

SEASONAL VARIATION IN THE THERMAL BIOLOGY OF THE ROCK HYRAX

(*PROCAVIA CAPENSIS*)

By

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## ABSTRACT

Animals in the Southern African sub-region are faced with unpredictable seasonal rainfall patterns and unpredictably low resource availability due to the influence of the El Niño Southern Oscillation System. This has led to conservative energetic traits in animals that offset the costs of maintaining homeostasis in the unpredictable environments they inhabit.

One of these animals is the rock hyrax (*Procavia capensis*). Past research has looked at the thermoregulation of rock hyrax in the laboratory. Results indicated that rock hyrax had labile body temperatures that reached lethal levels at ambient temperatures above 39°C. Laboratory studies separate endogenous thermoregulation from behavioural thermoregulation and do not reflect the overall thermoregulatory potential of the rock hyrax in maintaining body temperatures.

This study looked at the thermoregulation of rock hyrax in their natural environment. Body temperatures were measured in the field using Thermochron iButtons inserted into the intraperitoneal cavity of the animals. Behavioural observations were also recorded on subgroups and individually marked animals.

Rock hyraxes were exposed to large fluctuations in ambient temperatures and food availability during the course of this study. In winter, ambient temperatures ranged between 5-25°C and in summer between 18-42°C. Our results show that rock hyrax seasonally and daily altered both their physiological and behavioural thermoregulation to control body temperature efficiently.

The physiological alterations observed in rock hyrax differed between winter and summer. During winter, when food availability was low, rock hyrax maintained body

temperatures at a lowered level relative to summer. Body temperatures fluctuated to a greater extent during winter as a result of reduced body temperatures at night and increased body temperatures due to basking during the diurnal hours. During summer, rock hyrax displayed high body temperatures, which reached hyperthermic levels. This enabled rock hyrax to forage during midday hours since heat loads could be easily dissipated through passive conduction in the cooler rock crevices.

Rock hyrax employed different behavioural patterns in winter and summer. It is proposed that rock hyraxes are unable to meet energetic demands on a low quality and patchy food resource under low ambient temperatures. Predation is also a cost to foraging and becomes increasingly important when rock hyraxes have to move large distances away from crevices to find food. The most frequent behaviour recorded in rock hyrax during winter was basking. Basking enabled rock hyrax to maintain body temperatures with very little thermoregulatory cost. Differences were also recorded in behavioural patterns in rock hyrax of different sizes. Juveniles, due to their small body size and high energetic demands foraged more frequently than adult rock hyrax.

During summer, rock hyrax spent considerable time in the rock crevices. This was because ambient temperatures exceeded the upper limit of the thermoneutral zone of the rock hyrax throughout most of the day. Rock hyrax therefore escaped the excessive temperatures by utilizing the cooler rock crevices, which remained at temperatures within the rock hyraxes thermoneutral zone. The most frequent behaviour recorded in rock hyrax aboveground was foraging. Since forage was abundant around the rock crevices during summer, predation risk was less of a factor influencing foraging behaviour.

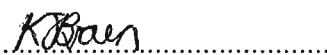
Since basking is an essential component of the rock hyraxes thermal biology during winter we examined basking behaviour in more detail. Basking in the morning was not used to increase body temperatures from hypothermic levels as otherwise thought. Instead, it was used to maintain body temperatures at low ambient temperatures by altering posture, orientation to the sun and basking bout lengths. During the early morning, when heating rates were greatest, rock hyrax orientated their bodies exposing the greatest surface area to solar radiation. During midday, reduced basking bout lengths and the reduction of surface areas exposed to the sun reduced the heat loads during the hottest parts of the day. Rock hyrax appeared to utilize the warm rock surfaces during the late afternoon when the sun was setting to maintain body temperatures before entering the crevices for the night.

The combination of physiological and behavioural thermoregulation therefore enables rock hyrax to maintain homeostasis with very little energetic costs in an environment that displays variability in both ambient temperatures and resource availability.

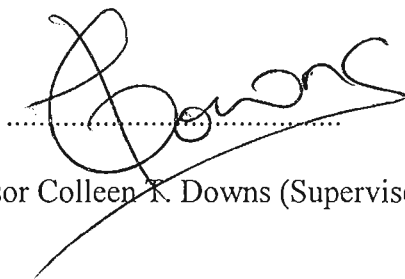
## PREFACE

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg, from March 2002 to December 2003, under the supervision of Professor Colleen T. Downs.

These studies represent original work by the author and have 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. The thesis is structured with each chapter is written in the format of submission for a particular journal. Any repetition was unavoidable. Chapter one, two and five follow the format of Physiological and Biochemical Zoology. Chapter three follows the format of Journal of Zoology, London and chapter four follows the format of Comparative Biochemistry and Physiology.



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Professor Colleen T. Downs (Supervisor)

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## CHAPTER FIVE

### CONCLUDING REMARKS - THE EVOLUTIONARY SUCCESS OF THE THERMAL BIOLOGY OF THE ROCK HYRAX (*PROCAVIA*

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## CHAPTER ONE

### INTRODUCTION

#### **The history of the Afrotheria clade**

The hierarchical grouping of eutherian mammals and the divergence events that led to their assemblage have been a contentious issue amidst morphologists, paleontologists and molecular evolutionists for many years (Murphy et al. 2001). Advances in molecular techniques have led to new eutherian groupings vastly different from those developed on morphological grounds (Novacek 1992; Stanhope et al. 1998; Murphy et al. 2001). Recent genetic studies have ‘shaken’ the phylogenetic tree, splitting what were thought to be ancient monophyletic groups (based on numerous morphological features) into paraphyletic groups (Springer et al. 1997; van Dijk et al. 2001). One group that has undergone considerable rearranging over the years is the Afrotheria.

Traditionally, divergence times between lineages were obtained from fossil records (Kumar & Hedges 1998). Molecular studies however, suggest that estimates of divergence times of groups are much older than suggested by their oldest fossil records (Kumar & Hedges 1998; Foote et al. 1999). Where molecular times coincide with Cenozoic fossil-based times, considerable gaps appear in the Mesozoic fossil record (Kumar & Hedges 1998). At least four lineages of eutherian mammals arose more than 100 million years ago (mya) prior to the Cretaceous/Tertiary extinction of the dinosaurs (Hedges et al. 1996; Kumar & Hedges 1998). This evidence suggests that mammalian diversification corresponded not to the filling of vacant niches left by the dinosaurs but rather with the breaking up of the continents (Hedges et al. 1996; Springer et al. 1997).

It appears that the earliest divergence that took place was between Afrotheria and Xenarthra when tectonic forces caused the geological separation of the southern supercontinent Gondwanaland between 111-118 mya (Madsen et al. 2001; Murphy et al. 2001). Both primitive orders underwent parallel adaptive radiations, filling the ecological niches being vacated by dinosaurs (Hedges et al. 1996; Madsen et al. 2001; Murphy et al. 2001).

Molecular genetics suggest that the adaptive radiation of the Afrotheria occurred during Africa's window period of isolation between the separation of Gondwanaland in the Late Cretaceous period and the joining to Europe via land connections in the Cenozoic period (Springer et al. 1997; Stanhope et al. 1998; van Dijk et al. 2001). This led to an ancient African grouping with all its species having their origins in Africa, most of which are still confined to this continent today (Gerbrandt et al. 1996; Stanhope et al. 1998).

This all African superordinal clade now contains six orders (nearly one-third) of extant placental mammals (Stanhope et al. 1998). These are the hyraxes (Hyracoidea), elephants (Proboscidea), elephant-shrews (Macroscelidea), armadillos (Tubulidentata), golden moles (Chrysochloridae), tenrecs (Tenrecidae) and the dugongs and manatees (Sirenia) (Springer et al. 1997; Stanhope et al. 1998; van Dijk et al. 2001). The tenrecs and golden moles were previously placed in the monophyletic group, Insectivora, due to their morphological affinities (Stanhope et al. 1998). Genetic sequences have not only shown that they are more closely related to the Afrotheria but that their ancestor resided in Africa some 70 mya (Springer 1997; Stanhope et al. 1998).

Morphologically this African superordinal clade appears to be an improbable grouping (Novacek 1992; Springer et al. 1997; Stanhope et al. 1998; Madsen et al. 2001; van Dijk et al. 2001). The African clade, boasts a range of body masses from <50g (golden moles and elephant shrews) to more than 6 000 kg (african elephants) showing a variety of ecological and morphological specializations (Springer et al. 1997, Lovegrove et al. 1999).

Since these groups belong to such an ancient lineage originating in Africa, one might assume that they must all have some sort of adaptation to the climatic conditions experienced on the continent. This is especially the case in the southern African sub-region, which experiences variable climatic conditions. El Niño Southern Oscillations (ENSO) are a source of unpredictable rainfall patterns in southern Africa (Philander 1983; Stone et al. 1996). Unpredictable seasonal rainfall results in animals being subjected to unpredictably low resource availability, similar, but on a less frequent scale, to that which occurs in arid regions (Philander 1983; Philander 1990; Stone et al. 1996). The magnitude of these stresses rather than the frequency associated with low resource availability in arid areas leads to conservative energetic traits that offset the costs of maintaining homeostasis in desert animals (Parsons 1991). Thus, a similar occurrence should be found in animals inhabiting ENSO affected mesic zones (Parsons 1991).

### **The Hyracoidea**

During Africa's window period of isolation, about 36 million years ago, the Hyracoidea were the most important medium-sized herbivores roaming Africa's landscape (Estes 1997). This very successful group contained at least seven genera during this time ranging in size from that of present day hyraxes to the *Megalohyrax* which was



as large as a hippopotamus (Kingdon 1971; Hoek 1979; Skinner & Smithers 1990). Fossil evidence from Egypt and East Africa indicates that much larger hyrax species occurred during the Oligocene and lower Miocene (Kingdon 1971). The extremely long gestation period, heavy birth mass and precocious young suggest these are phylogenetically determined, and may be further evidence that recent hyrax have become smaller compared to their ancestors (Sale 1965a).

The Miocene epoch saw the joining of Africa and Europe via land connections and led to the invasion and radiation of ungulates following the expansion of grassland savanna in Africa (Kingdon 1971). With the rapid expansion of the ungulates came the first carnivores to Africa (Ewer 1973). This period saw a rapid reduction in hyrax diversity.

The hyrax's inefficiency in feeding, low metabolic rates and short plantigrade foot structure, proved them to be an inadequate competitor for the ungulates on the open plains (Kingdon 1971; Estes 1997). Built for speed, with high metabolic rates and unguligrade feet, the ungulates quickly filled nearly every niche left by the out-competed slower hyraxes (Kingdon 1971).

To avoid being outcompeted, the Hyracoidea had to be able to adapt to a niche where they could avoid direct competition with ungulates. It was only those species of hyraxes that were small enough to utilize rocky outcrops and trees to escape predators that persisted (Estes 1997). A small animal with a plantigrade structure could be flexible and proved advantageous in climbing of trees and agility over rocks (Gould 2001). Most large animals show greater specialization. This specialization makes structural changes more difficult in adapting to a changing environment (Gould 2001). Broken rocks prove

difficult for all ungulates except for the klipspringer (*Oreotragus oreotragus*), while climbing trees is beyond the adaptive powers of bovids. This has led to the successful exploitation of hyraxes in these two habitats (Kingdon 1971; Fairall et al. 1983).

In the past, the absence of predators meant hyraxes could move great distances to get the quantity and quality of food they required to meet energetic demands. However, the low metabolic rates and plantigrade foot structure were a hindrance in moving large distances away from refugia in the presence of predators.

The extant Hyracoidea group contain three genera, *Procavia* (rock hyrax), *Heterohyrax* (bush hyrax) and *Dendrohyrax* (tree hyrax) based on both anatomical features and behavioural characteristics (Hoek 1979; Eisenberg 1981). *Procavia* is the most common and extensive genus found in both arid regions (Sinai, Syria and Arabia) as well as in the more temperate climates of North and South Africa (Rübsamen et al. 1982).

Rock hyraxes inhabit areas that vary considerably in ambient temperature, water availability and good quality forage. Low metabolic rates and labile body temperatures have probably contributed to the successful utilization of isolated rocky outcrops by rock hyrax (*Procavia capensis*) throughout its distribution. A reduction in size from the ancient hyrax groups meant an increase in surface area to volume ratio and a potential to lose more heat. To survive on a herbivorous diet at such an intermediate size would require a low metabolic rate and the ability to utilise a relatively variable and poor quality food source efficiently (Ashby 1971).

The digestive system of the rock hyrax is extremely complex and specially adapted to a high fibrous diet. Three separate areas of microbial digestion (the sacculated stomach, the midgut sacculatation and the pair of caecae) contribute to the efficiency of

digestion of a poor quality food source (Clemens 1977; Clemens & Maloiy 1978). To digest high fibrous diets efficiently, digesta are also retained for longer periods in the gastrointestinal gut thereby allowing further substrate fermentation (Clemens 1977; Eloff 1983).

Past research has concentrated on hyrax metabolism and body temperature regulation in the laboratory (Taylor & Sale 1969; Bartholomew & Rainy 1971; Louw et al. 1972; McNairn & Fairall 1979; Rübsamen et al. 1979; Fairall et al. 1983; McNairn & Fairall 1984). These laboratory studies separate behaviour from the thermoregulatory system in order to identify the extent to which the physiological control regulates body temperature in rock hyrax. The metabolic rate of rock hyrax was found to be lower than predicted by Kleiber (Fairall et al. 1983). Results also displayed a higher degree of thermolability in hyrax and from a physiological point of view, are considered poor thermoregulators (Louw et al. 1972; McNairn and Fairall 1984).

At lower ambient temperatures, body temperatures of laboratory hyrax showed pronounced decrease with very little increase in metabolic rate (Bartholomew & Rainy 1971; Louw et al. 1972; McNairn & Fairall 1979; Fairall et al. 1983; McNairn & Fairall 1984). McNairn and Fairall (1984) found that at low ambient temperatures, juvenile hyrax reduced thermolability and decreased conductance whilst adults showed a high degree of thermolability with no change in conductance.

At the other end of the temperature spectrum, hyraxes have been found to have poor heat tolerance (Louw et al. 1972). At temperatures at and above 35°C, rock hyrax develop hyperthermia, with lethal limits around 40°C (Bartholomew & Rainy 1971; Louw et al. 1972). At these temperatures hyrax display profuse nasal and foot sweating,

increased breathing rate and a decrease in skeletal muscle tonus (Bartholomew & Rainy 1971; Louw et al. 1972).

The efficient physiological mechanisms, such as a low metabolic rate, a complex and efficient digestive system and efficient renal function have all contributed to the long-term success of hyrax in their natural environment (Louw et al. 1972; Maloiy & Sale 1976; Fairall et al. 1983).

The rock hyrax, however, thermoregulates most efficiently using both physiological and behavioural mechanisms (Rübsamen et al. 1982). Behaviour patterns employed by rock hyrax that contribute to the efficient control of body temperature include: diurnality, basking, long periods of inactivity (mostly in dens) and gregarious fossorial habits (Sale 1965b, Bartholomew and Rainy 1971).

It has been proposed that the low metabolic rates and labile body temperatures of rock hyrax are an energy-conserving strategy, which utilizes an external solar energy source to override hypothermia (Taylor & Sale 1969; Bartholomew & Rainy 1971, McNairn & Fairall 1984). Alternatively, the low metabolic rate may be a phylogenetic trait associated with the primitive Paenungulata group, which has proved to be advantageous in hot and dry environments (Rübsamen et al. 1982).

### **Statement of intent**

Knowing that the basal metabolic rate is lower than predicted and that the rock hyrax possesses a labile body temperature in the laboratory, it was decided to examine seasonal body temperature in their natural environment. At the same time it was intended to

measure behavioural patterns and environmental parameters. The following were specific objectives of the study.

- (i) To examine the daily and seasonal differences in the body temperature of the rock hyrax (*Procavia capensis*).
- (ii) To examine to what extent environmental factors influence thermoregulation in rock hyrax.
- (iii) To examine the effect of behaviour on the temperature regulation of the rock hyrax.

I hypothesized that the (i) body temperature of the rock hyrax would be labile and fluctuate with daily and seasonal environmental temperatures; (ii) the rock hyrax would behaviourally select microhabitats that maintain their body temperature within the thermoneutral zone; and (iii) basking is necessary to increase body temperature substantially after overnight hypothermia.

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CHAPTER TWO  
SEASONAL CHANGES IN DAILY RHYTHMS OF BODY TEMPERATURE IN  
FREE-LIVING ROCK HYRAX (*PROCAVIA CAPENSIS*)

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Formatted for Physiological and Biochemical Zoology

**Abstract**

Rock hyraxes are faced with large daily fluctuations in ambient temperature during both summer and winter periods. The large range in body temperature of rock hyrax recorded in this study reflects the adaptability of this animal to the wide range of ambient temperatures experienced in its natural environment.

During winter, when low ambient temperatures and the low food supply is prevalent, rock hyraxes maintained a lowered body temperature relative to summer. Diurnal body temperatures were more variable than nocturnal body temperatures in winter. This variability is likely a result of body temperatures being raised through basking in the sun. Body temperatures recorded during winter never fell to levels recorded in previous laboratory studies. Huddling in crevices probably prevented excessive heat loss during nocturnal hours.

During summer, the ambient temperatures exceeded the thermoneutral zone of the rock hyrax throughout most of the day, while the crevice temperatures remained within

the thermoneutral zone of rock hyrax. Minimum and maximum body temperatures did not coincide with minimum and maximum ambient temperatures. Constant body temperatures were also recorded when ambient temperatures reached lethal limits. During summer it is likely that rock hyraxes select cooler refugia to escape lethal temperatures and prevent excessive water loss.

### **Introduction**

Daily rhythms of body temperature show the extent to which an organism stores heat and the degree to which the thermoregulatory system allows body temperature to fluctuate (Whittow 1966). Daily oscillations in body temperature of an endotherm are a result of a relationship between heat production and heat dissipation and show raised body temperatures during the active phase and reduced values during the resting phase (Aschoff and Pohl 1970; Aschoff 1982). Circadian rhythms are daily oscillations of body temperature, which are generated endogenously but under constancy of conditions (Refinetti and Menaker 1992; IUPS Thermal Commission 2003).

The body temperature of organisms may undergo not only short-term (daily) fluctuations but also seasonal ones (Rodríguez-Gironés 2002). Seasonal changes in organisms are controlled by changes in light intensity, temperature and food availability (Enright 1970). Anticipating seasonal changes can have economic value to organisms (Enright 1970). Most endotherms maintain a fairly constant core-body temperature that fluctuates within a narrow range (Rodríguez-Gironés 2002). Since endogenous heat production constitutes the largest portion of an endotherm's daily energy expenditure (Bartholomew 1977; Chappell 1980; Lovegrove et al. 1991), maintaining constant body

temperatures becomes extremely costly under unfavourable conditions (Sibly and Calow 1986; Schmidt-Nielsen 1990).

When challenged energetically under conditions of low ambient temperatures or decreased food supply, some mammals may lower their body temperature (Pereira et al. 2002). Reductions in the minimum body temperature during the rest phase could represent a mechanism for conserving energy (Bakko et al. 1988; Fielden et al. 1990; Lovegrove and Heldmaier 1994). A reduction in the minimum body temperature increases the amplitude or range in body temperature. Similarly, in hot arid environments, the amplitude of body temperature may increase as a result of organisms allowing themselves to become hyperthermic in order to increase surface activity during extremely hot days (Chappell and Bartholomew 1981; Rodriguez-Gironés 2002). The amplitude of the daily rhythm of body temperature is important in determining an organism's ability to regulate body temperature in the maximum range of ambient temperatures experienced in its environment (Refinetti and Menaker 1992; Lovegrove and Heldmaier 1994).

In addition to endogenous thermoregulatory responses, some mammals make use of behavioural responses when exposed to cold or hot environments (Refinetti 1995). Instead of maintaining constant body temperatures through the generation of endogenous heat, they rely on heat gained directly from their surroundings (Whittow 1966). Since behavioural thermoregulation assists in heat gain or heat loss, one would expect that it would also participate in the generation of the oscillation in body temperature of an organism in its natural environment (Refinetti 1995).

Rock hyraxes (*Procavia capensis*) occupy regions that show great daily and seasonal fluctuations in ambient temperatures. They may be exposed in winter to a low of  $-2^{\circ}\text{C}$  up to  $25^{\circ}\text{C}$  in the early afternoon and in summer to a peak of close to  $40^{\circ}\text{C}$  (McNairn and Fairall 1984). Laboratory experiments have shown that rock hyrax display labile body temperatures under constant environmental conditions (McNairn and Fairall 1984). Ranges in body temperature have been reported to be up to  $4.5^{\circ}\text{C}$  (Sale 1970). In the laboratory, rock hyrax reduced body temperature with a reduction in ambient temperature (McNairn and Fairall 1984) whereas at high ambient temperatures, rock hyraxes become hyperthermic (Louw et al. 1972). Although the body temperature of rock hyrax display a wider range than most mammals (Rübsamen et al. 1982), their body temperatures never dropped below  $32^{\circ}\text{C}$  even at ambient temperatures of between  $4-40^{\circ}\text{C}$  (Taylor and Sale 1969; McNairn and Fairall 1984). This indicates that the internal physiological mechanisms of rock hyrax are primarily responsible for daily body temperature regulation (Taylor and Sale 1969; Sale 1970).

Although much of the research has shown that rock hyrax display labile body temperatures, these results reflect only laboratory studies. These laboratory studies separate behaviour from the thermoregulatory system in order to identify the extent to which the physiological control of hyrax regulates body temperature. Thermoregulation in hyraxes involves a combination of physiological and behavioural control of body temperature (Rübsamen et al. 1982).

The aim of this study was to determine body temperatures of rock hyrax in the field. Any potential rhythms were expected to be entrained by the light/dark cycle or

temperatures experienced throughout the day. The objective was to determine the daily rhythms of body temperature of free-living rock hyrax and to determine whether:

- i) they differed between individuals in the field
- ii) they differed on a seasonal basis in the field
- iii) the amplitude in the daily rhythms differed on a seasonal basis in the field.
- iv) the range ( $R_t$ ) differed under natural conditions to published laboratory data.

### **Materials and Methods**

The present study was conducted in the Klipbank suburb of Ladysmith, KwaZulu Natal, South Africa (28°30'S and 29°45'E) during a winter season (July 2002) and a summer season (February 2003). A total of eight hyraxes were captured (six in winter and two in summer) using wire mesh (10mm) box cages measuring 400 x 400 x 750 mm, with a hinged trapdoor. Trapdoors opened inwards allowing animals to enter traps but prevented departure. The traps were baited with cabbage leaves, carrots and potatoes. Cages were originally lined with hessian to prevent facial injuries. Trapping, however, was unsuccessful and the hessian was later removed. Trapping of individuals was more successful in winter than in summer. This was probably due to the lack of good quality food available close to crevices in their natural environment encouraging foraging from the cages during winter. The abundance of forage close to crevices during summer equated to rock hyraxes being less eager to enter traps.

When a rock hyrax was caught in a cage a blanket was immediately placed over the cage to calm the individual down. The animal was then taken directly to a local

veterinarian for surgical implantation of pre-calibrated temperature dataloggers (DS1921 Thermochron *i*Buttons® (Dallas Semiconductor)).

Rock hyraxes were anaesthetized using ketamine. The prescribed dosage was determined according to the mass of the animal (20 mg ketamine per ml/kg) and injected intramuscularly. Two Thermochron *i*Buttons were implanted into the intraperitoneal cavity of each animal. The *i*Buttons were enclosed in surgical wax to prevent tissue attachment over the experimental period.

*i*Buttons are miniature dataloggers encapsulated in stainless steel caps. Each *i*Button contains a thermometer (measured to 0.5° C), a clock and calendar weighing on average three grams (including wax encasing). The *i*Buttons were programmed to record body temperatures every 10 minutes over a period of 14 days. The second *i*Button was programmed to start measuring as the first one ended, hence body temperature could be measured continuously for approximately 28 days.

Animals were fitted with brightly coloured neck collars to assist in recognition of individuals for recapture. Animals were then released again in their natural environment after a recovery period of approximately 3 to 4 hours. Towards the end of the recording period animals were retrapped and the *i*Buttons were removed. Only four individuals were recaptured during the winter period as a consequence of collar loss and trap shyness.

The data from the *i*Buttons were downloaded using a DS1921 Thermochron *i*Button Software Download programme (Dallas). Daily rhythms of body temperature were determined for each individual as well as the average of the total number of rock hyrax caught in both winter and summer. Daily temperature ranges as well as active and

rest phase ranges were calculated. Active phase was taken to be from sunrise to sunset while rest phase was from sunset to sunrise. Body temperature rhythms were compared to daily ambient temperature rhythms over the respective seasons. Independent t-tests and ANOVAs were used to compare body temperature data both within and between seasons using STATISTICA © ('98 Edition, Statsoft Inc.). Data was analysed to determine physiological trends in individuals.

Ambient temperatures were recorded every 10 minutes using standard thermocouple probes connected to a MCS 120-02EX datalogger (MC Systems, Cape Town). Ambient temperatures were measured outside of the crevices in a Stephenson's screen. The thermocouple probe was placed approximately one metre down into the entrance of a rock crevice. Only seven to eight days of continuous environmental temperature data was recorded over summer and winter respectively. This was due to disruptions in data collection by dataloggers and the difficulty in finding a location to avoid human interference. Results using a combination of ambient temperatures and body temperatures used only the data where both environmental and body temperatures coincided.

## **Results**

The mean body mass of the rock hyrax caught in this study was 3.03 kg ( $\pm$  0.34 kg). The four individuals captured in winter ranged in body mass from 2.45 to 4.35 kg (Mean 3.21  $\pm$  0.41 kg; Table 1), while the two individuals captured in summer weighed 1.95 kg and 3.35 kg respectively (Mean 2.65  $\pm$  0.70 kg; Table 2).



### Daily rhythms

Both winter and summer body temperatures of free-living rock hyrax showed definite daily rhythms, but to varying degrees (Figure 1a-d, 2a-b). In summer, maximum body temperatures were reached some time before the onset of the dark/rest phase (Figure 1a-d), whereas maximum body temperatures peaked for a short time after sunset in winter (Figure 2a-b).

#### *i) Winter daily body temperatures*

Winter mean diurnal body temperature of rock hyrax was significantly greater than mean nocturnal body temperatures (Table 1; independent t-test:  $t = 6.73$ ,  $df = 61$ ,  $P < 0.05$ ). The lowest and highest body temperatures recorded during winter were 34.5 and 39°C respectively. Three of the four individuals showed an overall winter range of 4.5°C, while the smallest individual had a range of 3°C. Minimum body temperatures were recorded mostly during nocturnal hours, but it occurred at 12h00 on one occasion.

In winter the body temperature of rock hyrax was more variable during the day (Mean range ( $R_t$ ) =  $2.39 \pm 0.09^\circ\text{C}$ ) than at night ( $R_t = 1.70 \pm 0.09^\circ\text{C}$ ) (Table 1). Although there was a significant difference between mean day and night range (independent t-test:  $t = 6.28$ ,  $df = 61$ ,  $P < 0.05$ ), there was no significant difference between mean diurnal and nocturnal minimum body temperatures. The difference between the mean diurnal and nocturnal ranges can be accounted for by the significantly greater mean maximum body temperatures during the day than at night (independent t-test:  $t = 8.08$ ,  $df = 61$ ,  $P < 0.05$ ).

The lowest body temperatures of rock hyrax generally occurred at night or early morning between 19h00 and 10h00 (Figure 3a-d). However, there was much individual variation in the frequency of minimum and maximum body temperatures. This may be a consequence of body mass (Chapter 3) and greater sample size will have confirmed this. Between 08h00 and 13h00, the frequency of minimum and maximum body temperatures overlapped (Figure 3a-d). Minimum ambient and crevice temperatures mostly occurred between 03h00 - 07h00 (Figure 4a-b).

Maximum body temperature of rock hyrax in winter mostly occurred between 10h00 - 18h00 and showed less variability between individuals than minimum body temperatures (Figure 3a-d). These maximum body temperatures coincided with the occurrence of maximum ambient temperatures (Figure 4a).

ii) *Summer daily body temperatures*

At night during summer, the mean body temperature of rock hyrax was significantly lower than by day (independent t-test:  $t = -8.50$ ,  $df = 53$ ,  $P < 0.05$ ). The highest body temperature recorded for the season was 40.5°C in the larger individual during the early afternoon and the lowest body temperature was 33.5°C recorded in the smaller individual in the early hours of the morning. The larger individual showed an overall summer range of 5°C whereas the smaller individual had a range of 6°C.

During the summer, the mean range in body temperature in rock hyrax during the day was more than double the range during the nocturnal hours (Table 2). Mean day minimum body temperatures were significantly lower than mean night minimum body temperatures (independent t-test:  $t = -4.70$ ,  $df = 53$ ,  $P < 0.05$ ), while mean maximum day

body temperatures were significantly greater than mean maximum night temperatures (independent t-test:  $t = 13.44$ ,  $df = 53$ ,  $P < 0.05$ ).

There was no particular period of the day in summer when minimum body temperatures of rock hyrax occurred (Figure 5a-b). The majority of the daily maximum body temperatures occurred between 12h00 - 20h00 (Figure 5a-b). Minimum ambient temperatures occurred between 04h00 - 06h00 (Figure 5c-d). Surprisingly, this is not when the minimum body temperatures occurred most frequently. Maximum ambient temperatures occurred between 11h00 - 17h00 (Figure 5c-d). The most frequent time at which maximum ambient temperatures occurred was 13h00 (Figure 5c). However, the highest frequency of maximum body temperatures did not occur at this time. Maximum body temperatures mostly occurred at 16h00, which was not in accordance with maximum air temperatures (Figure 5a-b). Interestingly, maximum crevice temperatures occurred mostly between 17h00 – 18h00 (Figure 5d), following maximum body temperatures.

### Seasonal differences in daily rhythms in free-living rock hyrax

#### *i) Periodicity*

Sunrise and sunset occurred at different times between the two seasons. This had an effect on the daily rhythms of rock hyrax in the different seasons. Sunrise occurred at 07h00 and sunset at 17h30 in winter producing a 10.5 L : 13.5D light cycle. The sunrise in summer occurred at 06h00 and sunset at 19h00 producing a 13 L : 11 D light cycle. These seasonal light cycles affected rock hyrax by increasing day length in summer and therefore increasing the above ground activity time.

ii) *Amplitude and mean*

Summer animals had a significantly higher mean 24-hour body temperature than winter animals (ANOVA:  $F_{1,114} = 90.74$ ,  $P < 0.05$ ). The mean body temperature of rock hyrax for winter was  $0.36^{\circ}\text{C}$  lower than summer (Table 1 and 2).

Both mean minimum and maximum body temperatures of rock hyrax were significantly different between the seasons (ANOVA of  $T_b$  min,  $F_{1,114} = 17.97$ ,  $P < 0.00001$ ;  $T_b$  max,  $F_{1,114} = 42.38$ ,  $P < 0.000$ ). There was however, no significant difference between the mean ranges of summer and winter body temperatures of rock hyrax.

