

https://dspace.org/

The effect of pregnancy and lactation on the body temperatures of free-living vervet monkeys

Roberts, Carmen

2019

https://hdl.handle.net/10539/29848

Roberts, Carmen (2019) The effect of pregnancy and lactation on the body temperature of free-living vervet monkeys, University of the Witwatersrand, Johannesburg, <http://hdl.handle.net/10539/29848>

Downloaded from a DSpace repository. https://dspace.org/

THE EFFECT OF PREGNANCY AND LACTATION ON THE BODY TEMPERATURES OF FREE-LIVING VERVET MONKEYS

Carmen Roberts

A dissertation submitted to the Faculty of Health Sciences, School of Physiology, University of Witwatersrand, in fulfilment of the requirements for the degree of Master of Science in Medicine.

Johannesburg, South Africa

DECLARATION

I, Carmen Roberts, declare that this dissertation is my own work, except where others have helped as indicated in the acknowledgements and the reference list. It is being submitted for the Degree of Master of Science in Medicine at the University of the Witwatersrand, Johannesburg. The work herein has not been submitted before for any degree or examination at any other University.

_____

Carmen Roberts

Signed in Johannesburg on the _____day of _____2019

I certify that all the experimental procedures used in this dissertation were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC numbers: 2010/41/04 and 2015/04/14/B).

ABSTRACT

Reproduction is physiologically challenging for female mammals, requiring an increase in food and water intake to meet the demands of gestation and lactation. One way to assess how free-living female mammals cope with these increased demands in changing environments (e.g., fluctuating environmental temperatures and resource availability) is by assessing their body temperature patterns through biologging. As part of a long-term project to investigate the behavioural and physiological mechanisms employed by free-living vervet monkeys (*Chlorocebus pygerythrus*) in the semi-arid Nama Karoo in the Eastern Cape, South Africa, I investigated how well female monkeys regulated their body temperatures during gestation and lactation.

Body temperature (T_b) data were collected from 30 female vervet monkeys over a seven-year period. During that period, we recorded 27 pregnancies. Mean air temperature (T_a) was 23.0 ± 3.1 °C in summer and 11.4 ± 4.6 °C in winter. Early stages of pregnancy coincided with mid-winter conditions, with pregnancy progressing through spring when mean T_a was 17.3 ± 4.1 °C. Lactation generally started in mid-summer and lasted through autumn when mean T_a was 17.4 ± 4.8 °C. In one year, the vervet monkeys were exposed to drought with total annual rainfall of only 132 mm, compared to the average annual rainfall of 292 ± 99 mm per year. Rain fell predominantly in the summer months peaking between December and March, while the winter months were drier months. Normalized difference vegetation index (NDVI) (i.e., vegetation greenness) was used as a proxy for food availability.

As shown for other mammals, pregnant vervet monkeys displayed gestational hypothermia with a progressive decline in overall 24-h T_b (i.e., 24-h minimum, 24-h maximum and 24-h mean) as gestation progressed, such that mean 24-h T_b was 0.4 °C lower at the end of

pregnancy compared to the start of pregnancy. Despite later stages of pregnancy coinciding with warmer conditions and increased food abundance, mean 24-h T_b progressively declined up until the day of parturition. Gestational hypothermia in free-living vervet monkeys was therefore independent of environmental conditions. Pregnant females also displayed improved homeothermy compared to lactating and non-lactating females, where 24-h amplitude of the T_b rhythm was 0.1 - 0.2 °C lower in pregnancy.

During lactation, minimum 24-h T_b of females was slightly higher (0.1 °C) than that of non-lactating females but there was no significant difference in maximum 24-h T_b between lactating and non-lactating females. The similar T_b patterns in lactating females suggest that they received adequate water and energy intake to meet the demands of lactation. The 24-h amplitude of the T_b rhythm of lactating females was on average 0.1 °C lower than non-lactating females. Over the course of lactation minimum 24-h T_b and mean 24-h T_b did not change but maximum 24-h T_b increased slightly by approximately 0.2 °C and the 24-h amplitude of the T_b rhythm increased by 0.1 °C. The small increase in maximum 24-h T_b and the 24-h amplitude of the T_b rhythm over the course of lactation indicates that lactating females generally maintained T_b very well, especially considering the increasing energetic and water demands of caring for a growing infant.

