studies. PET indices may be valuable in behavioural studies as they provide accurate time series measurements and take temperature, solar radiation, humidity and wind speed into account, providing a biologically relevant thermal index (Hill *et al.* 2004). It was expected that measured black-bulb and computed PET1 would have similar values due to the method of computation. It was also expected that PET1 would have the highest mean value and greatest range of the three indices due to the cumulative method of computation. The initial temperature was the black-bulb temperature, which was greater than 24ºC during photophase, both in winter and summer. The heat index was then based upon this value, which was only computed for values greater than 24ºC. Thus humidity is taken into account for all temperatures greater than 24ºC. This cumulative sequence of calculations may be the cause of PET1 indices being higher than the other two indices during photophase, resulting in significant differences between PET1 and the other indices. This would also account for the reverse situation during scotophase, resulting in lack of significant differences. Computation of PET2 does have sequential procedures, but separates the 'heating' and 'cooling' elements, resulting in lower temperatures when compared to PET1. PET3 alleviates any problems due to sequential procedures, but it does not account for any interactions between the variables resulting in cumulative thermal effects, underestimating the actual 'perceived' temperature (Hill *et al.* 2004).

It is important to note that the relative importance of the factors used to compute the PET indices may vary between habitats and this should be considered in studies. For example, the importance of solar radiation intensity may be greatest for primates in open habitats, while for arboreal species humidity is likely to be of greater significance to thermal loads (Hill *et al.* 2004). The similarity, due to the method of computation, between all PET indices and black-bulb temperatures in this study suggests that black-bulb temperatures could suffice for behavioural studies in open habitats as an index of T_a.

As predicted, black-bulb and copper model temperatures did provide the most accurate and precise measure of T_e during photophase when compared with other direct measurement devices, and black-bulb recorded the greatest variation in temperatures. However, all methods were accurate for general trends in terms of the thermal microenvironment. Black-bulb and copper models should be the favored devices for studies requiring accurate time series measurements, due to their rapid response to thermal change. In accordance with Vitt & Sartorius (1999), we suggest that direct methods should be avoided in studies requiring accurate time series measurements. However, the utility of black-bulb and copper models is limited to studies on diurnal endotherms where the researcher is interested in the maximum temperatures reached during photophase and the effect of these temperatures on behavioural thermoregulation, for example. For studies on nocturnal endotherms and/or diurnal endotherms that avoid the maximum daytime temperatures in refugia, simple direct measurement devices, such as iButtons® would produce accurate thermal profiles of temperatures to which the animal is exposed. Although temperatures of such devices may not provide an estimate of 'instantaneous' operative temperatures, they still show the variation in temperature available to the animal in the same micohabitat, since they respond faster than animal temperatures (O'Connor *et al.* 2000). Devices could be placed in all microhabitats used by the study animal thereby providing a reference thermal map for the study species. This may elucidate heterogeneity in T_e which might be useful to the study animal.

In conclusion, the decision as to whether T_e should be measured as opposed to a direct measurement of the microclimate of the study animal depends on the research question. For studies necessitating instantaneous measurements of the diurnal thermal environment, it is suggested that T_e is measured using a black-bulb or suitable models.

However, simpler direct temperature measurement devices would suffice for studies requiring an estimate of the temperature trends of the microclimate of the study animal.

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Legends for Figures (see text):

Fig. 1: Mean winter temperatures (± SE) in Molopo (a), Haina (b) and Weenen (c). No data were recorded for model (elevated) in Haina. Weenen model (elevated), model (base) and iButton data were excluded due to incomplete datasets (see text for abbreviations and explanations).

Fig. 2: Mean summer temperatures (± SE) in Molopo (a), Haina (b) and Weenen (c) (see text for abbreviations and explanations).

Fig. 3: Mean winter temperatures (± 95% CI) in Molopo (a), Haina (b) and Weenen (c) after randomization. No data were recorded for model (elevated) in Haina. Weenen model (elevated), model (base) and iButton data were excluded due to incomplete datasets (see text for abbreviations and explanations).

Fig. 4: Mean summer temperatures (± 95% CI) in Molopo (a), Haina (b) and Weenen (c) after randomization (see text for abbreviations and explanations).

Table 1a. Mean, range, minimum and maximum temperatures (ºC) measured using different methods during winter at the three study sites (see text for abbreviations and explanations).

Site	Variable	N	Mean	Minimum	Maximum	Range
Molopo	PET1	283	11.70 ± 0.65	-5.39	31.77	37.16
	PET2	283	10.85 ± 0.55	-4.93	27.97	32.90
	PET3	283	10.65 ± 0.53	-4.78	27.50	32.28
	Black bulb	283	11.70 ± 0.66	-5.39	33.68	39.07
	model (base)	283	10.98 ± 0.46	-0.92	25.65	26.57
	model (elevated)	283	10.38 ± 0.44	-3.40	25.20	28.60
	shade	283	10.09 ± 0.47	-4.47	25.17	29.64
	iButton	283	10.18 ± 0.38	-1.93	22.62	24.55
	Kestrel	283	9.80 ± 0.41	-3.90	22.70	26.60
Haina	PET1	376	17.23 ± 0.62	2.06	42.78	40.72
	PET2	376	16.36 ± 0.52	2.60	35.53	32.94
	PET3	376	16.23 ± 0.50	2.77	33.84	31.06
	Black bulb	376	17.76 ± 0.66	2.06	42.08	40.02
	shade	376	15.55 ± 0.43	3.13	30.68	27.55
	iButton	376	16.94 ± 0.33	6.00	31.00	25.00
	model (base)	376	19.55 ± 0.55	7.10	42.60	35.50
	Kestrel	376	15.56 ± 0.40	3.60	33.60	30.00
Weenen	PET1	440	16.86 ± 0.45	5.10	43.12	38.02
	PET2	440	15.47 ± 0.35	4.85	35.14	30.29
	PET3	440	14.91 ± 0.31	4.77	31.10	26.33
	Black bulb	440	16.51 ± 0.42	5.10	39.14	34.04
	shade	440	14.10 ± 0.26	4.60	27.66	23.06
	model (base)	269	15.29 ± 0.24	8.61	25.16	16.55
	model (elevated)	270	14.69 ± 0.22	8.18	23.73	15.55
	iButton	199	14.24 ± 0.28	8.12	24.14	16.02
	Kestrel	440	13.97 ± 0.25	5.20	29.80	24.60

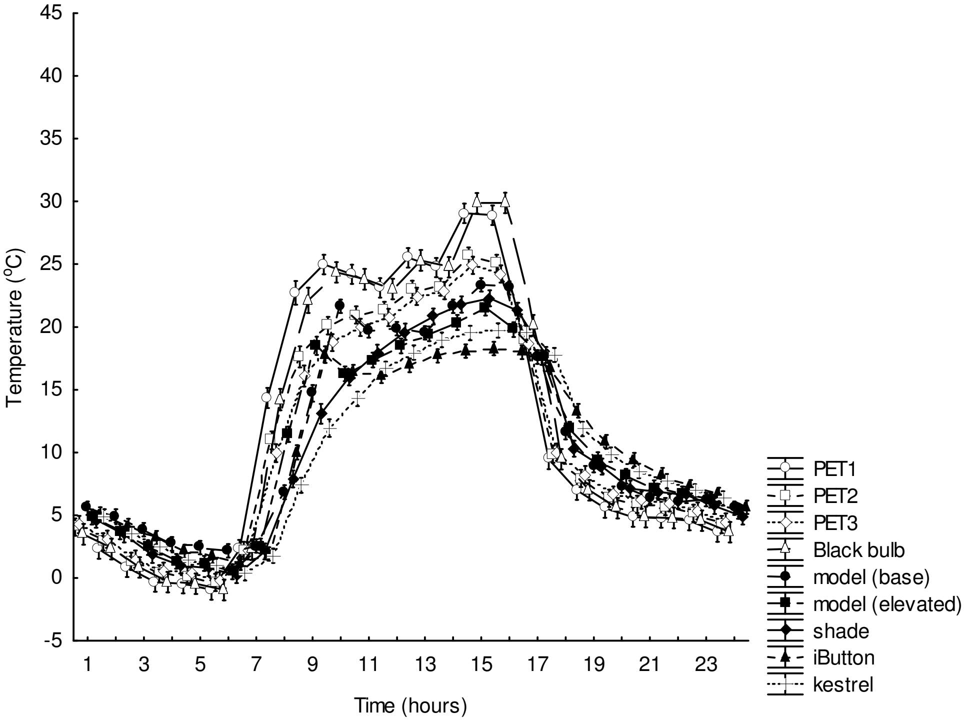
Table 1b. Mean, range, minimum and maximum temperatures (ºC) measured using different methods during summer at the three study sites (see text for abbreviations and explanations).

Site	Variable	N	Mean	Minimum	Maximum	Range
Molopo	PET1	498	30.69 ± 0.42	19.16	64.10	44.94
	PET2	498	29.28 ± 0.32	19.42	50.13	30.71
	PET3	498	28.52 ± 0.27	19.51	41.90	22.39
	Black bulb	498	29.26 ± 0.33	19.16	49.10	29.94
	shade	498	27.96 ± 0.24	19.68	38.67	18.99
	model (elevated)	498	28.59 ± 0.28	19.21	43.17	23.96
	model (base)	498	27.94 ± 0.23	20.65	45.60	24.95
	iButton	498	29.37 ± 0.32	19.35	52.33	32.98
	Kestrel	498	27.72 ± 0.24	19.10	40.50	21.40
Haina	PET1	440	27.54 ± 0.37	16.61	51.04	34.43
	PET2	440	26.35 ± 0.32	9.59	49.52	39.93
	PET3	440	25.92 ± 0.25	16.65	37.04	20.39
	Black bulb	440	26.35 ± 0.30	16.61	42.58	25.97
	shade	440	25.48 ± 0.22	16.67	34.67	18.00
	iButton	440	26.03 ± 0.19	19.12	34.11	14.99
	model (base)	440	26.60 ± 0.17	20.66	36.65	15.99
	model (elevated)	440	26.35 ± 0.29	17.05	45.05	28.00
	Kestrel	440	25.09 ± 0.22	16.80	34.50	17.70
Weenen	PET1	488	23.50 ± 0.33	11.63	47.91	36.28
	PET2	488	22.75 ± 0.31	11.38	42.03	30.65
	PET3	488	22.45 ± 0.30	11.30	38.32	27.02
	Black bulb	488	23.13 ± 0.30	11.63	41.13	29.50
	shade	488	22.03 ± 0.29	11.13	36.65	25.52
	model (base)	488	23.04 ± 0.24	14.14	35.65	21.51
	model (elevated)	488	22.40 ± 0.29	11.19	38.21	27.02
	iButton	488	22.65 ± 0.23	13.13	34.14	21.01
	Kestrel	488	21.75 ± 0.28	11.10	36.50	25.40

Table 2. Relationship between temperatures produced by different methods at all sites during winter and summer (see text). Values are R^2 values for 25% sub-sample of the dataset. R^2 values for 10% sub-sample of the dataset are shown in parenthesis when they differ from the 25% sub-sample. Blanks indicate missing model (elevated) dataset for Haina in winter. The Weenen dataset for winter was excluded due to an incomplete dataset. (See text for abbreviations).

	Winter		**Summer**		
Comparison	**Molopo**	**Haina**	**Molopo**	**Haina**	**Weenen**
Bbulb v Kestrel	0.89	0.90	0.87	0.94	0.97
Bbulb v model (base)	0.94	0.93	0.81 (0.82)	0.89	0.96
Bbulb v model (elevated)	0.95		0.91	0.96	0.96
Bbulb v iButton	0.89	0.72	0.79 (0.80)	0.89	0.94
Bbulb v shade	0.94	0.95	0.91 (0.92)	0.94	0.98
model (base) v Kestrel	0.93	0.80	0.89	0.87 (0.88)	0.94
model (base) v iButton	0.90	0.64 (0.65)	0.62 (0.63)	0.84	0.91
model (elevated) v Kestrel	0.96		0.96	0.95	0.97
model (elevated) v model (base)	0.92		0.90 (0.91)	0.92	0.92
model (elevated) v iButton	0.97		0.71 (0.72)	0.92	0.95
iButton v Kestrel	0.94	0.90	0.69 (0.70)	0.97	0.96
Shade v Kestrel	0.92 (0.98)	0.86 (0.98)	0.77 (0.97)	0.92 (0.96)	0.96 (0.98)
Shade v model (base)	0.95 (0.96)	0.86	0.88 (0.89)	0.89	0.93
Shade v model (elevated)	0.96		0.96	0.93	0.97
Shade v iButton	0.95 (0.92)	0.86	0.88 (0.78)	0.89 (0.92)	0.93 (0.96)

a)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Black bulb
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model (elevated)
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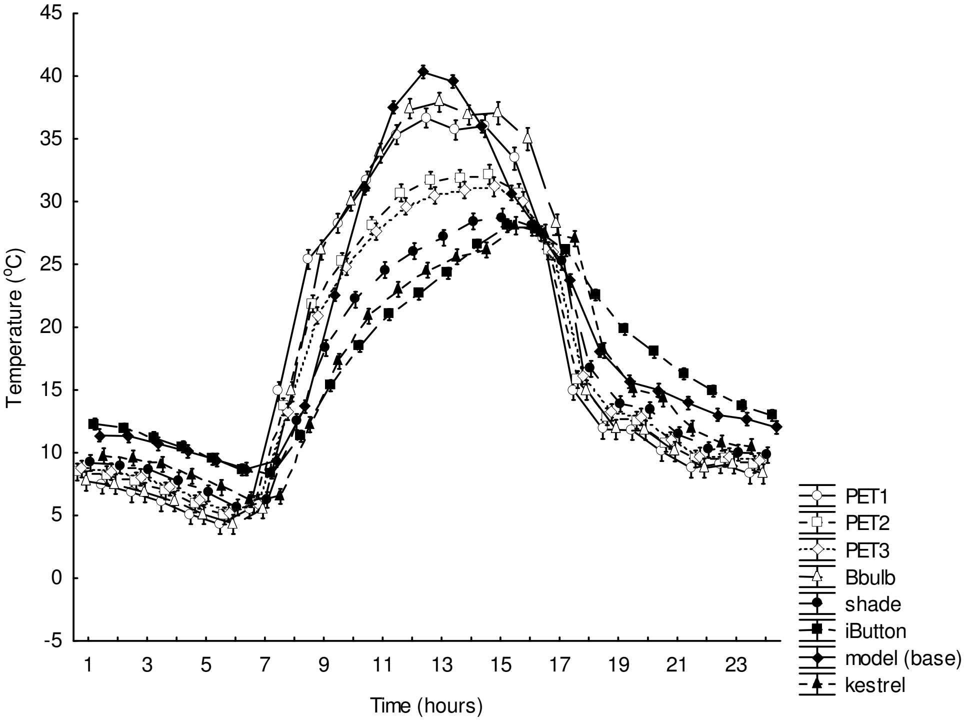
kestrel

b)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model (base)
kestrel

c)