Although mean maximum day body temperatures were significantly different between the seasons, mean maximum night body temperatures did not differ. Consequently despite the mean daily body temperatures being maintained at different levels (Figure 6), body temperature fluctuated by a similar amount in each season.

iii) *Hourly differences*

Body temperatures of rock hyrax during summer differed significantly with result to time (ANOVA:  $F_{1,4606} = 89.76$ ,  $P < 0.00$ ; Figure 7a). A Post hoc Scheffé test indicated that body temperature between 14h00 – 20h00 was significantly different from the morning hours of the day (00h00 – 12h00) and the evening (21h00 – 23h00). Winter body temperatures also differed significantly with respect to time (ANOVA:  $F_{3,5705} = 160.52$ ,  $P < 0.05$ ; Figure 7b). A Post hoc Scheffé test showed that body temperature between hours 06h00 and 07h00 was significantly different from 00h00 – 03h00, 13h00 – 18h00 and 21h00 – 23h00. It also showed that during the early morning (00h00 – 05h00) body

temperature was significantly different to mid-morning through to early evening hours (10h00 – 18h00). The midday to early evening hours (13h00 – 17h00) body temperatures were significantly different from early morning hours (00h00 – 11h00) and the evening hours (18h00 – 23h00).

In both winter and summer, the body temperature of rock hyrax started to increase prior to the onset of light, peaking at sunrise (Figure 7a-b). After reaching a peak at the onset of light, body temperature decreased steadily and became fairly constant between 11h00 and 14h00 in summer, but increasing substantially after 10h00 in winter (Figure 7b). The late afternoon peak tended to be much higher than the morning peak. In winter, body temperatures rose from approximately 36.5°C at 10h00 to a peak of approximately 37.8°C between 14h00 - 17h00 (Figure 7a). Summer body temperatures only started to rise only from 14h00 ( $\pm 37^\circ\text{C}$ ) and reached a peak of approximately 37.6° C between 16h00 and 19h00 (Figure 7b). Following the late afternoon/evening peaks, and prior to the morning peaks, a period of reduced body temperature occurred in both seasons.

### Environmental temperatures

Seasonally, both ambient temperature and crevice temperatures showed definite daily cycles. Overall ambient temperatures experienced in summer ranged by 23.27°C from a minimum of 18.79°C to a maximum of 42.06°C. Winter ambient temperatures fluctuated by 19.79°C from 5.34°C to 25.13°C. Crevice temperatures during winter showed similar fluctuations with similar minimum and maximum temperatures (Table 3). Overall crevice temperatures in summer, showed much lower fluctuations than ambient temperature, fluctuating by only 9.8°C (Table 3).

Mean daily crevice temperatures fluctuated by 5.15°C in summer and 5.10°C in winter, whereas mean ambient temperatures outside the crevices fluctuated between 13.67°C in summer and 7.65°C in winter (Table 4). Both the mean ambient and crevice temperatures were significantly higher in summer than in winter (ANOVA ambient  $T_a$ :  $F_{1,14} = 68.80$ ,  $P < 0.001$ ; crevice  $T_a$ :  $F_{1,14} = 101.93$ ,  $P < 0.001$ ). Although there was a significant difference in the mean range in ambient temperature between the two seasons (ANOVA,  $F_{1,14} = 6.07$ ,  $P < 0.05$ ), there was no significant difference in the mean range of crevice temperatures between summer and winter (Table 4). The mean day and night ranges in crevice temperature were not significantly different between winter and summer. In winter the only significant difference in crevice temperature was between the mean maximum and minimum temperatures (independent t-test:  $t = 7.47$ ,  $df = 9$ ,  $P < 0.001$ ). Summer crevice temperatures displayed differences between day and night mean maximum temperatures (independent t-test:  $t = 5.45$ ,  $df = 9$ ,  $P < 0.001$ ).

In winter there was no significant difference between mean air temperatures and crevice temperatures. However, in summer crevice temperatures were nearly always significantly lower than ambient temperatures, with no significant difference displayed in mean night ranges (Table 4). This indicates that the use of crevices may be far more important for thermoregulation in summer than in winter.

#### Body temperature and ambient temperature

There was no correlation between body temperature of rock hyrax and ambient temperature in either winter (linear regression:  $R^2 = 0.02$ ,  $F_{1,3811} = 76.92$ ,  $P < 0.05$ ) or in summer (linear regression:  $R^2 = 0.02$ ,  $F_{1,864} = 12.70$ ,  $P < 0.0039$ ). Although there was no

linear relationship between ambient and body temperature during winter, the body temperature appears to follow the same trajectory as the ambient temperature, both peaking between 11h00 and 18h00 (Figure 7a). In summer however, there does not appear to be a clear tracking of body temperature with ambient temperature (Figure 7b). The body temperature peaks at a later hour than the ambient temperature peak.

As shown earlier, both ambient and crevice temperatures undergo daily cycles. Crevice temperatures exhibit less variation than ambient temperatures (Figure 8a-b). The thermoneutral zone of the rock hyrax has a span over the ranges of 20-30°C (McNairn and Fairall 1984). In winter, both the ambient temperature outside the crevice and the crevice temperature rarely reached temperatures inside the thermoneutral zone of the rock hyrax (Figure 8a). In summer, air temperatures were only found within the thermoneutral zone at night and during the early morning (Figure 8b). Between 09h00 and 22h00 ambient temperatures outside the crevice often exceeded the thermoneutral zone while crevice temperatures remained within the thermoneutral zone throughout the day (Figure 8b).

## **Discussion**

The climatic conditions experienced by rock hyrax in this study showed large daily fluctuations both in summer and winter. The summer varied from mild nights to very hot days (18.79 – 42.06°C), whereas the winter showed fluctuations between cold nights and warm days (5.34 – 25.13°C). The selected use of rock crevices by rock hyrax is thought to be an adaptation to escape the temperature extremes experienced in their natural environment (Sale 1970; Hoek 1975). The availability of stable microclimatic refugia

would thus allow rock hyrax to maintain fairly constant body temperatures when the outside temperature went above the upper critical limit of their thermoneutral zone. The rock crevices were found to fluctuate to a much lower degree (9.8°C and 7.65°C in winter and summer respectively) than the outside environmental temperatures. Although outside ambient temperatures often exceeded the thermoneutral zone of rock hyrax during summer (McNairn and Fairall 1984), crevice temperatures were found to fall within the thermoneutral zone. Winter crevice temperatures fluctuated by similar amounts to outside temperatures and mostly fell below the rock hyrax thermoneutral zone. Rock crevice temperatures measured in this study fluctuated by a greater degree than those found in closed soil burrow systems (Bennett et al. 1988; Fielden et al. 1992).

The isolated nature of their rocky habitats further accentuates the unfavourable conditions experienced by rock hyrax. Coupled with extreme temperature fluctuations are limited water supply and a sub-optimal diet (Rübsamen et al. 1982; McNairn and Fairall 1984). Although rock hyrax had free access to water (a river flowed about 100 metres from rock crevices) in the present study, both the quantity and quality of the diet was considerably reduced during winter (they consumed large proportions of *Syringa* bark). Thus, during winter rock hyrax have to contend with both low ambient temperatures and low digestibility of a poor quality diet. When food quality is low, thermoregulation at low ambient temperatures becomes costly (Pereira et al. 2002).

Despite the large fluctuations in the environment, rock hyrax body temperatures fluctuated overall by 4.5°C in winter and 6°C in summer. However, in this study the fluctuations in body temperature measured in their natural environment showed a greater range than found in laboratory studies (Taylor and Sale 1969; Rübsamen et al. 1979;



Rübsamen and Kettembiel 1980; McNairn and Fairall 1984). This is surprising, since the rock hyraxes were able to utilize microhabitats and behaviour in their natural habitat, and therefore were expected to maintain body temperature at a fairly constant level. The large range in body temperature of rock hyrax in the field is not a consequence of substantial lowering of body temperature during the rest phase, but rather as a result of body temperatures reaching hyperthermic levels during the active phase. Louw et al. (1972) recorded on one occasion the range of one individual to be 6.7°C after exposure to extremely high ambient temperatures in the laboratory.

#### Winter body temperatures

Although rock hyrax showed lower mean nocturnal than diurnal body temperatures during winter, our studies showed that mean body temperatures were higher than those recorded in laboratory studies over similar ambient temperatures (McNairn and Fairall 1984). This difference is not a consequence of the rock hyrax escaping cold temperatures by utilizing rock crevices at night as was suggested by Yom-Tov (1993). Crevice temperatures during winter showed little deviation from the ambient temperatures outside the crevices and very rarely fell within the thermoneutral zone of the rock hyrax (Table 2 a-b). It is therefore unlikely that the rock crevices are the distinguishing factor causing the discrepancy between laboratory and field results. Rock crevices are therefore not likely to play a thermoregulatory role during winter but rather have advantages in predator avoidance and escaping from wet and windy conditions.

The lowest body temperature recorded in rock hyrax in winter was 34.5°C, which is higher than that recorded in the laboratory (McNairn and Fairall 1984). This suggests

that rock hyrax may be utilizing a different form of thermoregulatory response to maintain fairly constant body temperatures under low ambient temperatures. When individuals were provided with artificial 'crevices' in the laboratory, rock hyraxes were found to huddle together under low ambient temperatures (Sale 1970). Huddling of individuals reduces the surface area to which they can lose heat to their surroundings and thereby reduces energy expenditure during the rest phase (Weatherhead et al. 1985). The social behaviour of rock hyrax may, therefore, play a significant role in thermoregulation during cold winter nights. Further research is required both in the field and the laboratory to further substantiate this.

During winter the body temperature of rock hyrax was highest just before retreating to the rock crevices for the night. It appears that rock hyraxes store heat when animals are subjected to the high external temperatures and during activity. When individuals retreat into the crevices their high body temperatures started to decrease possibly as a consequence of the lower temperatures of the crevice. This also appears to raise the temperatures of the crevice, thereby resulting in a lower temperature differential between the rock hyrax and the crevice.

Mean daily winter body temperatures of rock hyrax in the field were lower than during summer. Mean body temperatures were maintained at a lower level during winter than summer throughout most of the day. Only between 13h00 and 17h00 did winter body temperatures reach similar levels to summer body temperatures (Figure 6) after a period of basking (personal observation, Chapter 4). Laboratory results have also shown that rock hyrax maintain lower body temperatures at lower ambient temperatures (McNairn and Fairall 1984). The ability to maintain a low body temperature under

conditions of cold stress clearly confers energetic benefits, since less energy is required to maintain an elevated body temperature.

### Summer body temperatures

As mentioned above rock hyrax display a very different thermoregulatory response in summer compared to winter. Higher body temperatures recorded in summer are as a result of the ambient temperatures lying within the thermoneutral zone of the rock hyrax and, therefore, no energy conserving mechanisms are required. However, rock hyrax experienced outside ambient temperatures of over 35°C on most summer days. High ambient temperatures not only causes body temperatures to rise but also increases water loss through evaporation. For an animal that has a low daily water intake (predominantly from the diet), evaporative water loss may be costly to the organism and only a short-term mechanism (Louw et al. 1972; Meltzer 1976; Rübsamen et al. 1979).

The highest ambient temperature recorded during our study period was 42°C. Laboratory studies have shown that rock hyrax increase their body temperature with an increase in ambient temperature (Rübsamen and Kettembeil 1980). Body temperature was recorded to reach lethal limits at ambient temperatures of just under 40°C (Louw et al. 1972). Rock hyrax must, therefore, have some thermoregulatory response to avoid direct exposure to these high ambient temperatures.

Taylor and Sale (1969) suggest that rock hyrax select their thermal environment so as to avoid increasing evaporative water loss to keep cool. Extreme heat has been found to force rock hyrax to retreat to their crevices (Hoek 1975). Throughout the summer period crevice temperatures were fairly constant and never reached temperatures

above the upper critical limit of the thermoneutral zone of the rock hyrax. Body temperatures remained fairly constant throughout the period of maximum ambient temperatures indicating that rock hyrax are probably utilizing the crevices as protective microhabitats to avoid the stress of extreme temperatures and low humidity during the hottest parts of the day. It therefore appears that rock crevices are primarily used for thermoregulation during summer rather than winter.

The body temperatures of rock hyrax in summer peaked between 16h00 and 19h00 that coincided with the most intensive period of feeding (Hoek 1975). During this period body temperature fluctuated slightly, this may be because rock hyraxes shuttle between rock crevices and feeding sites. Body temperatures apparently reach a maximum through heat storage, which is then dissipated fairly quickly in the cooler crevices due to the high temperature gradient between their bodies and the crevice. Body temperature would be reduced with a minimal loss of water (Sale 1970). Rock hyraxes were seen to feed for short periods during the hotter parts of the day (13h00 to 15h00) (personal observation, Chapter three). During this period both individuals during the summer showed alternate hourly minimum and maximum body temperatures. It is possible that the rock hyrax use this shuttling behaviour to ensure that their body temperature never reaches lethal limits.

#### Daily phase and period

The onset of the active phase in most mammals is often regulated by light intensity (Decoursey and Menon 1991). Often, however, other factors such as temperature and

food availability or a combination of factors may act as stimuli for increased heat production at the onset of the active phase (Enright 1970).

Rock hyraxes spend the nocturnal hours deep within rock crevices. It is not known what factor stimulates the onset of the active phase in rock hyrax in their natural habitat. The active phase in both winter and summer was chosen in this study to begin at sunrise. Sunrise occurred before any emergence of individuals from the rock crevices. However it did become fairly light before the sun had risen.

Body temperature started to increase from about 02h00 during both winter and summer. This occurs well before the onset of twilight or sunrise and therefore indicates that light may not be the dominant zeitgeber influencing the onset of the active phase. Body temperature increases steadily until it reaches a small peak at 07h00 during winter and between 05h00 and 06h00 during summer. Both of these peaks coincided with sunrise. Sunrise may, therefore, be a stimulus for rock hyrax to emerge from their crevices. Endogenous heat production from about 02h00 may be necessary to heat body temperature just sufficiently enough to allow them to emerge from the crevices at sunrise. However, more research is required on the mechanisms used. More data is required from other small free ranging mammals to determine if this is a common trend.

The commencement of body temperature heating seems to coincide with the beginning of a decrease in ambient temperature and reaches a maximum when ambient temperature reaches a minimum. The stimulus for the onset of the active phase may, therefore, in fact be temperature or a combination of temperature and light.

### Control of thermoregulation

The wide range of body temperatures recorded in rock hyrax appears to have energy conservation benefits in winter and water saving benefits during summer. Reduced energetic costs during winter are as a result of a drop in body temperature with little or no increase in metabolic rate at lower ambient temperatures (McNairn and Fairall 1979; McNairn and Fairall 1984). Taylor and Sale (1969) showed that *Procavia capensis* only started increasing oxygen consumption at ambient temperatures below 15°C. At high ambient temperatures rock hyrax allow their body temperatures to increase until they develop hyperthermia at temperatures above 35°C. It is only at these temperatures that rock hyrax exhibit any form of evaporative cooling (Louw et al. 1972).

It is possible that rock hyrax utilize a two-tier thermoregulatory control (Bligh 1966), which displays both a narrow and wide band of body temperature control. The wide band control is controlled endogenously when the fine thermoregulatory control (behaviour) fails to maintain body temperature between certain limits. The practicality of this is that the fine control allows the animal to maintain a body temperature close to an optimum by means of an energetically cheap mechanism, that being behaviour.

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Table 1: Comparison of mean, minimum and maximum daily, active phase ( $\alpha$ ), and rest phase ( $\rho$ ) body temperatures ( $^{\circ}\text{C}$ ) in four free-living rock hyrax during winter (2002).

	Individual A	Individual B	Individual C	Individual D	Average
Mass (kg)	4.35	3.2	2.85	2.45	$3.21 \pm 0.41$
$T_b$ minimum	$35.87 \pm 0.11$	$35.29 \pm 0.11$	$35.36 \pm 0.14$	$36.08 \pm 0.08$	$35.64 \pm 0.07$
$T_b$ maximum	$38.26 \pm 0.07$	$38.47 \pm 0.07$	$37.96 \pm 0.16$	$38.17 \pm 0.11$	$38.23 \pm 0.05$
$T_b$ average	$36.95 \pm 0.06$	$36.75 \pm 0.04$	$36.66 \pm 0.05$	$36.96 \pm 0.04$	$36.83 \pm 0.03$
$R_t$	$2.39 \pm 0.11$	$3.18 \pm 0.15$	$2.61 \pm 0.24$	$2.08 \pm 0.12$	$2.60 \pm 0.09$
$\alpha T_b$ min	$36.13 \pm 0.09$	$35.53 \pm 0.12$	$35.32 \pm 0.15$	$36.38 \pm 0.09$	$35.85 \pm 0.08$
$\rho T_b$ min	$36.13 \pm 0.14$	$35.74 \pm 0.11$	$36.07 \pm 0.10$	$36.38 \pm 0.09$	$36.03 \pm 0.07$
$\alpha T_b$ max	$38.20 \pm 0.06$	$38.47 \pm 0.06$	$38.04 \pm 0.12$	$38.17 \pm 0.11$	$38.23 \pm 0.05$
$\rho T_b$ max	$37.88 \pm 0.11$	$37.95 \pm 0.13$	$37.50 \pm 0.09$	$37.50 \pm 0.09$	$37.73 \pm 0.06$
$\alpha T_b$ average	$37.13 \pm 0.06$	$37.11 \pm 0.05$	$36.73 \pm 0.06$	$37.31 \pm 0.07$	$37.07 \pm 0.04$
$\rho T_b$ average	$36.82 \pm 0.07$	$36.47 \pm 0.07$	$36.55 \pm 0.07$	$36.74 \pm 0.05$	$36.76 \pm 0.05$
$\alpha R_t$	$2.08 \pm 0.10$	$2.95 \pm 0.14$	$2.71 \pm 0.20$	$1.79 \pm 0.16$	$2.39 \pm 0.09$
$\rho R_t$	$1.68 \pm 0.13$	$2.21 \pm 0.16$	$1.43 \pm 0.10$	$1.25 \pm 0.12$	$1.70 \pm 0.09$

Table 2: Comparison of mean, minimum and maximum daily, active phase ( $\alpha$ ), and rest phase ( $\rho$ ) body temperatures ( $^{\circ}\text{C}$ ) in two free-living rock hyrax during summer (2003).

	Individual A	Individual B	Average
Mass (kg)	3.35	1.95	$2.65 \pm 0.70$
$T_b$ minimum	$36.20 \pm 0.09$	$35.96 \pm 0.13$	$36.08 \pm 0.08$
$T_b$ maximum	$38.98 \pm 0.12$	$38.70 \pm 0.09$	$38.84 \pm 0.08$
$T_b$ average	$37.25 \pm 0.03$	$37.13 \pm 0.03$	$37.19 \pm 0.02$
$R_t$	$2.78 \pm 0.18$	$2.74 \pm 0.18$	$2.76 \pm 0.13$
$\alpha T_b$ min	$36.30 \pm 0.10$	$35.96 \pm 0.13$	$36.13 \pm 0.08$
$\rho T_b$ min	$36.52 \pm 0.07$	$36.56 \pm 0.08$	$36.54 \pm 0.05$
$\alpha T_b$ max	$38.98 \pm 0.12$	$38.70 \pm 0.09$	$38.84 \pm 0.08$
$\rho T_b$ max	$37.67 \pm 0.09$	$37.54 \pm 0.06$	$37.60 \pm 0.06$
$\alpha T_b$ average	$37.34 \pm 0.03$	$37.24 \pm 0.04$	$37.29 \pm 0.02$
$\rho T_b$ average	$37.11 \pm 0.04$	$36.99 \pm 0.04$	$37.05 \pm 0.03$
$\alpha R_t$	$2.69 \pm 0.19$	$2.74 \pm 0.18$	$2.71 \pm 0.13$
$\rho R_t$	$1.15 \pm 0.10$	$0.98 \pm 0.07$	$1.06 \pm 0.06$

Table 3: Comparison of the, minimum and maximum daily, active phase ( $\alpha$ ), and rest phase ( $\rho$ ) ambient temperatures ( $^{\circ}\text{C}$ ) inside and outside of rock crevices during summer and winter experienced by the rock hyrax.

	SUMMER		WINTER	
	Ambient	Crevice	Ambient	Crevice
$T_a$ minimum	18.79	18.2	5.34	6.25
$T_a$ maximum	42.06	28	25.13	21.94
$R_t$	23.27	9.8	19.79	15.69
$\alpha T_a$ min	19.38	18.2	5.34	6.25
$\rho T_a$ min	18.79	18.93	5.34	6.46
$\alpha T_a$ max	42.06	28.00	25.13	21.94
$\rho T_a$ max	34.80	27.36	20.93	20.2
$\alpha R_t$	22.58	9.8	19.79	15.69
$\rho R_t$	16.01	8.43	15.59	13.74

Table 4: Comparison of mean minimum, maximum and range of daily, active phase ( $\alpha$ ), and rest phase ( $\rho$ ) ambient temperatures ( $^{\circ}\text{C}$ ) inside and outside of rock crevices during summer ( $n = 8$  days) and winter ( $n = 10$  days) as experienced by rock hyrax.

	SUMMER		WINTER	
	Ambient	Crevice	Ambient	Crevice
$T_a$ minimum	$20.69 \pm 0.55$	$19.64 \pm 0.44$	$8.36 \pm 0.91$	$8.47 \pm 0.89$
$T_a$ maximum	$34.36 \pm 2.16$	$24.79 \pm 0.79$	$16.01 \pm 1.90$	$13.57 \pm 1.40$
$T_a$ average	$26.60 \pm 1.15$	$22.45 \pm 0.59$	$11.53 \pm 1.58$	$11.52 \pm 1.02$
$R_t$	$13.67 \pm 1.88$	$5.15 \pm 0.49$	$7.65 \pm 1.16$	$5.10 \pm 0.68$
$\alpha T_a$ min	$21.50 \pm 0.66$	$20.23 \pm 0.57$	$9.28 \pm 1.26$	$9.52 \pm 1.14$
$\rho T_a$ min	$21.34 \pm 0.65$	$20.15 \pm 0.46$	$9.07 \pm 0.97$	$9.33 \pm 0.91$
$\alpha T_a$ max	$34.36 \pm 2.16$	$24.79 \pm 0.79$	$16.01 \pm 1.90$	$13.58 \pm 1.39$
$\rho T_a$ max	$28.87 \pm 1.57$	$24.10 \pm 0.84$	$14.18 \pm 1.56$	$12.63 \pm 1.07$
$\alpha T_a$ average	$28.45 \pm 1.38$	$22.86 \pm 0.66$	$13.13 \pm 1.60$	$12.07 \pm 1.20$
$\rho T_a$ average	$24.40 \pm 0.96$	$21.96 \pm 0.55$	$11.18 \pm 1.16$	$11.09 \pm 0.90$
$\alpha R_t$	$12.86 \pm 2.06$	$4.56 \pm 0.50$	$6.73 \pm 1.08$	$4.06 \pm 0.62$
$\rho R_t$	$7.53 \pm 1.20$	$3.95 \pm 0.60$	$5.11 \pm 0.74$	$3.30 \pm 0.46$

### Figure legends

Figure 1a-d: Double daily plots of body temperature in four free-living rock hyraxes during winter (n = 10 days), where 1a: Individual A, 1b: Individual B, 1c: Individual C and 1d: Individual D.

The dark horizontal bars on top indicated the dark phase of the 24-hour daily rhythm. The body temperature scale ranges from 34°C to 41°C.

Figure 2a-b: Double daily plots of body temperature in two rock hyraxes during summer (n = 26 days), where 2a: Individual E and 2b: Individual F.

The dark horizontal bars on top indicated the dark phase of the 24-hour daily rhythm. The body temperature scale ranges from 33.5°C to 41°C.

Figure 3a-d: Frequency distributions of minimum and maximum body temperatures (°C) throughout winter of free-living rock hyrax where: 3a: Individual A, 3b: Individual B, 3c: Individual C and 3d: Individual D.

Figure 4: Frequency distributions of minimum and maximum ambient temperatures (°C) throughout winter experienced by rock hyrax, where 4a: Ambient temperatures outside crevices and 4b: Ambient temperatures inside crevices.

Figure 5a-b: Frequency distributions of minimum and maximum body temperatures (°C) in free-living rock hyrax throughout summer, where 5a: Individual E, 5b: Individual F.

Figure 5c-d: Frequency distributions of minimum and maximum ambient temperatures (°C) throughout summer, where 5c: Ambient temperatures outside the crevice and 5d: Ambient temperatures inside the crevice



Figure 6: Mean body temperatures ( $\pm$  SE) ( $^{\circ}$ C) of free-living rock hyrax for summer and winter throughout the day.

Figure 7: Mean daily body temperature ( $\pm$  SE) ( $^{\circ}$ C) of free-living rock hyrax and ambient temperatures ( $^{\circ}$ C) throughout the day, where 7a: Winter and 7b: Summer.

Figure 8a-b: Continuous ambient and crevice temperatures ( $^{\circ}$ C) experienced by rock hyrax measured over 7 days, where 8a: Winter and 8b: Summer. The thermoneutral zone (20-30 $^{\circ}$ C) in Figure 8a & 8b is taken from McNairn and Fairall (1984).

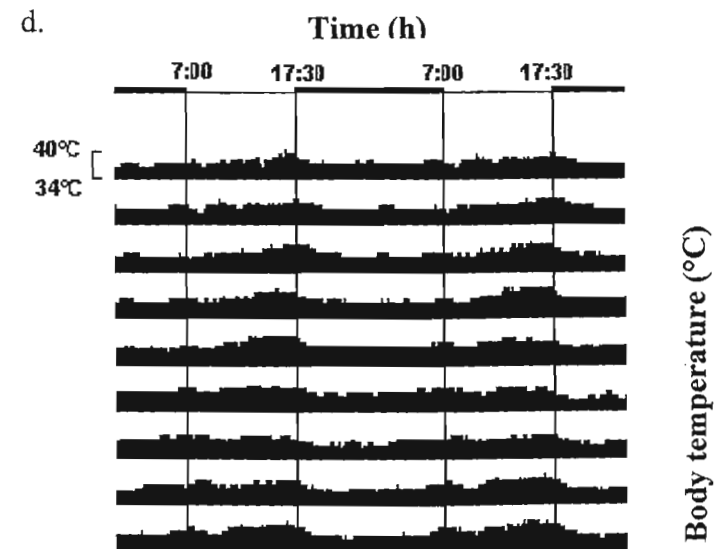
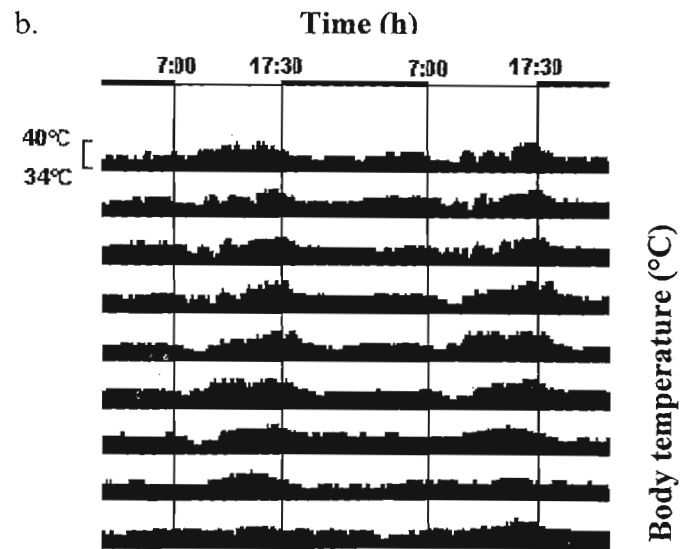
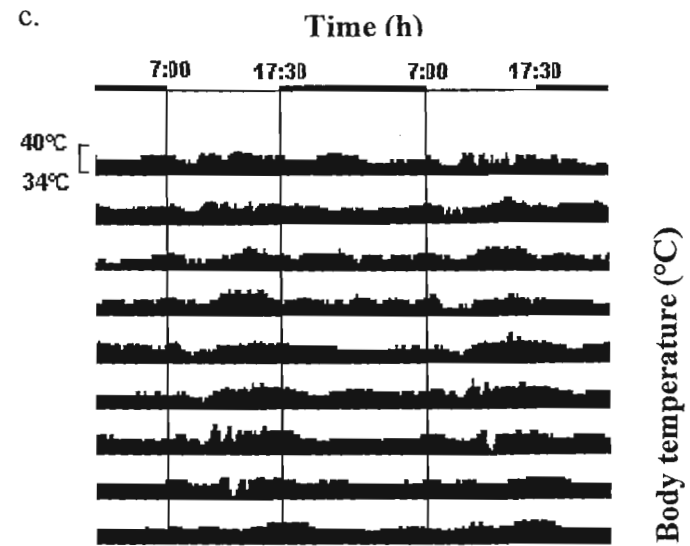
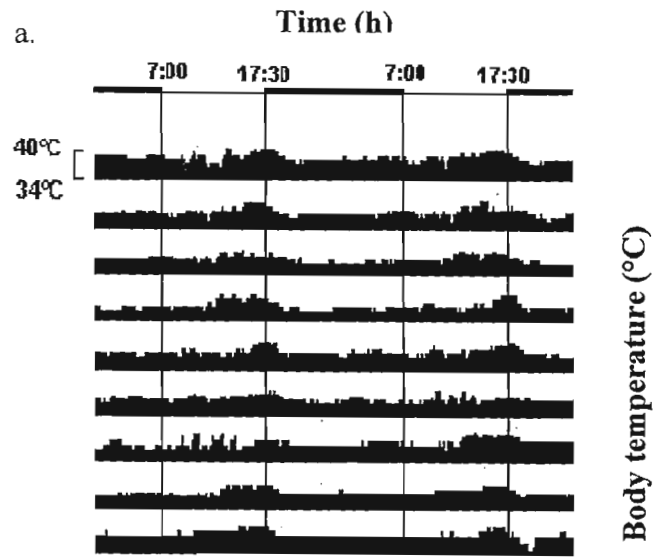