During drought conditions, lactating females experienced a decrease in minimum 24-h T_b associated with poor energy availability, and an increase in maximum 24-h T_b associated with water stress, compared to normal years. As a result, they exhibited an increase in the 24-h amplitude of the T_b rhythm, likely reflecting a trade-off in allocating limited food and water supplies to other homeostatic systems rather than to thermoregulation. In general, lactating females regulated body temperature relatively well, without severe hyperthermia or

hypothermia, indicating that they were able to cope with the energetic and water demands of lactation during a period of poor resource availability.

My study has contributed valuable insights into understanding how female vervet monkeys respond to environmental (e.g., fluctuating environmental temperatures and resource availability) and physiological (e.g., reproduction) stressors through investigating body temperature patterns. Although female vervet monkeys coped very well with the energetic and water demands of reproduction in their semi-arid environment, future climate change predictions are likely to exacerbate the seasonal characteristics of the Karoo, which may result in increased environmental stress (e.g., higher ambient temperatures and more frequent droughts). Biologging of body temperature provides insights on reproductive phenology and the physiological welfare of mothers and may be a valuable tool to assess how various free-living mammals cope with changes in their environments.

ACKNOWLEDGEMENTS

My research and, ultimately, my dissertation are the result of countless hours of hard work and the assistance of several people whom I would like to thank and express my appreciation for their contribution to the successful completion of this study.

I want to start off by thanking my supervisors, Andrea Fuller, Robyn Hetem and Louise Barrett for giving me the opportunity to conduct this research. Robyn's guidance and assistance during data analysis and understanding the reasons behind the statistics was invaluable. Andrea's extensive knowledge on the topic of climate change and thermoregulation, as well as scientific writing helped a lot during the entire process of my write-up and is much appreciated. Louise Barrett's knowledge and insight into primatology, especially the vervet monkeys used in this study, gave me the right platform onto which I could build my newfound knowledge.

I am also grateful to the University of the Witwatersrand and the School of Physiology for accepting me as a graduate student and the Brain Function Research Group for giving me the opportunity and providing me with the resources to follow my dreams as a field researcher. I would also like to thank the National Research Foundation for funding my two years of study.

I would like to thank every person that was involved in the logistics of field surgery. Zipho Zwane, for always organizing the vehicle for surgery trips and helping pack and unpack the mammoth load. Arista Botha and Valery Phakoago that made themselves available to help pack for surgery trips. Mary-Ann Costello, for her assistance and monitoring of the animals during surgery. Central Animal Services at the University of the Witwatersrand, for providing

us with surgical equipment. I owe a large debt of gratitude to the study veterinarian, Jessica Briner, for not only helping to organize and pack for surgery trips, the hours of driving down to the study site, her expertise during field surgery, but also the companionship and friendship that was much needed during challenging times.

Thank you to Richard McFarland and Chris Young for all their hard work and long hours in the field during captures, which left them pretty banged-up and exhausted by the end of every day. Their determination kept everyone in the field motivated. They also provided me with the retrospective temperature and climate data without which my study would not have been successful. Thanks to Marcus Dostie, for providing me with satellite climate and imaging data. To the field researchers, and study leaders Peter Henzi and Louise Barrett, thank you for the data collection and knowledge on vervet identifications. Thanks to Peter Kamerman for showing me the ropes of R-studio and guiding the way through analysing a very large and complicated dataset.

I am grateful for the support from my friends and family who kept me going, even during the hard times where the finish line seemed out of reach. Their constant encouragement made this two-year journey possible. All of their messages, e-mails, phone calls and lunchtime conversations kept me motivated. To my family, thank you for all that you have done for me by giving me the opportunities to further my education and to pursue my passion. I know it wasn't always easy, but it was definitely worth it.