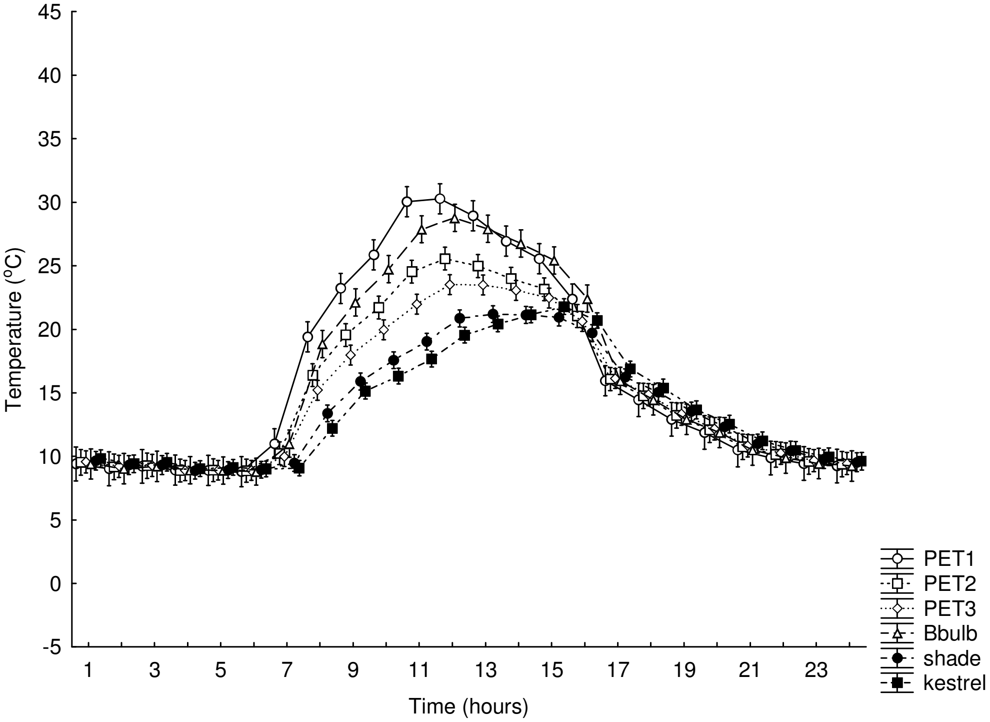
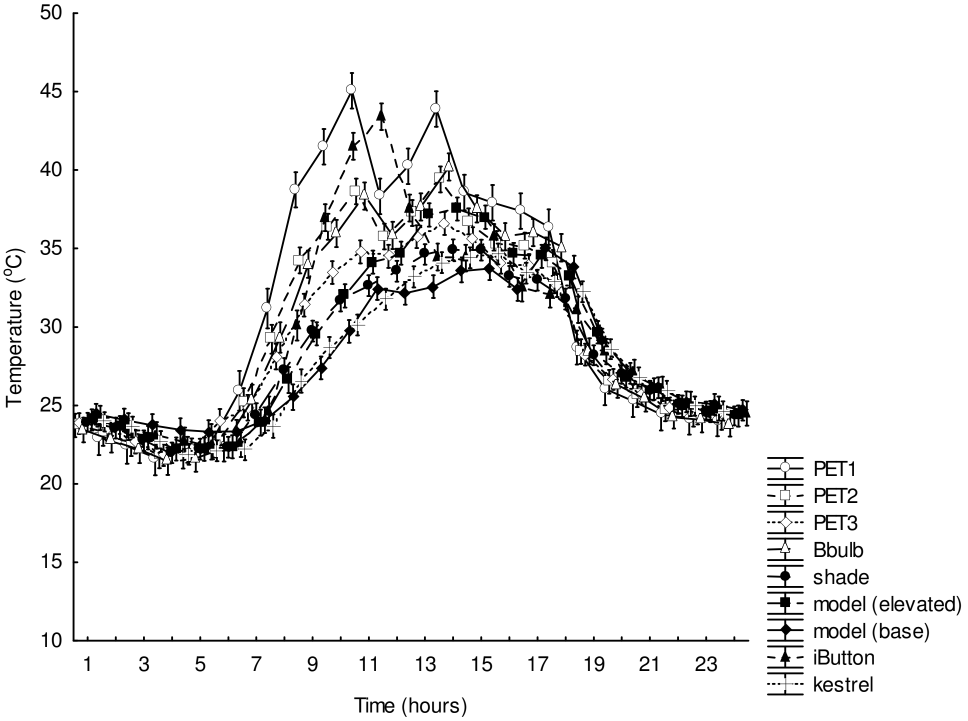


Fig. 1. Mean winter temperatures (± SE) in Molopo (a), Haina (b) and Weenen (c). No data were recorded for model (elevated) in Haina. Weenen model (elevated), model (base) and iButton data were excluded due to incomplete datasets (see text for abbreviations and explanations).

a)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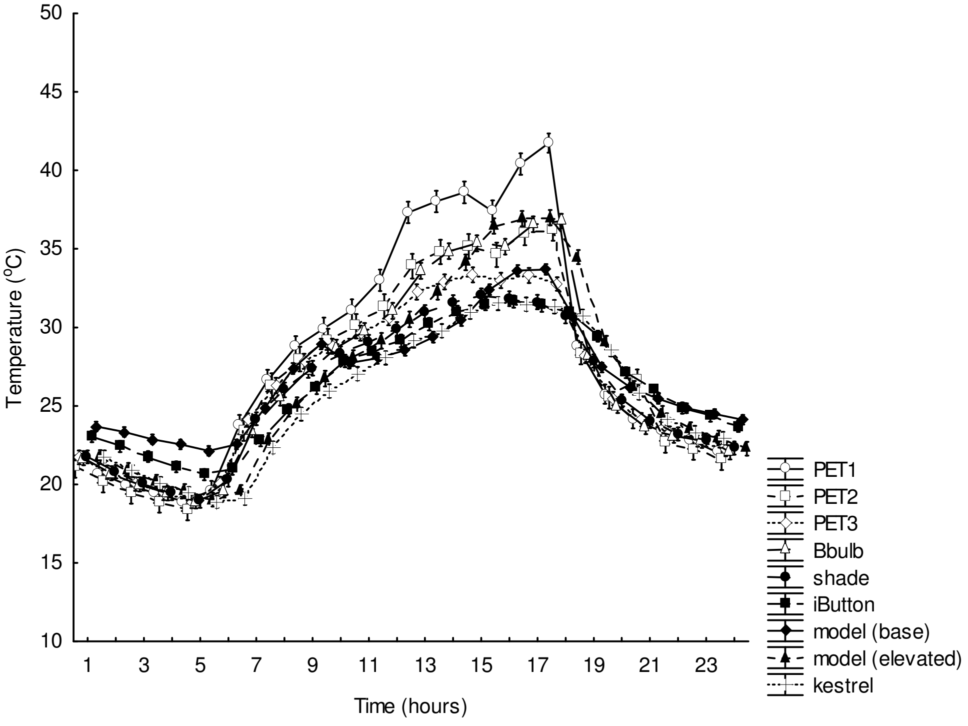
model (elevated)
model (base)
iButton
kestrel

b)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Time (hours)
PET1
PET2
PET3
Bbulb
shade
iButton
model (base)
model (elevated)
kestrel

c)

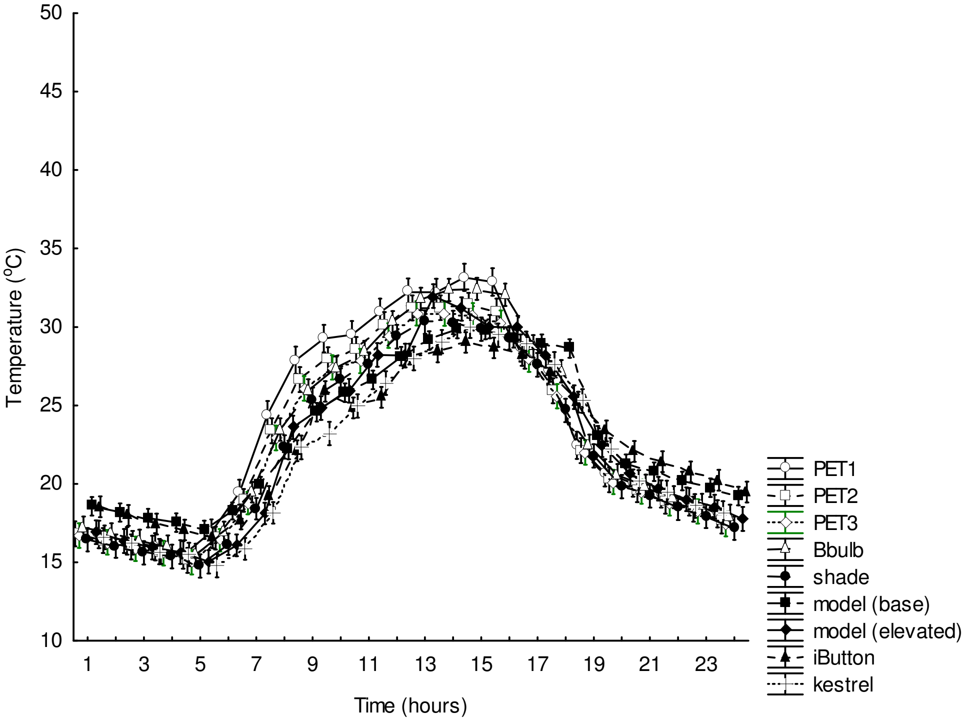

Fig. 2. Mean summer temperatures (± SE) in Molopo (a), Haina (b) and Weenen (c) (see text for abbreviations and explanations).

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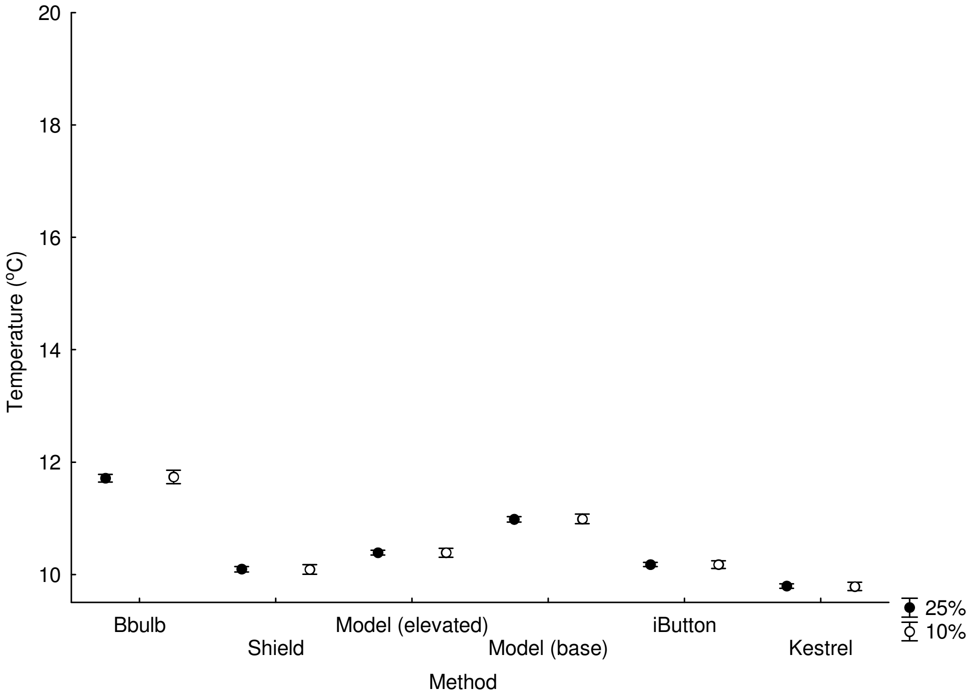
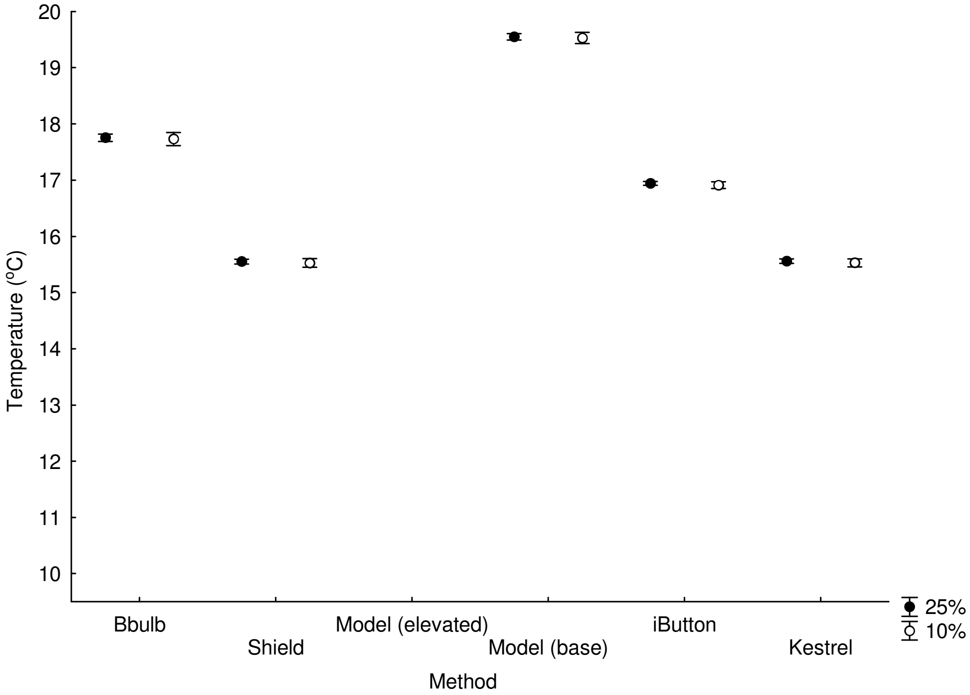
a)



Temperature (°C)
20
18
16
14
12
10
Bbulb
Shield
Model (elevated)
Model (base)
iButton
Kestrel
Method
25%
10%

b)



Temperature (°C)
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19
18
17
16
15
14
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12
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Bbulb
Shield
Model (elevated)
Model (base)
iButton
Kestrel
Method
25%
10%

c)

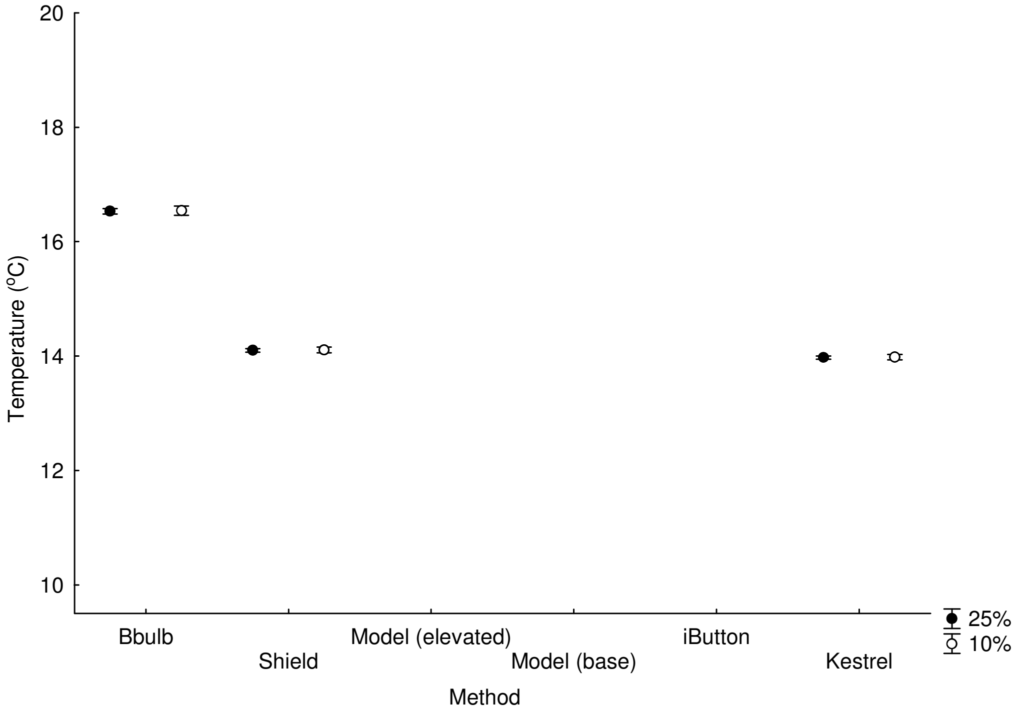
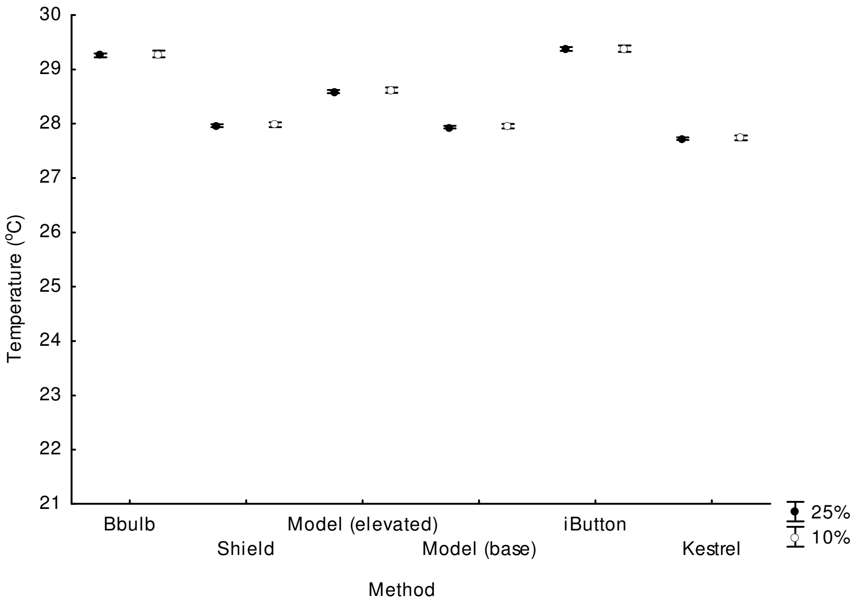