Figure 1

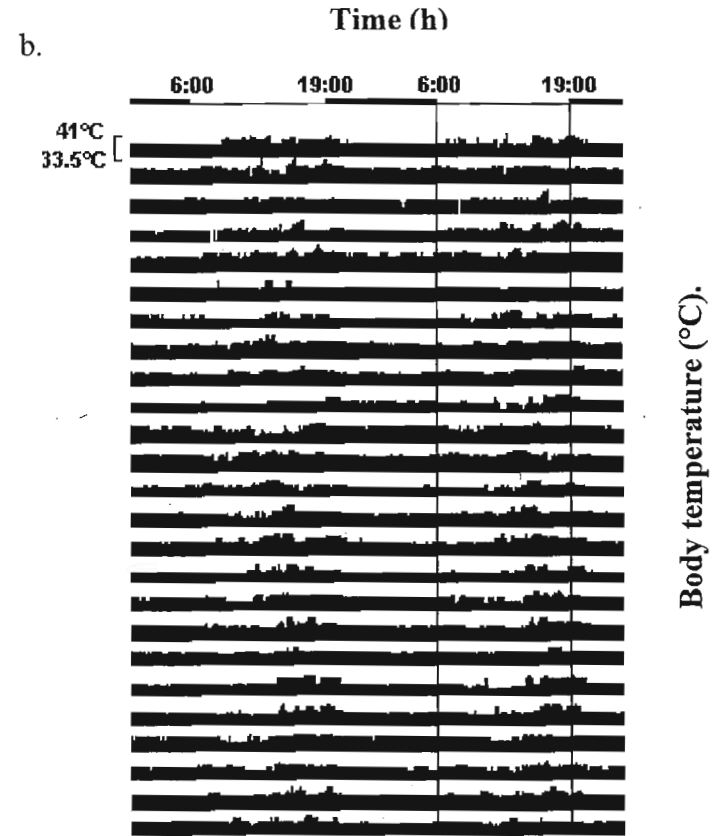
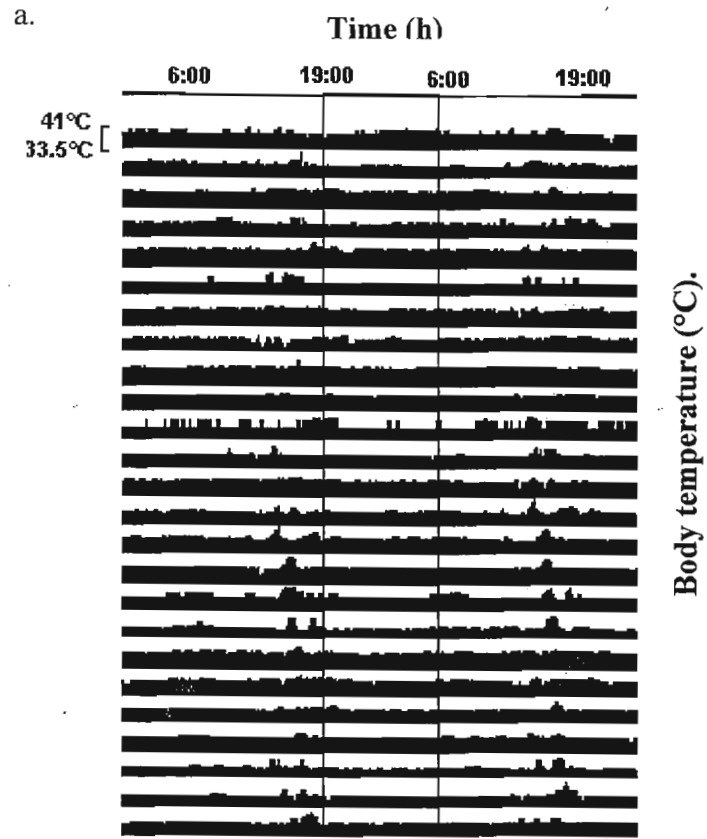


Figure 2

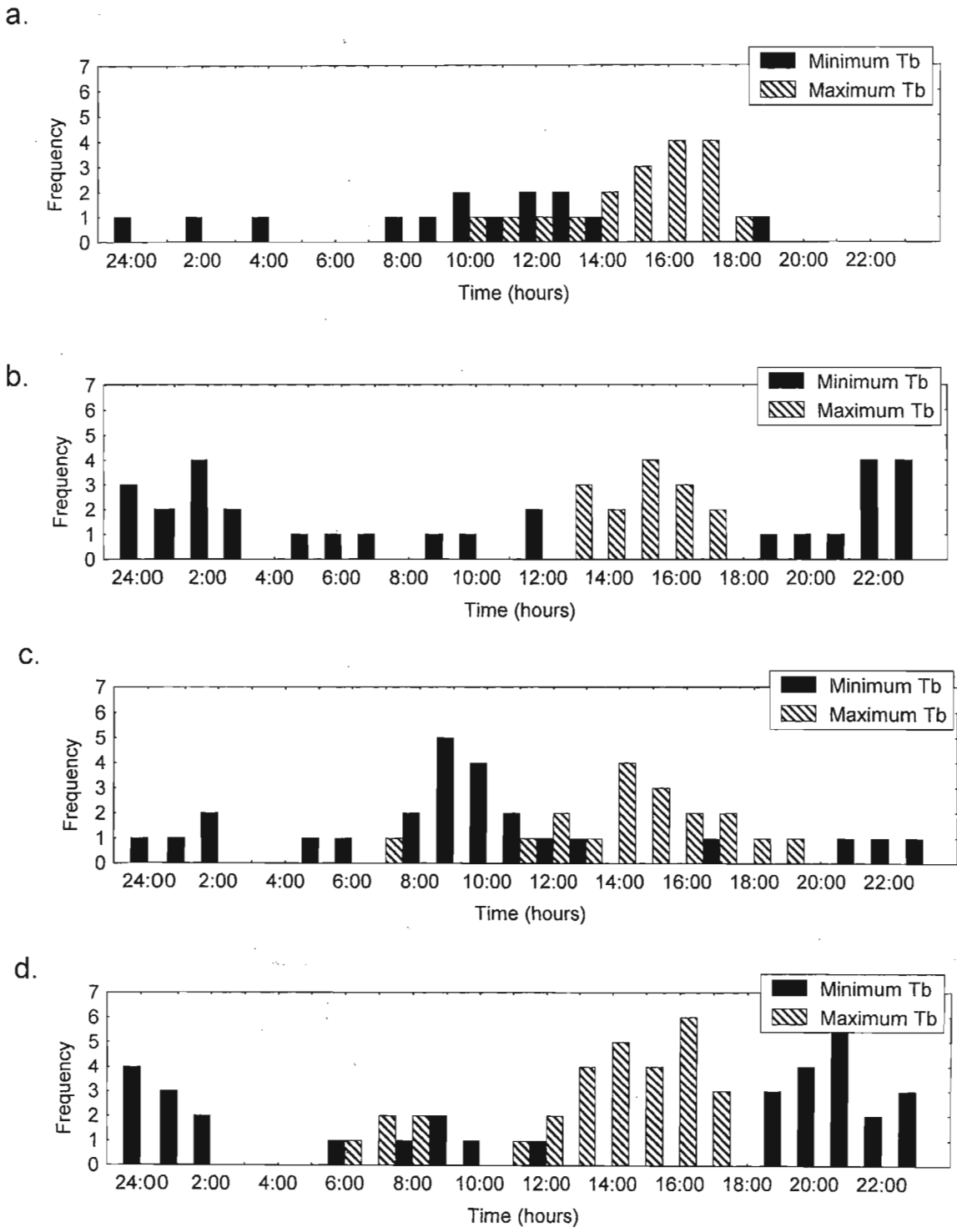
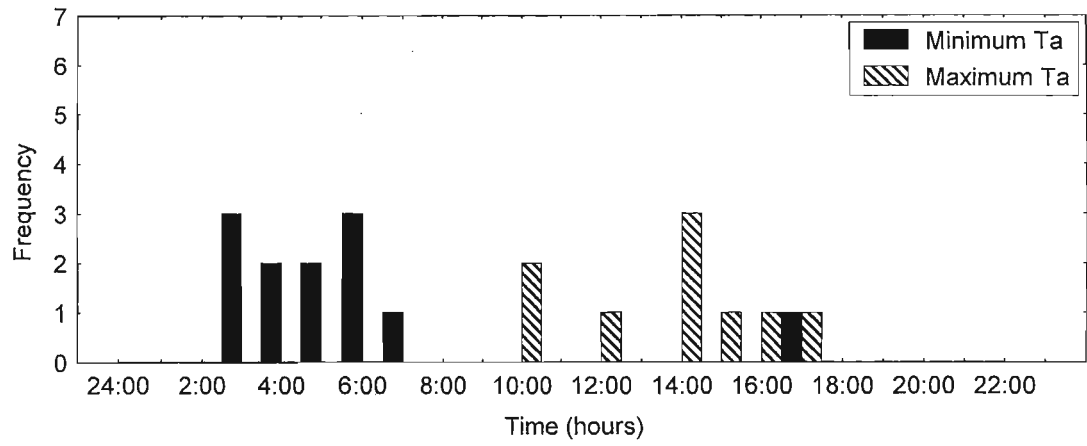


Figure 3

a.



b.

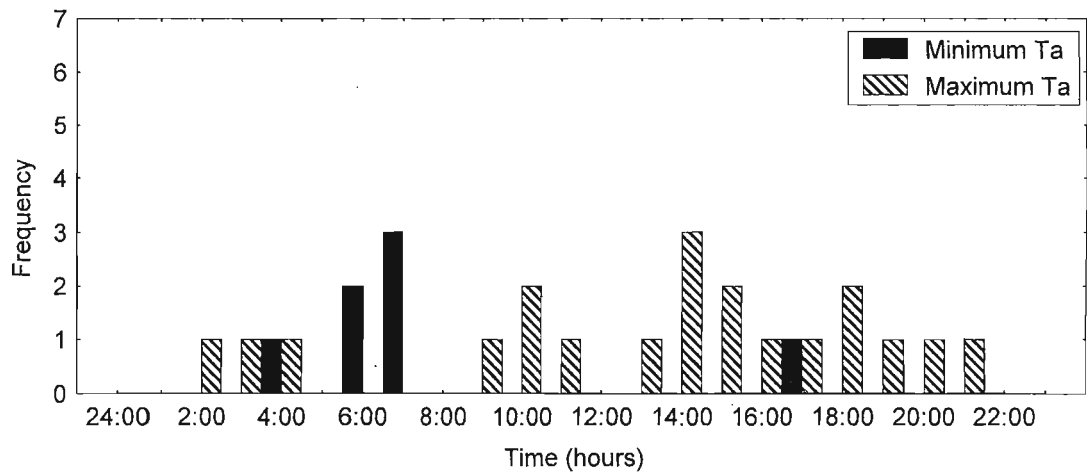


Figure 4

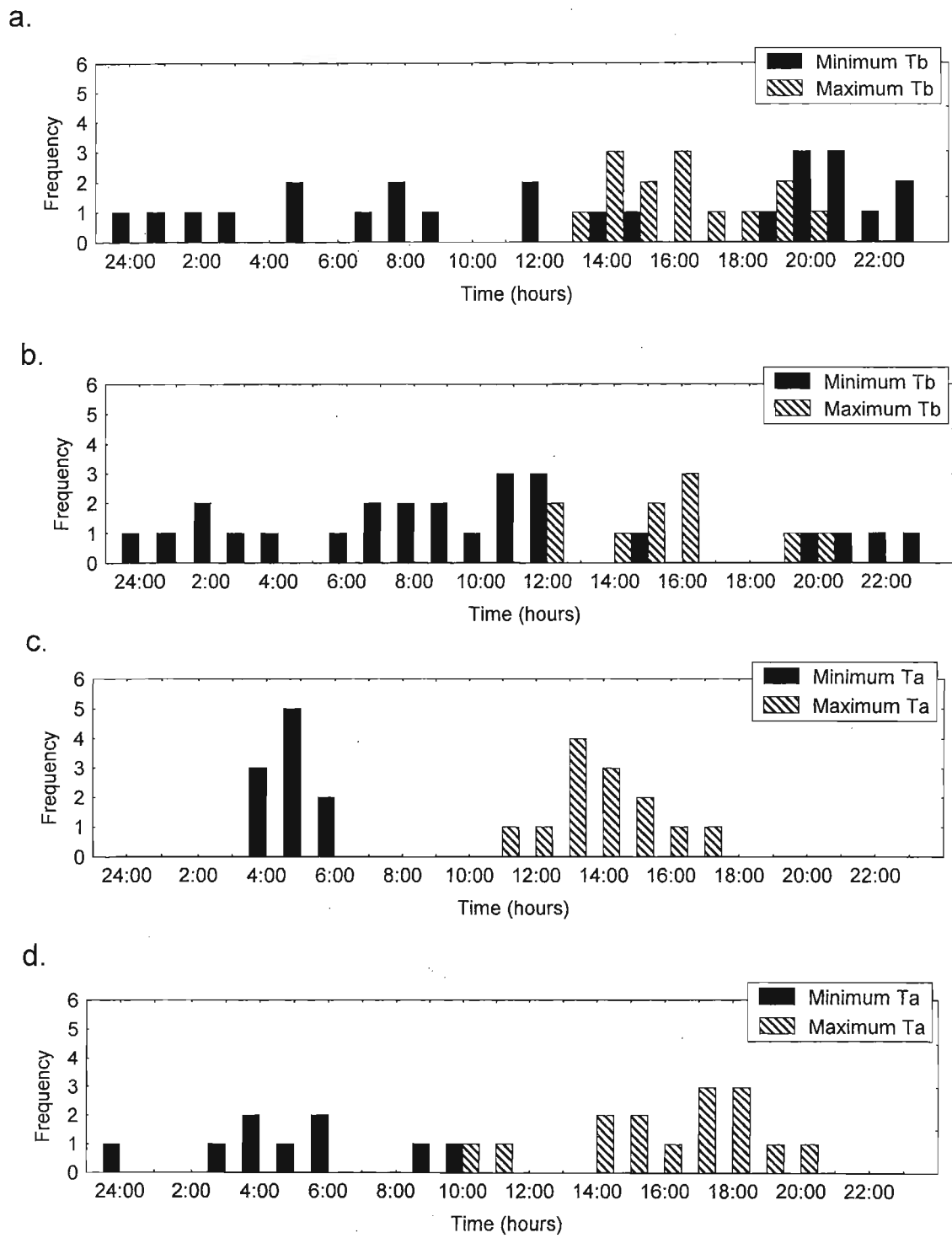


Figure 5

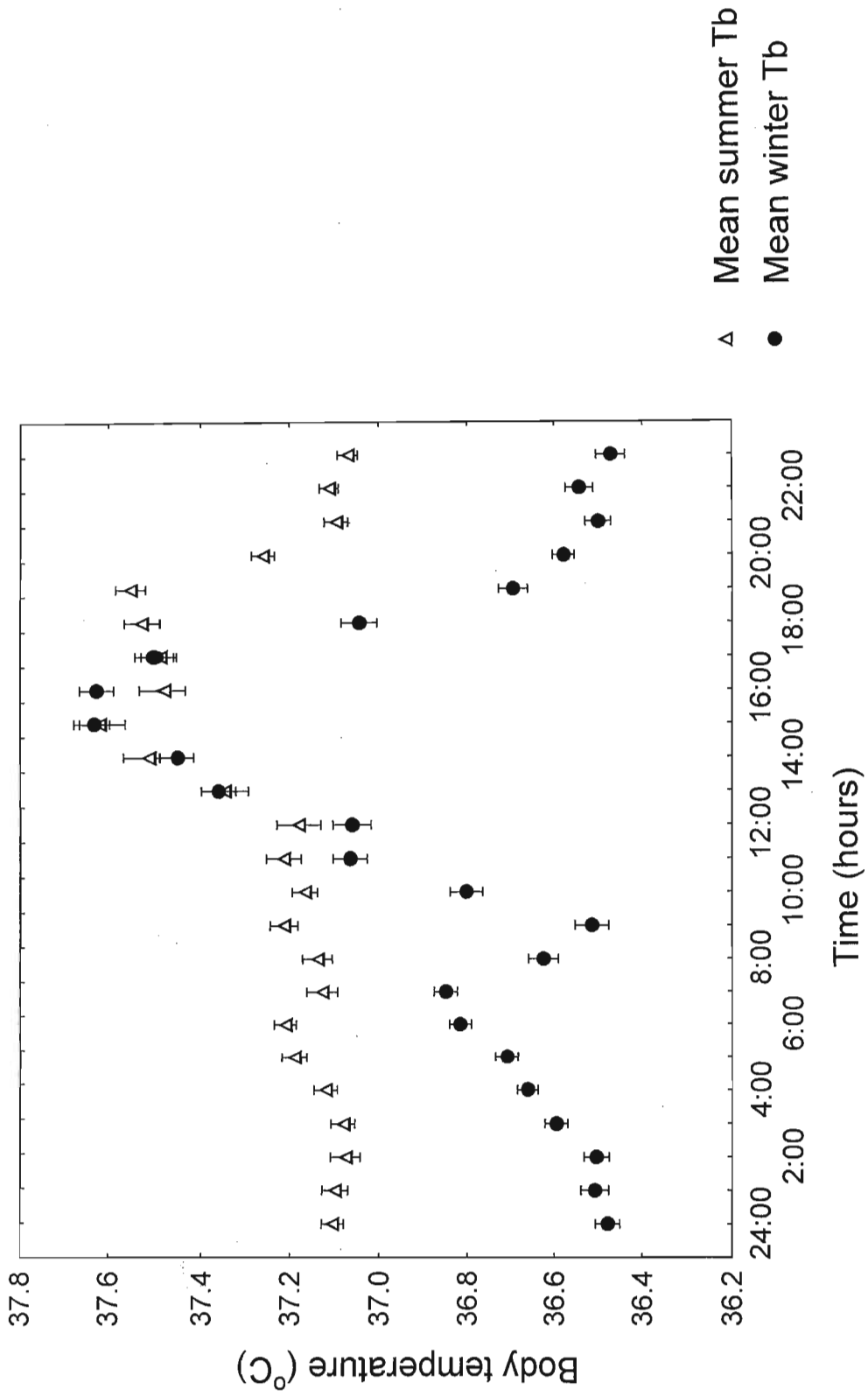


Figure 6

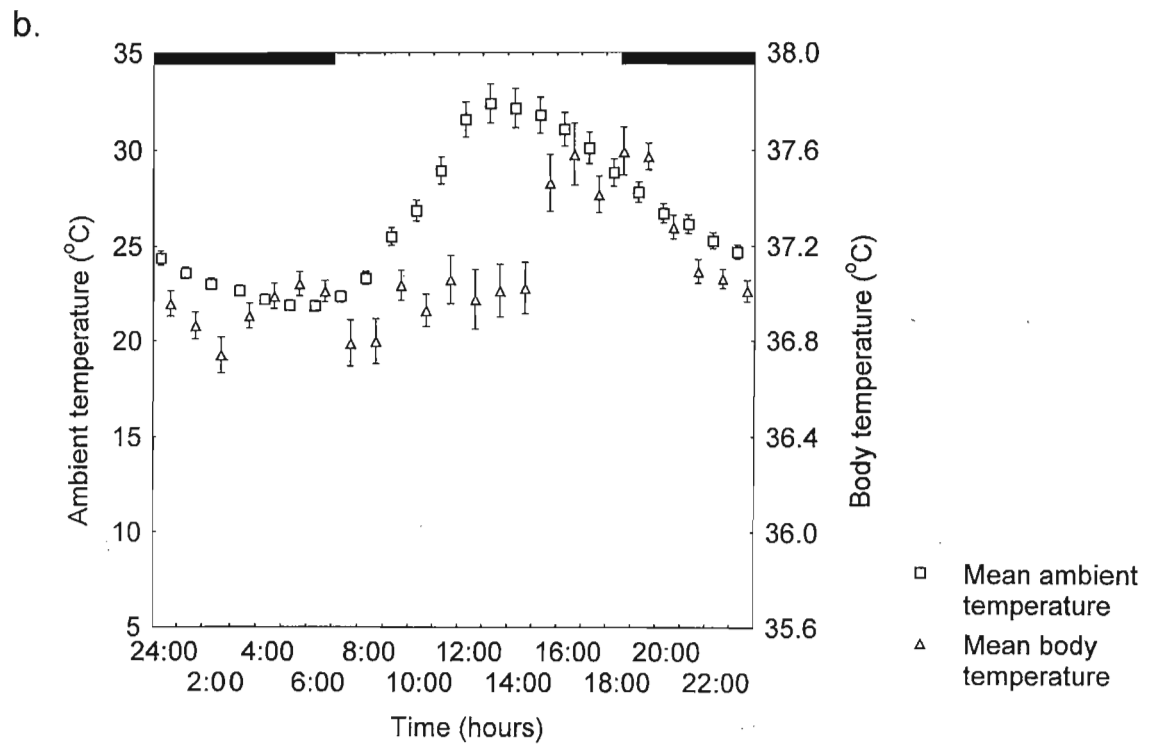
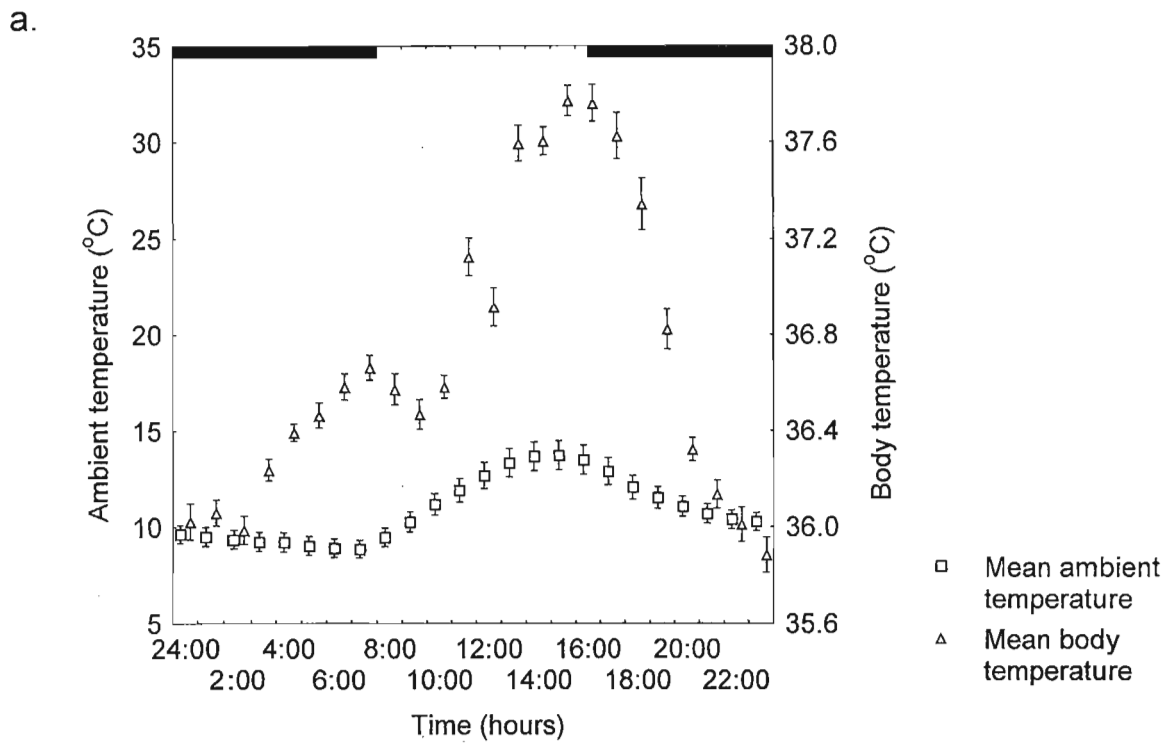
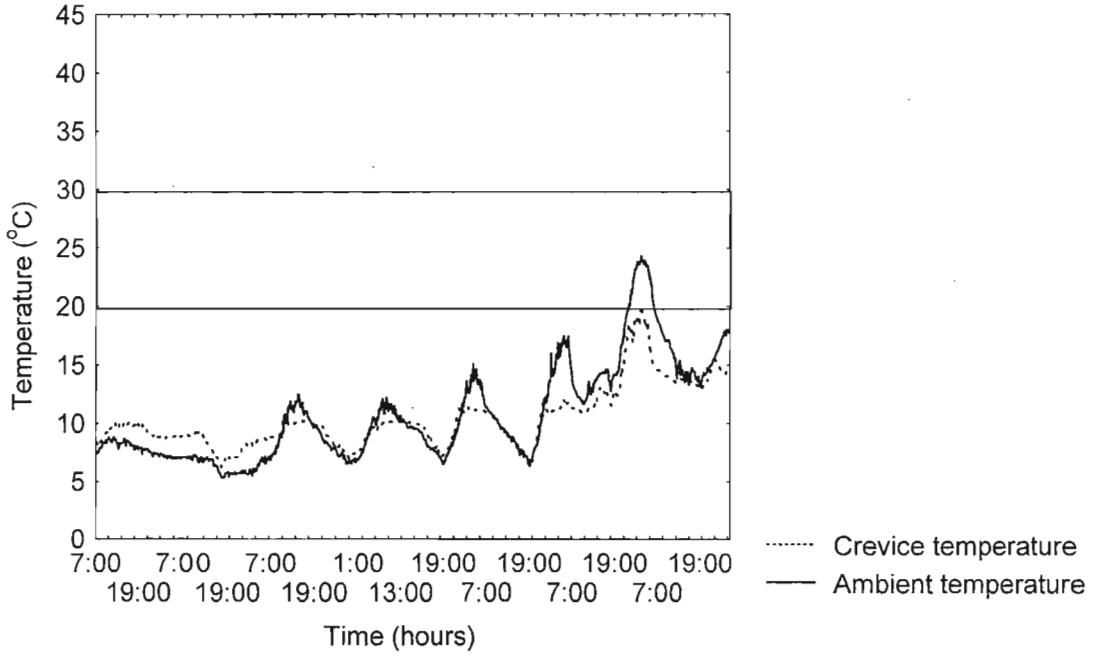


Figure 7



a.



b.

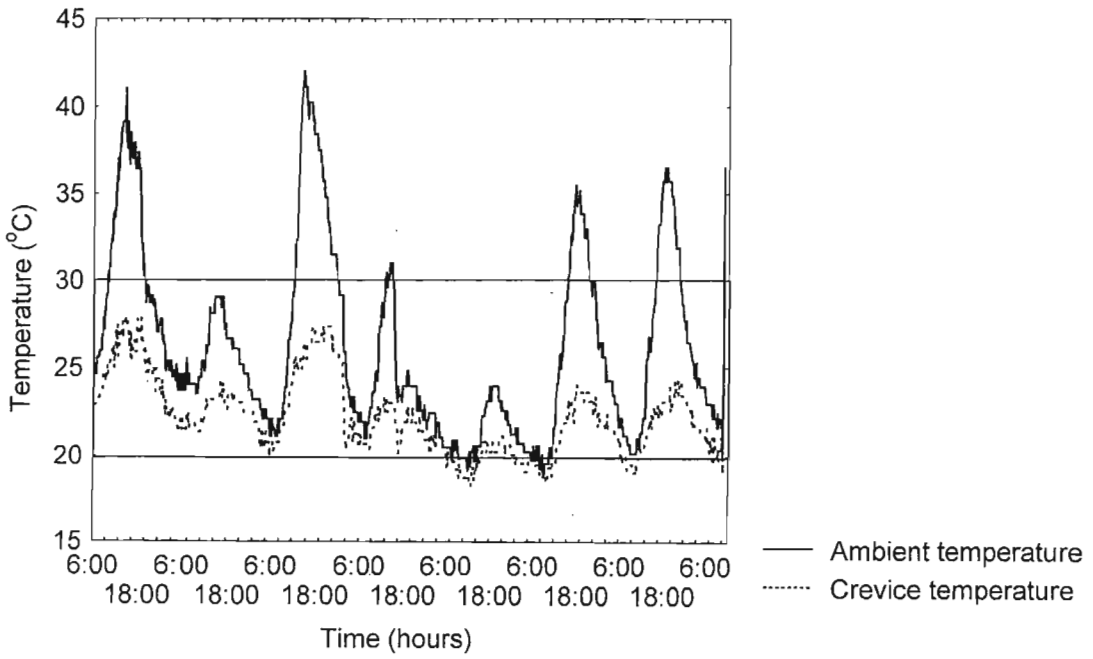


Figure 8

CHAPTER THREE  
SEASONAL BEHAVIOURAL PATTERNS OF FREE-LIVING ROCK HYRAX  
(*PROCAVIA CAPENSIS*)

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**Abstract**

The activity pattern of rock hyrax is not only related to the periodically changing environmental stimuli but also involves the physiological attributes of the animals. The activity pattern displayed by this species indicates how it is adapted to the conditions that prevail in its natural habitat.

Juvenile rock hyraxes have higher surface area to volume ratio and are more vulnerable to low ambient conditions than adults. As a result they display a slightly different behaviour pattern to adult rock hyrax during winter. They required larger amounts of food to meet their energetic requirements while adults spent greater amounts of time basking.

The behavioural utilization of rock crevices by rock hyrax was essential in avoiding harsh environmental conditions during summer. Foraging was the most dominant aboveground behaviour exhibited by rock hyrax during summer. Most ambient temperatures in the early morning of summer fell within the rock hyrax thermoneutral

zone, which enabled rock hyrax to forage without the need for prior heating from a solar energy source.

Basking was an essential behaviour displayed by rock hyrax in winter. The low quality and scarce food source may be inadequate to meet the metabolic requirements of rock hyrax at low ambient temperatures. It therefore appears that basking is not only an energy conservation mechanism but also essential for the survival of rock hyrax during winter.

The extent to which rock hyrax meet energetic requirements depends on the interaction of ambient temperature, food availability, food quality and foraging efficiency in the presence of predators. The extent to which each of these factors influences behaviour differed on a daily and seasonal basis.

## **INTRODUCTION**

The environment, which an animal inhabits, can influence the expression of its behaviour in such a way that different behaviour patterns are expressed under varying environmental conditions (Delany & Happold, 1979; Sharpe & Van Horne, 1999). Some behaviours may be suppressed or accentuated in response to varying environmental factors (Aschoff, 1966). Environmental conditions do not produce the activity pattern but rather entrains an already existent endogenous rhythm (Aschoff, 1966; Enright, 1970; Aschoff, 1982; Refinetti & Menaker, 1992). Behaviour is thus the result of an interaction between exogenous and endogenous factors.

The timing of mammalian behaviour is essential under field conditions and is usually an outcome of the internal endogenous rhythm (Enright, 1970). The periodicity of

activity under natural conditions usually approximates 24 hours and is often entrained by the periodicity of changes in light intensity (Ashby, 1971). Synchronizing activity with recurrent environmental conditions is advantageous to organisms as it enables them to anticipate seasonal changes (Enright, 1970; Rubal *et al.* 1992). It also ensures that organisms perform the appropriate activity in the right place at the right time of day or season (Enright, 1970). These factors have important consequences for fitness if the animal is to survive and reproduce successfully in its natural environment.

Terrestrial mammals may be classified as being diurnal (predominantly active during light phase), nocturnal (predominantly active during the dark phase) or crepuscular (active around dawn and dusk) (Woolley *et al.* 1991). It is essential that mammals are highly adapted to the conditions prevailing during these times, and use the whole of their activity time efficiently (Ashby, 1971). Various factors are important as determinants of activity patterns limiting organisms to different places at different times. Trade-offs between the cost of thermoregulation, foraging efficiency and predator avoidance often limit activity of mammals (Chappell, 1980; Chappell & Bartholomew, 1981; Lima & Dill, 1990; Hainsworth, 1995).