TABLE OF CONTENTS **PAGE**

DECLARATION ..... **ii**
ABSTRACT ..... **iii**
ACKNOWLEDGEMENTS ..... **vi**
LIST OF FIGURES ..... **ix**
LIST OF TABLES ..... **xii**
LIST OF ABBREVIATIONS ..... **xiii**
PRECLUDE ..... **xiv**
CHAPTER ONE – INTRODUCTION **1**
1.1 Cost of gestation 4
1.2 Cost of lactation 7
1.3 Implications for thermoregulation 14
1.4 Dissertation aims and hypotheses 17
CHAPTER TWO – STUDY SITE AND METHODS **21**
2.1 Study species 21
2.2 Study site 24
2.3 Study subjects 27
2.4 Surgical procedures 31
2.5 Body temperature measurements 34
2.6 Identifying pregnancies, births and lactation periods 35
2.7 Environmental measurements 39
2.8 Data analysis 40
CHAPTER THREE – RESULTS **44**
3.1 Environmental conditions during the study period 44
3.2 Reproductive status 45
3.3 Progression of pregnancy 51
3.4 Days of lactation 55
CHAPTER FOUR – DISCUSSION **59**
4.1 Gestational hypothermia 63
4.2 Lactation 70
4.3 Consequences of climate change for reproduction 78
CHAPTER FIVE – CONCLUSION **82**
REFERENCES **89**

LIST OF FIGURES **PAGE**

Figure 2.1: The vervet monkey distribution range as of 2008, with Samara Private Game Reserve indicated by the red location pin 23
Figure 2.2: The location of Samara Private Game Reserve in South Africa and the reserve boundary 25
Figure 2.3: Vegetation types at Samara Private Game Reserve with the location of the study troops home ranges centered on the Melk river 26
Figure 2.4: Total annual rainfall for the study period (2010 –2017) 27
Figure 2.5: All three troop territories situated along the Melkriver 28
Figure 2.6: Summary of all 30 female vervet monkeys implanted over a seven-year period (September 2010 – June 2017) 29
Figure 2.7: Original 5-minute body temperature of a male and a non-reproductive female exposed to the same environmental conditions over a year (June 2014 – June 2015) 30
Figure 2.8: Temporary surgical theatre 32
Figure 2.9: Veterinarian and veterinary nurses preparing an anaesthetized vervet monkey for surgery to implant the temperature-sensitive data logger. 33
Figure 2.10: A) Temperature-sensitive data logger (mlog T1C), used from September 2010 to March 2013, uncoated and in inert wax. A 9V battery is used as a size reference (Lubbe, 2013), B) temperature-sensitive data logger (DST centi-T) used from December 2013 to June 2017 34
Figure 2.11: Original 5-minute body temperature and mean 24-h body temperature of a non-reproductive female over a year (June 2014 - June 2015). 35
Figure 2.12: Mean 24-h body temperature of 12 females (1 non-pregnant female and 11 pregnant females) July 2014 – July 2015 36
Figure 2.13: a) Mean 24-h body temperature of a pregnant female over 12-months, b) mean 24-h body temperature before and after birth, c) 5-minute body temperature on the day of birth. 37
Figure 2.14: 5-minute body temperature of six pregnant females on the day of parturition.. 38
Figure 2.15: Mean 24-h body temperature of a pregnant female over a 12-month period with pregnancy and the lactation period indicated by the shaded blocks 39

Figure 2.16: Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h air temperature, vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and reproductive status (pregnancy, lactation and non-lactation) on 24-h body temperature while controlling for body mass 42
Figure 2.17: Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h air temperature, vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and pregnancy progression on 24-h body temperature while controlling for body mass 42
Figure 2.18: Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h air temperature, vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and lactation on 24-h body temperature while controlling for body mass 43
Figure 3.1: Cumulative monthly rainfall, mean monthly vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and mean 24-h air temperatures for the duration of the study period (September 2010 to June 2017) 45
Figure 3.2: Mean 24-h body temperatures of four individuals, (a) non-reproductive individual (male), (b) female who gave birth once over a period of two years and had a complete lactation period (203 days), (c) female who gave birth twice over a period of two years and had a shorter lactation period (53 days) due to the death of the infant and a (d) female who gave birth twice over a period of two years where lactation and pregnancy overlapped 47
Figure 3.3: Generalized linear mixed-effects model (GLMM) marginal effects of reproductive status on 24-h body temperature while controlling for air temperature, vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and body mass 49
Figure 3.4: Mean 24-h body temperature of two females during pregnancy leading up to the birth. Female in (a) was pregnant during a normal year while female in (b) was pregnant during cold and dry environmental conditions 51
Figure 3.5: Generalized linear mixed-effects model (GLMM) marginal effects of pregnancy progression in days on 24-h body temperature, while controlling for air temperature, vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and body mass 53
Figure 3.6: Generalized linear mixed-effects model (GLMM) marginal effects of lactation progression in days on 24-h body temperature, while controlling for air temperature,

vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and body mass.....56
Figure 3.7: Maximum 24-h body temperature of three females from different cohorts during the lactation period starting immediately after birth. Female in (a) is from the 2014-2015 cohort where the lactation period coincided with favourable environmental conditions. Females in (b) and (c) are from the 2016-2017 cohort where the first three months of lactation coincided with dry and warm environmental conditions. Rain fell during the fourth month of lactation.....58