Fig. 3. Mean winter temperatures (± 95% CI) in Molopo (a), Haina (b) and Weenen (c) after randomization. No data were recorded for model (elevated) in Haina. Weenen model (elevated), model (base) and iButton data were excluded due to incomplete datasets (see text for abbreviations and explanations). Note small confidence intervals.

a)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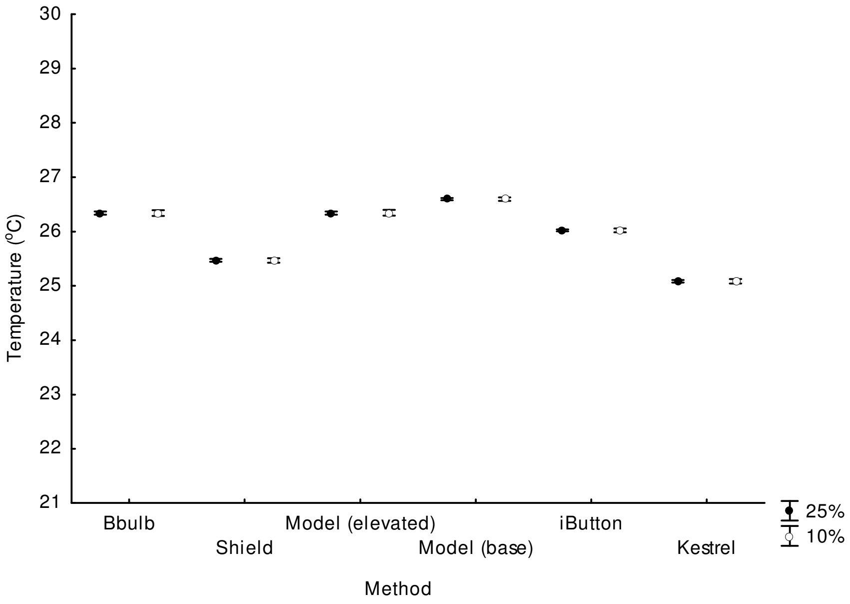
26
25
24
23
22
21
Temperature (°C)
Bbulb
Shield
Model (elevated)
Model (base)
iButton
Kestrel
Method
25%
10%

b)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Temperature (°C)
Bbulb
Shield
Model (elevated)
Model (base)
iButton
Kestrel
Method
25%
10%

c)

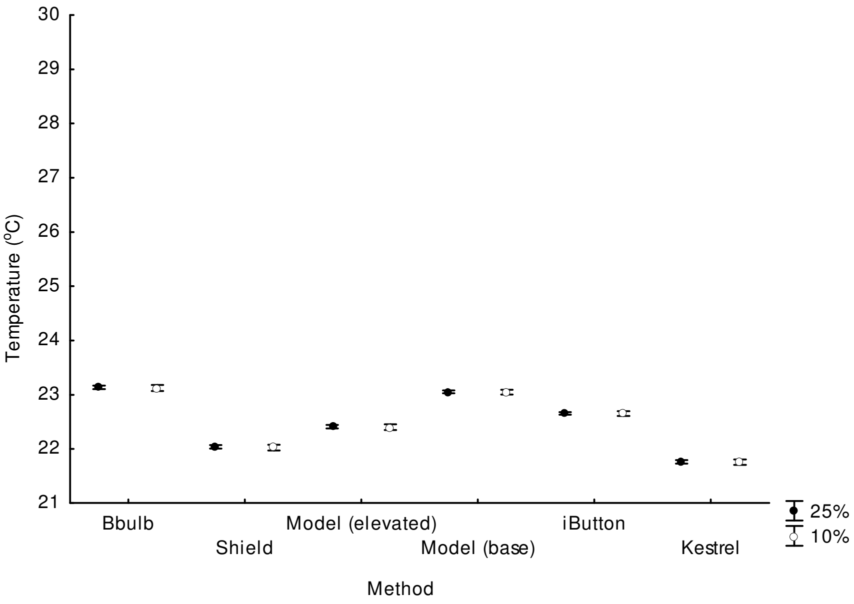

Fig. 4. Mean summer temperatures (± 95% CI) in Molopo (a), Haina (b) and Weenen (c) after randomization (see text for abbreviations and explanations). Note small confidence intervals.

Chapter 5

Daily rhythms of body temperature and activity in free-living Black-tailed Tree Rats (*Thallomys nigricauda)* along an aridity gradient

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Formatted for Physiology and Behaviour – note that the references have been included in text at this stage.

Abstract

It has been shown that some species of mammals have flexible body temperature (T_b) as an energy saving mechanism. Since Black tailed Tree Rats, *Thallomys nigricauda,* face variable thermal environments in their extensive range in southern Africa, one would expect flexibility in their physiological and behavioural responses to the wide range of T_a's to play a role in the success and range of the species. Body temperature (T_b) and activity patterns of free-ranging Tree Rats were investigated during winter and summer at three study sites along an aridity gradient. We measured abdominal T_b using implanted iButtons®. All but three Tree Rats displayed significant 24 h T_b rhythmicity. The T_b range for Tree Rats was 32.33-40.63 °C (n = 13) and 32.69-40.15 °C (n = 17) in winter and summer respectively. Although there was variation in T_b profiles, Tree Rats generally displayed a bimodal distribution of T_b, with high and low T_b values during scotophase and photopase respectively. Body temperature range ($T_b$range) was significantly greater in winter, when Tree Rats reduced their minimum body temperature ($T_b$min). It was shown that the maximum amplitudes of circadian rhythms of body temperature (R_t) was on average 259.7% of expected values. To determine the extent to which the microclimate of Tree Rat cavities assists in the maintenance of T_b, we measured the temperatures of cavities, providing an indication of the degree of buffering provided by refugia. Compared with operative temperature, cavities had stable microclimates, displaying smaller ranges in temperature, and this buffering capacity of the cavities was similar between seasons. To determine whether Tree Rats alter their length of exposure in response to lower ambient temperatures in winter as a means of maintaining T_b, we measured the activity of Tree Rats defined as the proportion of fixes outside the home cavity of the individual. Male Tree Rats spent a greater proportion of the active phase away from their home cavity in summer and significantly in winter when compared to females, but no there were no differences between seasons. It is suggested that Tree Rats realize energy savings by lowering their T_b during the day allowing them to maintain nocturnal activity and overall energy balance.

Keywords: Body temperature; iButton®; Cavity temperature; Operative temperature; Ambient temperature; Telemetry; Activity

1. Introduction

Terrestrial habitats represent the most complex and variable thermal environments on earth (Walsberg *et al.* 1997). Extreme environments place severe demands on the thermoregulation of the smallest birds and mammals (Schmidt-

Nielsen 1964; Porter & Gates 1969) and the influence of temperature on energy exchange and behaviour is large, with thermoregulation representing the largest component of an animal's energy budget (Bennett 1987). One of the climate change predictions in southern Africa is an increase in temperature (Hulme 2005; Lovett *et al.* 2005), resulting in possible shifts in the range of species from west to east (Erasmus *et al.* 2002) coinciding with the aridity gradient in an east-west direction (Rutherford & Westfall 1994; Schulze *et al.* 1997). Phenotypic flexibility, as a category of phenotypic plasticity (Piersma & Drent 2003), would allow individuals to maintain fitness in changing environments (Sultan 1995). Information on the degree to which behavioural and physiological flexibility affect species range in southern Africa is scant which is surprising given its importance with regard to climate change.

Body temperatures (T_b) of most mammals are not fixed, but vary within a range of values around a fairly constant core (McNab & Morrison 1963; Refinetti 1995; Rodriguez-Girones 2002) controlled by an internal circadian clock (Refinetti & Menaker 1992; Weinert & Waterhouse 1998). The variation is influenced by several factors (Gebczynski & Taylor 2004) other than $\mathrm{T_a}$, most variations in an animal's T_b reflecting the state of activity (McNab & Morrison 1963). The rhythms of activity and T_b normally proceed synchronously (Refinetti & Menaker 1992).

Tolerance of a wide range of T_a's allows animals to survive in energetically and thermally stressful environments. When challenged energetically under conditions of low T_a or decreased food supply, some mammals may allow T_b to fluctuate with ambient conditions (Lehmer *et al.* 2006), by lowering T_b, for example (Perreira *et al.* 2002; Geiser 2004). Numerous small mammals decrease their T_b during the rest phase (Jones *et al.* 1997; Cooper & Withers 2004) thereby reducing the cost of euthermy (Barclay *et al*. 2001). This decrease results in a lowered minimum T_b and increases the amplitude or body temperature range ($T_b$range).

In addition to endogenous thermoregulatory responses, some mammals make use of behavioural responses to T_a's, suggesting that behavioural thermoregulation also plays a role in the fluctuation of T_b of an animal in its environment (Refinetti 1995; 1996; 1997; Refinetti & Menaker 1992). Behaviour is primary and sometimes the crucial means by which an animal copes with an environmental challenge (Bennett 1987), when environmental conditions exceed the capacities of physiological systems to achieve homeostasis (Goldstein & Pinshow 2006), particularly for small mammals living in areas with wide ranges in temperature (Long *et al*. 2005).

Nocturnalism allows small mammals to avoid the problems of high temperature stress (MacMillan 1983; Fielden *et al*. 1990), and this may be a reason for nocturnal rodents being largely ignored. For many nocturnal rodents which occupy xeric environments, the principal thermoregulatory problem is coping with very low nighttime temperatures during the winter (Bartholomew & Dawson 1974), a neglected aspect of the physiology of xeric organisms (Hadley 1979; Goodfriend *et al.* 1991). Activity periods are important components of behaviour, since they determine the length of exposure to surface conditions (MacMillen 1972) and variability in the thermal environment could influence activity, which could have fitness consequences for animals (Sharpe & Van Horne 1999).

The 24 h activity rhythms displayed by animals in the field are a result of the interaction between endogenous physiological and environmental factors (Aschoff 1966; Ashby 1972; Rezende *et al*. 2003) with most animals having two alternative behavioural states: rest and activity. The demands that influence how an animal allocates its time budget to different activities are often conflicting (Rosenzweig

1974; Schwaibold & Pillay 2006) and in thermally stressful environments and can create trade-offs between daily energy needs from foraging and costs of thermoregulation (Melcher *et al.* 1990). In addition, foraging organisms must avoid predators, and change location to seek suitable environmental conditions. In order to do this, animals may compensate or adjust their behaviour and/or physiology, for example by changing the duration or frequency of exposures to stressful conditions (Bozinovic *et al*. 2000). Results of studies suggest that desert rodents retain much flexibility in foraging behaviour and that foraging decisions involve coincident monitoring of resource availability and predator risk (Bowers 1988).

Seasonal patterns of activity of rodents are influenced by changes in photoperiod and temperature (Lockard & Owings 1974; Lockard 1978; Hanski *et al.* 2000; Waulters *et al*. 2000). The capacity for thermogenesis and energy intake are important for the survival of small winter active nocturnal mammals (Song & Wang 2006) since the seasonal decline in T_a increases the cost of both thermoregulation and foraging (Kronfeld-Schor *et al.* 2001; Song & Wang 2006). The problem is especially acute for non-hibernating small mammals because they lose heat rapidly and need to consume large amounts of food relative to their body mass (Bozinovic *et al*. 1997; Schwaibold & Pillay 2006). In such cases, in addition to physiological mechanisms discussed, additional behavioural mechanisms to maintain body weight and temperature and to conserve energy can be expected to occur (Contreras 1984; Vickery & Millar 1984). Animals may make use of buffered refugia which provide a thermal environment resulting in energetic benefits to the inhabitants (Stains 1961; Robb *et al*. 1996) in addition to reducing the cost of foraging (Ashby 1972; Bozinovic *et al.* 2000). Moreover, animals may huddle in refugia thereby reducing heat loss (Madison *et al.* 1984; Kaufman *et al*. 2003).

Thallomys nigricauda, the Black-tailed Tree Rat (hereafter referred to as Tree Rat), is a small (32-116g) arboreal, nocturnal, murid rodent, occurring in mesic to xeric regions of South Africa, Botswana, Swaziland, Zimbabwe and Namibia (Skinner & Chimimba 2005). They are folivores, feeding on young *Acacia erioloba* leaves and fine twigs and the outer green coating of seed pods, but may supplement their diets with insects and gum (de Graaff 1981; Skinner & Chimimba 2005). This is in contrast with the majority of xeric rodents, which are predominantly granivorous or opportunistically insectivorous. While the vast majority of rodent species evade the harsh conditions by burrowing, Tree rats have adopted an arboreal lifestyle with nests situated in forks and hollows of trees (mainly *Acacia erioloba*) (Skinner & Chimimba 2005). Being arboreal, Tree Rats are exposed to greater daily temperature fluctuations and lower humidities in their nests compared to most other southern African xeric rodents which use subterranean microhabitats to escape daytime heat. There are possible thermal costs resulting from an arboreal lifestyle which are reduced in the thermal refuge of a burrow. It is expected that Tree rats are exposed to greater daily temperature fluctuations in their arboreal nests compared to most other southern African xeric rodents which use subterranean microhabitats with stable milieux to escape daytime heat (de Graaff 1981; Lovegrove & Knight-Eloff 1988; Downs & Perrin 1989; Skinner & Chimimba 2005).

Since Tree rats occur along an east-west aridity gradient in southern Africa, one would expect phenotypic flexibility in physiological and behavioural traits in response to the diverse environmental conditions to be related to the success and range of the species. Their size, wide distribution, arboreal lifestyle and nocturnal habits suggest that Tree Rats are exposed to greater extremes of temperature than fossorial rodents, making them an ideal species to test this assumption. Hence we expected that Tree Rats would exhibit variation in physiological and behavioural traits in response to the thermal environment measured along an aridity gradient. This has important implications in predicting the survival of small mammal species in the light of climate change in southern Africa.