The variability in the thermal environment within and between microhabitats could strongly influence an organism's behavioural pattern (Turk & Arnold, 1988; Sharpe & Van Horne, 1999). Thermoregulation may be fairly costly to an animal and can have serious consequences on fitness. There is, therefore, a need for animals to limit the time spent in microhabitats where thermal equilibrium cannot be maintained (Sharpe & Van Horne, 1999).

For mammals the trade-off between foraging efficiency and cost of thermoregulation becomes particularly apparent in hot arid environments. The scarcity of both food and water provide energetic challenges to smaller mammals under extremely hot conditions. The hot desert surface often limits activity and therefore shortens valuable foraging time (Chappell & Bartholomew, 1981). Behavioural selection of thermal refugia often plays an important role in thermoregulation in these environments. Some small mammals display shuttling behaviour to balance foraging efficiency and thermoregulation (Chappell & Bartholomew, 1981; Hainsworth, 1995). Burrows provide cool surfaces where animals are able to transfer excessive heat loads through conduction following foraging expeditions and allow these organisms to extend surface activity in order to meet energetic demands (Chappell & Bartholomew, 1981; Hainsworth, 1995).

During cold nights refugia provide a buffer against low ambient temperatures and therefore reduce the amount of energy mammals require for thermoregulation (Chappell, 1981). Small mammals in desert environments escape the extreme heat of the day by being active at night (Fielden *et al.* 1990). This reduces evaporative water loss and may extend foraging times. There is, however, a cost to thermoregulation involved in nocturnal activity. Colder temperatures at night increase heat loss and although animals may be able to forage for longer periods, they have to consume larger quantities of food to thermoregulate efficiently (Chappell, 1980).

For many mammals, a trade-off between conflicting demands of foraging efficiency and predator avoidance may become important (MacWhirter, 1991). The balance between the profitability of foraging and predation risk may vary between habitats or patch type (Lima & Dill, 1990) and will determine the amount of time an

animal is active in each area. Predation risk may be influenced strongly by vegetative cover. This may vary between and within patches on a seasonal basis. Vegetative cover may provide concealment from predators and obstacles to pursuing predators (Wywiałowski, 1987).

In some cases body temperature may have a large impact on the locomotor abilities of animals. Many ectotherms and some endotherms are unable to forage efficiently or avoid predators unless their body temperatures are sufficiently high enough (Rodríguez-Gironés, 2002). Basking behaviour by many small mammals helps overcome nocturnal hypothermia and reduces the cost of endogenous heating (Geiser *et al.* 2002). This becomes increasingly important when they are thermally challenged and food supplies are low and patchy. Basking in the sun speeds up the re-warming process to a level that permits unimpeded activity with very little thermoregulatory cost (Sale, 1970; Geiser *et al.* 2002).

Among small mammals rock hyraxes (*Procavia capensis*) display a number of behaviours, which appear to bear a relationship to the environmental conditions experienced in their natural habitat (Sale, 1970). The activity pattern of rock hyrax can be considered to follow a bimodal distribution (Sale, 1965; Sale, 1970; Hoek, 1975). For a large part of the day (80-95%) rock hyrax appear to be inactive (Sale, 1970; Fourie & Perrin, 1987). Apart from intense feeding periods which are usually concentrated in the cooler parts of the day (Taylor & Sale, 1969), rock hyrax spend most of their time resting either in a basking posture or sitting in the shade of trees and crevices (Sale, 1970).

In the rock hyrax emergence is thought to be associated with illumination rather than ambient temperature (Coe, 1962). Aschoff (1966) found that the most dominant

zeitgeber to be the onset of activity in the day-night cycle of illumination. Although rock hyrax are considered to be diurnal (Sale, 1970), they have been observed to forage on moonlit nights (Coe, 1962). Thus both sunlight and moonlight have profound effects on rock hyrax activity (Coe, 1962).

The sluggishness of rock hyrax coupled with basking behaviour in the early hours of the morning appears to suggest that environmental heat is also necessary for their thermoregulation (Taylor & Sale, 1969). The first feeding period of the day often commences after a warming-up period and a second, longer feeding period occurs in the late afternoon/evening (Sale, 1970; Hoek, 1975). Sale (1970) noted that rock hyrax spent less than one hour in feeding per day, while Fourie & Perrin (1987) observed foraging excursions that lasted between 0.5 – 8 hours. Large amounts of time are spent in refuges and are considered to be associated with thermoregulation during the hottest parts of the day (Sale, 1970; Hoek, 1975).

Being slow moving and with few defenses against predators, rock hyraxes depend on rock crevices to escape their natural enemies (Fairall *et al.* 1983). There must therefore be a trade-off between foraging efficiency and predator avoidance. This therefore limits the area in which rock hyraxes are able to forage. Foraging by adults generally takes place no more than 50 metres away from rock crevices (Sale, 1965), although they have been known to move distances of greater than 500 metres (Fourie, 1983). Juveniles, however, never venture more than 40 metres from the safety of rock crevices (Fourie, 1983).

Although the behavioural pattern of rock hyraxes has been described in much detail (Sale, 1970; Hoek, 1975), little is known about the seasonal differences in rock

hyrax behaviour. The aim of this study was therefore to determine whether seasonal differences occur in the activity pattern and behaviour of the rock hyrax (*Procavia capensis*).

Specific objectives were to determine whether:

- i) the time spent in different behaviours differed between winter and summer,
- ii) behaviour differed between adults and juveniles,
- iii) ambient temperatures affected behavioural patterns, and
- iv) forage availability altered behavioural patterns between the seasons.

## **METHODS**

A small population of rock hyrax (13 adults and 11 juveniles) was observed in the Klipbank suburb of Ladysmith, KwaZulu-Natal, South Africa (28°30'S and 29°45'E) during winter (July 2002) and summer (February 2003). Binoculars were used to observe rock hyrax from a vehicle, which was situated in an area that gave the best vantage point of the colony. To obtain a better understanding of overall rock hyrax activity, we took scan samples at this site at 10 minute intervals. Scan samples occurred for a maximum of 5 hours a day due to observer fatigue. Scan sampling occurred over eleven days in winter and seventeen days in summer. The number of juveniles and adults involved in different behaviours aboveground was recorded during each scan. This allowed us to estimate the proportion of rock hyrax active (% population) at each sampling period by dividing the number observed during a single scan by the maximum number observed during any scan within the same area. Those individuals not seen during each scan were assumed to be



inactive in the crevices. Data was analysed separately for juveniles and adults. There were 11 juveniles present in both the winter and summer seasons.

Furthermore, the daily and seasonal range in body temperature, which depends on ambient temperature, increases with a decrease in body size (Aschoff, 1982). Since body temperature influences activity to a large degree, one would expect behavioural patterns of smaller individuals to differ from larger individuals. It was, therefore, decided to examine adult and juvenile behavioural patterns separately.

Behavioural data collected every 10 minutes was further analysed to determine number of individuals displaying each specific behaviour. Chi-square analysis tests ( $\chi^2$ ) were performed to test for the goodness-of-fit of specific behavioural categories in order to determine whether a significant difference existed between observed and expected numbers of animals in each behavioural category. Therefore, for winter and summer, chi-square tests were performed to determine whether there was a significant difference between observed and expected numbers of individuals displaying various behaviours within the different time categories of the day. Chi-square analysis tests were also used to determine whether different behaviours differed from expected between summer and winter. Thus, in each chi-square the hypothesis was that there was no difference between the observed and expected frequencies of behaviours within the various categories.

Whenever the chi-square test showed that there was an overall significance, a Bonferroni Z-statistic was performed to determine where the significance lay. The Bonferroni Z-statistic confidence interval technique determines which behaviour is displayed more or less than expected (Byers & Steinhorst, 1984). If the expected proportion of usage ( $P_i$ ) does not fall within the interval, it is concluded that the expected

and observed utilization is significantly different. If the expected proportion of usage is greater than the limits of the confidence interval then the behaviour was concluded to be less than expected by chance. Conversely, if the expected proportion of usage was smaller than the limits calculated, then it was concluded that it was displayed more than expected by chance. Animals moved independently to one another and half an hour intervals were used to ensure that the temporal spacing of observations were not autocorrelated (Byers & Steinhorst, 1984).

A Mann-Whitney U-test (STATISTICA © ('98 edition StatSoft inc)) was used to determine whether there was a significant difference between winter and summer in the occurrence of various behaviours at different temperature ranges.

The behavioural categories observed in this study are described in detail below.

*Basking:* This involved rock hyrax resting, usually on a rock, and exposing some area of the body to the sun. Basking was further divided in some instances into basking hunched or basking flat.

*Basking hunched:* This usually occurred when rock hyrax initially emerged from the crevice. This behaviour is described as a sitting position with the hind legs tucked under the body and the front legs held vertically erect. Very little body surface area was in contact with the rock surface.

*Basking flat:* The animals' body was stretched flat. It was usually lying on its side or belly exposing the greatest area of its body to the rock

surface and to solar radiation. Legs were usually extended outward from the rest of the body.

*Foraging:* Foraging was considered to be any rock hyrax movement away from the rock crevices in search for food or active feeding. This category in some instances was divided into foraging close (<50 m) or foraging far (>50 m).

*Foraging close:* This was observed when individuals fed in the trees or on grass less than 50 m away from the rock crevices.

*Foraging far:* This was observed when individuals foraged more than 50 m away from rock crevices and usually involved moving through open areas where they were exposed to solar radiation and a lack of cover.

*Resting in the shade:* This behaviour of rock hyrax involved lying either in a hunched or flat position under the shade of a rock or tree.

*Playing:* This was only observed in small individuals (juveniles) and involved chasing each other over the rocks, always close to the crevices.

*Den:* This behaviour was assumed when individuals moved out of view amongst the rocks. Individuals are assumed to have retreated into the rock crevices.

Microclimatic conditions were recorded every 10 minutes using standard thermocouple probes connected to a MCS 120-02EX datalogger (MC Systems, Cape Town). Ambient temperatures were measured outside the crevices in a Stephenson's screen.

Since rock hyraxes showed a bimodal pattern of activity it was decided to combine data into five periods, which were identified as early morning, mid-morning, midday, early afternoon and late afternoon. Since the lengths of the days in winter and summer differed, the total day length was divided into five equal parts.

In winter early morning spanned from 07h30-09h29, mid-morning from 09h30-11h29, midday from 11h30-13h29, early afternoon from 13h30-15h29 and late afternoon from 15h30-17h29. In summer early morning spanned from 05h30-08h29, mid-morning from 08h30-11h29, midday from 11:30-14h29, early afternoon from 14h30-17h29 and late afternoon from 17h30-19h29.

## RESULTS

Rock hyraxes are diurnal, hence the periodicity of activity closely resembles the periodicity of daylight. In this study the periodicity of the light/dark cycle differed on a seasonal basis producing a 10.5L:13.5D cycle in winter and a 13L:11D cycle in summer. Thus, rock hyrax experienced 2 ½ more hours of light during the day in summer compared with winter, which was available for foraging, basking and other activities.

In both summer and winter rock hyrax display a bimodal activity pattern (Fig. 1a-b). However, the times of day in which the peaks occur differ between summer and winter. In summer, the first peak of activity occurs within the first two hours of daylight followed by a long period of low activity before peaking once again prior to sunset (Fig.

1a). In winter, the first peak in activity occurred four and a half hours after sunrise with a much smaller bout of low activity and peaking again before sunset (Fig. 1b). Surprisingly, the first activity peak in winter occurred during the period when activity was at its lowest in summer (Fig. 1a-b). This may be related to the temperature of the surrounding environment.

The main behaviours observed during the activity phase of the study period were basking, foraging and resting in the shade. Other activities noted on a much smaller scale included playing, suckling, and sunbathing in summer whereas in winter huddling and mating were observed. In some instances basking and foraging behaviour were further divided into two categories to assist in the explanation of different aspects of the thermal biology of rock hyrax.

### **Winter daily behavioural patterns**

In winter, adult and juvenile rock hyrax followed similar bimodal activity patterns (Fig. 2a-b). The first main peak occurred around 11h00 in both adults and juveniles. However, adults showed a small peak in activity at about 08h30. Both adults and juveniles reduced activity between 12h00 and 14h00 before peaking again between 15h30 and 16h30. Although the percentage time spent outside the crevice by adults and juveniles was similar, the percentage of time involved in particular various behaviours differed between the two age groups throughout the day (Fig. 2a-b).

i) *Juvenile winter behavioural pattern*

There was a significant difference between the expected and observed frequency of behaviours displayed by rock hyrax juveniles during different periods of a winter day ( $\chi^2 = 82.7$ , d.f. = 12,  $P < 0.001$ ).

Bonferroni confidence intervals revealed that juveniles displayed basking flat and foraging less frequently than expected in the early morning, but displayed the den more than expected during this time (Table 1). During the mid-morning, juveniles were less likely to bask flat, whereas other behaviours did not differ significantly from expected (Table 1). The midday period showed no significant deviation from the expected utilization of the different behaviours. However, during the early afternoon significantly less hunched and more flat behaviour occurred than expected (Table 1). During late afternoon juveniles showed significantly more foraging than expected, and utilized the dens less significantly than expected (Table 1).

ii) *Adult winter behavioural pattern*

There was a significant difference between the expected and observed utilization of behaviours by adult rock hyrax during different periods of a winter day ( $\chi^2 = 121.2$ , d.f. = 12,  $P < 0.001$ ).

Adults unlike juveniles displayed significantly greater use of the basking hunched behaviour than expected during the early morning (Table 2). Adults however, also showed significantly less utilization of basking flat in the early morning (Table 2). They also showed very different proportional use of behaviours during the mid-morning period compared to juveniles. Foraging was displayed significantly less than expected and the

den/shade significantly more than expected during this period. As with juveniles, adults displayed the different behaviours similar to expected at midday. The early afternoon showed that adult rock hyrax displayed only basking hunched significantly less than expected (Table 2). Adults utilized dens significantly less than expected. However, unlike juveniles they displayed basking flat behaviour significantly more than expected instead of foraging in the late afternoon (Table 2).

### **Summer daily activity patterns**

In summer both adult and juvenile rock hyrax displayed a fairly bimodal activity pattern with peaks occurring in the early morning just after sunrise and again just before sunset (Fig. 3a-b). Between 08h30 and 16h00 less than 20 percent of adults were active outside the crevices (Fig. 3a). However, this period of lowest activity was much shorter in juveniles. Between 08h30 and 12h00 most of the juveniles remained in the crevices (Fig. 3b). This period of inactivity was followed by progressively more individuals exiting the crevices between 12h30 and 19h00. Although the activity pattern of both adults and juveniles show a similar trend, the types of behaviours performed during this period differed between the age groups (Fig. 3a-b).

#### *i) Juvenile summer behavioural pattern*

Juvenile rock hyrax displayed very little basking 'flat' during summer and therefore all the basking was placed into one category (emerge/hunched). Foraging and playing were also placed into one category for the ease of analysis. Both of these behaviours involved

activity and moving distances away from the crevice and therefore could be grouped together.

Bonferroni confidence intervals revealed that during summer juvenile rock hyrax displayed basking behaviour in the early morning significantly more than expected (Table 3). They also utilize the dens significantly less than expected during the early morning. During mid-morning, juveniles displayed basking and foraging significantly less than expected while utilizing the dens significantly more frequently (Table 3).

During midday and early afternoon juvenile rock hyraxes displayed all behaviours in the same proportions as expected. In the late afternoon, however, it appeared that foraging and playing became the most important activity since they were displayed significantly more than expected, while the crevices were utilized significantly less (Table 3).

*ii) Adult summer behavioural pattern*

Unlike juveniles, adult rock hyrax displayed basking flat behaviour but never more than expected. Playing appeared to be the only behaviour only displayed in juveniles and therefore was excluded from adult analysis.

Adult rock hyrax displayed a similar use of the behavioural types as juveniles in the early morning and mid-morning. Basking hunched was displayed significantly more than expected and the dens were utilized significantly less in the early morning (Table 4). During the mid-morning period both basking and foraging were displayed significantly less than expected and dens/shade was used significantly more than expected (Table 4).



Adult rock hyrax differed from juveniles in their use of behaviours from midday onwards. At midday adults basked hunched significantly less and used the den significantly more than expected (Table 4). Both types of basking behaviour were displayed significantly less than expected during the early afternoon when foraging became significantly more important (Table 4). During the late afternoon adults exhibited no difference in the use of any of the behaviours.

### **Seasonal differences in behavioural patterns**

There was a significant difference in the use of behavioural types between winter and summer in adults ( $\chi^2 = 115.6$ , d.f. = 3,  $P < 0.001$ ) and in juveniles ( $\chi^2 = 136.1$ , d.f. = 2,  $P < 0.001$ ).

Bonferroni confidence intervals showed that significantly less basking behaviour (hunched and flat) was displayed by adult rock hyrax in summer, whereas significantly more was displayed in winter (Table 5). In winter adults foraged significantly less than expected while in summer adult rock hyrax utilized dens significantly more than expected (Table 5).

Juvenile rock hyraxes also showed significantly reduced basking behaviour in summer and significantly more basking in winter than expected (Table 6). This is in contrast to foraging behaviour where juveniles foraged significantly more in summer than in winter (Table 6). Significantly fewer juveniles were observed in crevices during summer than expected (Table 6).

These results indicate that basking is the most dominant behavioural type displayed by both adult and juvenile rock hyrax during winter, and foraging is of primary importance during summer.

### **Behaviour and ambient temperature**

In winter the predominant behavioural type noted in both adult and juvenile rock hyrax was that of basking (Fig. 4 a-b). Foraging was the primary behaviour displayed by rock hyrax under most ambient temperatures in summer (Fig. 5 a-b).

#### *i) Winter behaviour under different ambient temperatures*

At cooler temperatures (5-10°C and 10-15°C), adults showed significantly more basking hunched than expected (Fig. 4a, Table 7). Juveniles only showed basking hunched significantly more than expected between 10-15°C (Fig. 4b, Table 8). Both adults and juvenile rock hyrax showed less basking flat than expected at the lower temperatures (5-15°C) (Fig. 4a-b, Tables 7-8).

At temperatures of between 15-20°C both adults and juveniles showed significantly less hunched behaviour. However, adults showed significantly more basking flat whereas juveniles preferred to forage during this temperature range (Fig. 4a-b, Table 7-8). Juveniles showed no significant preference for behavioural types between 20-25°C, whilst adults showed significantly more foraging during these temperatures. At temperatures of 25-30°C, both adults and juveniles preferred basking flat, whereas showed significantly less basking hunched or foraging.

Foraging at distances further than 50 m away from refuges never occurred at low (0-5°C) or high temperatures (25-35°C) in adult rock hyrax (Fig. 4a). No foraging occurred in either group at temperatures above 30°C (Fig. 4a-b).

ii) *Summer behaviour under different ambient temperatures*

During summer adult rock hyrax showed significantly more hunched behaviour and less basking flat at temperatures between 15-20°C (Table 9, Fig. 5a). Juveniles however, did not differ from expected in any behavioural types at these temperatures. Both adult and juvenile hyrax showed significantly more hunched behaviour, and less foraging behaviour at temperatures between 20-25°C than expected (Table 9-10, Fig. 5a-b).

At temperatures between 25-35°C juvenile rock hyrax behaviour did not differ from that expected. However, at these temperatures adults showed significantly less basking hunched than expected (Table 9, Fig. 5a). Adults also showed significantly more basking flat at temperatures between 25-30°C, however this behaviour switched to foraging significantly more at temperatures between 30-35°C (Table 9, Fig. 5a).

At high temperatures (35-40°C) both adults and juveniles follow a similar behaviour pattern whereby significantly less basking hunched was displayed and significantly more foraging occurred than expected (Table 9-10, Fig. 5a-b).

Foraging close to the crevices was the most frequent behaviour observed under all temperature ranges in both adult and juvenile rock hyraxes (Fig. 5 a-b). Both adult and juvenile rock hyrax foraged at distances greater than 50 m at temperatures between 15-35°C. Surprisingly, foraging behaviour was observed in both adults and juveniles at temperatures above 30°C in summer.

iii) *Differences in behaviours between seasons at different temperatures*

During winter, ambient temperatures did not exceed 35°C, whilst in summer ambient temperatures never fell below 15°C. Winter and summer ambient temperature ranges overlapped between 15 and 35°C. If temperature is the primary regulator of rock hyrax behaviour, then one would expect similar behaviour patterns during both winter and summer over this temperature range.

At ambient temperatures of 15-20, 20-25, 25-30 and 30-35°C adult rock hyrax showed significantly more basking flat in winter than in summer (Table 11), whereas significantly more foraging occurred in summer than in winter (Table 11). There were no differences in the frequency of behaviours displayed over winter and summer.

At ambient temperatures of 15-20°C, juvenile rock hyrax showed significantly more basking flat in summer than in winter (Mann-Whitney U-test:  $z = 5.53$ ,  $p < 0.00$ ). There was no significant difference between foraging in winter and summer at these temperatures. At temperatures between of 20-35°C, juveniles followed a similar trend to the adults, whereby significantly more basking flat in winter than in summer, and significantly less foraging in winter than in summer (Table 12).

## **DISCUSSION**

Seasonality has long been recognized to have a profound influence on animal behaviour under natural environmental conditions (Enright, 1970; Vispo & Bakken, 1993). Climate affects the seasonal availability of food, the occurrence of food in space and time, and the cost involved in foraging at different times of the day (Porter *et al.* 2000). Temperature

dependent behaviours allow animals to select microhabitats where thermal equilibrium can be maintained at low thermoregulatory cost (Sharpe & Van Horne, 1999; Porter *et al.* 2000).

Rock hyraxes have little physiological capacity for heat loss at ambient temperatures above 35°C (Louw *et al.* 1972). They do not pant and only have sweat glands on the soles of their feet and consequently behavioural thermoregulation via choice of location is to be expected.

### **Thermoregulatory behaviour during winter**

Juvenile rock hyrax are more vulnerable to lower ambient temperatures than adults. Having a smaller body mass, juveniles as a consequence have a high surface area relative to body volume ratio and are therefore experience excessive heat loss when ambient temperatures fall below thermoneutrality (Pereira *et al.* 2002). This difference in morphology between adult and juvenile rock hyrax has led to a variation in thermoregulatory behaviour when exposed to low ambient temperatures.

In winter juvenile rock hyrax spent more time than expected in the dens during the early morning, whilst adults preferred to bask in a hunched position during this period of the day. In the early morning, rock surfaces have not heated up significantly from the absorption of solar radiation. Adults, therefore, reduce the surface area in contact with the rock surface. It is likely that a combination of cold rock surfaces and low ambient temperatures prevent juveniles from emerging in the early mornings during winter. They, therefore, prolong the time in the dens where they are buffered from the early morning

chill and only emerge when conditions are more favourable for smaller individuals to bask and forage.

Seasonal daily comparisons indicated that both adult and juvenile rock hyraxes basked significantly more during winter than during summer. Previous studies suggest that basking allows rock hyrax to increase body temperature from a nocturnal hypothermia using an external energy source, the sun (Taylor & Sale, 1969; Sale, 1970, Bartholomew & Rainy, 1971, Fairall *et al.* 1983). Thus basking would restore the heat lost overnight at little to no thermoregulatory cost.

During winter, the period of highest rock hyrax activity occurred during midday when ambient temperatures were within the thermoneutral zone and body temperatures had reached a level that allowed unimpeded activity. During this time both adults and juveniles displayed no difference between any observed and expected behaviour, indicating that when ambient temperatures were significantly warm enough, rock hyrax displayed all behaviours under observation.

Adult rock hyrax spent more time basking in winter than juveniles. This was especially true in the late evening prior to entry into crevices for the night. The smaller size of juveniles imposes greater thermoregulatory costs during the nocturnal hours. High heat loss must be met by endogenous heat production in order to maintain homeostasis (Aschoff & Pohl, 1970; Aschoff, 1982). Larger quantities of food must therefore be consumed in order to meet the energetic demands of juveniles overnight (Chappel, 1980).

While in winter, adult rock hyrax spent the last few daylight hours basking; juveniles on the other hand spent more time than expected foraging prior to entry into the crevices for the night. Rather than consuming large quantities of food for

thermoregulation, adults preferred to gain heat from the environment enabling them to increase their body temperature prior to nightfall probably as a heat-sink against the cool to cold nights.

Adult rock hyraxes, due to their larger size, have the capacity to store more fat during the season of high food quality and availability. Although juveniles bask significantly more in winter than in summer, they have to forage considerably more than adults during winter. The combined effect of reduced activity; high body fat storage and the use of an external energy source would allow adults to survive through the winter with a lower food intake than juveniles.

### **Thermoregulatory behaviour during summer**

During summer, when ambient temperatures often reach levels above the upper critical limit thermoneutral zone, rock hyrax increase the time they spent in the crevices. The bimodal aboveground activity pattern observed in summer is therefore due to the rock hyrax retreating to the burrows during midday, probably for the purpose of cooling. In summer most frequent aboveground behavioural type displayed by both adults and juveniles is foraging. Rock hyrax exhibited significantly lower amounts of basking in summer than in winter. The higher ambient temperatures during summer equates to little need for rock hyrax to heat their body temperatures in the early hours of the morning.

Juvenile rock hyraxes are vulnerable to low ambient temperatures because of their size as well as being susceptible to overheating. Juvenile rock hyraxes in the laboratory are unable to thermoregulate above 30°C (McNairn & Fairall, 1984). Surprisingly, in summer juveniles spent less time than expected in the dens than when compared to

winter. This is probably because their smaller size not only causes their body temperature to rise quickly but also assists in rapid heat loss. Thus, the larger surface area of juveniles enables them to spend less time in the dens cooling off than adults. It is likely that juveniles displayed quick shuttling between the hotter microhabitat and the cooler rock crevices, which was not revealed in our results due to large sampling intervals.

In summer, both adult and juvenile rock hyrax forage after sunset when it was too dark to observe efficiently (K.J. Brown personal observation). The percentage activity reached a peak at sunset (Fig. 1b). It is likely that feeding after dark, when high ambient temperatures can be avoided, may be energetically profitable for both adults and juveniles in summer.

#### **A trade-off between foraging and thermoregulation**

Herbivores in temperate zones are faced with a short growing season (Neuhaus, 2000). Both day length and the length of the plant-growing season thus limit the total foraging time available to herbivores in the different seasons (Turk & Arnold, 1988). In winter both food quality and quantity is low, and animals must eat more to acquire the same amount of energy as they would during the summer months (Neuhaus, 2000). In response to low ambient temperatures, many mammals increase food intake to match energetic demands (Haim *et al.* 1990). The variation in the availability and the nature of the diet could therefore be an important factor in the activity pattern of animals (Ashby, 1971).

Since basking was the prominent behaviour displayed by rock hyrax during winter and foraging was utilised more in summer, it is thought that the determining factor of the behaviours may be ambient temperature. We thus looked at ambient temperatures



that overlapped between winter and summer to determine whether behaviours were similar at the same ambient temperature across seasons.

At all the prescribed temperatures, both juvenile and adult rock hyrax foraged significantly more in summer and basked significantly more in winter. Thus, it appears that temperature is not the single determinant of foraging behaviour and that other environmental factors are governing the onset of foraging in rock hyrax.

In winter, the major food items of the rock hyrax were scarce and of low quality. Much of the rock hyrax diet that was close to the crevices comprised of dry grass, with a high fibre content in winter and the exotic *Syringa* trees. Due to these trees containing very little foliage for food consumption, rock hyrax consumed large proportions of their bark. Cellulose-based high fibre diets require prolonged digestion to efficiently gain sufficient energy for optimal metabolism (Ashby, 1971). Animals must either spend large parts of the day foraging to balance energetic demands or they must utilise other means of energetic gain (Ashby, 1971). During summer it appears that a herbivorous diet is sufficient to meet the rock hyraxes metabolic demands.

Fairall *et al.* (1983) found that even on a poor quality laboratory diet, rock hyrax maintained their metabolic energy requirements. Only when rock hyrax were subjected to ambient temperatures within their thermoneutral zone did they maintain their energy requirements. At lower ambient temperatures rock hyrax increased their metabolic rates such that they had higher digestive energy requirements than could be supplied by the laboratory diets (Fairall *et al.* 1983). Thus, it is probable that rock hyrax may not be able to meet their energetic requirements during the winter season on a low quality diet and require energy conserving mechanisms to remain homeothermic. In most instances small

mammals will enter torpor or go into hibernation when deprived of food and water at low ambient temperatures (Semenova *et al.* 2001; Lehmer *et al.* 2003). Rock hyraxes were never observed to go into torpor (Chapter two). The body size of rock hyrax may be slightly too large for any substantial energy saving after re-warming from a heterothermic state.

A combination of a low quality diet and the length of time required for the digestion of the high fibre diet implies that rock hyraxes must display behavioural thermoregulation in the form of basking to meet energetic demands and to ensure their survival through winter.

#### **A trade-off between foraging and predator avoidance**

During winter, rock hyrax spent more time foraging at distances greater than 50 metres than in summer. The availability of food was scarcer during winter and rock hyrax had to move greater distances to find sufficient food. Rock hyraxes that foraged close to the crevices were often involved in grazing and the greater distances travelled allowed them to browse on more nutritious *Acacia* leaves (personal observation).

In summer, forage was abundant close to the crevices and most foraging occurred close to this location. Vegetation type may affect the energetics of an animal by providing a significant amount of shade or by providing surfaces whereby cool air is radiated back to the animals (Porter *et al.* 2000). Thus, the dense cover of the vegetation around the crevices enabled rock hyraxes to forage throughout most of the day.

Both juveniles and adults foraged far in winter at almost all ambient temperatures encountered particularly between 15-20°C. Juveniles also spent a considerable

percentage of time foraging further at temperatures of 5-10°C (below the lower critical limit of thermoneutrality) indicating that they required to forage more than adults at colder ambient temperatures. In summer rock hyrax only foraged far when ambient temperatures reached temperatures within the thermoneutral zone. However, in summer foraging at a distance occurred mostly during early morning and sunset (Fig. 3a-b). Thus, ambient temperature may not be the only factor influencing foraging at distances greater than 50 m from the rock crevices.

Body size has an influence on the likelihood of being predated (Brown *et al.* 1993). The small body size and the slow movement of rock hyrax makes them extremely vulnerable to aerial predators when they are exposed at large distances away from the shelter of their crevices. In the early morning just as the sun rises and at sunset most aerial predators are grounded (McNair, 1982). Thus, foraging greater distances from the crevices during the darker parts of the day ensure that rock hyraxes are less vulnerable to predators.

In winter foraging at a distance occurred at all hours of the day. Rock hyraxes were consequently far more prepared to risk the possibility of predation throughout the day in winter when food quality and quantity was low.