LIST OF TABLES **PAGE**

Table 2.1: The number of males and females implanted in each troop, the number of births, and average body mass for males and females during the different study cohorts.....29
Table 3.1: Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and reproductive status with body temperature (T_b) of 30 female vervet monkeys over the duration of the study period (September 2010- June 2017). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor.....50
Table 3.2: Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and progression of days of pregnancy with body temperature (T_b) of 17 pregnant female vervet monkeys over the duration of the study period (September 2010- June 2017). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor.....54
Table 3.3: Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and the progression of the lactation period with body temperature (T_b) of 17 female vervet monkeys over the duration of the study period (September 2010- June 2016). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor.....57
Table 4.1: Average decrease in mean body temperature (T_b) (gestational hypothermia) and average decrease in the 24-h amplitude of the T_b rhythm (improved homeothermy) during pregnancy, as well as living conditions of the animals, and the method through which body temperature was measured.....65

LIST OF ABBREVIATIONS

GLMM – Generalized linear mixed-effects model

HDL – Heat dissipation limitation

I.D. – Identification

MODIS – Moderate resolution imaging spectroradiometer

NDVI – Normalized difference vegetation index

PT – Picnic troop

RBM – Riverbend mob

RST – Riverside troop

T_a – Air temperature

T_b – Body temperature

PRECLUDE

This dissertation attempts to understand the body temperature plasticity of reproductively active female vervet monkeys (*Chlorocebus pygerythrus*) inhabiting the semi-arid Nama-Karoo, in response to high costs of reproduction while simultaneously being exposed to high day time temperatures, low night time temperatures and fluctuating food and water availability. Long-lived animals that have slow reproductive cycles, such as the vervet monkey, are likely vulnerable to rapid environmental changes (Lubbe, 2013), such as those occurring as a result of climate change and habitat destruction. Future climate change scenarios predict that the seasonal fluctuations in the Karoo will be exacerbated, resulting in higher environmental temperatures, extended summer conditions, decreased rainfall and more frequent extreme climatic events such as droughts (Engelbrecht *et al*., 2015), which will significantly impact species survival and distribution.

If we wish to predict the future survival and distribution of species in the face of climate change, long-term studies are required to determine the extent of the phenotypic plasticity of animals to respond to climate change. Knowledge on an animal's phenotypic plasticity to cope with climate change, will improve our ability to employ successful conservation strategies. I had the opportunity to examine a long-term data set, including a drought year, for my study. My study aims to investigate the physiological mechanisms employed by free-living vervet monkeys in response to environmental stresses during the costly reproductive period. I therefore investigated the pattern of the body temperature rhythm in free-living pregnant, lactating and non-lactating vervet monkeys to investigate how they cope with the physiological demands of gestation and lactation during changing and often harsh environmental conditions.

CHAPTER ONE – INTRODUCTION

The primary goal of an animal's life is to reproduce. Those animals that are more successful in their reproduction are the ones that will be favoured in terms of natural selection because of their greater genetic contribution to the gene pool of future generations (Speakman, 2008). Therefore, animals will invest heavily in reproduction, especially long-lived species that produce fewer offspring. In contrast, short-lived species that have fast life-histories characterized by rapid maturation, breeding only once and producing small offspring in large numbers (Rowe, 2008), do not invest as heavily in getting those large numbers of offspring to maturity. Long-lived species, including many mammals, have slow life-histories characterized by long lives, slow growth rates, reach sexual maturity late in life, breed multiple times and have fewer offspring in which they invest heavily (Pianka, 1970) to ensure the survival of those few offspring to maturity. Female mammals have high individual investment in their offspring by carrying their young during gestation and feeding their young through lactation, both of which come at a cost to the mother.