As part of a broader study of aspects of the physiology and behaviour of the Tree Rat, the aims of the current study were to (i) measure and describe T_b daily rhythms, (ii) determine whether these rhythms differed along an aridity gradient and between seasons (iii) determine and compare cavity temperatures with operative temperature (T_e), and (iv) to determine and compare activity patterns between sexes and seasons. We predicted that Tree Rats would display a T_b daily rhythm typical of an endotherm T_b daily pattern and that T_b would be maintained, irrespective of season or aridity site. In addition, we expected that cavity temperatures would buffer T_a and that maintenance of T_b would influence activity patterns.

2. Materials and methods

2.1. Study sites

The study was conducted at three sites along an east-west aridity gradient (Rutherford & Westfall 1994; Schulze *et al.* 1997): mesic locality Weenen Game Reserve (KwaZulu-Natal Province, South Africa, 28°50'43"S; 29°59'12"E); semi-xeric site Haina Game Farm (Botswana 20˚56'56"S; 23˚40'40"E) and xeric site Molopo Nature Reserve (southern Kalahari savannah, North-West Province, South Africa 25˚50'52"S; 22˚55'37"E) (Chapter 2). Degree locations were plotted using a Magellan GPS 4000 XL. Vegetation, rainfall and temperature data for the three sites are detailed elsewhere (Chapter 2). Aridity index data for the three sites are presented elsewhere (Chapter 3).

2.2. Daily rhythms of body temperature (T_b)

Tree Rats were trapped at each study site during winter (May – July) in 2006 and 2007 and in summer (January – February 2007) using Elliot live-traps. Cavities and resting places of Tree Rats were recognised by examining the stems and bases of trees with potential cavities for faeces and the smell of excreta. Traps were also placed at sites where study animals had been previously seen and/or trapped. Traps were placed on the branches and at the base of potential trees and baited with oats and peanut butter. Traps were set in the late afternoon, checked shortly after sunrise and removed from trap sites. Tree Rats were transported to a veterinarian within 36 h of capture. Rats were sexed, weighed, ear clipped and reproductive status was noted. Tree Rats (>40g) were anaethesized using isoflorthane (2%) or Anakel – V (100mg/ml) and Chanazine (20 mg/ml).

Body temperatures were measured with surgically implanted precalibrated temperature dataloggers (DS 1922L Thermochron iButtons® (Dallas Semiconductor, California)). These miniature dataloggers were encapsulated in stainless steel caps with a thermometer (measured to 0.5 °C), a clock and calendar, and weighed on average 3 g. iButtons® were calibrated with mercury thermometers (0.05 °C) in a water bath at temperatures from 5-45 °C. Buttons® were surgically implanted at the veterinarian in the peritoneal cavity of each individual animal and were programmed to record body temperature every 15 mins. After the veterinarian procedure, animals were given 4-12 h to recover before being released at their point of capture. At the end of the study, animals were recaught, sacrificed and the iButtons® removed.

Aschoff (1982) showed that there is an allometric relationship between body size and the maximum amplitude of the circadian increase in T_b between an animal's daily rest and activity phase:

$$R_\mathrm{t} = 4.762M_\mathrm{b}^{-0.197} \qquad \text{(Equation 1)}$$

where M_b is body mass in grams. R_t was computed using equation 1.

2.3 Cavity Temperatures (T_{cavity}) and environmental parameters

Temperatures of cavities (hereafter referred to as T_cavity) were measured using Thermochron iButtons® programmed to record temperatures every 15 mins. One iButton® was implanted just inside the cavity (hereafter referred to as T_cavity (shallow) and a second was implanted at a depth of approximately 30 cm inside the same cavity (hereafter referred to as T_cavity (deep). In Weenen in summer, Tree Rats were found to be nesting within a wall of an outbuilding structure. The wall was composed of a double layer of bamboo stems positioned and secured vertically. At this site, we positioned iButtons® between the two layers of wall in an identical manner to those in tree cavities. iButtons® were positioned in two cavities at each study site during winter 2006 and summer 2007. An additional two cavities were monitored at Weenen in summer 2007. Where two cavities were monitored at a study site, T_cavity were measured simultaneously. Within a season, data were not collected from cavities at different study sites at the same time, although there were periods when simultaneous data were recorded. iButtons® in cavities were not removed when moving to a different study site, providing continuous data.

Ambient temperature is not the actual thermal condition experienced by the animal in its natural environment (Chappell & Bartholomew 1981a; Bakken 1992). A useful index of the thermal potential driving heat flow between animals and their thermal environments, which takes into account radiation, air temperature, wind and humidity (Porter & Gates 1969) is operative temperature (T_e) (Byman 1985). This thermal index thus gives an indication of the thermal conditions experienced by an animal in its natural surroundings (Chappell & Bartholomew 1981a). Sphere thermometers may provide a reasonably accurate thermal index of an animal's environment (Walsberg & Weathers 1986), with copper casts being the most accurate T_e models available (Dzialowski 2005).

Operative and T_a were recorded in the vicinity of cavity sites. Operative temperature was measured using back bulb solar radiation temperatures recorded using an iButton® placed in a black copper ball (1mm thickness,10cm diameter) that was exposed to direct sunlight throughout the day at a height of 1 m. Unlike cavity iButtons®, within a season, the black bulb was moved from Molopo to Haina and replaced on the return visit, resulting in discontinuous T_e data for Molopo. Ambient temperature was measured using a calibrated DS 1921 Thermocron iButton® placed in a Stevenson's screen (temperature shield) and suspended in a tree at a height of 1.25 – 2 m. Temperature shields were not removed when moving between study sites, providing continuous T_a data. Minimum and maximum T_{cavity}'s (shallow) were compared to T_{cavity}'s (deep) and compared between seasons. Minimum and maximum T_{cavity}'s (shallow) and T_{cavity}'s (deep) were compared to T_e. Sunrise and sunset times for the winter and summer study periods at the three study sites were recorded.

2.4. Activity

Tree Rats were fitted with radio-transmitters (C. Dearden, Pietermaritzburg) after the surgical implanting of iButtons®. Transmitters were two-stage radio-transmitters encased in epoxy resin and attached to a cable-tie collar with a 15 cm vertical whip aerial. Radio-transmitters were powered by a single silver oxide 1.5V watch battery and weighed 3.0g, which was less than 5% of the average animal's body mass (2-4% of body mass). The transmitters had 60 days of battery life and an average range of 1 km. We analysed activity data for Tree Rats with T_b data. Based on this, 31 Tree Rats, 10 in winter 2006, 18 in summer 2007 and three in winter 2007 were included for the analyses. Three Tree Rats had faulty transmitters and hence no activity data were available, resulting in activity data for a total of 28 Tree Rats.

Tracking was conducted on foot with a hand-held, three-element aerial and an Alinco DJ-X10 receiver (Osaka, Japan). Fixes (the location of an animal at one point in time) were recorded by their grid co-ordinates using a handheld GPS (Magellan GPS 4000 XL). Locations of Tree Rats were obtained from direct sightings/homing in (White & Garrott 1990) and activity, where possible, was recorded with each fix. Use of homing techniques had no effect on diurnal locations. In addition, there was no evidence that nocturnal locations were affected by homing techniques since our close proximity to Tree Rats rarely appeared to affect their behaviour or movement patterns. We divided the nights from 17:00-07:00 into 14 hourly intervals in winter and from 19:00-06:00 into 11 hourly intervals in summer. Days were divided from 07:00-17:00 into 10 hourly intervals in winter and from 06:00-m19:00 into 13 hourly intervals in summer.

Tree Rats were always in a "home cavity" during the day and thus assumed to be inactive. It was not possible to determine the exact nocturnal activity of Tree Rats at each fix due to their size and elusive behaviour. Moreover, it is crucial that disturbance was minimised, so as not to interfere with their routine activities. When Tree Rats were inside their cavities, permanent or temporary, during the night, it was not possible to ascertain whether they were active or not. Whereas authors have used a fluctuating signal to determine activity, we found this to be an unreliable measure of activity. To determine nocturnal activity patterns, we used all fixes made at night (the hour which included sunset to the hour that included sunrise). Activity for an animal was defined as the proportion of fixes outside the cavity, expressed as a percentage.

2.5. Data analysis

iButton® data were downloaded using the DS1921 Thermochron iButton Software Download programme (Dallas). The periodicity and significance in the T_b cycles was analysed for individual Tree Rats using the X^2 Periodogram (Refinetti 1993; http://www.ciircadian.org/periodogram.html). This calculates ratios of variances (Q_p) for each possible circadian period and the period with the highest Q_p value is considered the true circadian pattern (Refinetti 1993). Statistical analyses were performed using the Statistica 7 package (Statsoft Inc., USA). All values are presented as mean ± SE, N is the number of animals and n is the number of measurements (or days, as indicated).

3. Results

3.1. Ambient conditions (T_a)

During the study, the mean T_a was 14.10 ± 0.26 ºC (range 4.60 – 27.66 ºC) and 22.03 ± 0.29 ºC (range 11.13 – 36.65 ºC) in winter and summer respectively at Weenen. At Molopo, the mean T_a was 11.50 ± 0.22 ºC (range -4.94 – 28.12 ºC) and 28.34 ± 0.19 ºC (range 12.14 – 42.12 ºC) in winter and summer respectively. The T_a was 15.55 ± 0.43 ºC (range 3.13 – 30.68 ºC) and 25.47 ± 0.26 ºC (range 16.61 – 38.10 ºC) in winter and summer respectively at Haina.

3.2. Daily rhythms of body temperature (T_b)

No T_b data were recorded for Weenen in winter 2006 due to malfunctioning iButtons®. We experienced Tree Rat deaths, mainly due to predation and veterinary procedure. In addition, a number of iButtons® could not be retrieved due to faulty transmitters. Consequently, we obtained continuous T_b measurements for a total of 13 and 17 Tree Rats in winter and summer respectively (Table 1). The T_b range for Tree Rats was 32.33-40.63 °C (n = 13) and 32.69-40.15 °C (n = 17) in winter and summer respectively. All, with the exception of three Tree Rats, had a significant 24 h T_b rhythmicity ($P < 0.05$; 15 min resolution) using the X^2 Periodogram analysis (Q_p range 156-1316, df = 94-98). Non-significant 24 h T_b rhythmicity was the result of insufficient data points.

Thermal profiles of the T_b of Tree Rats revealed several trends in winter (Fig. 1 a-c) and summer (Fig. 2 a-c). Although thermal profiles varied between individuals, there was little variation in T_b within individuals as indicated by low SE (Table 2, Figs 1 and 2). Tree rats had a distinct nychthermeral T_b pattern, being lower during the day and higher at night (Figs 1 and 2). In winter and summer, generally, T_b peaked at different times during scotophase, generally a few hours after the onset of dark. Some individuals reached a second T_b peak a few hours before first light. Mean core T_b declined from the onset of light and reached minimum T_b ($T_\mathrm{b}$min) around midday, after which it steadily increased. The T_b rhythms of individual Tree Rats were not highly synchronized, with increases and decreases in T_b between rest and activity often several hours apart (Figs 1 and 2). Using frequency distributions of the time at which maximum T_b ($T_\mathrm{b}$max) and $T_\mathrm{b}$min occurred each day, although Tree Rats varied in the time of day when $T_\mathrm{b}$max and $T_\mathrm{b}$min were reached, there was a clear bimodal distribution of T_b data, with $T_b$max values during the night and $T_b$min values during the day (but see below). (Fig. 3a, b).

T_b varied seasonally. There was a significant effect of season on $T_b$min and $T_b$max (RMANOVA, $F_{2,27} = 5.42$, $P < 0.05$) and on $T_b$range (ANOVA, $F_{1,28} = 9.89$, $P < 0.05$). The mean range in winter was 6.41 ± 0.51 °C and 4.72 ± 0.26 °C in summer. In winter, lower mean $T_b$min's were recorded than in summer, although this was not significant. The variation in the $T_b$range between sites in winter (Table 2), was not significant. In summer (Table 2), this variation was significant (ANOVA, $F_{2,14} = 8.83$, $P < 0.05$), with the $T_b$range in Molopo greater than in Weenen and Haina (Post-hoc, Tukey, $P > 0.05$).

Despite the low winter night-time ambient temperatures, there was no evidence of torpor in Tree Rats. However, a single individual, Tree rat 28, dropped T_b from 36.14 °C to 27.65 °C in 30 minutes at 00:52 on a single morning in winter in Molopo (Fig. 4). Besides this single bout, $T_b$min for Rat 28 occurred during the day (rest phase).

The mean Rt was 5.42 ± 0.30 (range 2.99 - 11.48) which is 259.66% (136.96 to 557.35%) of the predicted maximum circadian amplitude in body temperature. Rt was significantly higher in winter than summer (independent *t*-test: $t = 2.95$, df = 29, $P < 0.05$).

3.3. Cavity Temperatures (T_{cavity}) and environmental parameters

No T_{cavity}'s were recorded for Weenen in winter 2006 due to malfunctioning iButtons®. A deep iButton® was removed from a single cavity in Haina in winter 2006 and summer 2007 presumably by Tree Rats, and hence temperatures from these cavities could not be used. Temperatures of three cavities were thus recorded in winter and for seven cavities in summer. Cavities used by Tree Rats varied greatly in position and structure including cavities in live trees or in dead tree stumps lying horizontally on the ground. Only one male Tree rat in Molopo used a typical bird “nest”.

Since temperature profiles of cavities, T_e and T_a at the ten locations revealed similar patterns, a single cavity, T_e and T_a for winter in Molopo and Haina (Fig. 5 a-b; Table 3) and in Molopo, Haina and Weenen in summer (Fig. 6 a-c; Table 3) were chosen to represent this data. During the day, T_{cavity}’s did not fluctuate as greatly when compared to T_e and T_a, reaching lower maximum temperatures. When compared to T_e and T_a, the response of T_{cavity}’s to changes in outside temperature was slower as they heated up and cooled down at a slower rate. Maximum T_{cavity}’s were reached later in the day than maximum T_e and T_a. Since T_{cavity}’s lagged behind T_e and T_a, the highest T_{cavity}’s were reached either late in the day or at night, when black-bulb temperatures and T_a had already begun to drop. The magnitude of the temperature lag varied between cavities. During the night, minimum T_{cavity}’s were higher than T_e and T_a, which dropped to the lowest minimum temperatures, with the exception of Molopo and Weenen in summer. When considering day and night, deep cavity temperatures generally displayed a slight delay response (lag) when compared to shallow temperatures. The magnitude of this temperature lag between shallow and deep regions varied between cavities. There was no significant difference between minimum T_{cavity} (shallow) when compared with T_{cavity} (deep) (RMANOVA, $F_{1,8}$ = 0.03, $P > 0.05$, Fig. 7) or between maximum temperatures (RMANOVA, $F_{1,8}$ = 0.46, $P > 0.05$, Fig. 7). On average, the minimum and maximum daily T_{cavity}’s (deep) were 0.38 ºC warmer and 0.47 ºC cooler than the minimum and maximum daily T_{cavity}’s (shallow), respectively. There was a significant difference between minimum T_{cavity}

(shallow) and T_{cavity} (deep) in winter and summer (RMANOVA, $F_{1,8} = 21.76$, $P < 0.05$, Fig. 8) and between maximum temperatures in the cavity in winter and summer (RMANOVA, $F_{1,8} = 24.56$, $P < 0.05$, Fig. 7). There were significant differences between minimum T_{cavity} (shallow) when compared to T_e (RMANOVA, $F_{1,8} = 13.82$, $P < 0.05$, Fig. 7) and maximum temperatures (RMANOVA, $F_{1,8} = 41.33$, $P < 0.05$, Fig. 8). There were significant differences between minimum T_{cavity} (deep) when compared to T_e (RMANOVA, $F_{1,8} = 19.91$, $P < 0.05$, Fig. 7) and maximum temperatures (RMANOVA, $F_{1,8} = 37.42$, $P < 0.05$, Fig. 8). Mean daily ranges of T_{cavity} (shallow) and T_{cavity} (deep) in winter were 22.72 ºC and 23.05 ºC, respectively, by comparison with operative temperature range ($T_e$range) of 39.55 ºC. In summer, mean daily ranges of T_{cavity} (shallow) and T_{cavity} (deep) were 22.35 ºC and 20.99 ºC, respectively, by comparison with $T_e$range of 27.60 ºC (Table 4).