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Table 1: Chi-square analysis showing differences in observed and expected proportions of juvenile rock hyrax displaying different behaviours during different parts of a winter day (Z=2.498)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Early morning (n = 141)</b>							
Emerge/hunched	13	15.8	0.483	0.112	0.092	0.031 < p < 0.153	
Flat	0	15.3	15.340	0.109	0.000	0.000 < p < 0.000 *	less
Foraging	5	14.1	5.855	0.100	0.035	-0.003 < p < 0.074 *	less
Den	123	95.8	7.709	0.680	0.872	0.802 < p < 0.943 *	more
<b>Mid-morning (n = 194)</b>							
Emerge/hunched	25	21.7	0.507	0.112	0.129	0.069 < p < 0.189	
Flat	12	21.1	3.929	0.109	0.062	0.019 < p < 0.105 *	less
Foraging	14	19.4	1.489	0.100	0.072	0.026 < p < 0.119	
Den	143	131.8	0.945	0.680	0.737	0.658 < p < 0.816	
<b>Midday (n = 147)</b>							
Emerge/hunched	21	16.4	1.271	0.112	0.143	0.071 < p < 0.215	
Flat	24	16.0	4.009	0.109	0.163	0.087 < p < 0.239	
Foraging	14	14.7	0.031	0.100	0.095	0.035 < p < 0.156	
Den	88	99.9	1.417	0.680	0.599	0.498 < p < 0.700	
<b>Early afternoon (n = 112)</b>							
Emerge/hunched	6	12.5	3.394	0.112	0.054	0.000 < p < 0.107 *	less
Flat	23	12.2	9.600	0.109	0.205	0.110 < p < 0.301 *	more
Foraging	16	11.2	2.075	0.100	0.143	0.060 < p < 0.225	
Den	67	76.1	1.091	0.680	0.598	0.482 < p < 0.714	
<b>Late afternoon (n = 77)</b>							
Emerge/hunched	10	8.6	0.226	0.112	0.130	0.034 < p < 0.226	
Flat	14	8.4	3.774	0.109	0.182	0.072 < p < 0.292	
Foraging	18	7.7	13.829	0.100	0.234	0.113 < p < 0.354 *	more
Den	35	52.3	5.738	0.680	0.455	0.313 < p < 0.596 *	less
<b>Total chi-square = 82.7, d.f. = 12, p &lt; 0.001</b>							
* = significant difference at p < 0.05							

Table 2: Chi-square analysis showing differences in observed and expected proportions of adult rock hyrax displaying different behaviours during different parts of a winter day (Z=2.498)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Early morning (n = 273)</b>							
Emerge/hunched	59	32.1	22.500	0.118	0.216	0.154 < p < 0.278	* more
Basking flat	0	27.2	27.193	0.100	0.000	0.000 < p < 0.000	* less
Foraging	19	24.4	1.199	0.004	0.070	0.031 < p < 0.108	
Den/shade	195	189.3	0.173	0.693	0.714	0.646 < p < 0.783	
<b>Mid-morning (n = 351)</b>							
Emerge/hunched	42	41.3	0.012	0.118	0.120	0.076 < p < 0.163	
Basking flat	27	35.0	1.813	0.100	0.077	0.041 < p < 0.112	
Foraging	14	31.4	9.629	0.089	0.040	0.014 < p < 0.066	* less
Den/shade	268	243.4	2.495	0.693	0.764	0.707 < p < 0.820	* more
<b>Midday (n = 262)</b>							
Emerge/hunched	22	30.8	2.526	0.118	0.084	0.041 < p < 0.127	
Basking flat	30	26.1	0.584	0.100	0.115	0.065 < p < 0.164	
Foraging	30	23.4	1.845	0.089	0.115	0.065 < p < 0.164	
Den/shade	180	181.7	0.015	0.693	0.687	0.615 < p < 0.759	
<b>Early afternoon (n = 247)</b>							
Emerge/hunched	14	29.1	7.804	0.118	0.057	0.021 < p < 0.092	* less
Basking flat	38	24.6	7.295	0.100	0.154	0.098 < p < 0.21	
Foraging	31	22.1	3.599	0.089	0.126	0.074 < p < 0.177	
Den/shade	164	171.3	0.307	0.693	0.664	0.591 < p < 0.737	
<b>Late afternoon (n = 142)</b>							
Emerge/hunched	13	16.7	0.822	0.118	0.092	0.047 < p < 0.136	
Basking flat	32	14.1	22.541	0.100	0.225	0.161 < p < 0.29	* more
Foraging	20	12.7	4.201	0.089	0.141	0.087 < p < 0.195	
Den/shade	77	98.5	4.675	0.693	0.542	0.465 < p < 0.619	* less
<b>Total chi-square = 121.2, d.f. = 12, p &lt; 0.001</b>							
* = significant difference at p < 0.05							

Table 3: Chi-square analysis showing differences in observed and expected proportions of juvenile rock hyrax in displaying different behaviours during different parts of a summer day ( $Z=2.394$ )

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Early morning (n = 298)</b>							
Emerge/basking	28	14.7	12.160	0.049	0.094	0.053 < p < 0.134	* more
Forage/play	56	46.3	2.023	0.155	0.188	0.134 < p < 0.242	
Den	214	237.0	2.237	0.795	0.718	0.656 < p < 0.781	* less
<b>Mid-morning (n = 251)</b>							
Emerge/basking	0	12.3	12.341	0.049	0.000	0.000 < p < 0.000	* less
Forage/play	1	39.0	37.039	0.155	0.004	-0.006 < p < 0.014	* less
Den	250	199.6	12.700	0.795	0.996	0.986 < p < 1.006	* more
<b>Midday (n = 256)</b>							
Emerge/basking	12	12.6	0.027	0.049	0.047	0.015 < p < 0.079	
Forage/play	31	39.8	1.942	0.155	0.121	0.072 < p < 0.170	
Den	213	203.6	0.432	0.795	0.832	0.776 < p < 0.888	
<b>Early afternoon (n = 212)</b>							
Emerge/basking	6	10.4	1.877	0.049	0.028	0.001 < p < 0.056	
Forage/play	39	33.0	1.110	0.155	0.184	0.120 < p < 0.248	
Den	167	168.6	0.016	0.795	0.788	0.721 < p < 0.855	
<b>Late afternoon (n = 244)</b>							
Emerge/basking	16	12.0	1.336	0.049	0.066	0.028 < p < 0.104	
Forage/play	69	37.9	25.461	0.155	0.283	0.214 < p < 0.352	* more
Den	159	194.1	6.340	0.795	0.652	0.579 < p < 0.725	* less
<b>Total chi-square = 117.0, d.f. = 8, p &lt; 0.001</b>							
* = significance at p < 0.05							

Table 4: Chi-square analysis showing differences in observed and expected proportions of adult rock hyrax displaying different behaviours during different parts of a summers day (Z=2.498)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Obseved proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Early morning (n = 327)</b>							
Emerge/hunched	42	18.5	29.793	0.057	0.128	0.082 < p < 0.175	* more
Basking flat	10	8.0	0.497	0.024	0.031	0.007 < p < 0.054	
Foraging	70	51.8	6.403	0.158	0.214	0.157 < p < 0.271	
Den/shade	205	248.7	7.676	0.761	0.627	0.560 < p < 0.694	* less
<b>Mid-morning (n = 234)</b>							
Emerge/hunched	5	13.2	5.136	0.057	0.021	-0.002 < p < 0.045	* less
Basking flat	1	5.7	3.904	0.024	0.004	-0.006 < p < 0.015	* less
Foraging	18	37.1	9.803	0.158	0.077	0.033 < p < 0.120	* less
Den/shade	210	178.0	5.768	0.761	0.897	0.848 < p < 0.947	* more
<b>Midday (n = 246)</b>							
Emerge/hunched	5	13.9	5.723	0.057	0.020	-0.002 < p < 0.043	* less
Basking flat	4	6.0	0.679	0.024	0.016	-0.004 < p < 0.036	
Foraging	31	39.0	1.627	0.158	0.126	0.073 < p < 0.179	
Den/shade	206	187.1	1.912	0.761	0.837	0.779 < p < 0.896	* more
<b>Early afternoon (n = 130)</b>							
Emerge/hunched	2	7.4	3.904	0.057	0.015	-0.012 < p < 0.042	* less
Basking flat	0	3.2	3.183	0.024	0.000	0.000 < p < 0.000	* less
Foraging	38	20.6	14.723	0.158	0.292	0.193 < p < 0.392	* more
Den/shade	90	98.9	0.795	0.761	0.692	0.591 < p < 0.793	
<b>Late afternoon (n = 370)</b>							
Emerge/hunched	20	20.9	0.043	0.057	0.054	0.025 < p < 0.083	
Basking flat	17	9.1	6.961	0.024	0.046	0.019 < p < 0.073	
Foraging	50	58.6	1.262	0.158	0.135	0.091 < p < 0.180	
Den/shade	283	281.4	0.009	0.761	0.765	0.710 < p < 0.820	
<b>Total chi-square = 109.8, d.f. = 12, p &lt; 0.001</b>							
* = significant difference at p < 0.05							

Table 5: Chi-square analysis showing differences in expected and observed proportions of adult rock hyrax displaying different behaviours in summer and winter ( $Z=2.576$ )

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Summer</b>							
<b>(n = 1307)</b>							
Emerge/hunched	74	113.4	13.682	0.087	0.057	0.041 < p < 0.073	* less
Flat	32	80.5	29.208	0.062	0.024	0.014 < p < 0.035	* less
Foraging	207	162.5	12.193	0.124	0.158	0.133 < p < 0.184	* more
Den	994	950.6	1.978	0.727	0.761	0.731 < p < 0.790	* more
<b>Winter</b>							
<b>(n = 1275)</b>							
Emerge/hunched	150	110.6	14.026	0.087	0.118	0.095 < p < 0.140	* more
Flat	127	78.5	29.941	0.062	0.100	0.079 < p < 0.121	* more
Foraging	114	158.5	12.499	0.124	0.089	0.069 < p < 0.109	* less
Den	884	927.4	2.028	0.727	0.693	0.661 < p < 0.726	* less
<b>Total chi-square = 115.6, d.f. = 4, p &lt; 0.001</b>							
* = significance at p < 0.05							

Table 6: Chi-square analysis showing differences in observed and expected proportions of juvenile rock hyrax displaying different behaviours in summer and winter ( $Z=2.291$ )

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>Emerge/hunched</b>							
<b>(n = 210)</b>							
Summer	62	137.1	41.110	0.653	0.295	0.225 < p < 0.366	* less
Winter	148	72.9	77.258	0.347	0.705	0.634 < p < 0.775	* more
<b>Foraging/playing</b>							
<b>(n = 263)</b>							
Summer	196	171.7	3.452	0.653	0.745	0.685 < p < 0.805	* more
Winter	67	91.3	6.487	0.347	0.255	0.195 < p < 0.315	* less
<b>Den</b>							
<b>(n = 1459)</b>							
Summer	1003	952.3	2.702	0.653	0.687	0.660 < p < 0.715	
Winter	456	506.7	5.077	0.347	0.313	0.285 < p < 0.340	* less
	<b>1459</b>						
<b>Total chi-square = 136.1, d.f. = 2, p &lt; 0.001</b>							
* = significance at p < 0.05							

Table 7: Chi-square analysis showing differences in observed and expected proportions of adult rock hyrax displaying different behaviours at different temperature ranges in summer (Z=2.638)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi		Conclusion
<b>15-20 °C (n = 175)</b>								
Hunched	68	47.4	8.992	0.271	0.389	0.297 < p < 0.481	*	more
Flat	7	16.7	5.648	0.096	0.040	0.003 < p < 0.077	*	less
Shade	10	9.2	0.064	0.053	0.057	0.013 < p < 0.101		
Foraging	90	101.7	1.344	0.581	0.514	0.420 < p < 0.609		
<b>20-25 °C (n = 343)</b>								
Hunched	134	92.8	18.257	0.271	0.391	0.325 < p < 0.456	*	more
Flat	30	32.8	0.233	0.096	0.087	0.049 < p < 0.126		
Shade	18	18.1	0.000	0.053	0.052	0.022 < p < 0.083		
Foraging	161	199.3	7.366	0.581	0.469	0.402 < p < 0.537	*	less
<b>25-30 °C (n = 249)</b>								
Hunched	42	67.4	9.567	0.271	0.169	0.109 < p < 0.228	*	less
Flat	44	23.8	17.181	0.096	0.177	0.116 < p < 0.237	*	more
Shade	11	13.1	0.346	0.053	0.044	0.012 < p < 0.077		
Foraging	152	144.7	0.369	0.581	0.610	0.533 < p < 0.688		
<b>30-35 °C (n = 98)</b>								
Hunched	12	26.5	7.953	0.271	0.122	0.040 < p < 0.205	*	less
Flat	6	9.4	1.207	0.096	0.061	0.001 < p < 0.122		
Shade	7	5.2	0.649	0.053	0.071	0.006 < p < 0.136		
Foraging	73	56.9	4.525	0.581	0.745	0.635 < p < 0.855	*	more
<b>35-40 °C (n = 140)</b>								
Hunched	16	37.9	12.647	0.271	0.114	0.047 < p < 0.181	*	less
Flat	9	13.4	1.430	0.096	0.064	0.013 < p < 0.116		
Shade	7	7.4	0.020	0.053	0.050	0.004 < p < 0.096		
Foraging	108	81.4	8.728	0.581	0.771	0.683 < p < 0.860	*	more
<b>Total chi-square = 106.5, d.f = 15, p &lt; 0.001</b>								
*=significant difference at p < 0.05								

Table 8: Chi-square analysis showing differences in expected and observed proportions of juvenile rock hyrax displaying different behaviours at different temperature ranges in summer (Z=2.498)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>15-20 °C (n = 86)</b>							
Hunched	25	23.2	0.147	0.269	0.291	0.173 < p < 0.408	
Flat	3	5.1	0.879	0.060	0.035	-0.012 < p < 0.082	
Foraging	58	57.7	0.001	0.671	0.674	0.553 < p < 0.795	
<b>20-25 °C (n = 237)</b>							
Hunched	99	63.8	19.410	0.269	0.418	0.341 < p < 0.494 *	more
Flat	9	14.1	1.853	0.060	0.038	0.008 < p < 0.068	
Foraging	129	159.1	5.687	0.671	0.544	0.467 < p < 0.622 *	less
<b>25-30 °C (n = 206)</b>							
Hunched	50	55.5	0.538	0.269	0.243	0.171 < p < 0.314	
Flat	18	12.3	2.678	0.060	0.087	0.040 < p < 0.134	
Foraging	138	138.3	0.001	0.671	0.670	0.591 < p < 0.748	
<b>30-35 °C (n = 114)</b>							
Hunched	24	30.7	1.459	0.269	0.211	0.119 < p < 0.302	
Flat	4	6.8	1.146	0.060	0.035	-0.006 < p < 0.076	
Foraging	86	76.5	1.175	0.671	0.754	0.658 < p < 0.851	
<b>35-40 °C (n = 163)</b>							
Hunched	19	43.9	14.111	0.269	0.117	0.056 < p < 0.177 *	less
Flat	14	9.7	1.898	0.060	0.086	0.033 < p < 0.138	
Foraging	130	109.4	3.876	0.671	0.798	0.722 < p < 0.873 *	more
<b>Total chi-square = 54.9, d.f = 8, p &lt; 0.001</b>							
* = significant difference at p < 0.05							



Table 9: Chi-square analysis showing differences in observed and expected proportions of adult rock hyrax displaying different behaviours at different temperature ranges during winter (Z=2.498)

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>5-10 °C (n = 69)</b>							
Hunched	48	24.0	24.066	0.348	0.696	0.563 < p < 0.828 *	more
Flat	11	35.4	16.828	0.513	0.159	0.054 < p < 0.265 *	less
Foraging	10	9.6	0.016	0.139	0.145	0.043 < p < 0.246	
<b>10-15°C (n = 68)</b>							
Hunched	44	23.6	17.559	0.348	0.647	0.508 < p < 0.786 *	more
Flat	18	34.9	8.182	0.513	0.265	0.137 < p < 0.393 *	less
Foraging	6	9.5	1.273	0.139	0.088	0.006 < p < 0.171	
<b>15-20°C (N=199)</b>							
Hunched	48	69.2	6.471	0.348	0.241	0.169 < p < 0.314 *	less
Flat	124	102.1	4.685	0.513	0.623	0.541 < p < 0.705 *	more
Foraging	27	27.7	0.019	0.139	0.136	0.078 < p < 0.194	
<b>20-25°C (n = 191)</b>							
Hunched	62	66.4	0.288	0.348	0.325	0.243 < p < 0.406	
Flat	85	98.0	1.730	0.513	0.445	0.359 < p < 0.531	
Foraging	44	26.6	11.372	0.139	0.230	0.157 < p < 0.303 *	more
<b>25-30°C (n = 155)</b>							
Hunched	35	53.9	6.606	0.348	0.226	0.145 < p < 0.306 *	less
Flat	112	79.5	13.241	0.513	0.723	0.636 < p < 0.809 *	more
Foraging	8	21.6	8.555	0.139	0.052	0.009 < p < 0.094 *	less
			120.890				
<b>Total chi-square = 120.9, d.f = 12, p &lt; 0.001</b>							
*=significant difference at p < 0.05							

Table 10: Chi-square analysis showing differences in observed and expected proportions of juvenile rock hyrax displaying different behaviours at different temperature ranges during winter ( $Z=2.498$ )

	Observed (n)	Expected (n)	Chi- square value	Expected proportion Pw	Observed proportion Pi	Bonferroni C.I. for Pi	Conclusion
<b>5-10°C (n = 37)</b>							
Hunched	17	11.723	2.375	0.317	0.459	0.263 < p < 0.656	
Flat	7	14.976	4.248	0.405	0.189	0.035 < p < 0.343 *	less
Foraging	13	10.300	0.708	0.278	0.351	0.163 < p < 0.539	
<b>10-15°C (n = 63)</b>							
Hunched	42	19.96154	24.33148	0.317	0.667	0.524 < p < 0.809 *	more
Flat	10	25.5	9.421569	0.405	0.159	0.049 < p < 0.269 *	less
Foraging	11	17.53846	2.437584	0.278	0.175	0.060 < p < 0.289	
<b>15-20°C (n = 166)</b>							
Hunched	35	52.59707	5.887341	0.317	0.211	0.135 < p < 0.287 *	less
Flat	66	67.19048	0.021093	0.405	0.398	0.307 < p < 0.489	
Foraging	65	46.21245	7.638025	0.278	0.392	0.301 < p < 0.482 *	more
<b>20-25°C (n = 165)</b>							
Hunched	54	52.28022	0.056573	0.317	0.327	0.240 < p < 0.415	
Flat	68	66.78571	0.022078	0.405	0.412	0.320 < p < 0.504	
Foraging	43	45.93407	0.187415	0.278	0.261	0.179 < p < 0.342	
<b>25-30°C (n = 115)</b>							
Hunched	25	36.43773	3.59028	0.317	0.217	0.125 < p < 0.309 *	less
Flat	70	46.54762	11.81616	0.405	0.609	0.500 < p < 0.718 *	more
Foraging	20	32.01465	4.508931	0.278	0.174	0.089 < p < 0.259 *	less
77.249							
<b>Total chi-square = 77.3, d.f = 12, p &lt; 0.001</b>							
* = significant difference at p < 0.05							

Table 11: Results from Mann-Whitney U-tests showing significant differences in adult rock hyrax behaviour between winter and summer at various temperature ranges

	U	Adjusted Z	P value	Conclusion (Winter)
<b>15-20°C</b>				
Hunched	833	-2.382	0.024	
Flat	405	5.851	0.000	more
Shade	1075	-0.872	0.633	
Foraging close	493	-5.796	0.000	less
Foraging far	1028	1.728	0.411	
<b>20-25°C</b>				
Hunched	2177	-2.116	0.034	
Flat	1470	5.251	0.000	more
Shade	2624	0.454	0.650	
Foraging close	1613	-4.725	0.000	less
Foraging far	2578	0.693	0.488	
<b>25-30°C</b>				
Hunched	2084	0.141	0.910	
Flat	788	6.600	0.000	more
Shade	1986	1.005	0.571	
Foraging close	1188	-5.247	0.000	less
Foraging far	2009	-1.119	0.645	
<b>30-35°C</b>				
Hunched	252	0.763	0.583	
Flat	40	5.836	0.000	more
Shade	252	-1.170	0.583	
Foraging close	150	-2.875	0.012	less
Foraging far	258	-1.037	0.662	

Table 12: Results from Mann-Whitney U-test showing significant differences in juvenile rock hyrax behaviour between winter and summer at various temperature ranges

	U	Adjusted Z	P value	Conclusion (Winter)
<b>15-20°C</b>				
Hunched	1106	0.282	0.801	
Flat	499	5.531	0.000	more
Shade	1100	1.191	0.773	
Foraging close	921	-2.038	0.108	
Foraging far	971	2.092	0.218	
<b>20-25°C</b>				
Hunched	2294	-1.664	0.096	less
Flat	1536	5.855	0.000	more
Shade	2651	-0.532	0.595	
Foraging close	1939	-3.659	0.000	less
Foraging far	2546	0.946	0.344	
<b>25-30°C</b>				
Hunched	1917	-1.098	0.375	
Flat	1263	4.911	0.000	more
Shade	2067	-0.538	0.848	
Foraging close	1556	-3.235	0.010	less
Foraging far	1999	-0.875	0.612	
<b>30-35°C</b>				
Hunched	196	2.045	0.104	
Flat	159	3.551	0.020	more
Shade	270	-0.721	0.831	
Foraging close	162	-2.682	0.023	less
Foraging far	252	-1.170	0.583	

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Figure 1: The percentage of rock hyrax observed outside of the rock crevices from sunrise to sunset in a. summer and b. winter.

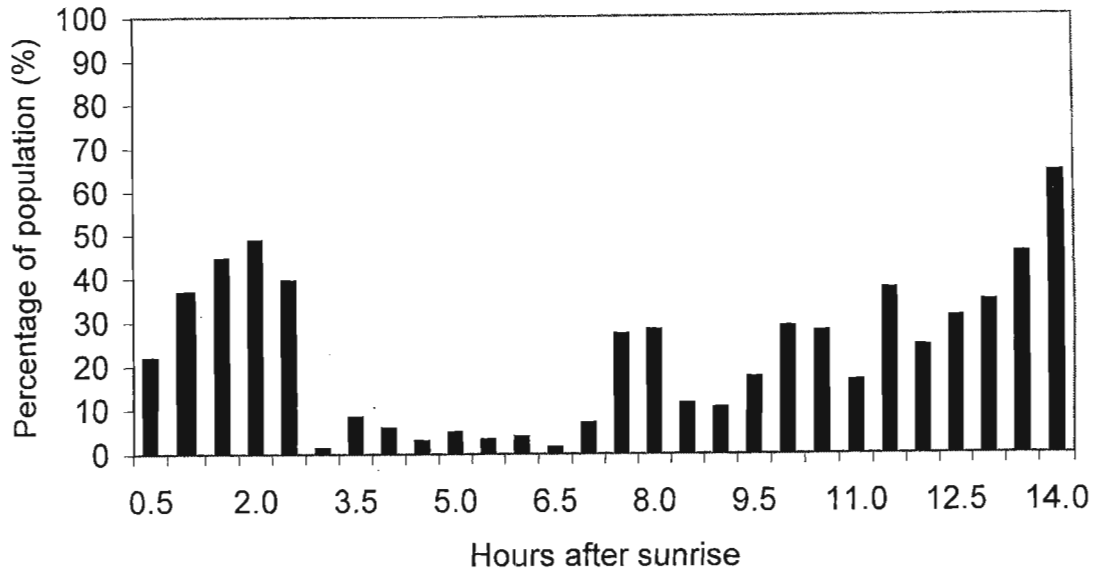
Figure 2: The percentage of rock hyrax displaying different behavioural types throughout a winter day where a. adults and b. juveniles.

Figure 3: The percentage of rock hyrax displaying different behavioural types throughout a summer day where a. adults and b. juveniles.

Figure 4: The percentage of rock hyrax displaying different behavioural types at different ambient temperature ranges during winter where a. adults and b. juveniles.

Figure 5: The percentage of rock hyrax displaying different behavioural types at different ambient temperature ranges during summer where a. adults and b. juveniles.

a.



b.

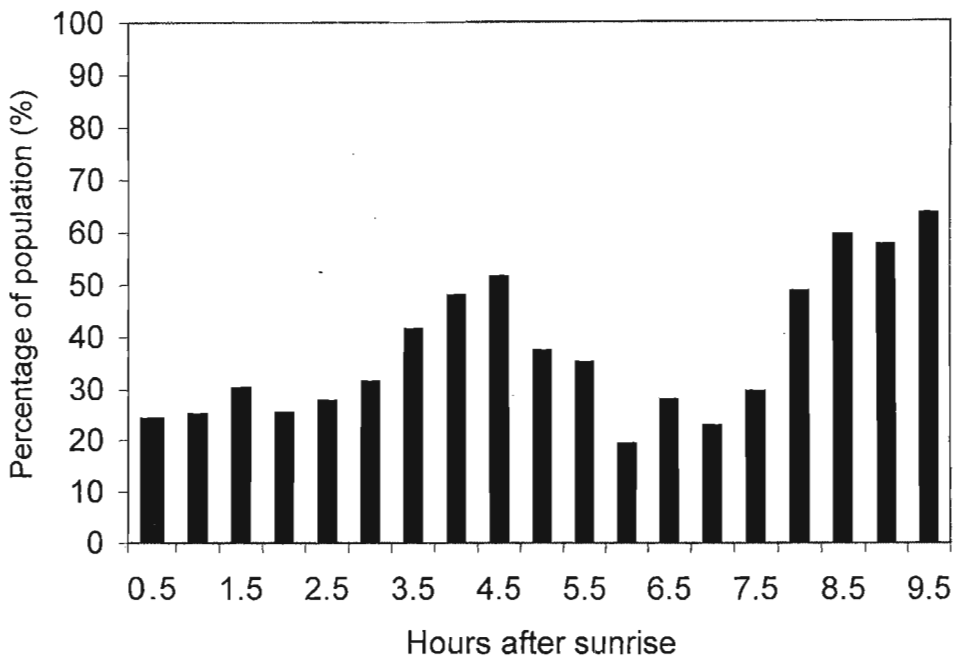


Figure 1

a.

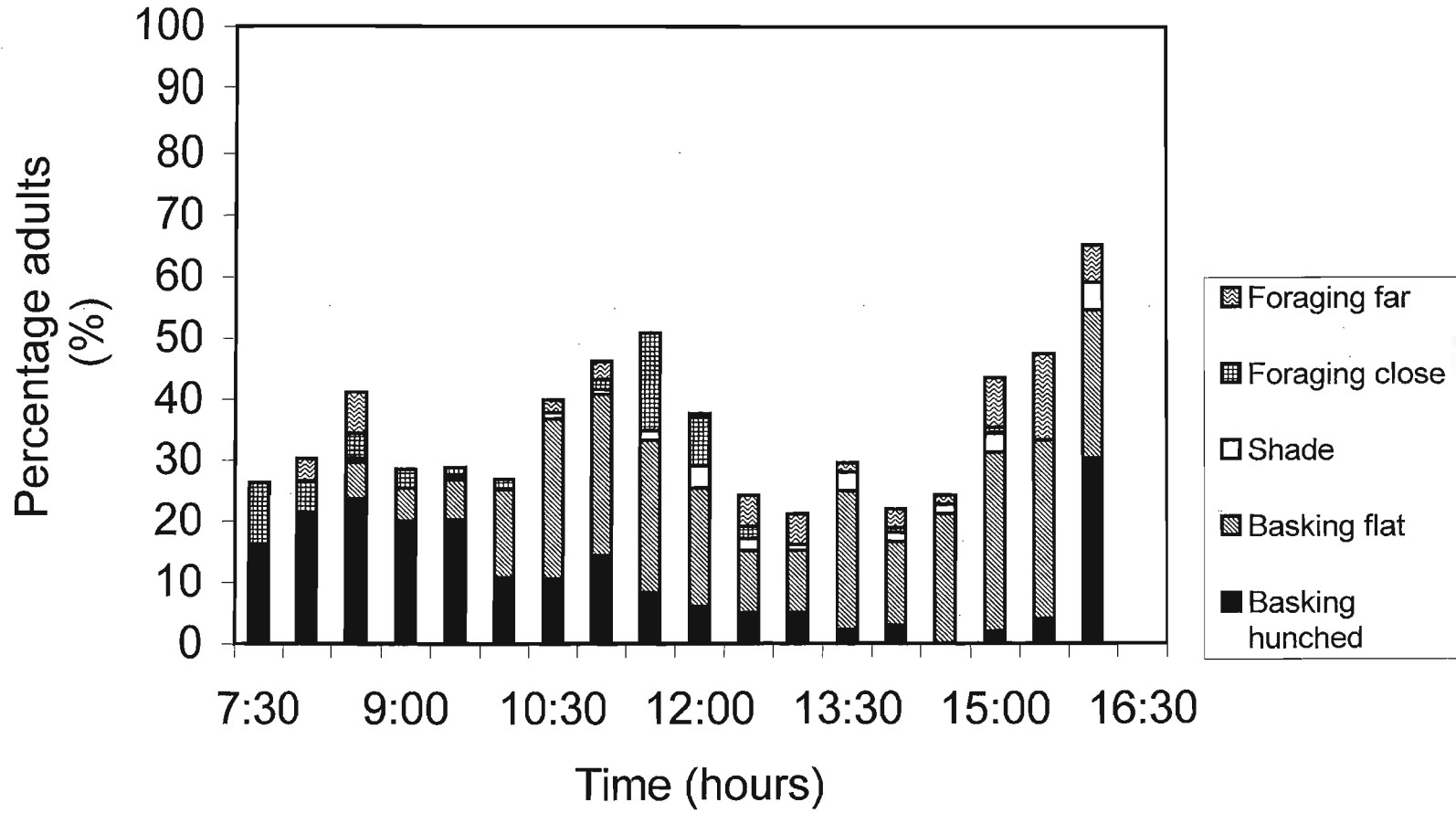


Figure 2

b.