The costs of parental investment depend on the number of offspring the mother gives birth to, whether or not the young are carried around and the length of the lactation period. The degree of parental investment varies greatly between species, which has led to debate among evolutionary biologists regarding the trade-offs between an energetically costly reproduction and the wellbeing of mothers and their offspring. The cost-benefit approach of parental investment was first introduced by Trivers (1972) who defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". Clutton-Brock (1991) later defined the cost-benefit approach of parental investment as costs being a decrease in the female's overall reproductive success and benefits

being an increase in the fitness of the current offspring. If a mother allocates substantial time and energy to her offspring's wellbeing, the cost may be a reduction in the time and energy required to look after herself in terms of foraging (Wright, 1984; Goldizen, 1987), thus compromising her future reproductive success or the welfare of future offspring. Successful reproduction requires animals to not only survive but to thrive, socialize, mate and rear offspring to maturity, all of which often have conflicting energetic demands (Dunbar, 1988). The demands for rearing offspring places female mammals under immense physical and physiological stress as a result of the energetic costs associated with gestation and lactation (Glittleman and Thompson, 1988). As a result of the costly nature of reproduction, trade-offs exist between the different life-history components. For example, maximizing fecundity to increase current reproductive output, may be done at the expense of future reproductive output (Stearns, 1992; Charnov, 1993). Mammals may therefore need to trade-off current and future offspring as well as the quantity and quality (i.e., individual fitness) of offspring (Stearns, 1992).

Reproduction is regarded as a physiologically challenging period for female mammals as gestation and lactation often require an increase in, or prioritization of resources, which can lead to energetic trade-offs if those resources are limited (Archie *et al*., 2014). For example, red deer (*Cervus elaphus*) hinds in nutrient-rich environments that are presumably in good physical condition, are able to transfer energy more efficiently to offspring by having a greater milk yield resulting in reduced frequency of nursing events compared to hinds in poor nutrient environments (Loudon *et al*., 1983). Poor quality food resources are associated with slow infant growth rates, increased infant rejection and higher infant mortality in several species, including sheep (*Ovis aries*: Arnold *et al*., 1979), rodents (Eastern woodrat *Neotoma floridana* and cotton-top rat *Sigmodon hispidus*: McClure, 1987) and primates (vervet

monkey *Chlorocebus pygerythrus*: Lee, 1984; Barbary macaque *Macaca Sylvanus*: Menard and Vallet, 1993). Vervet monkey mothers in both marginal versus prime physical condition had similar rates of infant rejection, both of which were higher than mothers in average reproductive condition (Fairbanks and McGuire, 1995). Despite similar levels of infant rejection, the consequences of that rejection for the infant and the mother differed depending on the mother's reproductive condition. Whereas the self-preservation behaviour of vervet monkey mothers that were in marginal reproductive condition resulted in high rates of infant mortality (40%) and low rates of fertility, mothers in prime physical condition were able to increase their fecundity by shortening birth intervals without jeopardizing infant survival by relying on other group members for infant care and potentially producing higher quality milk (Fairbanks and McGuire, 1995). Access to sufficient resources is therefore crucial to maintain energetic balance and ensure reproductive success.

Resource availability may dictate 'income versus capital' breeding strategies where capital breeders are defined as "an organism that uses stored energy for reproduction", while income breeders "use energy acquired during the reproductive period rather than stored energy for reproduction" (Stearns, 1989; Stearn, 1992). To sustain themselves throughout the costly reproductive period, large-bodied capital breeders are able to store energy reserves and reproduce independently of food availability, a strategy likely to be advantageous in highly seasonal environments (Sainmont *et al*., 2014). In comparison, small-bodied income breeders are at risk of dehydration and energy deficiency in highly seasonal environments, especially during the energetically costly reproductive period.