We calculated the $T_e$range and range of T_{cavity} (T_{cavity}range) for each cavity over each study period and computed the ratio of the two values (T_{cavity}range divided by $T_e$range) and expressed as a percentage. The ratios reflect the degree to which the cavities were buffered against T_e changes and allow comparison of the buffering effects of cavities when data are recorded on different days at different T_e (Moore & Roper, 2003). Cavities in winter provided significantly greater buffering than in summer (ANOVA, $F_{1,8} = 6.27$, $P < 0.05$, Table 4). However, in summer, Weenen Tree Rats were found to be living in an outbuilding which was covered by a corrugated iron roof, which would have increased the T_{cavity}range resulting in T_{cavity}range's greater than $T_e$range and hence very high ratios (Table 4). When Weenen data were excluded from analyses, winter cavities still provided greater buffering than summer, but there was less difference between the winter and summer ratios (ANOVA, $F_{1,10} = 0.22$, $P > 0.05$).

3.4. Activity

Tree Rats displayed several trends in their activity patterns. In summer, female Tree rats emerged from cavities later than male Tree rats. Although there was variation in the times in which female Tree rats were out of their home cavities, more time was spent out of cavities during the first half of the scotophase than in the second half of the scotophase during both winter and summer. This was in contrast to male Tree Rats where no such difference was evident (Fig. 8). In both seasons, females spent less time outside their home cavities in the early morning, although some left their home cavities once again just prior to sunrise. In contrast, male Tree Rat activity was more evenly distributed over the night in both seasons (Fig. 8). Male Tree Rats spent a greater mean proportion of time out of their cavities when compared to females in both seasons. However, due to high variation, this was only significant males only differed significantly from females in the cavities between 4 – 5 am in winter (Kruskal-Wallis, $H_{(1,11)} = 6.29$, $p < 0.05$) and between 3 – 4 am in summer (Kruskal-Wallis, $H_{(1,12)} = 4.88$, $p < 0.05$).

4. Discussion

Our study, which provides the first continuous T_b measurements for a free-living Tree Rat, shows that *T. nigricauda* has a nychthemeral T_b cycle typical of that for other endothermic animals (Refinetti & Menaker 1992) with two distinct temperature levels, the lower corresponding to resting and the higher to activity. Circadian patterns of T_b confirmed their nocturnalism (Skinner & Chimimba 2005). Lack of individual variation within hourly T_b measurements is supported by highly significant circadian rhythm patterns which supports the concept of internal circadian clock control of T_b (Refinetti & Menaker 1992; Weinert & Waterhouse 1998). Individual Tree Rats usually displayed a fairly constant T_b throughout the study, although every individual in winter had T_b's < 35 ºC and > 38 ºC and in summer < 37 ºC and > 38 ºC. The lability of T_b differed between different individuals, and reasons for this variation in thermal profiles are not known, but could be a consequence of variation in activity (McNab & Morrison 1963) as a result of foraging success, reproductive drive and predator-prey interactions (Warnecke *et al.* 2007), for example.

Generally, minimum T_b's were recorded during periods of rest, while max. T_b corresponded to periods of activity (except rat 28). Low T_b's are usually associated with rest phase and high T_b's with the active phase (Aschoff 1982) and although T_b rhythms are not generated by activity cycles, they are affected by them and usually correlated (Aschoff 1983). Thus the nychthemeral T_b rhythm of Tree Rats could be influenced by both the circadian rhythm and increased heat production due to activity. As above, variation in the time and number of peak T_b's could be a consequence of variation in activity (McNab & Morrison 1963). The peak T_b in the evening is consistent with the findings of Lovegrove & Heldmeier (1994) and lack of further peaks in his study (except for one rat) could be attributed to the fact that movement of captive Tree Rats in cages was restrained and at the same level of intensity throughout the active phase. Thus differences would presumably reflect some aspect of captivity, since captivity has an effect on movement and behaviour and thus possibly thermoregulatory patterns of Tree Rats.

Tree Rat's T_b showed a mean daily variation of 6.41 ºC during winter, significantly different to the summer range of 4.71 ºC. This large winter range, a result of allowing T_b to fluctuate with low T_a's, results from typical mean maximum

T_b values (38.5-40.63 ºC), but low mean minimum T_b values (27.65-34.66 ºC). This shallow hypothermia in winter when Tree Rats allowed lowered their minimum T_b‘s is presumably an energy saving device in response to lower T_a during the day (but see below) when compared to summer, allowing Tree Rats to spend less energy on thermoregulation. Similar variation in T_b, caused by reduced minimum T_b rather than increased maximum T_b has been found in numbats (*Myrmecobius fasciatus*), when not entering torpor (Cooper & Withers 2004) and in antelope ground squirrels (*Ammospermophilus leucurus*) (Chappell & Bartholomew 1981b).

It is difficult to define the drop in T_b of Tree Rat 28 on the single occasion in winter. A drop in T_b during periods of activity particularly in winter would incur a similar energetic advantage to the drop during periods of inactivity and has been shown in elephant shrews (Mzilikazi & Lovegrove 2005), providing an energetic benefit by reducing the T_b -T_a gradient during the coldest part of the night (Lovegrove & Raman 1998).

There are typically large differences between rest and active phase T_b values in animals that are strictly diurnal or nocturnal (Ashoff 1970), which translates into high R_t values, usually associated with energy savings through metabolic rate depression during the rest phase (Lovegrove & Heldmaier 1994). High R_t values are regarded as adaptive in environments with low productivity or variable energy inputs in time and space (Boix-Hinzen & Lovegrove 1998; McKechnie & Lovegrove 1999). Thus we expected the R_t to be greater than the value predicted by Ashoff’s (1982) allometric equation since some mammals may lower their T_b during their rest phase when exposed to low T_as (Perreira *et al.* 2002) as a mechanism of conserving energy, resulting in increased amplitudes of T_b.

The mean R_t in the present study was greater than that of six captive *T. paedulcus* individuals (152.5%), expressed as a percentage. However, this was expected and is in accordance with their observations. The rodents in their study may not have maintained minimum conductances as they were kept at a constant T_a higher than the lower critical limits of thermoneutrality, resulting in underestimated R_t values (Lovegrove & Heldmaier 1994). In addition, movement in the wild would increase T_b through muscular thermogenesis (Decoursey *et al.* 1998) and hence result in lower maximum $T_b$max's recorded in captive animals.

Results of this study highlight the buffering effect of cavities, albeit minor buffering when compared to the buffering of temperatures within burrows beneath the soil (Willmer *et al.* 2005). This is indicated by significantly lower maximum and higher minimum T_{cavity}'s, resulting in smaller temperature fluctuations and lower temperature ranges over a 24 h period within the cavities when compared to T_e. There was variation in the magnitude of the temperature lag between shallow and deep cavity regions and between T_{cavity}, T_e and T_a in different cavities, presumably since the structure of cavities affects the rate heat exchange (McComb & Noble 1981; Robb *et al.* 1996).

Variation in the magnitude of buffering in shallow and deep regions of cavities was similar between seasons, as indicated by similar ratios. Variation in the magnitude of buffering was also similar in both regions of cavities, minimum T_{cavity}'s (deep) slightly warmer and maximum T_{cavity}'s (deep) slightly cooler than T_{cavity} (shallow). Although this trend concurs with the findings of Lovegrove *et al.* (1991), the differences between the regions in the single nest in his study were more extreme, which could be due to the specific nest structure and presence or absence of Tree Rats. In addition, temperatures were measured in a nest, while the present study found only one Tree Rat residing in a nest, the others residing in cavities within living or dead tree trunks. The phase delay response reported for deep-nest temperatures is confirmed by the present study. Generally, cavities were cooler during the day and warmer during the night, when compared to T_e and fluctuation of the cavity temperature remained within the extremes of T_e. However, Tree Rats in cavities in winter were still exposed to low T_{cavity}'s and to sub-zero T_e's at night.

There were limitations in the techniques used in the present study of cavities. Openings of cavities were small and in some cases hidden and hence we were unable to determine the internal structure of the cavity. Due to the structure of cavities, some iButtons® could not be suspended within a cavity, resulting in contact with the cavity wall. This could have affected temperature readings. In addition, although we knew if study animals were inside the cavity, we did not know whether a cavity was occupied by other Tree Rats. Neither did we know whether there was nesting material or not, and if so, the amount and the composition. Thermoregulatory costs are reduced in cavities with nesting material (Havera 1979). Particular cavities were extensive structures in hollow trees and we were unable to determine the exact location of the part of the cavity being occupied. Tree Rats occupied various types of cavities, including cavities in live trees, dead tree stumps lying horizontally on the ground and crevices beneath the bark of old and dead trees. We did attempt to record variation in temperature within cavities by measuring shallow and deep cavity temperatures. Despite these factors, this study shows that cavities provide a different microclimate to external ambient conditions, as represented by T_e and T_a. However, they do not offer as stable a microclimate as burrows below the surface (Downs & Perrin 1989, Willmer *et al.* 2005).

The difference in time spent out of their home cavities between female and male Tree Rats during both seasons may be a consequence of reproductive patterns and behaviour in this species. In this study, male Tree Rats had larger home ranges than females (Chapter 2) which supports the promiscuous mating system as suggested by Eccard *et al.* (2004). This would explain the greater proportion of time spent outside cavities by males during summer as males search for possible mates. The difference in the proportion of time spent outside cavities between males and females in winter could be explained by the reproductive flexibility of Tree Rats. A lactating female with new-born offspring were found in July 2006 in Molopo, although Tree Rats are reported to have a summer breeding season (Skinner & Chimimba 2005). This observation implies that males were reproductively active during winter months and thus we would expect them spend more time away from their cavities when compared to females. Moreover, several male Tree Rats had more than one cavity tree and alternated between these trees on different days (pers. obs.). In addition, some had “temporary shelters”, at various distances from their home cavity which they used to varying degrees during the night (pers. obs.). When Tree Rats occupied these alternative and temporary sites, activity was noted as “active” since they were away from their home cavity. This may have resulted in the proportion of fixes away from their cavity tree to be overestimated. Male and female activity in summer and female activity in winter concur with the findings of a previous study (Eccard *et al.* 2004), and the greater proportion of time spent outside cavities by males in winter, when compared to the previous study can be attributed to the methods employed.

In summary, labile T_bs help maintain activity and energy balance in Tree rats. Our study showed that Tree Rats did maintain T_b at the three aridity sites but allowed T_b to fluctuate with T_a more than expected, by lowering $T_b$min during the rest phase as a mechanism to conserve energy. Nocturnal Tree rats face thermoregulatory challenges in winter and mechanisms to conserve energy would be selected for. In addition, cavities provide a buffered microclimate which may result in further energy savings by reducing the T_b - T_a gradient. These energy savings, a result of physiological and behavioural flexibility in response to the thermal environment are sufficient to negate the need to reduce their activity in winter and thus they are presumably able to meet their foraging needs. It seems probable that flexibility in measured traits in response to the diverse thermal conditions plays a role in the success and range of the species, which has implications for the survival of small mammal species in the light of climate change in southern Africa.

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Legends for Figures:

Fig. 1. Mean hourly winter body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall winter mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.

Fig 2. Mean hourly summer body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall summer mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.

Fig 3. Circular distributions of the time of day (degrees) of the daily minimum body temperature (unfilled circles) and daily maximum body temperature (filled circles) of Tree Rats at the three study sites in a) winter and b) summer.

Fig 4. Body temperature of Tree Rat 28, in winter in Molopo, recorded over the one day period during which the "torpor" bout occurred.

Fig 5. Mean hourly winter operative temperature, ambient temperature and cavity temperature (shallow and deep) in a) Molopo and b) Haina (see text for abbreviations and explanations).

Fig. 6. Mean hourly summer operative temperature, ambient temperature and cavity temperature (shallow and deep) in a) Molopo, b) Haina and c) Weenen (see text for abbreviations and explanations).

Fig. 7. Mean minimum and maximum operative temperature, ambient temperature and cavity temperature (shallow and deep) in summer and winter (see text for abbreviations and explanations).

Fig. 8. Nocturnal activity profiles of male and female Tree Rats in a) winter and b) summer. Bars show the mean ± *SE* of the percentages of fixes where animals were

located out of their home cavity in one hour intervals. The horizontal dashed line indicates a mean of 50% of fixes out of the home cavity. The dark bar indicates scotophase as determined by sunset and sunrise times.

Table 1
Summary of Tree Rat deaths and numbers used for body temperature data at the three study sites in winter and summer.

			Deaths					
Season	Site	Number. implanted	Unknown cause	Veterinary procedure	Predation	No recapture	Faulty transmitter	N
W	M	7		1				6
	H	6		1	1			4
	W	8	2			2	1	3
S	M	8		2	1		1	4
	H	7	1		1	1		4
	W	15	1	2	1	1	1	9

W = winter; S = summer; M = Molopo; H – Haina; W = Weenen.

Table 2
Mean, minimum and maximum body temperature of Tree rats at the three study sites in winter and summer respectively where n = the number of measurements.