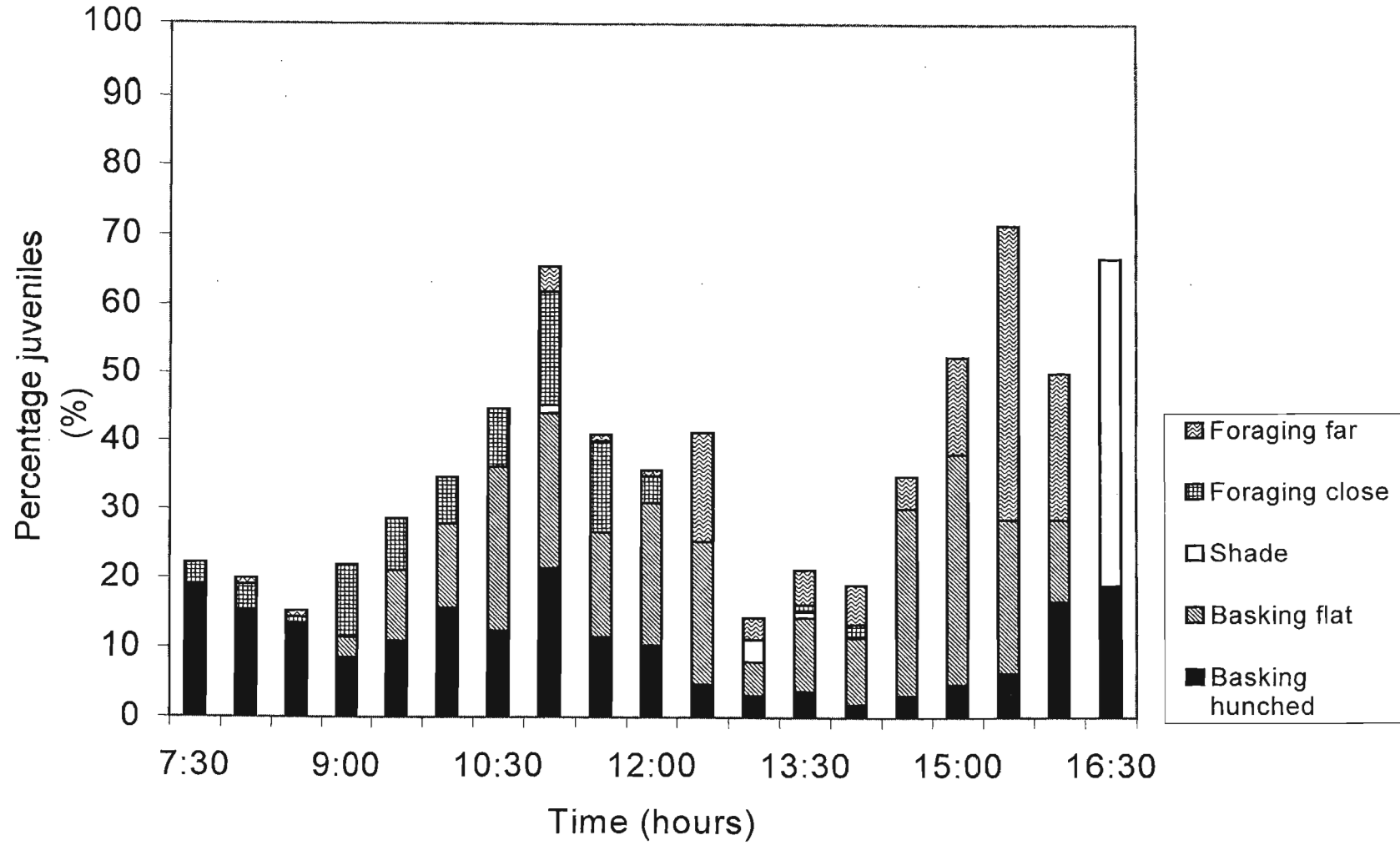


Figure 2



a.

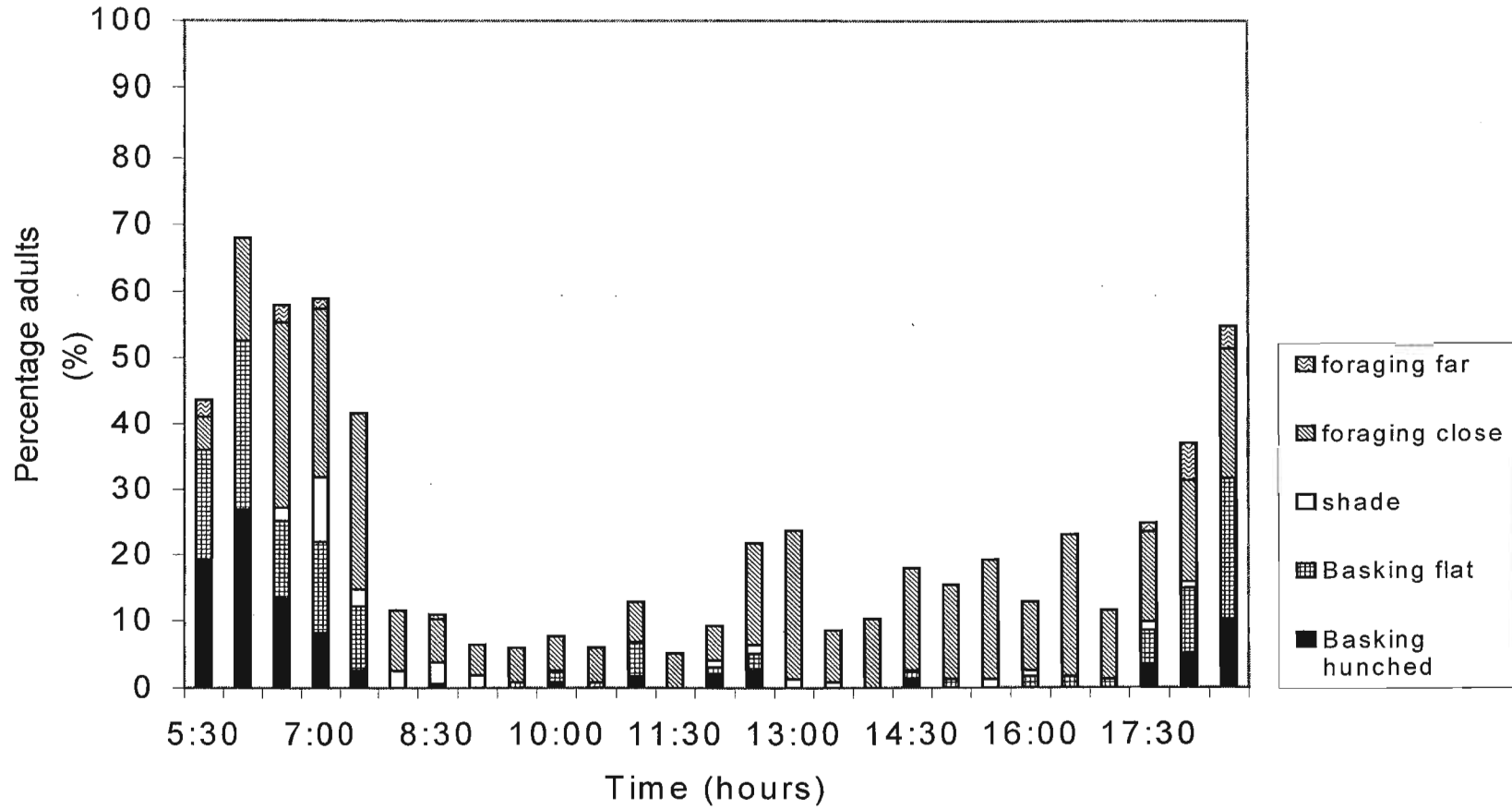


Figure 3

b.

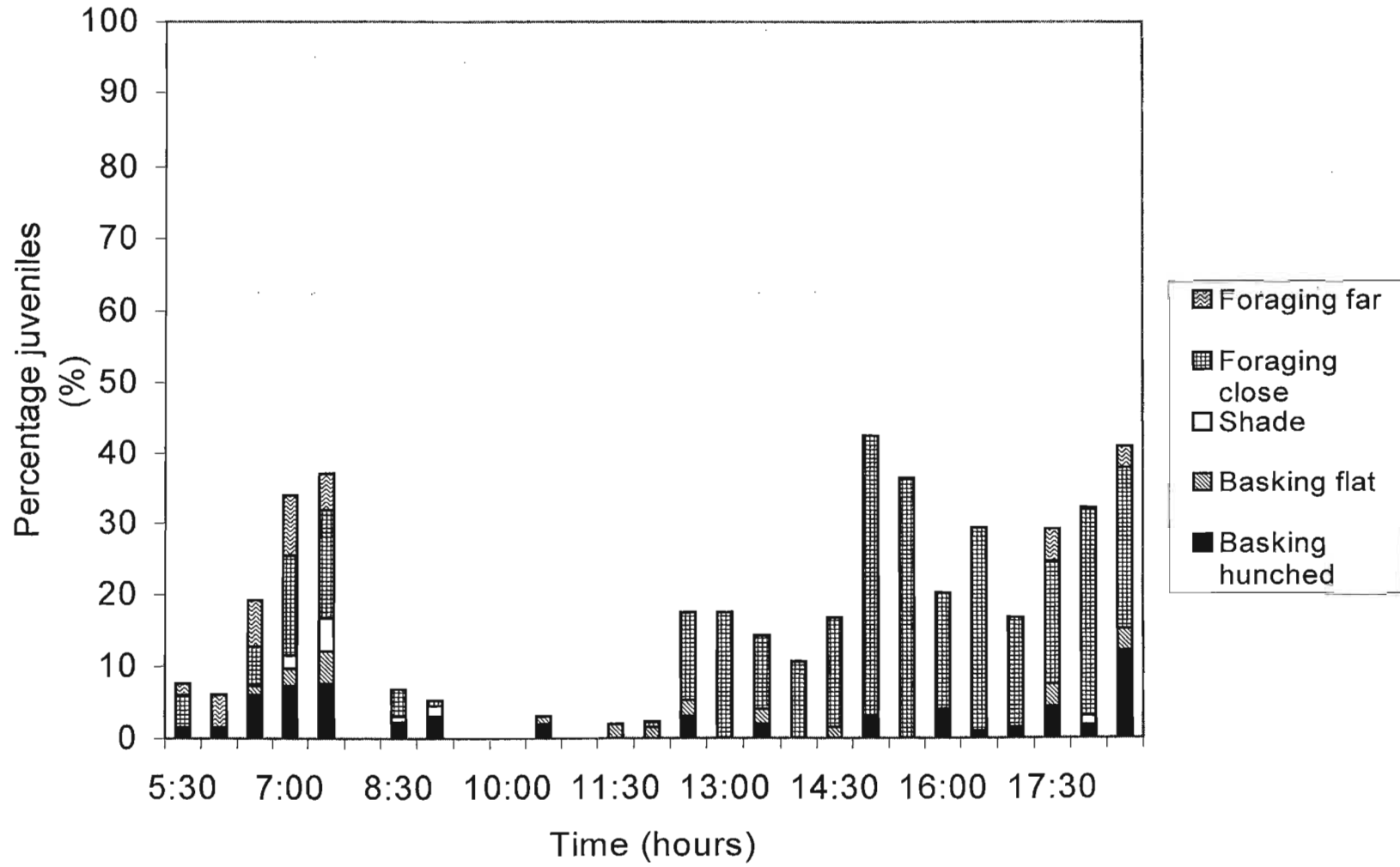
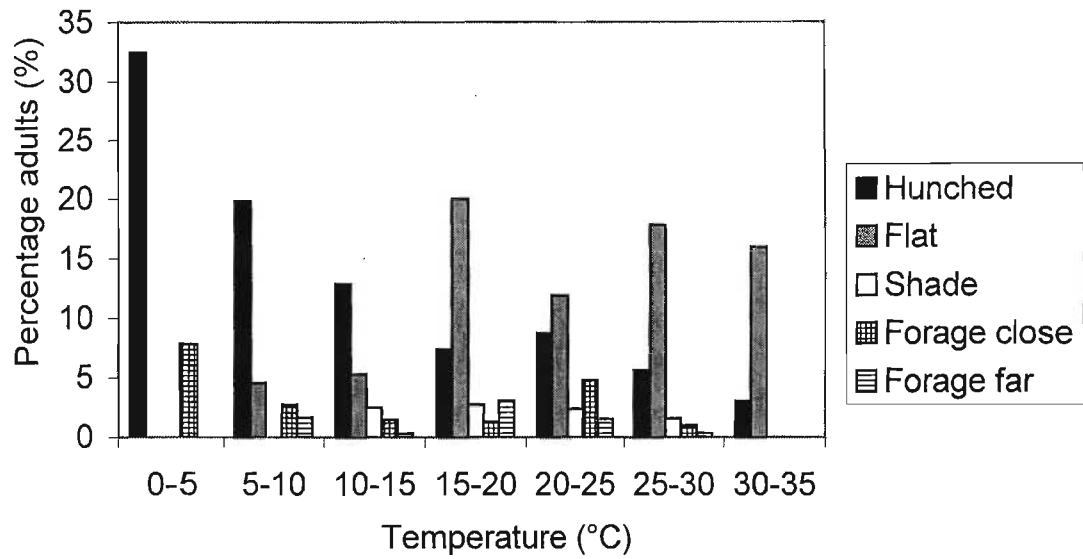


Figure 3

a.



b.

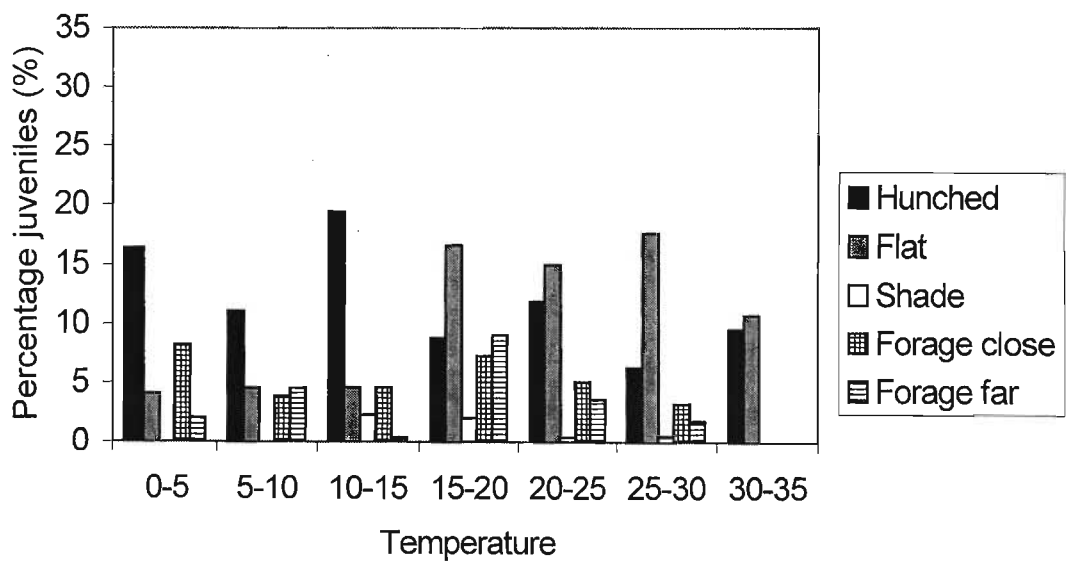
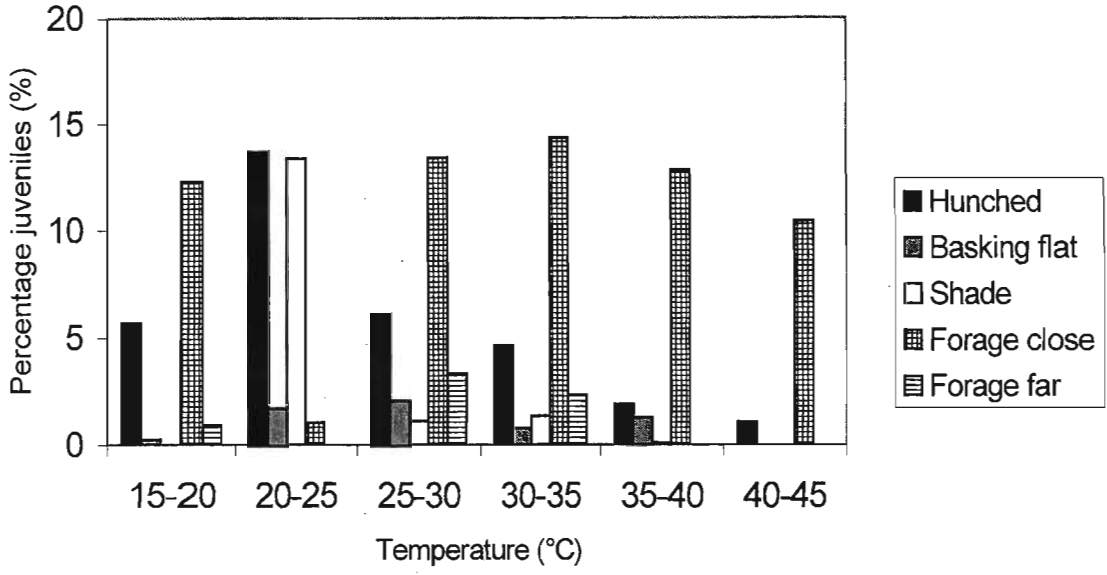


Figure 4

a.



b.

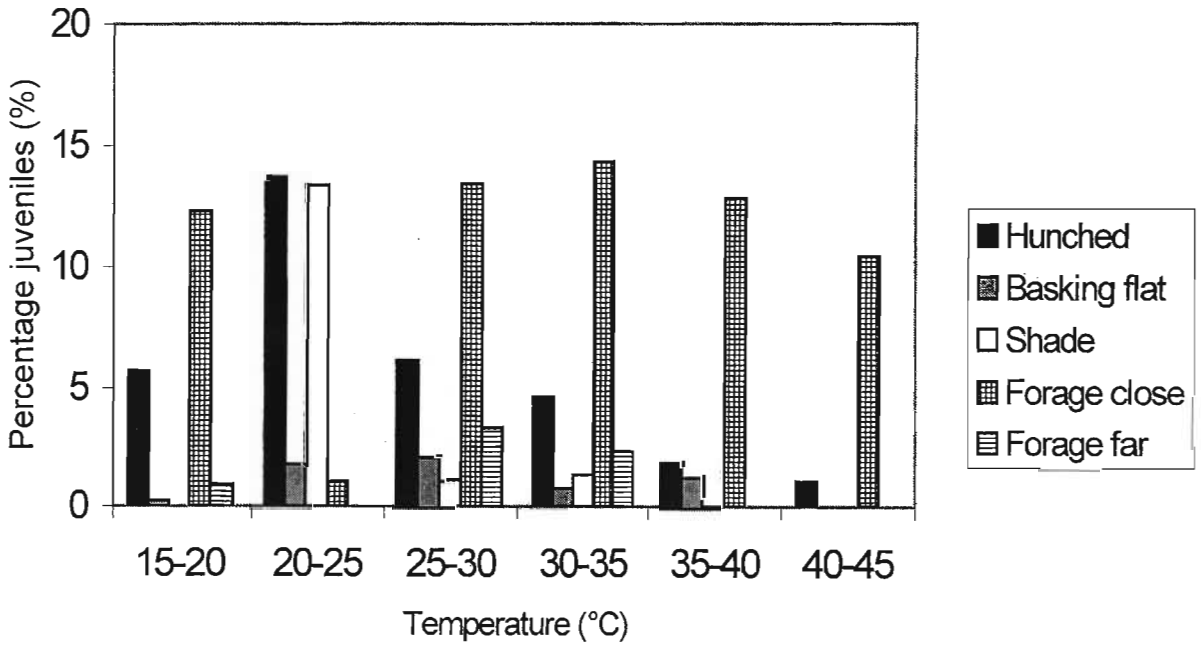


Figure 5

CHAPTER FOUR  
BASKING BEHAVIOUR IN ROCK HYRAX (*PROCAVIA CAPENSIS*) DURING  
WINTER

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**Abstract**

Basking is a behaviour frequently observed in rock hyrax during winter. It is thought that this behavioural type plays a significant role in rewarming from nocturnal hypothermia. This behaviour was investigated using operative temperatures and body temperatures in the natural environment.

In this study, rock hyrax (*Procavia capensis*) did not reduce their body temperature substantially overnight and thus basking was not used for rewarming but rather to maintain constant body temperatures under low ambient conditions.

The frequency of basking changed throughout the day as operative temperatures increased and decreased. Different basking postures (hunched or flat), orientations to the sun and basking bout lengths were used depending on the operative temperatures experienced. There was no difference in body temperature between the two basking postures at any operative temperature. Therefore, rock hyraxes maintained body temperature at all operative temperatures with the efficient use of basking behaviour.

*Keywords:* Basking, orientation, posture, operative temperature, body temperature.

## Introduction

The terrestrial environment displays diverse and variable thermal conditions. A small change in the position of an animal in this complex thermal mosaic can significantly alter the affect of environmental factors on the energy and water balance of animal [12]. The energy balance of small mammals is tightly coupled to environmental conditions experienced in their natural habitat [6]. Animals can exert significant control over their body temperature both hourly and seasonally through successful habitat utilization [5]. An animal in direct sunlight will increase its body temperature rapidly, whereas selecting shaded areas may reduce the heat loads with which an animal must contend and maximum body temperatures are reached over much longer periods [5].

Basking in the sun or rewarming with ambient temperature has recently been found to be a common behaviour utilized by many heterothermic mammals [8]. Torpor is of particular importance for small endotherms in realizing substantial energy savings overnight [9]. A disadvantage to this is thought to be the high-energy expenditure associated with endogenous re-warming [8]. Recent research has shown that the utilization of radiant heat substantially reduces energy expenditure in mammals [8]. This is equally so in slightly larger mammalian species who reduce their body temperature overnight by only a few degrees [5]. Under clear skies, the heat gain from short-wave solar radiation with maximal surface area exposed to the sun can exceed  $1000\text{W/m}^2$  that approximates 10-20 times the area-specific basal metabolic rates of typical endotherms [22].

The heat flow, to or from a mammal, is determined by a combination of microclimate selection, the shape (posture) and the orientation to the sun's rays of the

mammal [10, 22]. The magnitude of these effects is dependent on the angle of incidence of the solar beam, which varies, with time of day [5].

Heat gain from solar radiation may also be a function of the properties of a mammal's coat and skin [22]. Studies have shown that changes in coat structure can produce differences of up to 40% in solar heat gain between mammals of similar colour [22].

The rock hyrax, *Procavia capensis*, is a small mammal, which inhabits rocky outcrops. They are frequently seen to be basking on rocks in the morning hours of the day, especially during winter [15]. Rock hyraxes display a marked basking period in the morning shortly after sunrise [14, 15, 17, Chapter three]. This behaviour is thought to play a significant role in thermoregulation and that rock hyrax need to warm up before any sort of active behaviour such as feeding can be undertaken [15, 17].

In a previous laboratory study heating lamps were used to simulate sunrise for rock hyrax. The body temperature of animals increased from nocturnal hypothermia by about 2°C within 2 hours under a heat lamp [13]. Although animals in the absence of an external heat source increased their body temperature by a similar amount, the increase was much slower [15].

If basking behaviour has a significant thermoregulatory function, then rock hyrax should display differences in both posture and orientation as well as body temperature in response to changes in ambient temperature conditions throughout the day. Our particular study set out to determine whether free-living rock hyrax (*Procavia capensis*) display behavioural thermoregulation by predictably changing postures and orientation during clear winter days.

## Materials and Methods

The study was conducted at Ladysmith, in the Klipbank suburb, KwaZulu-Natal, South Africa (28° 30'S and 29° 45'E) during the winter of July 2002. All observations were done using binoculars from a vehicle, which was situated in an area that gave the best vantage point of the rock hyrax (*Procavia capensis*) colony. Observations occurred over a period of 12 days

### *Operative temperature ( $T_e$ ) measurements*

Ambient temperature ( $T_a$ ) does not portray a suitable reflection of the thermal conditions that a mammal experiences in its natural environment [5]. Thus, a more useful thermal index has been used to show the potential driving flow of heat between an animal and the environment, known as  $T_e$  (the effective or operative environmental temperature) [4].

The  $T_e$  is the equilibrium temperature of an inanimate object of zero heat capacity that has a similar size, shape and radiative properties of the animal in question when exposed to the same microclimate [2, 5, 18]. This thermal index therefore gives an indication of the thermal conditions experienced by an animal in its natural environment and is a result of a combination of the air temperature, ground temperature, solar radiation and wind velocity prevalent in the environment [5].

Although air temperature ( $T_a$ ) is an extremely useful meteorological measurement to show general trends,  $T_e$  is considered to be the true environmental temperature encountered by the animal and is necessary when looking at behaviour in response to environmental conditions [2].



It has been suggested [12] that circular cylinders or spheres using the diameter of the animal may be used to measure convection relations. A comparison study [22] showed that painted metal spheres or cylinders are acceptable  $T_e$  thermometers for analyses involving multiple measurements over moderately long time-scales. Since hollow copper models of animals covered by a fur are fairly difficult to produce, requiring substantial experience in taxidermy and electroplating [21], we modeled rock hyrax as a cylindrical metal tin (radius: 8.5 cm, length: 24 cm, circumference: 63 cm) to measure  $T_e$  directly. Three tins were placed on the rock surface parallel, perpendicular and at an angle to the sun's rays in order to measure  $T_e$  at different orientations. These tins were painted with black paint and their internal temperatures were measured using calibrated DS1921 Thermochron iButtons (Dallas Semiconductor) suspended in the centre of the tins by cotton. The  $T_e$  models were placed at a permanent location on the site for which behavioural observations were being conducted and were set up and removed each day to avoid possible human or animal interference.

### *Behavioural observations*

During winter continuous observations of rock hyrax over basking periods were recorded concurrently with operative temperature ( $T_e$ ) measurements. A focal group was sampled during these observations. The data recorded during basking included: the period of time spent basking, orientation of individual to the sun and animal posture.

The two postures recorded are described as basking hunched and basking flat. Basking hunched can be described as a rounded sitting position where the animals' tuck their hind legs under the bodies and the front feet are held vertically erect. We recorded a

rock hyrax lying in a basking flat posture when it either lay on its side or belly exposing the greatest area of its body to the rock surface and to solar radiation (Chapter three). The forefeet are extended in front with their soles on the rock and the hind feet are sprawled out backwards [15, personal observation].

Orientation was estimated according to 45 segments and were categorized as 1) parallel (animals orientated  $0^\circ$  facing straight into the sun or  $180^\circ$  facing directly away from the sun exposing the minimum surface area to solar radiation). 2) Left side (animals orientated with longitudinal axis  $90^\circ$  to suns rays thereby exposing their left flank to solar radiation. 3) right side (animals orientated with longitudinal axis  $270^\circ$  to suns rays exposing the right flank to solar radiation). Fig. 1 shows a diagrammatic version of parallel, left side and right side. 4) Left angle (animals orientated with longitudinal axis at  $45^\circ$  exposing left flank and head to the suns rays or  $135^\circ$  exposing left flank and rump to the suns rays. 5) right angle (animals orientated with longitudinal axis at  $225^\circ$  exposing right flank and rump to the suns rays or  $315^\circ$  exposing right flank and head to the suns rays. Fig. 2 illustrates left and right angle orientation diagrammatically.

Oriana © (Kovach computing services, Pentraeth, Wales) was used to analyze orientation data measured in degrees and time of day. Chi-square tests ( $\chi^2$ ) were performed to determine differences in basking orientation at various times of the day. Short intermittent behaviours of less than 10-minute duration were neglected from analyses.

*Body temperature measurements*

Rock hyraxes were captured during winter (July 2002) using wire mesh box cages measuring 400 x 400 x 750 mm, with a hinged trapdoor (Chapter two). The animals were taken directly to a local veterinarian for surgical implantation of pre-calibrated temperature dataloggers (DS1921 Thermochron iButtons® (Dallas Semiconductor)).

Rock hyraxes were anaesthetized using intramuscular injections of ketamine. Dosages were determined according to the animal's weight (20 mg/ml ketamine per kg). The iButtons were programmed to record body temperature every 10 minutes and were implanted into the intraperitoneal cavity of the rock hyrax. Surgical wax enclosed the iButtons to prevent tissue attachment over the experimental period.

Each trapped rock hyrax was fitted with unique brightly coloured neck collars to assist in recognition of individuals for behavioural observation and recapture. Animals were released back into their natural environment after a 3-4 hour recovery period. Collared animals were observed for as long as they were visible (the focal-animal sampling method) [1]. Approximately 4-5 weeks later animals were retrapped and the iButtons were removed and the data downloaded using a DS1921 Thermochron iButton Software Download Programme (Dallas).

**Results***Operative temperature changes*

Comparisons of the heating rates during winter of three black painted tins placed at different orientations are shown for one day (Fig. 3). The tin that was orientated at an angle (45°, 135°, 225° and 315°) to the solar beam experienced the highest operative

temperature throughout the day, while up until midday the tin orientated parallel ( $0^\circ$  and  $180^\circ$ ) to the solar beam experienced the lowest  $T_e$ . The only difference in heating rate, however, was in the early morning. A rock hyrax orientated at an angle or side-on to the solar beam experiences a  $T_e$  several degrees higher than does an animal facing directly into or away from the sun. The angled tin heated  $16.20^\circ\text{C}$  over the early morning period at a rate of  $0.18^\circ\text{C}/\text{min}$  (Fig. 3). The tin orientated with its side exposed to solar radiation heated at a slightly slower rate of  $0.17^\circ\text{C}/\text{min}$ , whereas the tin parallel to the solar beam heated only  $12.5^\circ\text{C}$  during the early morning at a rate of  $0.14^\circ\text{C}/\text{min}$  (Fig. 3).

During the mid-morning period the heating rates of the black painted tins slowed down substantially and were similar between the three orientated tins ( $0.04^\circ\text{C}/\text{min}$ ) (Fig. 3). During midday the angle of incidence changes and has differential effects on the heating rates at the different orientations [5]. This resulted in the heating rates of the tins orientated at an angle and side-on to the solar beam continuing to decline to a rate of  $0.01^\circ\text{C}/\text{min}$ . However, the tin angled parallel to the solar beam showed a higher heating rate of  $0.03^\circ\text{C}/\text{min}$ . This resulted in a maximum  $T_e$  ( $39.5^\circ\text{C}$ ) being reached at 12h40 prior to those reached by the other tins. Both the angled tin and the side-on tin displayed maximum  $T_e$ 's at 13h00, however the former measured  $42^\circ\text{C}$  and the latter  $40^\circ\text{C}$ . In the early afternoon all tins started to cool at a rate of  $0.04^\circ\text{C}/\text{min}$ .

When the long axis of an animal is perpendicular to the sun, absorption of short-wave radiation is maximized and when the long axis is parallel to the direction of the sun, absorption of short-wave radiation is minimized [18]. The mean heating rates of tins orientated at an angle to the sunbeam were compared with those orientated with their sides exposed to test for a difference during cooler days. Table 1 and Fig. 4 show that

there was no difference in heating rates or maximum  $T_e$  reached between angled and side orientated tins during winter cooler days.

Mean heating rates were compared between side-orientated tins and tins lying parallel to the solar beam on hot days during winter to see if any differences occurred between them. The side-orientated tin heated up at a much faster rate and had a higher  $T_e$  than parallel facing tins in the early morning on hot days (Table 2 and Fig. 5). From midday onwards the heating rate between these two orientations were similar with both reaching maximum  $T_e$  at 13h00.

#### *Basking behaviour in rock hyrax population in winter*

##### *i) Basking orientation*

During winter in the early morning (07h30-09h30) rock hyrax orientated themselves with the highest frequency at 135° and 315° (Fig. 6a). At this orientation the animals primarily exposed both their right flank and head and their left flank and rump to the solar radiation in the early morning.