1.1 Cost of gestation

The cost of reproduction is high, especially in mammals where gestation is an energetically expensive reproductive period. Energy investments during gestation involve several components such as the production of uterine, placental, foetal and mammary tissue as well as the increased metabolic costs of the newly produced tissue (Brody, 1945). Many studies have focused on caloric intake as an indicator of the energetic costs associated with gestation. Placental and uterine tissue proliferations account for ~ 20 % of caloric investment during pregnancy (Oftedal, 1985). To supply enough nutrients to a developing foetus, as well as tissue growth, pregnant females need to increase their food intake. Several studies have found that pregnant females significantly increase their food intake compared to non-reproductive females (cotton-top rat Mattingly and McClure, 1982; white-toothed shrew *Crocidurinae*: Mover *et al*., 1988; guinea pig *Cavia porcellus*: Künkele, 2000; mice *Mus musculus*: Gamo *et al*., 2013; yellow baboons *Papio cynocephalus*: Altmann, 1980; Muruthi *et al*., 1991; olive baboons *Papio anubis*: Barton, 1989; ring-tailed lemurs *Lemur catta*: Sauther, 1994).

Females appear to distribute the increased energy intake to the growing foetus as they reduce other energetically demanding physical activity during pregnancy. Activity levels have been reported to be lower in pregnant females than in non-reproductive females in several species, including bats (*Chiroptera*: Racey, 1982), gerbils (*Meriones unguiculatus*: Weinandy and Gattermann, 1995), chimpanzees (*Pan troglodytes schweinfurthii*: Murray *et al*., 2009), mice (Gamo *et al*., 2013) and vervet monkeys (Sashaw, 2012). Reduced levels of activity are particularly evident during late pregnancy. Pregnant women reduced daily activity levels by 26 % from the second to third trimester (Rousham *et al*., 2006). Similarly, pregnant vervet monkeys moved and foraged less during the last month of pregnancy compared to the first couple of months of pregnancy (Sashaw, 2012). In addition to reduced movement and

foraging activity levels as pregnancy progresses, levels of vigorous activity are reduced during late pregnancy. For example, the dwarf hamster (*Phodopus campbelli*) reduced overall activity during early pregnancy and more strenuous activity, such as wheel-running during late pregnancy (Scribner and Wynne-Edwards, 1994). Allocating available energy to pregnancy rather than activity by reducing physical activity levels may provide an energy-conserving strategy to support the energetic demands of the growing foetus (Gamo *et al*., 2013).

Despite an increase in energetic demands during pregnancy, many animals improve their homeothermy during this period. Improved homeothermy has been recorded in large free-living mammals such as African lions (*Panthera leo*: Trethowan *et al*., 2016) and brown bears (*Ursus arctos*: Friebe *et al*., 2014), as well as in species under laboratory conditions, including rats (Eliason and Fewell, 1997), sheep (Laburn *et al*., 1992) and dogs (Concannon and Hansel, 1977). Pregnant lions regulated daily body temperature with greater precision, with the mean amplitude of the 24-h body temperature rhythm 0.6 °C lower than that of non-pregnant and lactating females (Trethowan *et al*., 2016). Similarly, body temperatures were tightly regulated towards the end of gestation in dunnarts (*Sminthopsis macroura*), echidnas (*Tachyglossis aculeatus*; Nicol and Andersen, 2006), rats (Kitrell and Satinoff, 1988), Djungarian hamsters (*Phodopus campbelli*), Siberian hamsters (*Phodopus sungorus*; Scribner and Wynne-Edwards, 1994) and bats (*Eptesicus fuscus*: Lausen and Barclay, 2003). This narrow rhythm of body temperature likely accelerates foetal development as a result of rapid cell division in optimum temperature conditions (Farmer, 2000; Trethowan *et al*., 2016), increasing the parental fitness benefits (Farmer, 2003; Koteja, 2004; Levesque and Lovegrove, 2014). Yet it comes at a cost to the mother because maintaining a narrow 24-h

amplitude of body temperature rhythm is energetically costly and requires sufficient food and water intake (Hetem *et al*., 2016).