	Site	Individual	n	Mean (°C)	Minimum (°C)	Maximum (°C)	Range (°C)
winter	Molopo	23	434	36.65 ± 0.05	32.66	39.15	6.49
		24	1432	36.31 ± 0.03	34.15	40.13	5.98
		26	1516	37.04 ± 0.03	33.15	40.63	7.48
		27	1516	36.48 ± 0.03	32.66	40.63	7.97
		28	1468	36.05 ± 0.04	27.65	39.13	11.48
		29	1432	36.91 ± 0.03	33.64	39.13	5.49
	Haina	45	376	36.39 ± 0.06	33.16	39.14	5.98
		47	374	35.83 ± 0.06	33.13	39.11	5.98
		49	376	35.48 ± 0.05	33.05	38.55	5.50
		50	376	35.31 ± 0.07	32.11	38.59	6.48
	Weenen	161	440	36.46 ± 0.03	34.66	38.65	3.99
		162	440	37.15 ± 0.05	34.18	40.15	5.97
		165	292	36.85 ± 0.04	34.57	39.06	4.49
summer	Molopo	89	1432	37.24 ± 0.02	34.17	40.14	5.97
		90	1391	36.85 ± 0.03	32.69	39.67	6.98
		91	943	37.08 ± 0.03	34.16	39.64	5.48
		95a	1437	36.96 ± 0.03	34.15	40.13	5.98
	Haina	111	464	37.22 ± 0.03	35.13	39.12	3.99
		113	456	36.53 ± 0.04	34.20	38.69	4.49
		115	464	36.37 ± 0.04	34.61	39.09	4.48
		117	464	37.19 ± 0.03	35.14	39.62	4.48
	Weenen	67	328	38.15 ± 0.04	36.63	40.12	3.49
		71	1220	36.55 ± 0.02	34.62	39.61	4.99
		72	2680	37.02 ± 0.02	34.12	39.11	4.99
		73	372	37.93 ± 0.03	36.68	39.67	2.99
		136	433	37.39 ± 0.03	35.66	39.15	3.49
		137	434	35.82 ± 0.07	33.69	38.68	4.99
		139	488	37.05 ± 0.04	35.17	39.66	4.49
		140	432	36.86 ± 0.05	33.57	39.06	5.49
		141	488	37.87 ± 0.03	36.66	40.15	3.49

Table 3

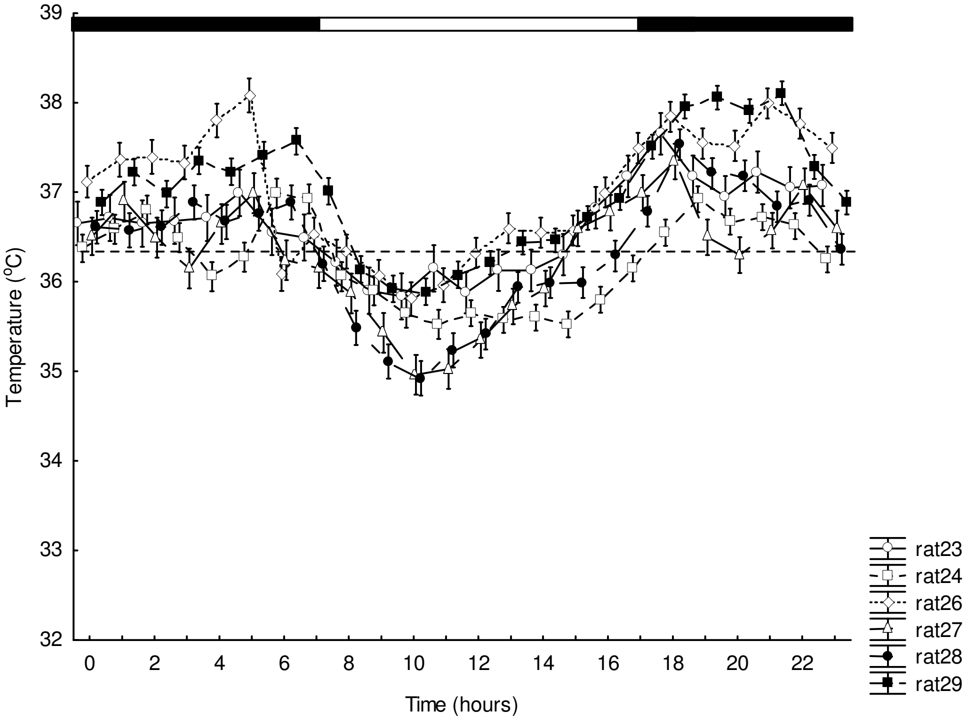
Mean, minimum and maximum cavity temperature, operative temperature and ambient temperature at the two study sites in winter and summer respectively (see text for abbreviations and explanations).

Site	Parameter	n	Mean (°C)	Minimum (°C)	Maximum (°C)	Range (°C)
Winter						
Molopo	Cavity (shallow)	1487	13.11 ± 0.12	1.58	23.67	22.09
	Cavity (deep)	1328	12.72 ± 0.14	0.04	25.10	25.06
	T_e	373	12.78 ± 0.55	-5.39	33.68	39.07
	T_a	1427	11.73 ± 0.22	-4.47	28.66	33.13
Haina	Cavity (shallow)	376	20.12 ± 0.35	9.09	32.61	23.52
	Cavity (deep)	376	20.02 ± 0.35	9.11	32.14	23.03
	T_e	376	17.76 ± 0.66	2.06	42.08	40.02
	$\mathrm{T_a}$	376	15.55 ± 0.41	3.57	28.62	25.05
Summer						
Molopo	cavity (shallow)	1432	27.72 ± 0.14	13.59	39.58	25.99
	cavity (deep)	334	25.94 ± 0.23	19.62	37.11	17.49
	Bbulb	498	29.26 ± 0.33	19.16	49.10	29.94
	T_a	1432	28.06 ± 0.16	13.67	39.17	25.50
Haina	Cavity (shallow)	438	26.16 ± 0.13	20.62	32.11	11.49
	Cavity (deep)	343	26.33 ± 0.15	21.15	34.64	13.49
	Bbulb	441	26.36 ± 0.29	16.61	42.58	25.97
	T_a	438	25.47 ± 0.26	16.61	38.10	21.49
Weenen	Wall (shallow)	488	22.82 ± 0.26	12.69	37.20	24.51
	Wall (deep)	488	22.11 ± 0.27	11.13	36.64	25.51
	Bbulb	488	23.13 ± 0.30	11.63	41.13	29.50
	T_a	488	22.34 ± 0.28	11.63	36.64	25.01

Table 4
Cavity temperature range, operative temperature range and ratio of cavity temperature range to operative temperature range for three and seven cavities in winter (w) 2006 and summer (s) 2007 respectively (see text for abbreviations and explanations).

Cavity	Season	Position	Range (^{o}C)	T_e range (^{o}C)	Ratio	%
1	w	Shallow	22.09	39.07	0.57	56.54
		Deep	25.06	39.07	0.64	64.14
2	w	Shallow	22.55	39.07	0.58	57.72
		Deep	21.07	39.07	0.54	53.93
3	w	Shallow	23.52	40.02	0.59	58.77
		Deep	23.03	40.02	0.58	57.55
4	s	Shallow	24.00	24.98	0.96	96.08
		Deep	23.99	24.98	0.96	96.04
5	s	Shallow	25.48	24.98	1.02	102.00
		Deep	25.98	24.98	1.04	104.00
6	s	Shallow	25.99	29.94	0.87	86.81
		Deep	17.49	29.94	0.58	58.42
7	s	Shallow	20.98	29.94	0.70	70.07
		Deep	16.49	29.94	0.55	55.08
8	s	Shallow	11.49	25.97	0.44	44.24
		Deep	13.49	25.97	0.52	51.94
9	s	Shallow	24.51	29.50	0.83	83.08
		Deep	25.51	29.50	0.86	86.47
10	s	Shallow	24.01	29.50	0.81	81.39
		Deep	24.01	29.50	0.81	81.39

a)



39
38
37
36
35
34
33
32
Temperature (°C)
0
2
4
6
8
10
12
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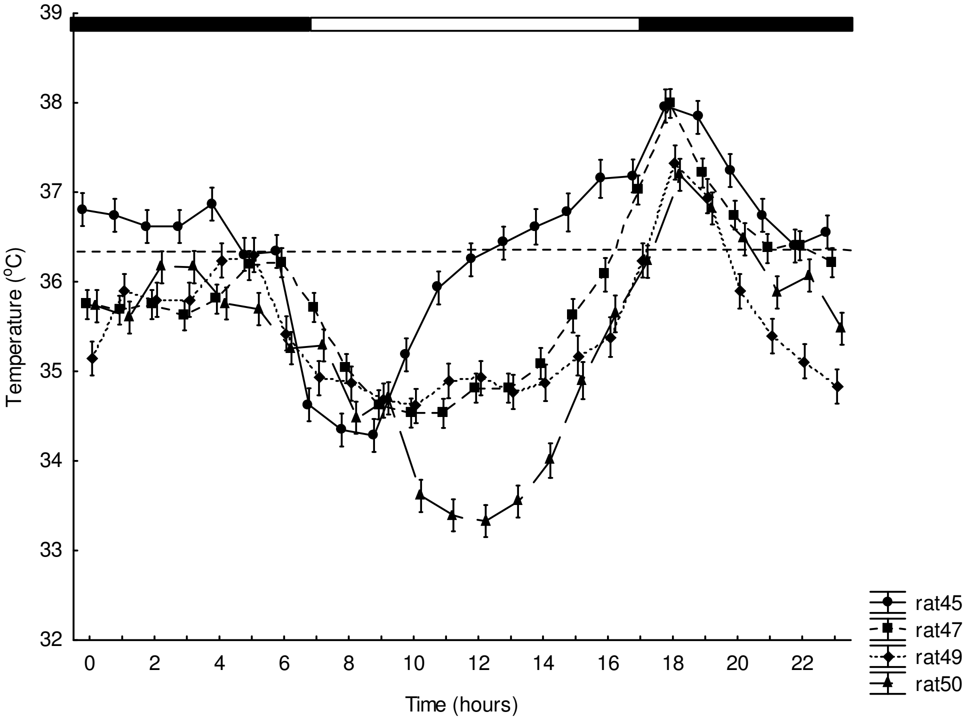
18
20
22
Time (hours)
rat23
rat24
rat26
rat27
rat28
rat29

b)



39
38
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36
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32
Temperature (°C)
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20
22
Time (hours)
rat45
rat47
rat49
rat50

c)

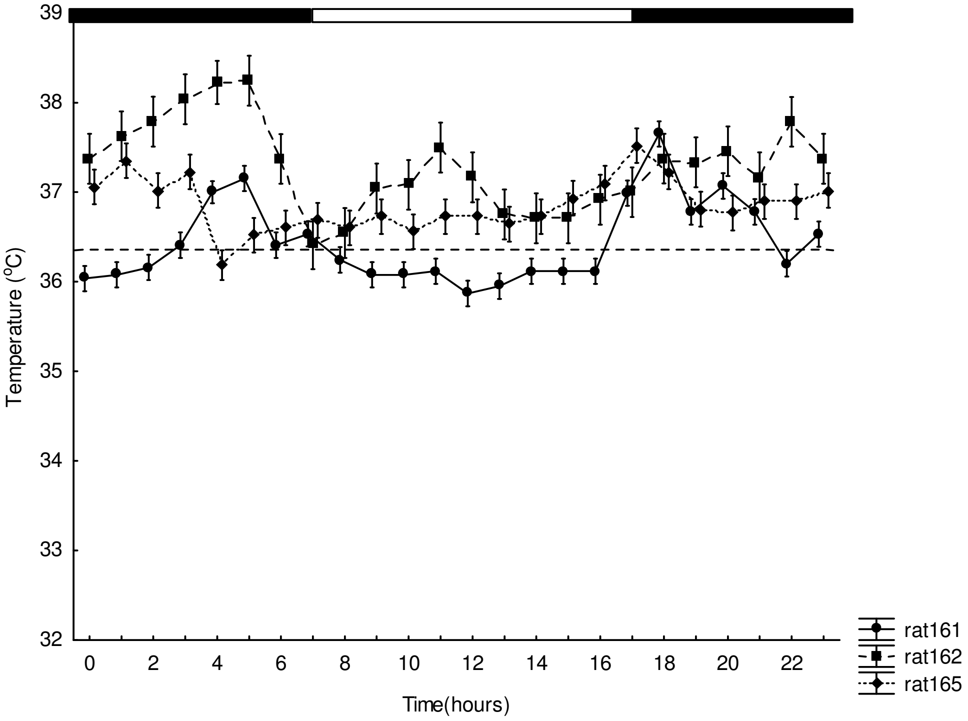
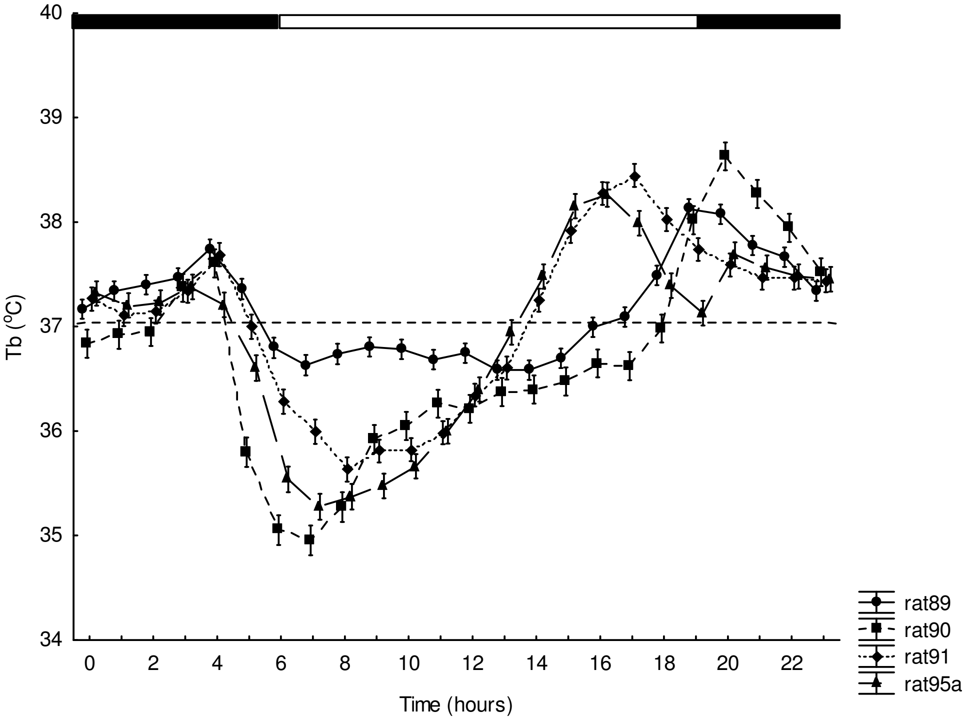


Fig. 1. Mean hourly winter body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall winter mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.

a)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Tb (°C)
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22
Time (hours)
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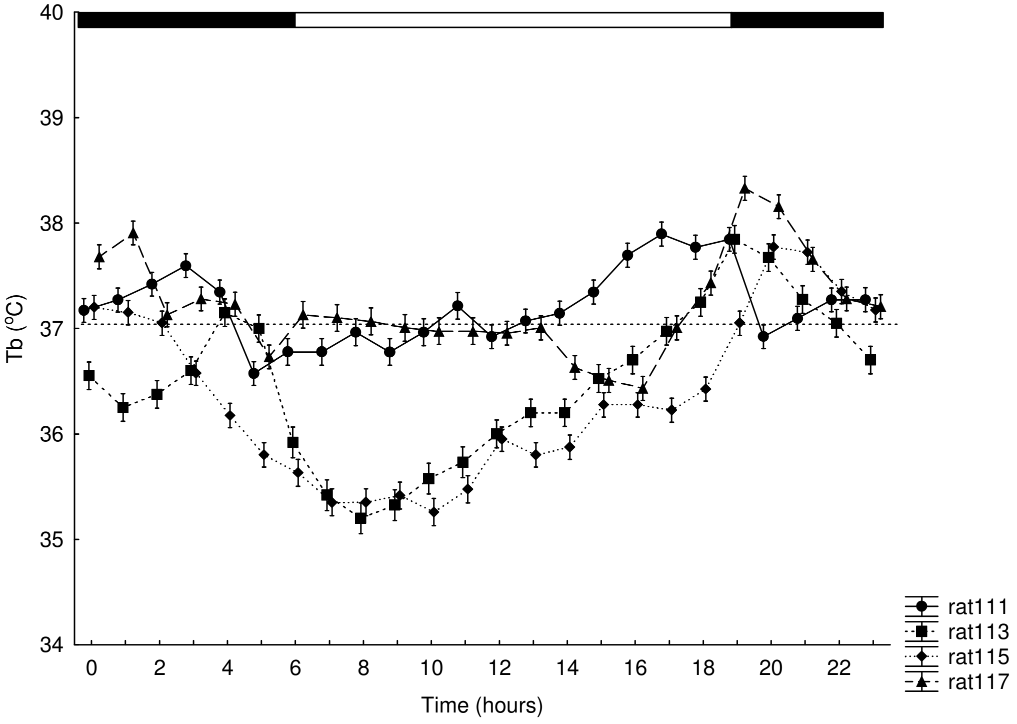
rat90
rat91
rat95a

b)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Tb (°C)
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20
22
Time (hours)
rat111
rat113
rat115
rat117

c)