Later on in the morning (09h30-11h30), rock hyrax switched their orientation to predominantly 45 and 225° (Fig. 6b). At these orientations, similar amounts of surface area are exposed to the solar radiation as in the early morning. At 45° the left flank and head are exposed to the greatest solar radiation and at 225° the right flank and rump are exposed.

At midday (11h30-13h30) during winter similar frequencies of orientation at 0, 45, 90, 225 and 270° were used by rock hyrax (Fig. 6c). Thus, rock hyrax did not show

any preference for a single orientation. During the midday period maximum and minimum surface areas were exposed to the sun.

The most frequent orientation displayed by rock hyrax in the early afternoon during winter was perpendicular to the solar beam. Rock hyrax showed a higher frequency of orientating at 90 and 270° respectively to the solar radiation (Figure 6d).

At the beginning of the late afternoon (15h30-17h30)  $T_e$  started to decline (Fig. 3). During this period there was no clear significant difference between the orientations displayed by rock hyrax. It is therefore likely that the rock hyrax were not orientating according to the solar radiation but were rather gaining heat from the rock surfaces and thus orientation was not significant.

Chi-square analyses with Bonferroni confidence intervals showed that rock hyrax orientated their bodies parallel to the solar beam significantly more than expected during winter midday and early afternoon (Table 3). They exposed both their left and right side of their bodies to the solar radiation significantly more in the early afternoon than expected (Table 3). Unexpectedly, the left angle was utilized significantly more than expected by rock hyraxes in the late afternoon whereas right angle was used significantly more than expected in the early morning (Table 3).

#### ii) *Basking bouts*

During winter rock hyraxes spent similar periods of time basking in the early morning and at midday (Table 4). Longer basking bouts occurred during the mid-morning period when heating rates had decreased substantially. The mean basking times declined from midday to early afternoon when  $T_e$ 's reached their maximum (Table 4).

The longest mean bouts of basking occurred during the late afternoon (Table 4). This was probably the result of rock hyraxes gaining heat from rock surfaces when  $T_e$  started to cool down.

#### *Thermal effects on basking posture and body temperature*

Since live animals can exert significant control over their body temperature in a given microhabitat using postural adjustment, we used collared rock hyrax, implanted with thermometers, to determine whether posture and body temperature varied at different  $T_e$ 's.

Rock hyraxes displayed considerable control over their body temperature at all operative temperatures by the selective use of basking postures. An ANCOVA showed that there was no significant difference in body temperature between basking flat and basking hunched with changes in  $T_e$ . There was also no significant difference in body temperature between the two basking postures (ANOVA:  $F = 1.58$ , d.f. = 1,  $P = 0.21$ ) (Fig. 7). However, there was a significant difference in the  $T_e$  at which the two basking postures were used by rock hyrax (ANOVA:  $F = 19.38$ , d.f. = 1,  $P < 0.0001$ ) (Fig. 8). Rock hyraxes basked flat significantly more than basking hunched at higher  $T_e$ 's.

Average, minimum and maximum body temperatures show that the body temperature of rock hyrax increased over the different periods of the day. The increase was slight and did not indicate that basking substantially increased body temperature in the early morning.

Rock hyrax spent longer periods basking hunched at low  $T_e$ 's and the shortest bouts occurred at  $T_e$ 's above 30°C (Table 6). Basking bouts when in a flat posture were

longest at temperatures of between 20 and 30°C and shortest between 10-20°C (Table 6). At all  $T_e$  ranges rock hyrax displayed longer basking bouts in a flat posture than in a hunched posture (Table 6).

## Discussion

Our results show that the function of basking behaviour in rock hyrax during the winter is not predominantly for rewarming after nocturnal hypothermia, as has been proposed in the past [15, 17]. The body temperature of rock hyraxes increased by no more than 1-1.5°C over the early morning period (4 hours) and thus would not have resulted in substantial energy savings. Furthermore, minimum body temperatures measured in rock hyrax on emergence from crevices was 35°C. Thus, rock hyraxes do not seem to reduce their body temperature considerably overnight and do not require substantial warming up in the early morning.

Why then do rock hyraxes still display considerable amounts of basking? There was no significant difference in rock hyrax body temperature between the two basking behaviours when measured at different operative temperatures. However, rock hyrax spent more time basking hunched at lower operative temperatures and basked flat at higher operative temperatures. Hence, the function of basking behaviour in rock hyrax may be to maintain a constant body temperature using solar radiation throughout the day rather than endogenously created energy. Rock hyraxes are therefore believed to be conserving energy at cooler ambient temperatures but in a different way to what was previously thought.



Some mammals have been observed to alter their orientation, posture and basking bout lengths according to the thermal conditions they are exposed to. Both antelope ground squirrels (*Ammospermophilus leucurus*) and Wyoming ground squirrels (*Spermophilus elegans*) reduce surface activity and alter posture and orientation to avoid lethal hyperthermia during high ambient conditions [4, 5]. Rock hyraxes have been observed basking in different positions throughout the day depending on the ambient temperatures to which they are exposed [15]. The function of changing orientation and posture in rock hyrax differed throughout the day. During the early morning (cold  $T_e$ s) basking behaviour was altered to maximize solar heat gain whereas at midday (hot  $T_e$ s) rock hyrax reduced exposure to the solar radiation by periodically orientating parallel to the sun's rays (Fig. 6c).

#### *Basking behaviour in the early morning*

The operative temperature index ( $T_e$ ) is considered the true environmental temperature encountered by the animal in its natural environment [2]. This thermal index has shown that in the early mornings (07h30-09h30), especially on cool winter days, temperatures often fall below the thermoneutral zone of the rock hyrax. The thermoneutral zone has been taken as between 20-30°C (Chapter 2). At these ambient temperatures heat loss exceeds heat production and increased metabolic energy is required to maintain a constant body temperature [11]. Heat loss may be further compounded through conduction on the cold rock surfaces in the early morning.

Thus, there appears to be a trade-off between solar heat gain and heat loss to the environment in the early morning. Rock hyraxes were frequently observed to perform

'test basks' when they first emerged in the morning. This behaviour can be described as individual rock hyraxes emerging and sitting for a couple of minutes before retreating again to the rock crevices. Therefore it appears that rock hyraxes will only fully emerge and bask if the heat gained from radiant energy exceeds the heat loss to the thermal environment.

In winter the predominant basking behaviour used by rock hyraxes in the early morning was the hunched posture. In this posture, with the feet tucked under the body, most of the body is lifted above the rock surface. The surface area in contact with the cooler rock surfaces is therefore reduced. In Wyoming ground squirrels, with just the feet touching the substrate, a countercurrent heat exchange in the legs prevents heat exchanged between the ground and the torso [4]. It is not known whether this mechanism exists in rock hyrax.

Orientation of the animals in winter determines the extent to which an animal will warm up and cool down. At low ambient temperatures in the early morning and midmorning rock hyrax orientated their bodies to expose the greatest surface area for solar heat gain. The  $T_e$  models demonstrated that the orientation resulting in the greatest heat gain throughout the day occurred when the longitudinal axis was at an angle to the solar beam. During the early morning rock hyrax orientated their bodies with the highest frequencies at 135 and 315°C, thus exposing the greatest surface area on both sides of their body. Sharpe and van Horne [16] also observed this type of behaviour. After having exposed one side of their bodies to the sun, rock hyrax were observed to deliberately get up and turn around, lying down again in the opposite direction so as to expose their other

flank to the warming rays [15]. During the midmorning period rock hyrax also orientated their bodies at an angle to the solar radiation but at 45 and 225°C.

In winter it appears that basking periods in rock hyrax bear some relationship to heating rates. Operative temperatures measured the highest heating rates in the early morning. The basking lengths were shorter than most other times of the day. As the  $T_e$  heating rates started to slow down during the midmorning, rock hyrax basked for longer periods of time.

#### *Basking behaviour during midday and early afternoon*

Basking behaviour in rock hyrax differed substantially during midday and early afternoon compared to the morning hours. Operative temperatures reached a maximum during this part of the day. Often during winter  $T_e$ 's reached temperatures above the upper critical limit of the thermoneutral zone. At midday, the operative temperatures of rock hyraxes orientated at an angle to the sun would rise to  $> 40^\circ\text{C}$ , whereas a rock hyrax basking perpendicular or parallel to reach operative temperatures to the solar beam would mostly be exposed to  $T_e$ 's  $< 40^\circ\text{C}$ .

Rock hyrax are unable to thermoregulate efficiently at ambient temperatures above  $39^\circ\text{C}$  [11]. One would therefore not expect rock hyrax to spend considerable amounts of time basking under these ambient conditions. The shortest basking times were therefore recorded during midday and early afternoon as expected, when  $T_e$ 's reached the maximum. Rock hyraxes are known to alternate basking with periods of resting in the shade or crevices [15]. As body temperatures of rock hyrax reach the upper critical limits they shuttled to the cooler crevices (Chapter three). Once the body temperatures are

substantially reduced basking was resumed. Therefore, even during midday, basking must play a role in regulating body temperature.

During winter the predominant basking behaviour utilized by rock hyraxes at high  $T_e$ 's is basking flat. One would expect rock hyrax to reduce the surface area exposed to the solar radiation to reduce heat gain. Turk and Arnold [19] observed that marmots (*Marmota marmota*) often stretched out on a boulder on warm and hot days. They concluded that boulders provided a better substrate for conductive heat loss and for a wider range in  $T_e$  and that this behaviour was the reverse of thermophilic 'basking' behaviour.

At midday during winter no particular angle of posture orientation was used more frequently than any other. This indicates that the animals are not lying in certain positions for long periods of time. Midday is the only period of the day when rock hyraxes display a high frequency of orientating parallel to the sun. This orientation minimizes the surface area exposed to the solar radiation and is therefore a predominant position used at high  $T_e$ 's.

The combination of a basking flat posture, shorter basking periods and orientations that minimize solar heat gain, thus contributed to the efficient maintenance of constant body temperatures under high operative temperatures in rock hyrax.

#### *Basking behaviour during the late afternoon/cooling down period*

A reduction in  $T_e$  occurred from 14h30 onwards during winter. This was probably as a result of the low angle of the sun's rays resulting in areas occupied by the colony gradually lying in shadow. Rock hyraxes were unlikely to be gaining much heat from

solar radiation during this part of the day. Rock hyraxes were observed lying on the rocks 'basking' even after the sun had set and they sat in shadow. Boulders and rocks retain heat for long periods of time after the sun has set [7]. It is probable that rock hyraxes were still gaining heat through conduction during this period of the day even though  $T_c$  was decreasing. The orientation of the animals during this period further emphasizes this point. There was no clear orientation used by rock hyrax in the late afternoon. Individuals displayed high frequencies of most angles indicating that they were not orientated in any specific direction for a specific purpose.

#### *Properties of the fur for solar heat gain of loss*

Basking in rock hyrax has different functions at differing times of the day. The extent to which an individual gains or loses heat is often a function of the properties of the pelage and skin [22]. The pelage of the rock hyrax has been shown to be highly suited to heat absorption from an external energy source [3].

The properties of the coat may change with posture. The complex and curved nature of whole animals compared with flat coats changes the angle of incidence of both sunlight and wind striking the fur and may change the degree to which sunlight and wind penetrates the coat [18]. Thus, the difference between the rounded shape of basking hunched and the flatter nature of basking flat may alter the extent to which individual gain or lose heat.

Dark skin has also been found to be of benefit in solar heat and may increase solar heat gain by about 5% [22]. Rock hyraxes however, have a pinkish-brown coloured skin and therefore it may not play a part in solar heat gain. Dark skin colouration may have

benefits during relatively cool periods for absorption of radiation, but may also create a stressful heat load during warm periods [22]. Since rock hyrax are exposed to both cold and fairly hot conditions, it is not surprising that they have a lighter skin colour beneath their darker fur.

The density and thickness of the pelage alters its insulative properties [18]. Some mammals show seasonal adjustment of radiative heat gain by changing fur thickness [18]. Marmots rather show differences in fur thickness over different areas of their body [19]. The ventral fur is shorter than its dorsal fur and is 2-3 times less dense [19]. The benefits of this are that insulation is poorer at the ventral fur and conduction is enhanced when lying. Since rock hyrax bask flat on rocks when temperatures exceed the thermoneutral zone, it was suspected that this was a mechanism to cool body temperatures through conduction. Further investigation on the properties of the ventral fur in contrast to dorsal fur surfaces may help to validate this.

#### *Predator detection and aggression*

The results from this study have shown that rock hyrax are most likely orientating their bodies in response to solar radiation during winter. There may however, be other reasons for them orientating in specific directions.

Aerial predators are a serious threat to rock hyraxes when they lie exposed outside of the rock crevices [15]. It is thus necessary for some individuals to be on guard. At any period of the day one can see that most of the individuals are basking at the same orientation, however, there are a few individuals that bask in other directions (KJ Brown

personal observation). These play the role of look-outs (KJ Brown personal observation) while most other individuals are maximizing heat gain in winter.

Aggression may also serve as a determinant of basking orientation in individual rock hyraxes. There is evidence that the rock hyrax is not basically an intensely social animal [15]. Aggressive behaviour is frequently observed between individuals. Within a group, rock hyraxes have been observed to orientate themselves so that they are facing away from their neighbours. This probably may explain why at each period of the day higher frequency of individuals is observed facing in opposite directions at the various angles. The function of this behaviour may be to avoid aggression but it does also have the secondary effect of predator detection [15].

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Table 1: Comparison of mean heating rates and temperature increase of  $T_e$  models orientated perpendicular and at an angle to the solar beam on cooler winter days.

	Perpendicular		Angle	
	Rate	Temperature rise	Rate	Temperature rise
	(°C/min)	(°C)	(°C/min)	(°C)
Early morning	0.13	14.29	0.13	14.04
Midmorning	0.06	6.55	0.06	6.04
Midday	0.01	1.96	0.02	1.75
Early Afternoon	-0.01	-2	-0.01	-0.25

Table 2: Comparison of mean heating rates and temperature increase of  $T_e$  models orientated perpendicular and parallel to the solar beam on hot winter days.

	Perpendicular		Parallel	
	Rate	Temperature	Rate	Temperature
	(°C/min)	rise (°C )	(°C/min)	rise (°C )
Early morning	0.22	25.70	0.19	22.80
Midmorning	0.05	5.15	0.06	6.65
Midday	0.01	0,63	0.02	1.75
Early Afternoon	-0.35	-1	-0.36	-6

Table 3: Chi-square analysis showing differences in observed and expected proportion of adult rock hyrax displaying different basking positions in each period of the day in winter (Z=2.638)

	Observed (n)	Expected (n)	Chi-square value	Expected proportion (Pw)	Observed proportion Pi	Bonferoni intervals for Pi	Conclusion
<b>Early morning (n=1592)</b>							
Back	134	206.9	25.708	0.130	0.084	0.066 < p < 0.102 *	less
Left side	139	163.8	3.769	0.103	0.087	0.069 < p < 0.106	
Right side	269	298.2	2.862	0.187	0.169	0.145 < p < 0.193	
Left angle	451	452.1	0.003	0.284	0.283	0.254 < p < 0.312	
Right angle	599	470.9	34.876	0.296	0.376	0.345 < p < 0.408 *	more
<b>Mid-morning (n=2089)</b>							
Back	205	271.5	16.306	0.130	0.098	0.081 < p < 0.115 *	less
Left side	181	215.0	5.377	0.103	0.087	0.071 < p < 0.102 *	less
Right side	417	391.3	1.686	0.187	0.200	0.177 < p < 0.222	
Left angle	622	593.3	1.389	0.284	0.298	0.272 < p < 0.324	
Right angle	664	617.8	3.448	0.296	0.318	0.292 < p < 0.344	
<b>Midday (n=1024)</b>							
Back	245	133.1	94.064	0.130	0.239	0.205 < p < 0.274 *	less
Left side	106	105.4	0.004	0.103	0.104	0.079 < p < 0.128	
Right side	109	191.8	35.757	0.187	0.106	0.082 < p < 0.131 *	less
Left angle	326	290.8	4.254	0.284	0.318	0.281 < p < 0.356	
Right angle	238	302.9	13.890	0.296	0.232	0.198 < p < 0.266 *	less
<b>Early afternoon (n=730)</b>							
Back	137	94.9	18.688	0.130	0.188	0.150 < p < 0.225 *	more
Left side	121	75.1	28.003	0.103	0.166	0.130 < p < 0.201 *	more
Right side	241	136.7	79.484	0.187	0.330	0.285 < p < 0.375 *	more
Left angle	107	207.3	48.549	0.284	0.147	0.113 < p < 0.180 *	less
Right angle	124	215.9	39.122	0.296	0.170	0.134 < p < 0.206 *	less
<b>Late afternoon (n=181)</b>							
Back	9	23.5	8.970	0.130	0.050	0.008 < p < 0.091 *	less
Left side	31	18.6	8.216	0.103	0.171	0.099 < p < 0.243	
Right side	16	33.9	9.456	0.187	0.088	0.034 < p < 0.143 *	less
Left angle	89	51.4	27.493	0.284	0.492	0.396 < p < 0.587 *	more
Right angle	36	53.5	5.742	0.296	0.199	0.122 < p < 0.275 *	less

Table 4: Mean basking bouts (minutes) observed in rock hyrax during different periods of the day

	Early morning	Midmorning	Midday	Early afternoon	Late afternoon
Mean	31.78	39.90	31.09	28.20	52.00
Standard Error	3.77	3.69	3.78	5.18	7.74

Table 5: Mean, range, minimum and maximum body temperatures (°C) recorded during different periods of the day.

	Early morning	Midmorning	Midday	Early afternoon	Late afternoon
Mean	36.15	36.49	36.79	37.40	37.95
Standard error	0.10	0.07	0.10	0.09	0.11
Range	2	2.5	4	1.5	1.5
Minimum	35	35	34.5	37	37
Maximum	37	37.5	38.5	38.5	38.5

Table 6: Mean basking bouts (minutes) in different postures at three different operative temperature ranges

	10 – 20 (°C)	20 – 30 (°C)	30 – 40 (°C)
Hunched	31.25 ± 10.41	27.10 ± 3.98	22.33 ± 7.29
Flat	34.33 ± 13.45	49.33 ± 25.46	33 ± 5.02



**Figure legends**

Figure 1: Diagrammatic representation of rock hyrax orientated parallel, and with their left and right sides exposed to the solar beam. The white shaded area represents the surface that is heated by the sun and the black shaded area represents the area of the body shaded from the solar radiation.

Figure 2: Diagrammatic representation of rock hyrax orientated at an angle to the solar beam. The white shaded area represents the surface that is heated by the sun and the black shaded area represents the area of the body shaded from the solar radiation

Figure 3: Comparisons of heating rates of three black painted tins orientated at different angles (angled, side and parallel) over one winter day.

Figure 4: Comparisons of mean heating rates of two black painted tins orientated at different angles (angled and side) on cool winter days.

Figure 5: Comparisons of heating rates of two black painted tins orientated at different angles (side and parallel) on hot winter days.

Figure 6: Rose diagram showing the frequency of observations of rock hyrax at different orientations during winter. The frequency of observations in each class is represented by the radius of the wedge. a) Early morning, b) Midmorning, c) Midday d) Early afternoon and e) late afternoon.

Figure 7 Mean ( $\pm$ SE) body temperature ( $^{\circ}$ C) recorded during winter when rock hyrax were basking hunched and basking flat.

Figure 8: Mean ( $\pm$ SE) operative temperatures ( $^{\circ}$ C) recorded during winter when rock hyrax were basking hunched and basking flat.