In addition to improved homeothermy, a gradual decline in mean body temperature over the course of gestation, termed gestational hypothermia (Kozak, 1997), has been reported in several mammalian species including rats (Kitrell and Satinoff, 1988; Eliason and Fewell, 1997; Cairns *et al*., 2005), sheep (Laburn *et al*.,1992), African lions (Trethowan *et al*., 2016) and dogs (Concannon and Hansel, 1977). Gestational hypothermia has also been recorded in other mammals that do not display improved homeothermy during pregnancy, such as arctic ground squirrels (Williams *et al*., 2011) and rabbits (Naccarato and Hunter, 1983). Foetal body temperature is ~ 0.5 °C higher than maternal body temperature in all species studied to date (Laburn *et al*., 1992), as a result of heat producing metabolically active foetal cells and accelerated cell division. Gestational hypothermia may provide a protective mechanism to facilitate a lower foetal temperature and thus prevent teratogenic effects caused by intrauterine hyperthermia (Edwards, 1986; Fewell, 1995; Laburn, 1996). Prolonged episodes of hyperthermia result in foetal death and consequently abortions, while shorter periods of hyperthermia result in congenital abnormalities (Asakura, 2004). The foeto-maternal temperature gradient allows heat transfer from the foetus to the mother to protect the foetus from damage caused by thermal stress.

Gestational hypothermia may also protect the foetus from hypoxia as a lowered maternal body temperature results in reduced metabolic activity, and therefore reduced oxygen demand in the mother and the foetus (Kozak, 1997). Lowered maternal body temperature has also been found to increase oxygen saturation by shifting the oxyhaemoglobin dissociation curve to the left (Kozak, 1997). The increased oxygen saturation associated with lower maternal

body temperature may reduce neuronal injury in the foetus in hypoxic conditions, such as asphyxia (Nishio *et al*., 2000), which further contribute to the idea that gestational hypothermia may be a neuroprotective mechanism. Although reduced maternal body temperature during gestation is advantageous to the foetus, there may be costs associated with lowering body temperature such as body water loss associated with evaporative cooling to maintain low body temperatures in hot environments (Hetem *et al*., 2016).

1.2 Cost of lactation

Although gestation is an energetically expensive period, it is generally less energetically expensive than lactation (Brody, 1945; Loudon and Racey, 1987; Altmann, 1980; Clutton-Brock *et al*., 1989). Lactation is the most energetically expensive periods of a mammal's life because of the cost of milk production (Altmann, 1980; Glittleman and Thompson, 1988; Strier, 1993; Lee, 1996; Dunbar *et al*., 2002). While pregnant northern female muriquis (*Brachyteles hypoxanthus*) were found to spend similar amount of time feeding compared to lactating females (Strier, 1987; Guedes *et al*., 2008), studies in yellow baboons (*Papio cynocephalus*: Altmann, 1980), gelada baboons (*Theropithecus gelada*: Dunbar *et al*., 2002), Japanese macaques (*Macaca fuscata*: Takahashi, 2002) and vervet monkeys (Lee and Hauser, 1998) found that pregnant females spent significantly less time feeding than did lactating females. A lower feeding time in pregnant females suggest that the energetic costs of gestation are not as high as those of lactation.

Lactating females increase their energy intake in order to maintain their increased metabolic costs (Johnson *et al*., 2001). For example, energy intake of lactating mice was found to be two to four times greater than that of non-lactating females (Speakman and McQueenie, 1996). In several non-human primates, lactating females fed more than non-lactating females

(Altmann, 1980; Strier, 1987; Dunbar and Dunbar, 1988; Koenig *et al*., 1997) and the lactating females may choose higher quality dietary items during lactation. For example, vervet monkey mothers in the semi-arid Karoo increased their protein intake as lactation progressed and the milk requirements of the infant increased (Sashaw, 2012), while the diet of lactating female chimpanzees consisted of a higher percentage of fruit compared to non-lactating females (Murray *et al*., 2009).

The risk of an energy deficit during lactation is exacerbated for small-bodied income breeders that rely on ingested energy to fuel reproduction and cannot pre-emptively accumulate large enough fat stores during pregnancy to fuel lactation (Lindstedt and Boyce, 1985). Although primates have the ability to store fat, they rarely do so in the wild (DuFour and Sauther, 2002) and they therefore need to forage after giving birth to support their own energetic needs and those of their growing infant. Cercopithecine primates, such as the vervet monkey, carry their young post-parturition, thereby further increasing energetic costs during lactation. Transporting infants was found to impose high energetic costs in marmosets (*Callithrix jacchus*) and tamarins (*Saguinus oedipus*) (Tardif, 1997; Sánchez *et al*., 1999). Species with highly precocial young, which either follow the mother or are carried, have highly diluted milk with a lower fat content compared to species that 'park' their young or leave them with other adolescent females ('allomothers') within their troop (Shad, 1963). Vervet monkey mothers give birth to highly precocial young and are in constant contact with their infants for the first two weeks of their lives (Lee, 1984), which places additional energetic stress on the mother while foraging. Thereafter, vervet monkeys will leave their young with allomothers while they forage, reducing their energetic burden. Vervet monkeys also use allomothers to increase the time between nursing bouts, thus allowing the mother to replenish milk stores (Fairbanks, 1990). Vervet monkey mothers in prime reproductive condition (i.e., those that