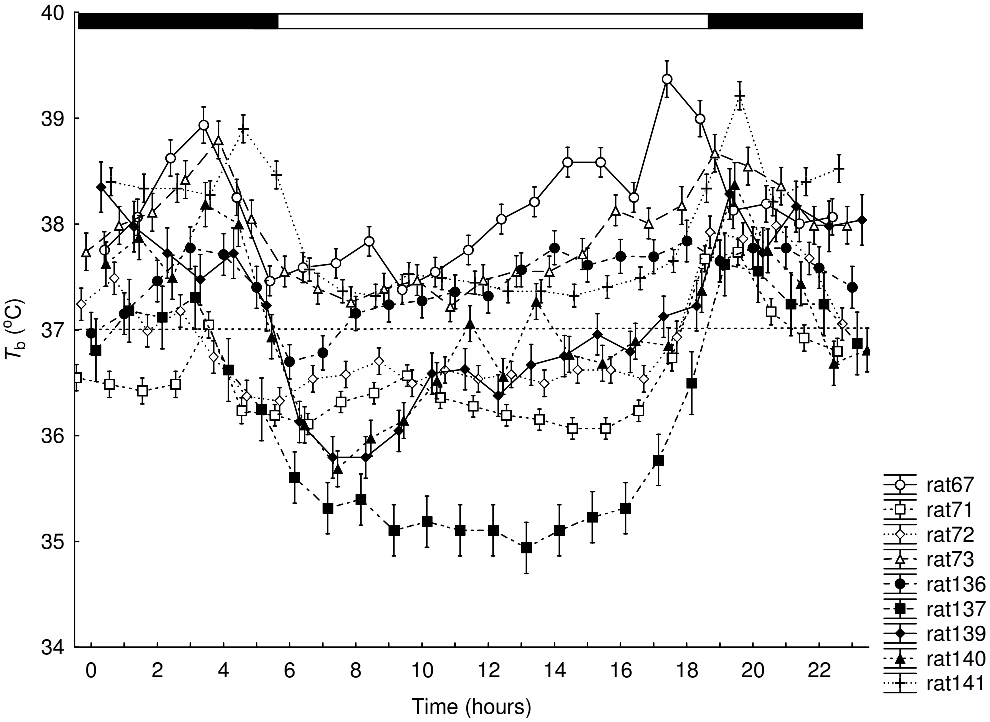
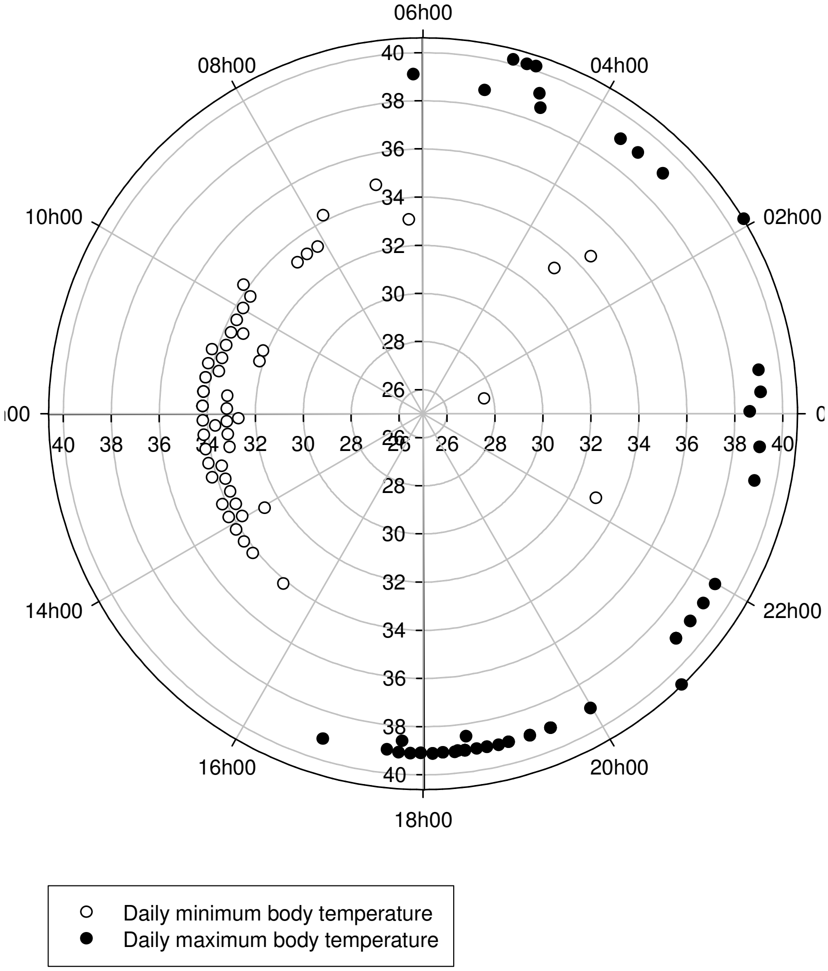


Fig 2. Mean hourly summer body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall summer mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.

a)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26
Daily minimum body temperature
Daily maximum body temperature

b)

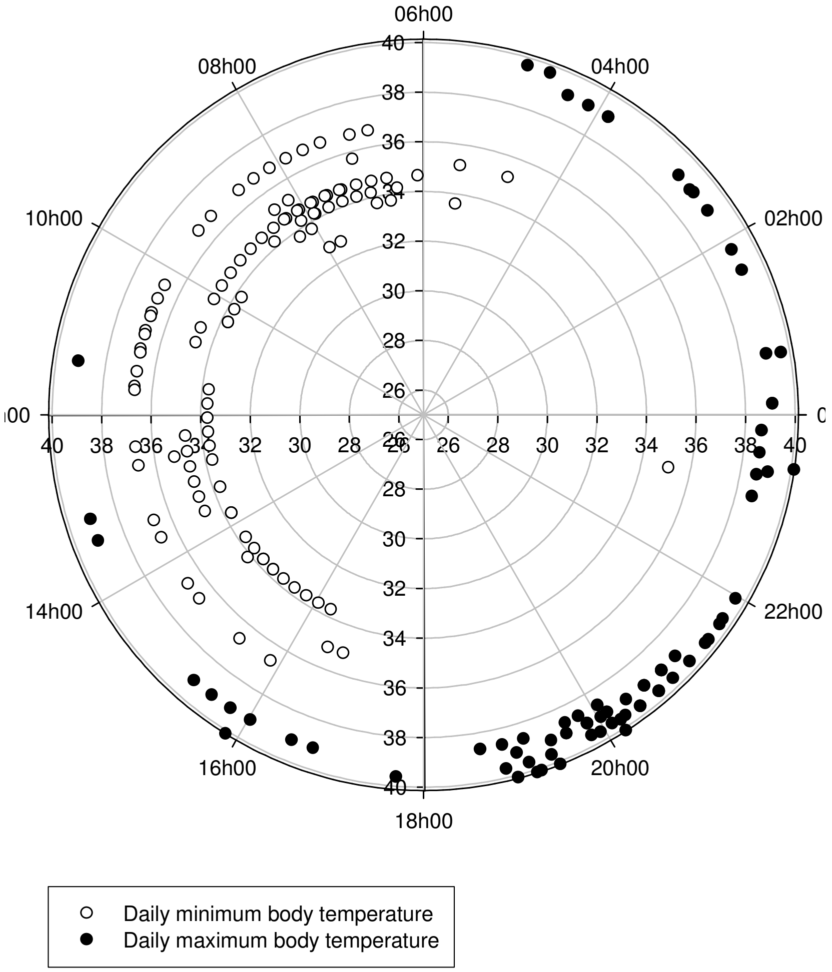


Fig 3. Circular distributions of the time of day (degrees) of the daily minimum body temperature (unfilled circles), and daily maximum body temperature (filled circles) of Tree Rats at the three study sites in a) winter and b) summer.

Fig 4. Body temperature of Tree Rat 28, in winter in Molopo, recorded over the one day period during which the "torpor" bout occurred.

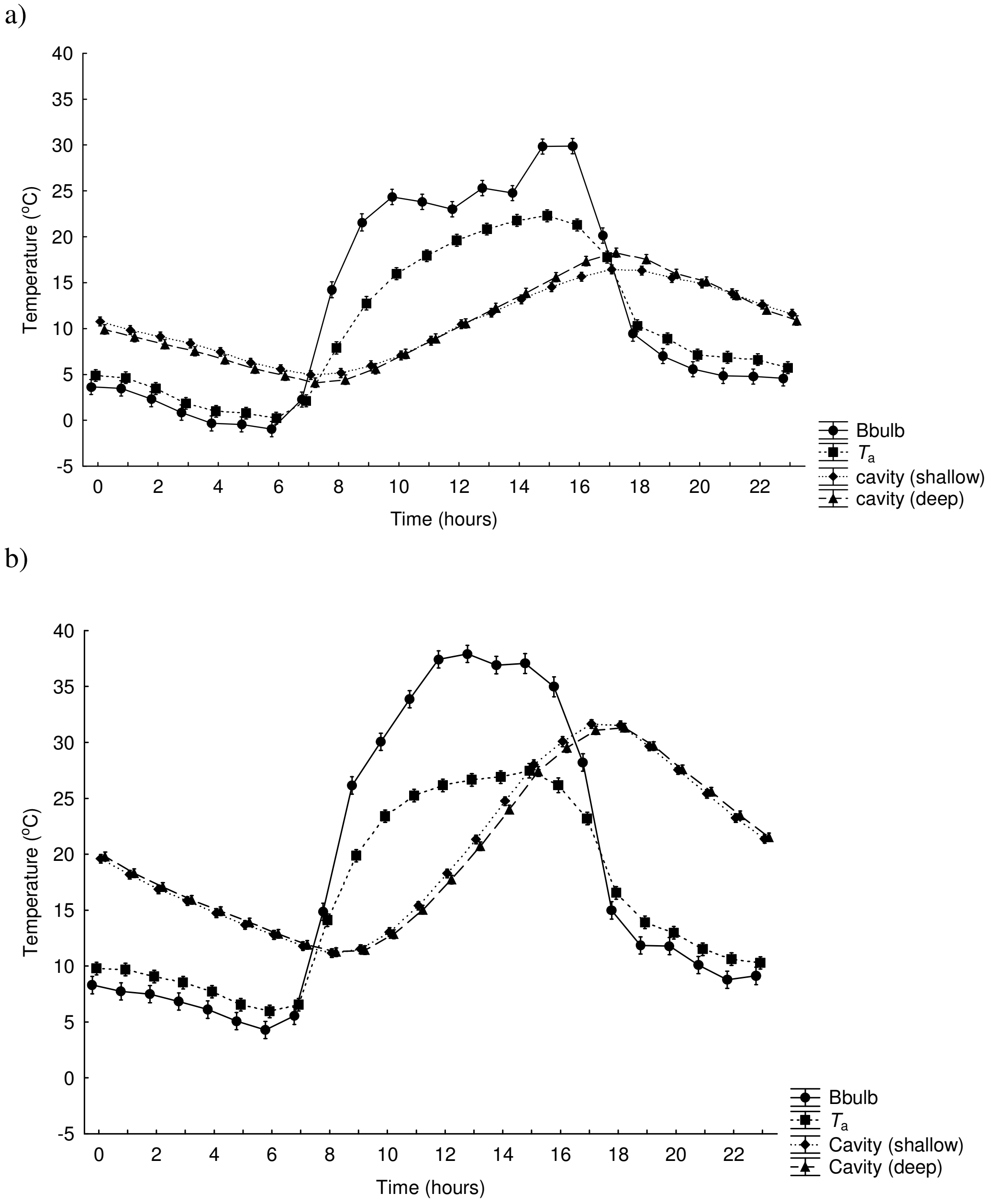
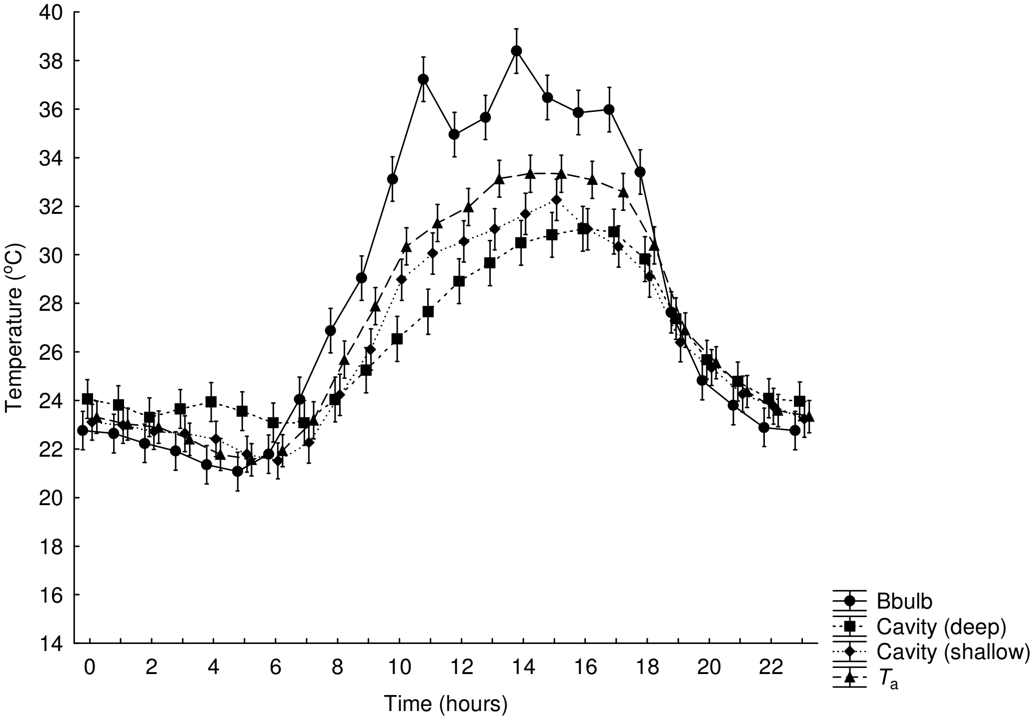


Fig 5. Mean hourly winter operative temperature, ambient temperature and cavity temperature (shallow and deep) in a) Molopo and b) Haina (see text for abbreviations and explanations).

a)


Temperature (ºC)
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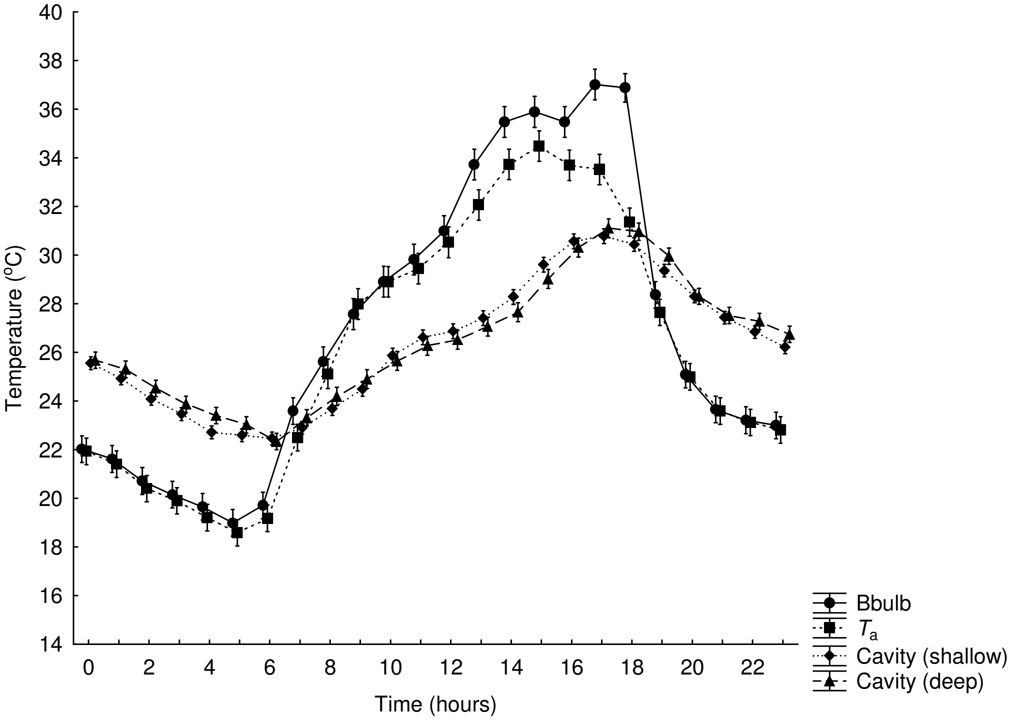
22
Time (hours)
Bbulb
Cavity (deep)
Cavity (shallow)
T_a

b)