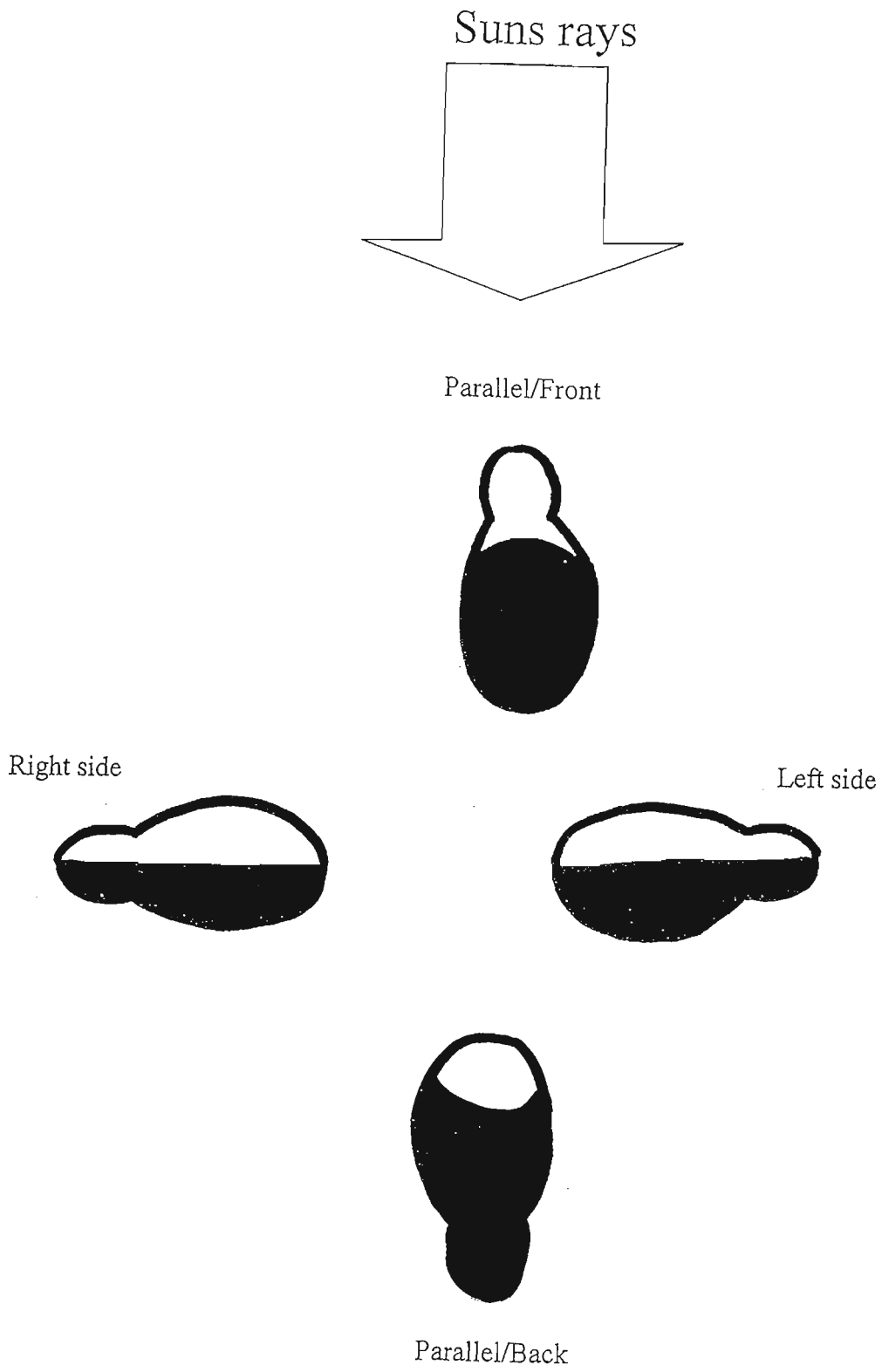


Figure 1

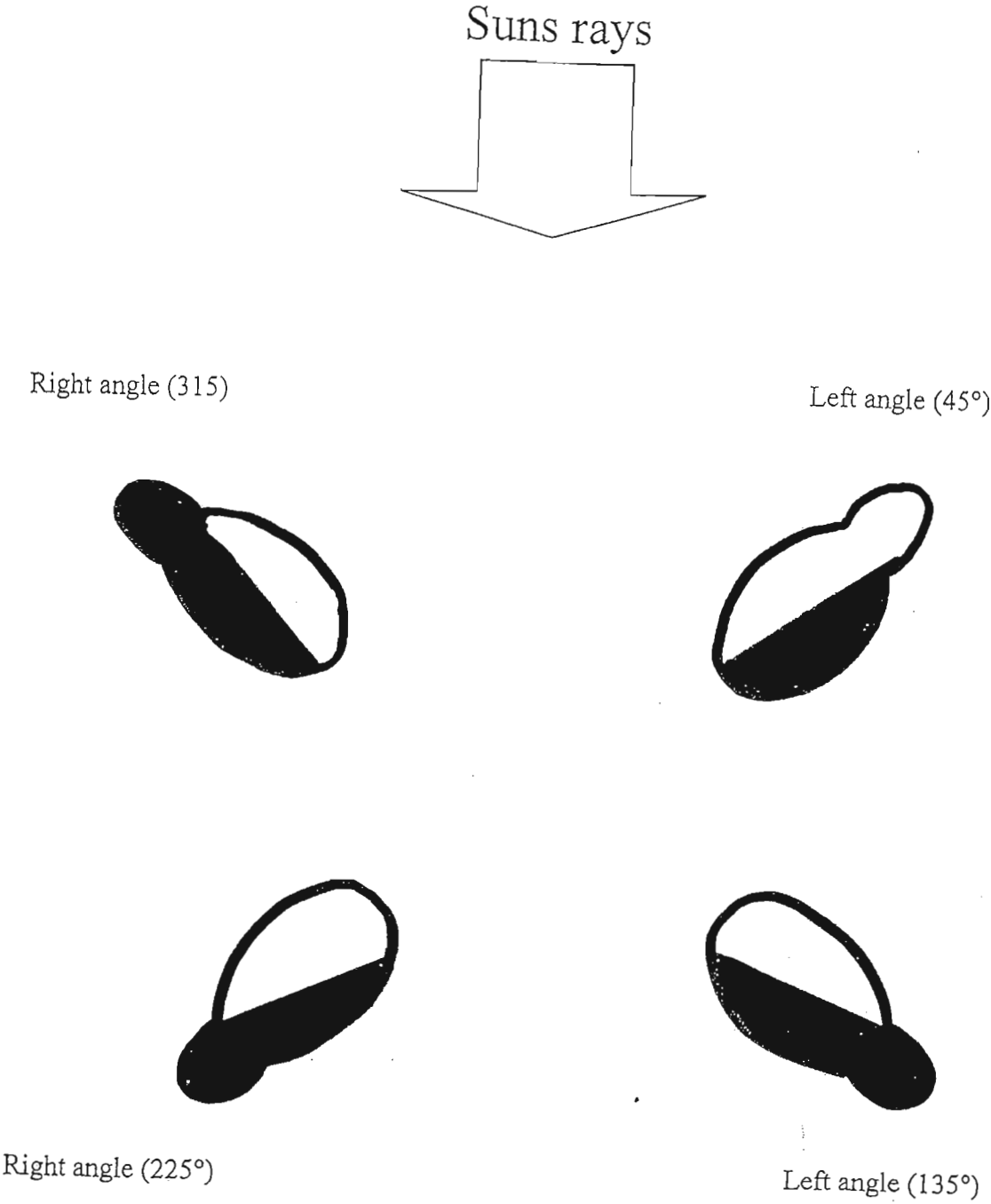


Figure 2

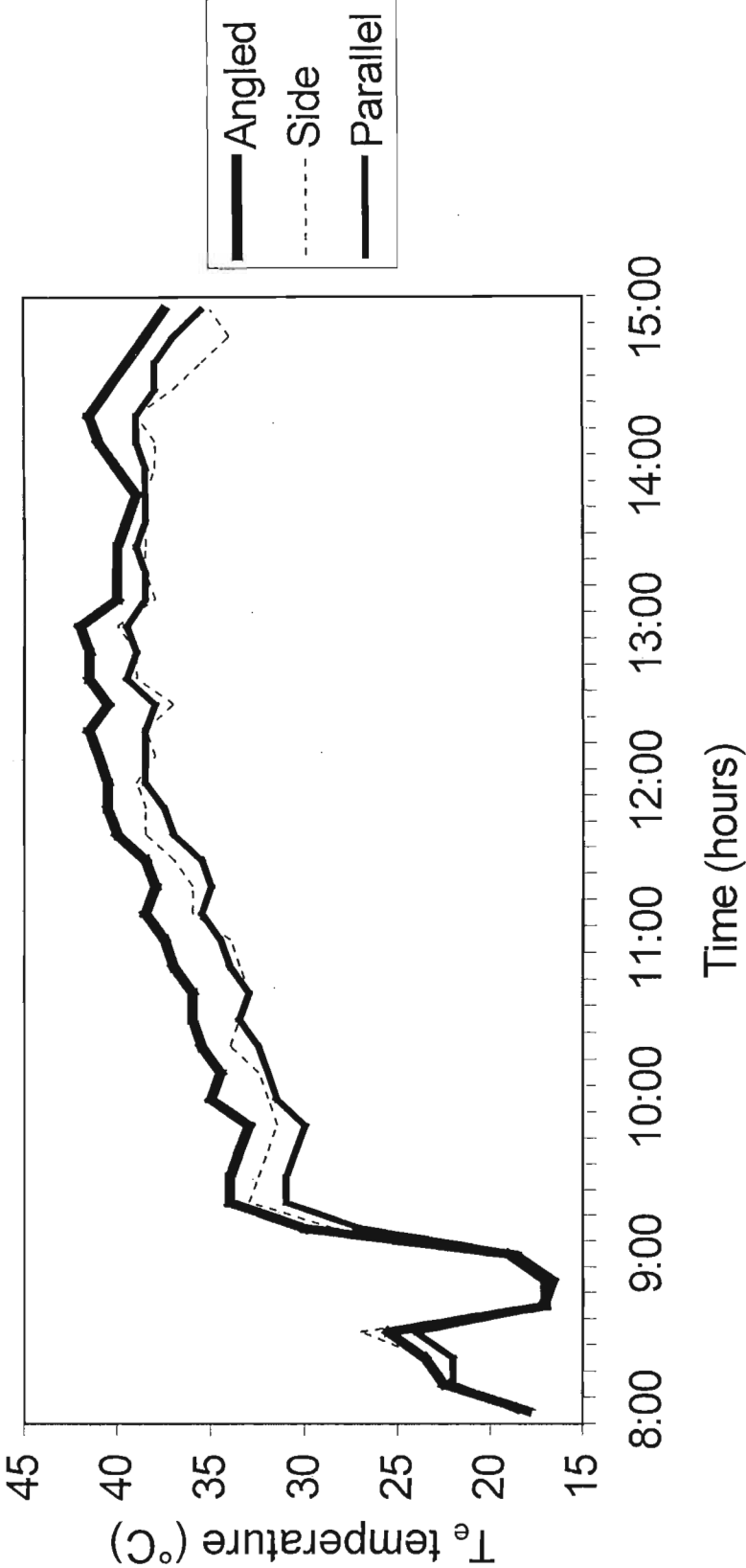


Figure 3

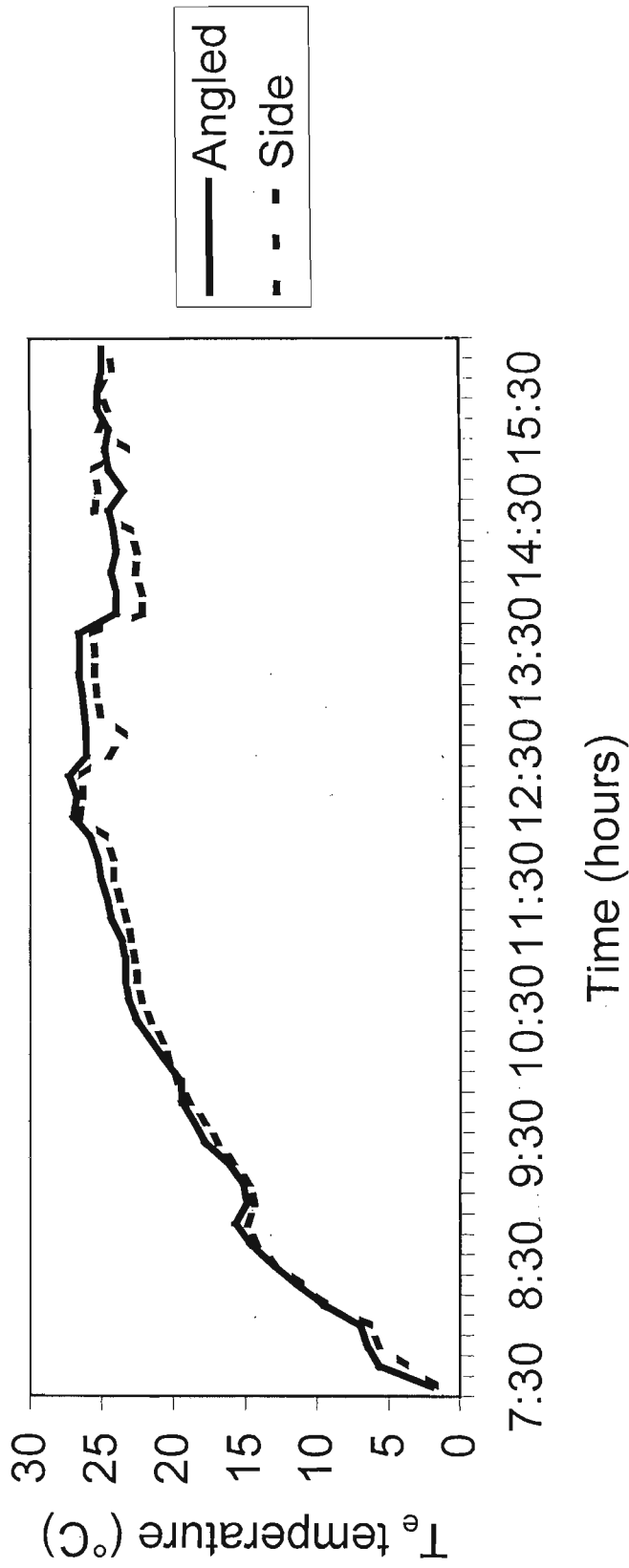


Figure 4

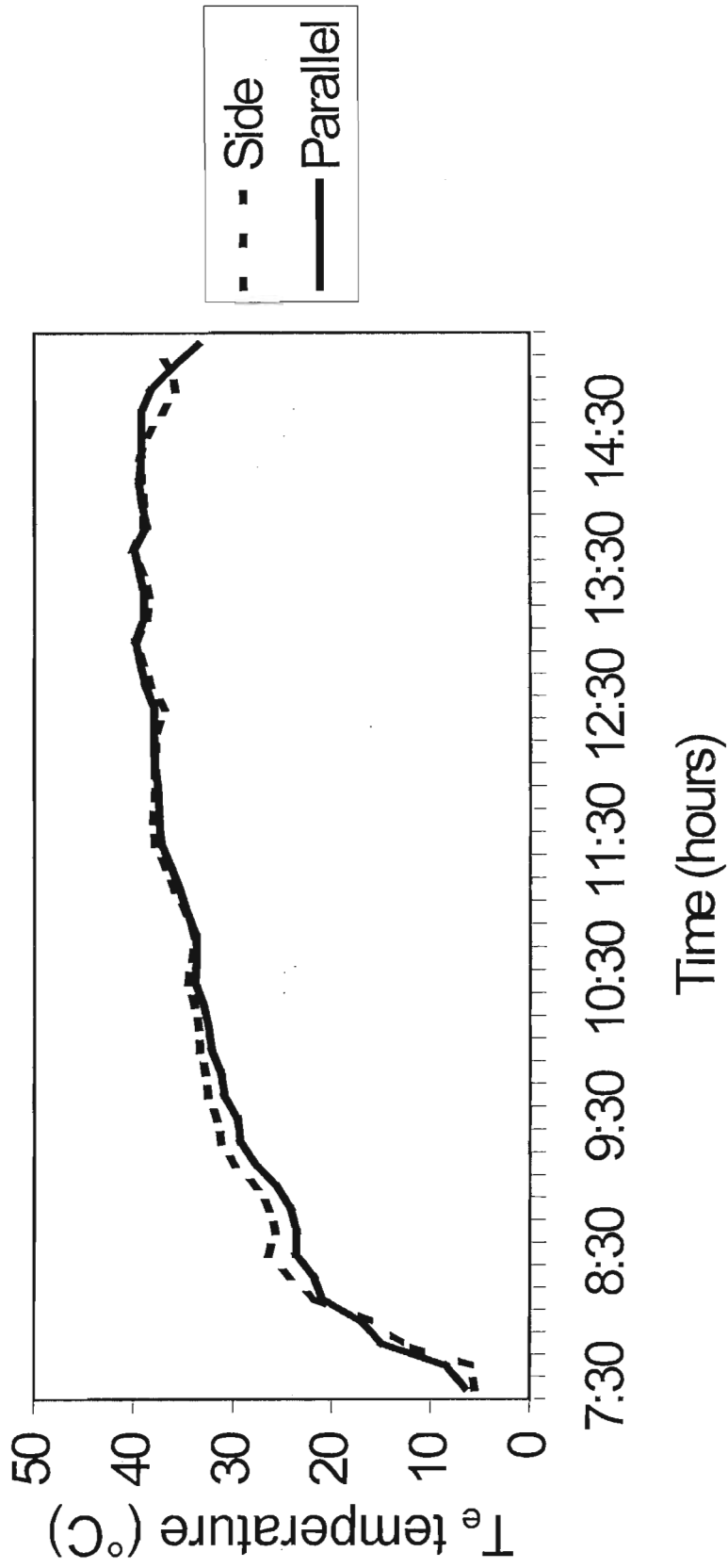
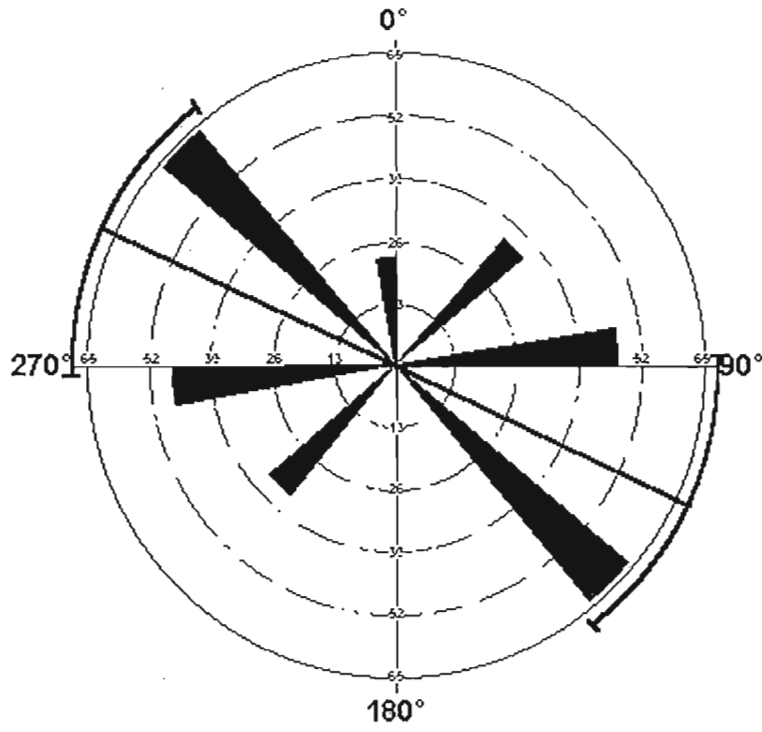


Figure 5

a.



b.

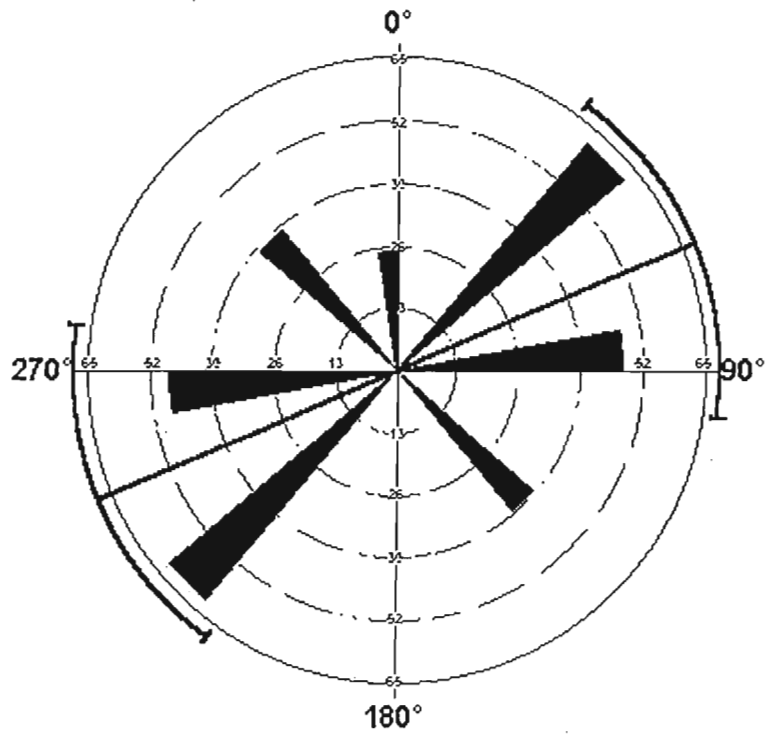
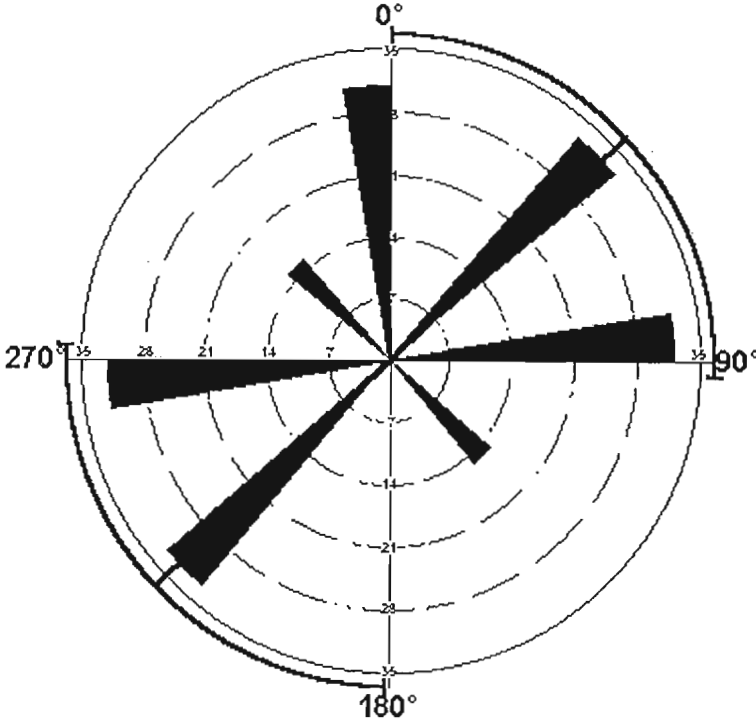


Figure 6

c.



d.

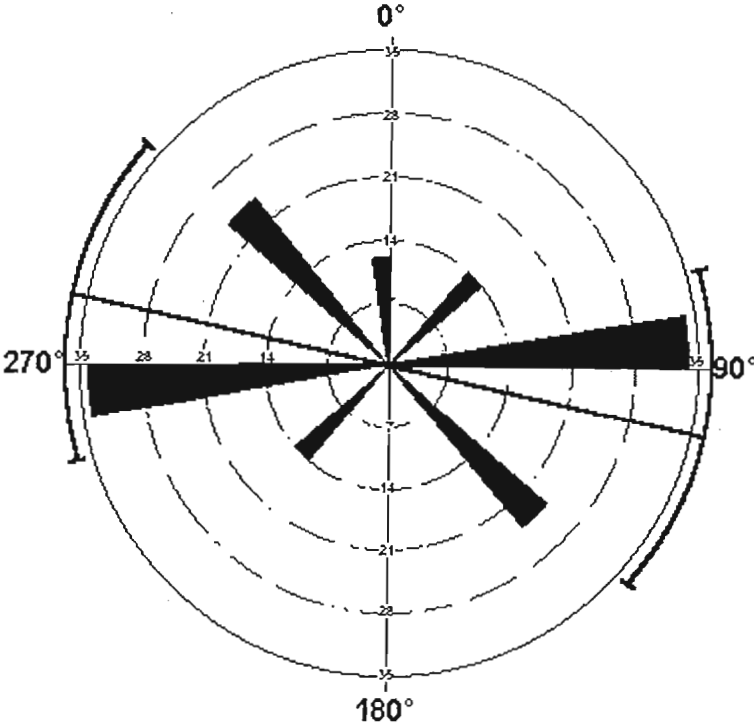


Figure 6



e.

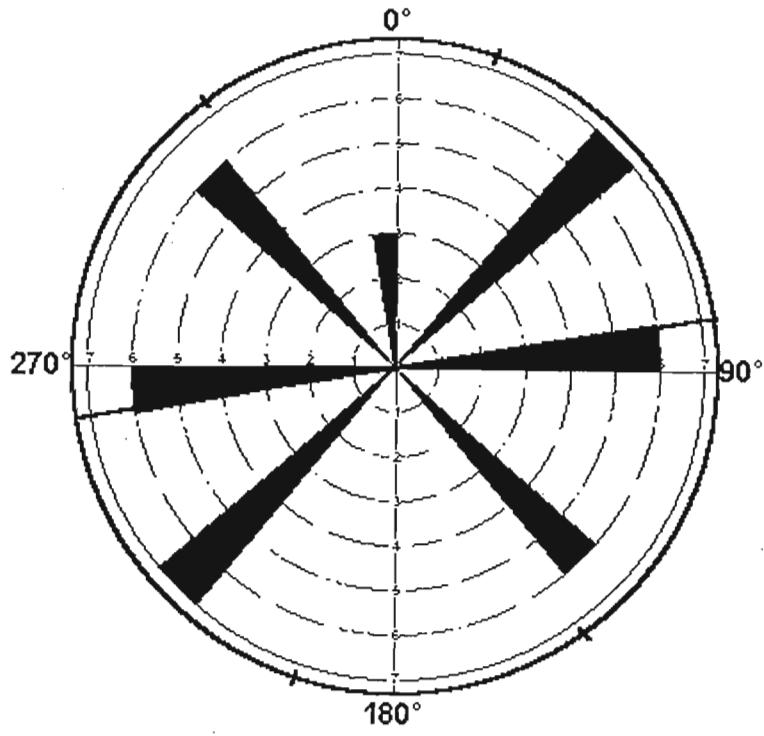


Figure 6

Figure 7

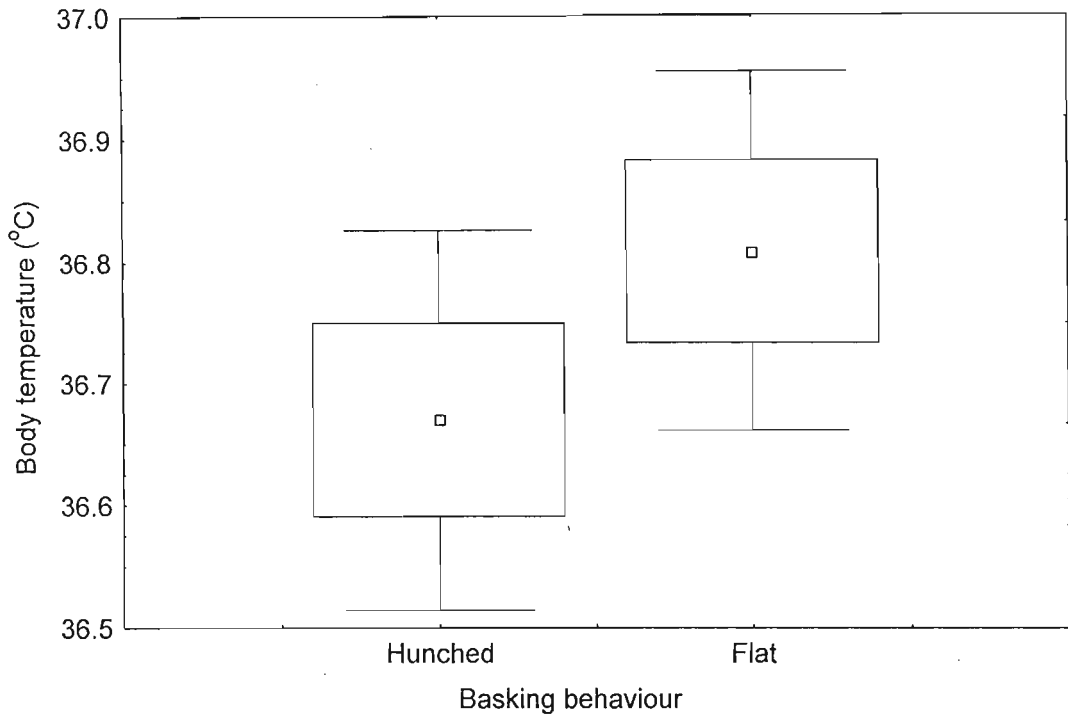


Figure 8



## CHAPTER FIVE

## CONCLUDING REMARKS

THE EVOLUTIONARY SUCCESS OF THE THERMAL BIOLOGY OF THE ROCK  
HYRAX (*PROCAVIA CAPENSIS*).

Ever since Darwin published his work on natural selection, scientists have been fascinated by the process surrounding how and why animals live where they do and what it is about their properties that allow them to survive in the environments they inhabit (Porter et al. 2000). This concluding chapter aims to shed some light on the evolutionary success of the Hyracoidea in Africa and the properties that they possess that have allowed them to appear where they do. The results from our study will be used to reinforce the argument presented.

The hyrax, 36 million years ago, was the dominant medium-sized to large herbivore on the continent of Africa (Estes 1997), while today it is a highly specialized 3-4 kg creature restricted to specific isolated habitats (Estes 1997). In the absence of predators, there is a weak selection for fast running speeds in animals, which may result in low basal metabolic rates (Lovegrove 2000). Consequently, the hyraxes were disadvantaged when the ungulates and large carnivores invaded Africa and may have caused the great reduction in rock hyrax diversity and body size.

Energetic fitness models have shown that in the absence of competitors, mammals should expect to be close to the optimal size (Brown et al. 1993). However, colonization and speciation tend to result in other sizes becoming established (Brown et al. 1993).

A reduction in body size results in a series of constraints. These constraints limit the variation in structure and function, and are a result of evolutionary history and phylogenetic relationships, which limit the variation in structure and function (Brooks and McLennan 1991; Harvey and Pagal 1991). Allometric relationships set fundamental limits on organic structure and function and determine the trade-off between the relative advantages of small and large body size (Brown et al. 1993).

#### *Consequences of reduced body size*

A reduction in size results in greater heat loss from body surfaces and consequently requires high metabolic rates to meet energetic demands (Schmidt-Nielson 1984; Lovegrove and Heldmaier 1994). The low metabolic rates displayed in all hyrax species to date are thought to be a phylogenetic trait retained from ancestral forms (Millar 1971). This phylogenetic constraint may be disadvantageous in smaller endotherms requiring high metabolic rates to balance heat loss. The range of thermal environments in which an endotherm can maintain a minimum metabolic rate and constant body temperatures becomes narrower as body size decreases (Tracy 1977). Therefore the smaller the endotherm, the more constant the environment must be to maintain constant body temperatures.

A smaller body size increases the cost of locomotion and thus the likelihood of predation (Schmidt-Nielson 1984; Lovegrove 2000; Porter et al. 2000). This in turn can be a cost to foraging efficiency. Smaller animals have reduced home ranges and are unable, in the face of high predation risk, to move over large distances in search of high quality food (Lima and Dill 1990). This has serious consequences for the smaller sized

rock hyraxes. A reduction in body size increases the likelihood of predation and thus decreases the area in which to forage. A reduced foraging range reduces the area in which hyrax are able to find good quality food in order to meet the increased energy demands imposed by the smaller body size.

Smaller body sizes, however, have the advantage of access to diurnal and/or nocturnal microclimate refugia, which partly offset the higher maintenance costs of smaller mammals, thereby reducing the energy costs of thermoregulation (Reichmann and Smith 1990; Porter et al. 2000). The smaller body size of the rock hyrax enabled them to utilize rock crevices to escape temperature extremes experienced in their environment.

Torpor is also widely used by animals of small body size. This periodic reduction in body temperature and metabolic rate during periods of unfavourable conditions is used primarily for energy conservation (Dunbrack 1993; Geiser and Ruf 1995; Boyer and Barnes 1999). The constraints on torpor as a means of conserving energy, however, often manifest itself at around 1kg (Aschoff 1982, Heldmaier 1989). Mammals larger than 1 kg rewarm from normothermic body temperatures at slow rates of 0.1 C/min or less (Geiser and Baudinette 1990). Hyraxes today range between 2-4 kg. Time and large costs involved in re-heating body sizes above 1 kg place limitations on the use of daily torpor by animals with these body sizes. Rock hyraxes were not recorded to employ torpor in our study and is likely due to their body size being slightly too large.

Physiological constraints preventing rock hyrax reducing size further:

A minimum body size is imposed that appears to be determined primarily as a function of the animals' maximum rate of endogenous heat production, the ambient thermal environment and the animals' ability to use daily or seasonal heterothermy (Tracy 1977).

Maximum rate of endogenous heat production is related to food assimilation efficiency and becomes progressively more restrictive with reduction in body size (Ashby 1971). Diet quality scales inversely and digestive efficiency scales directly with body size (Brown et al. 1993). Rock hyraxes are herbivores and consume large quantities of cellulose, which requires prolonged digestion by bacteria to render it assimilable (Ashby 1971). Increased body mass in animals requires larger and longer alimentary tracts, which enable them to ingest poorer-quality food and subject it to longer periods of digestion to extract sufficient energy and nutrients to meet energetic requirements (Brown et al. 1991; Brown et al. 1993). Limitations on a further reduction in body size in rock hyrax are probably a result of diet type and digestive physiology.

A further physiological constraint of body size in rock hyraxes is the extended gestation period of approximately 230 days, which is thought to be an evolutionary vestige from times when ancestral hyraxes were much larger (Millar 1971). Copulation usually takes place around March (Millar 1971) and therefore the bulk of the gestation period falls over winter when conditions are unfavourable. Hypothermic body temperatures during this time might compromise pregnancy and therefore torpor is not an option for female rock hyrax.

*An energetic definition of fitness*

Evolutionary constraints are associated with the availability of energy in time and space in the environment (Lovegrove 2003). This in turn is limited by the productivity of the continent (Burness et al. 2001). The Afrotropical mammals have been shown to be more sensitive to resource variability than to ambient temperature and mean productivity (Lovegrove 2003).

The evolutionary success of a lineage is determined by the making and breaking of constraints (Brown et al. 1993). This is certainly the story of the rock hyrax. Behavioural and physiological adjustments used by the rock hyrax have enabled this group of animals to break constraints imposed upon them by body size.

Evolutionary success is measured in terms of an energetic definition of fitness (Brown et al. 1993). Fitness is defined as the rate at which resources, in excess of those required for growth and maintenance, can be converted from the environment and used for reproduction (Calow and Townsend 1981; Brown et al. 1993; Lovegrove 2003). Climate at any given time and food quality and quantity affects the optimal body size that will maximize gross energy necessary for growth and reproduction (Porter et al. 2000; Lovegrove 2003).

The difference between energy intake and expenditure is the capital energy available for growth and reproduction (Waldschnidt et al. 1987; Porter et al. 2000). Limitations on food availability and quality are likely to have evolutionary consequences in an animal's energy budget (Lovegrove 2003). As the total amount of resources becomes more limited, growth and reproduction may become delayed (Dobson et al.

1992; Lovegrove 2003). An alternative to this is to keep maintenance costs low so that a higher proportion of net energy can be allocated to growth and reproduction. Studies on the thermal biology of the rock hyrax show that its evolutionary success is probably a result of following this trend.

*The rock hyrax – making and breaking constraints*

“ In the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favourable to the preservation of the species”

(Lotka 1922, p. 147)

The rock hyrax, known for its basking behaviour, has ‘energy-capturing devices’ far different to conventional methods used by most mammals. They also adjust their energy expenditure to reflect seasonal resource availability (McNab 1997). Energy expenditure may be characterized by the cost of body maintenance, various behaviours such as feeding, territorial defence, courting, escaping predators, and the cost of minimal and maximal rates of metabolism (McNab 1997).

My study on the thermal biology of rock hyrax has highlighted some interesting results. Rock hyraxes select lower body temperatures in response to low ambient temperatures and limited food supply during winter. So when the maximum amount of food required to obtain is too high, it is beneficial to consume less food and thus energetically advantageous to select a lower body temperature corresponding to the amount eaten (Prinzinger et al. 1991; Withers 1992; van Marken Lichtenbelt 1997). For endotherms, even moderately reduced body temperature during unfavourable



environmental conditions can result in substantial energy savings (Schmidt-Nielson 1990).

Rock hyraxes display a large range in body temperature, exceeding that calculated for its body size (Aschoff 1982). Lovegrove and Heldmaier (1994) have stated that a large range in body temperature is indicative of energy conservation and is an adaptive trait possessed by animals living in regions where resource availability is unpredictable in time and space. The large range in body temperature in rock hyrax is a result of higher body temperatures attained when exposed to heat loads in excess of the thermoneutral zone and maintenance of lower body temperatures during colder periods.

In summer, higher body temperatures reduce the thermal radiation gradient in eastern woodchucks (*Marmota monax*) and facilitate passive heat loss with little thermoregulatory cost (Zervanos and Salisbury 2003). The elevated body temperatures attained in rock hyrax during winter allow this particular mechanism to be utilized. In winter, elevated body temperatures of rock hyrax after sunset, appear to raise the temperatures of the crevices, thereby reducing the temperature differential from which heat can be lost overnight.

Not only do rock hyraxes adjust physiology by allowing their body temperatures to fluctuate but they also reduce energy expenditure imposed by its small body size through the use of behaviour. The 'energy-capturing device' used by rock hyrax is the capturing of solar radiation through basking. This is a prominent behaviour observed in rock hyrax, especially during winter. Our results have shown that the function of basking behaviour is to maintain body temperature during low ambient temperatures rather than for re-warming, as found in many other mammal species. This behaviour reduces the cost

of maintaining constant high body temperatures and therefore consequently increases the amount of energy that can be stored or allocated to reproduction.

A further behaviour that was not investigated in our study but has been noted by Sale (1965) is the use of huddling. Huddling decreases the high rates of heat loss associated with small size by a reduction in the surface area to volume ratio (Weatherhead et al. 1985). There is an overall increase in fitness with huddling, as heat loss is reduced and fat reserves are conserved in both adults and juveniles (Arnold 1990; McKechnie and Lovegrove 2001).

Preferred activity time is also a vital component related to individual energetics as well as population energetics. Fitness is affected by temperature dependent behavioural patterns that allow animals to move to less costly microenvironments at any time (Porter et al. 2000). Rock hyraxes have been observed to be inactive 95% of the time (Sale 1965). Most of this time is either spent in an inactive state basking or resting within crevices. Crevices provide fairly stable refugia for rock hyrax to retreat during periods of excessive heat. Retreating into the crevices reduces both energy expenditure and evaporative water loss.

During winter when food resources are scarce, rock hyraxes select basking over long periods of foraging. Foraging behaviour is costly, especially when food is patchy. Basking not only plays a role in energy conservation through reduced maintenance of body temperature, but the rock hyrax lie in an inactive state further reducing energy expenditure. Furthermore, by altering its posture and orientation towards the sun, rock hyrax can modify heat gain and heat loss in different environments and enhance the energy savings realised through basking (Porter et al. 2000).

Observations during this study on the thermal biology of the rock hyrax suggest that they seasonally implement physiological as well as behavioural tactics in their energy management to overcome constraints imposed by their small body size. They reduce energy expenditure by decreasing the costs of maintenance, minimal and maximal rates of metabolism and the costs of certain behaviours such as foraging and escaping predators. With a reduction in energy expenditure, rock hyraxes realize higher proportions of net energy, which can be allocated to growth and reproduction. This will increase the overall fitness and success of the species.

*Future with changing climate and landscape.*

It is well known that different body sizes interact differently with climate (Porter et al. 2000). With major shifts in the global climate and rapid global changes in land use, there is an increasing need to understand how and why animals are successful in their environments in order to be able to conserve the biodiversity of our flora and fauna (Porter et al. 2000).

The timing of activity, seasonal changes in food availability, environmental fluctuations, energy expenditure and the costs of reproduction are important determinants of the life history of an animal (Chappell 1981; Neuhaus 2000). Relationships between size and such traits as metabolic rate and turnover time, ontogenetic development time and life span all contribute to relative fitness under changing climatic conditions (Peters 1983; Calder 1984; Schmidt-Nielson 1984; Brown and Nicoletto 1991).

The small body size and the thermal biology of the rock hyrax have likely led to their success over millions of years until today. The small plantigrade structure provided

flexibility and proved advantageous in climbing trees and agility over rocks, when faced with the invasion and expansion of ungulates and carnivores. The small body size, however, also provided a greater flexibility in structure in adapting to a changing environment (Gould 2000).

We may ask whether physiological adaptation to homeostasis in unfavourable environments constrains the production of new phenotypic types if and when climate changes occur (Blomberg and Garland 2002). This may be the reason why the hyraxes have not diversified substantially after their adaptation to isolated habitats.

Rock hyraxes frequently have to move to a new series of rock crevices with the purpose of finding new vegetation (Sale 1965). This is particularly prevalent during periods of low productivity and low ambient temperature conditions (Sale 1965). The rapid changes in global land use and human expansion may have significant effects on rock hyrax survival.

The long gestation period, low specific foetal growth rate, relatively small litter size and a pubertal age of two years indicates a low reproductive potential in rock hyrax (Millar 1971). When faced with major shifts in the global climate and rapid global changes in land use, the survival of the rock hyrax may be uncertain.

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