Temperature (ºC)
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18
20
22
Time (hours)
Bbulb
T_a
Cavity (shallow)
Cavity (deep)

c)

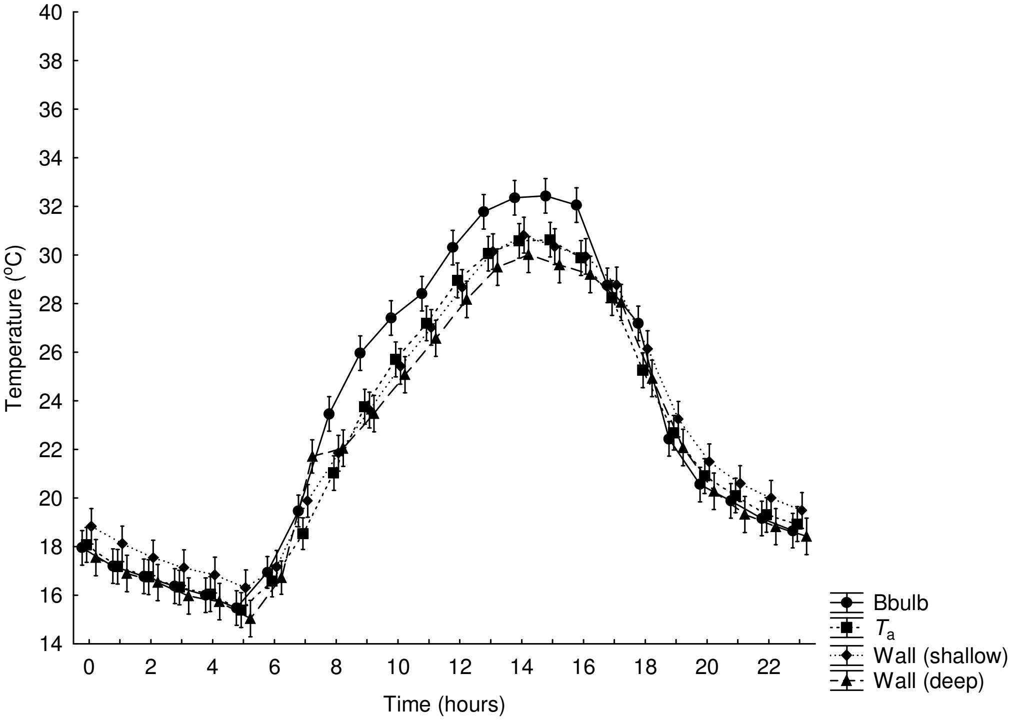


Fig. 6. Mean hourly summer operative temperature, ambient temperature and cavity temperature (shallow and deep) in a) Molopo, b) Haina and c) Weenen (see text for abbreviations and explanations).

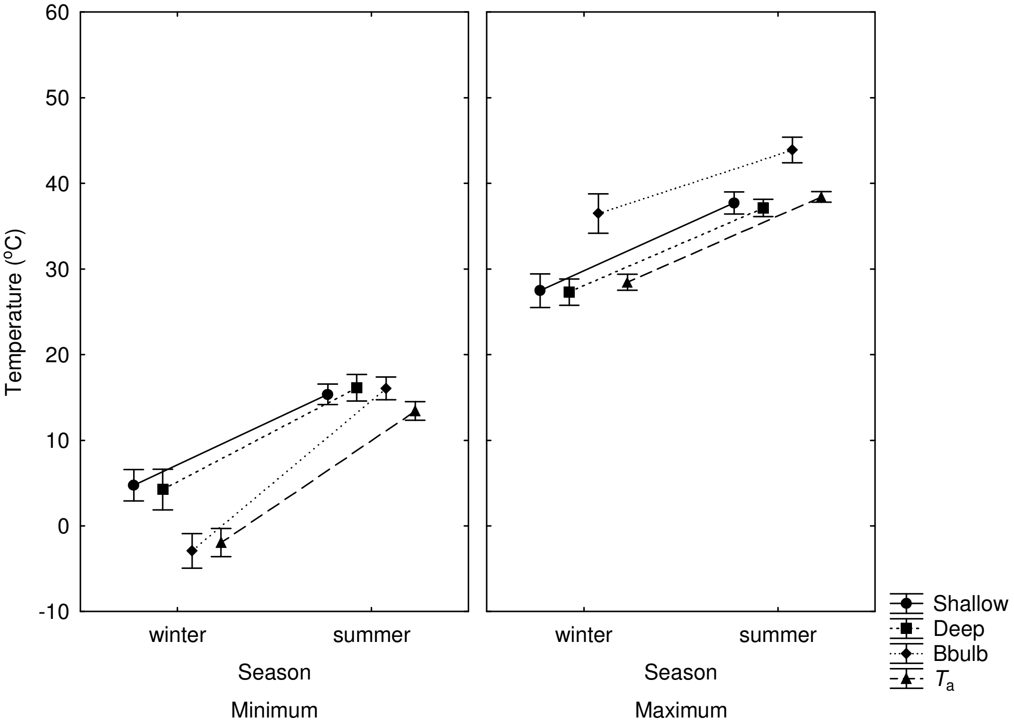
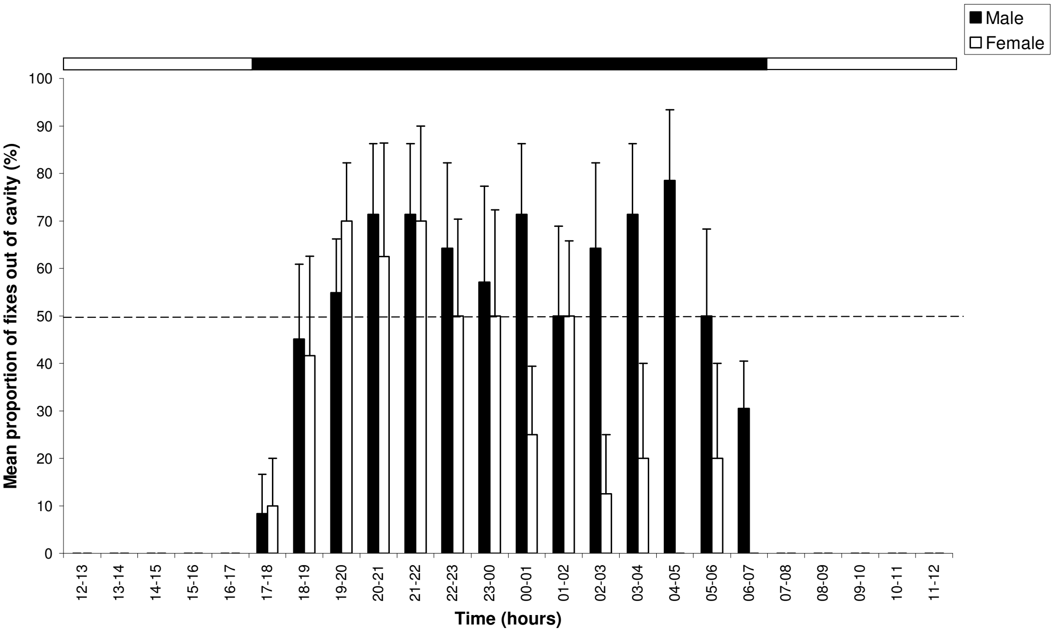


Fig. 7. Mean minimum and maximum operative temperature, ambient temperature and cavity temperature (shallow and deep) in summer and winter (see text for abbreviations and explanations).

a)



b)

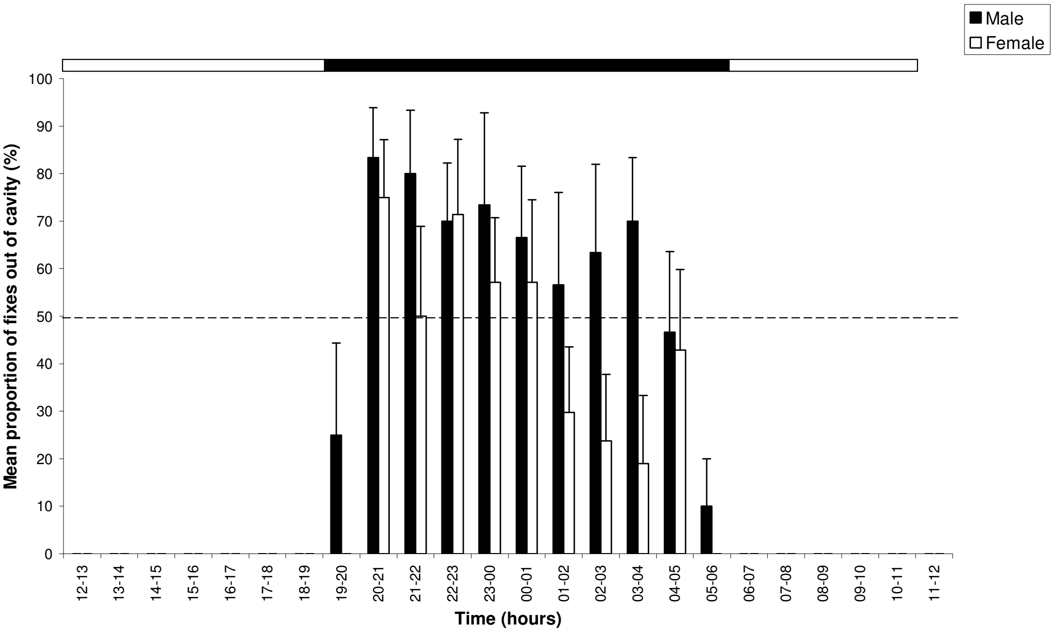


Fig. 8. Nocturnal activity profiles of male and female Tree Rats in a) winter and b) summer. Bars show the mean ± *SE* of the percentages of fixes where animals were located out of their home cavity in one hour intervals. The horizontal dashed line indicates a mean of 50% of fixes out of the home cavity. The dark bar indicates scotophase as determined by sunset and sunrise times.

CHAPTER 6

CONCLUSION

Regardless of its ultimate cause or duration, global warming appears to be having an effect on the distribution and survival of vertebrates and physiological ecology, which focuses on diversity of solutions to problems presented by the environment, is positioned by its approach to examine the causes of distribution changes and to help anticipate problems before they have an irretrievable impact on species (McNab 2002). Studying the physiological responses of free-living organisms allows us to understand the vulnerability of animals to physiological stress (Goldstein & Pinshow 2006). Water and energy are linked in the context of the environment and survival of organisms is a result of the complex interaction between these two factors. Adaptations for acquiring and conserving water have an effect on the intake and use of energy and this in turn affects the energy available for growth and reproduction (Lillywhite & Nevas, 2006).

This study investigated the presence and extent of physiological and behavioural flexibility as indicated by the intraspecfic variation in three populations of free-living Black-tailed Tree Rats, *Thallomys nigricauda,* along an aridity gradient. The wide distribution along an aridity gradient coupled with the arboreal habits of this species made it an ideal species to test the assumption that the species range shifts in southern Africa, as predicted by climate range models, may not be as marked if a species is able to adapt to the changed conditions (Erasmus *et* al. 2002). The results of this study confirm our expectation of physiological and behavioural flexibility in the three subpopulations of *T. nigricauda* and suggest that this flexibility plays a role in the successful colonization of mesic to xeric regions of southern Africa.

If home range size is a reflection of the physiological state and energetic requirements of *T. nigricauda*, low ambient temperatures at night and reduced primary productivity during winter had no influence on their range of movements. It is suggested that home range size of male and female *T. nigricauda* is influenced by a combination of precipitation, habitat productivity and breeding system and that there is sufficient flexibility in this behavioural trait as evidenced by the lack of difference in size between seasons and sites (Chapter 2). This is in accordance with the similarity in water balance between aridity sites and seasons, as indicated by urine osmolality and water flux in the three populations (Chapter 3). In addition, as might be expected, *T. nigricauda* did not alter nocturnal activity patterns between aridity sites or between seasons (Chapter 5).

I emphasise that the variation or flexibility in the physiological and behavioural traits measured could be related to the conditions of the microhabitat during a timeframe relevant to the measured response and not to aridity or season *per se*. The semi-xeric and xeric sites experienced greater than average summer rainfall (B Nkga; CJ Spykerman pers. comm.), resulting in a subsequent winter of greater than average primary productivity (pers. obs.). The quantity of preformed water available to T. nigricauda after the rainfall season may thus have been greater than expected. As a folivore, in response to more favourable conditions than expected, *T. nigricauda* would not need to curtail its range of movements, nor activity patterns. They would produce urine of similar osmotic concentration and be in a similar water balance when compared with summer months (Chapter 2). The energetic savings of *T. nigricauda* lowering body temperature during the day and spending its rest phase in a buffered cavity was sufficient to negate the need to reduce foraging during low ambient temperatures at night during winter (Chapter 5).

Thus it is essential that any study attempting to relate climatic conditions to the physiological and/or behavioural response of a free-living animal takes into account not only the conditions within the timeframe of the study, but microclimatic conditions at a scale relevant to the study animal. Because an animal lives in a specific environment, this does not mean that it experiences the environment as perceived by humans (Bennett 1987). Habitat-level measurements are not well-correlated to niche-level measurements (Helmuth 1998; Gilman *et al.* 2006). The choice of suitable climatic recording devices should be realistic to the study animal. For example, it was unrealistic to use operative temperature as a measure of the perceived temperature in this study due to nocturnal activity pattern of *T. nigricauda* and its daytime inactivity in a cavity (Chapters 2, 4, 5). In addition, results of this study suggest that more direct temperature recording devices, which may be more suitable to the particular research question, provide adequate estimates of the microclimate of the study animal (Chapter 4).

One of the concerns when examining subpopulations of a species across a gradient is the degree of speciation that may be occurring. This genetic divergence was not measured in the present study but forms part of a collaborative project that is not complete. However, it is expected that as Black-tailed Tree Rats have such a broad distribution that there is gene flow. The high degree of flexibility in the parameters measured in the present study supports this expectation.

The results of the present study are encouraging in terms of the survival of this species in southern Africa in the light of climate change. We suggest that the presence of physiological and behavioural flexibility in *T. nigricauda* may enable the species to respond to climate change in the same manner as the populations respond to differing climatic conditions in their range in southern Africa. This has important implications for the predicted survival and distribution changes of small endotherms in the region. It is hoped that the findings of this study will encourage similar field studies, such that data on species' physiology may be incorporated into predictions of the success of vertebrates in the face of global climate change, particularly if Africa is to be the most vulnerable, as predicted (Lovett *et al*. 2005).

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