rank higher in the female dominance hierarchy) have less contact with their infant than mothers in average reproductive condition (Fairbanks and McGuire, 1995), which may allow the mothers an opportunity to recoup energetic costs, improve body condition and reduce the interbirth interval. As infants mature and start to locomote independently, the energetic stress of infant-carrying will be reduced but the infant remains heavily dependent on their mother's milk for five to six months (Cheney *et al*., 1981) and the mother needs to produce increasing quantities of milk to feed the rapidly growing infant (Altmann and Samuels, 1992).

The lactation period starts immediately after birth with a gradual increase in milk production to sustain the growing infant. Maximum milk production, or peak lactation, occurs just before weaning; thereafter milk production declines as the infant starts to rely more on solid food. Primates have longer periods of lactation compared to other mammals of similar size due to late weaning of infants, high investment in individual infant development (Hayssen, 1993; Martin, 1995) and their slow life history traits (Hinde *et al*., 2009). These extended lactation periods can compromise both the mother's and infant's wellbeing if the mother's dietary needs are not met. Weight loss has been reported during lactation in primates such as olive baboons (*Papio anubis*: Bercovitch, 1987) and vervet monkeys (Fairbanks and McGuire, 1995), which suggests that lactating females resorted to using their own energy stores to fuel lactation. If a primate mother is unable to meet her energy requirements, she may either resort to using her own energy stores to fuel lactation, thus compromising her own wellbeing, or she may reduce milk output which may compromise the infant's survival (Roberts *et al*., 1985). Vervet monkey mothers in poor physical condition that are unable to meet her energetic requirements limit maternal investment by rejecting the infant, which often result in high infant mortality (Hauser, 1993; Fairbanks and McGuire, 1995). In addition, mothers that are

energy deficient may adjust their activity budgets in order to conserve energy and reduce energetic requirements.

Mothers may use an energy-sparing strategy by reducing their activity levels, thus reducing their energetic requirements so that they can meet their own needs and those of their growing infant (Kenyatta, 1995). When energy costs cannot be balanced by increased energy intake as a result of low food availability, an animal can either use its energy stores or reduce energy expenditure (Heasley, 1983). Small-bodied income breeding primates, which cannot rely on energy stores to fuel lactation when food availability is low (Lindstedt and Boyce, 1985), would need to adopt alternative feeding strategies. When possible, animals are predicted to use optimal foraging strategies that maximize their energy intake while at the same time minimizing the amount of time or energy spent on foraging (Emlen, 1966; MacArthur and Pianka 1966, Schoener, 1971). Altmann (1980) developed an analytical model to predict food intake of female yellow baboons in Amboseli, Kenya, for them to effectively deal with the increasing nutritional demands of a growing infant. In several populations of baboons (olive baboon *Papio anubis*: Nicolson, 1982; gelada baboon *Theropithecus gelada:* Dunbar and Dunbar, 1988; hamadryas baboon *Papio hamadryas anubis*: Kenyatta, 1995; chacma baboon *Papio cynocephalus ursinus*: Lycett *et al*., 1998) feeding time exceeded the predicted food intake requirements for lactating females to sustain their growing infant. After a comprehensive review of all previous baboon studies that tested Altmann's (1980) model, Barrett *et al*., (2006) showed that maternal feeding times in habitats with low mean annual temperature were above those of Altmann's predictions, while maternal feeding times in habitats with high mean annual temperature fell below Altmann's predictions. Poor habitat conditions and fluctuations in resource availability resulted in females spending more time

foraging in order to obtain similar nutrient and energy intake as compared to when conditions were favourable (Barret *et al*., 2006).

In addition to the energetic cost associated with infant carrying and milk production, lactating females also have the added energetic cost of having to protect their infants against predators. The risk of predation is higher for lactating females than non-lactating females because their infants are more likely to be targeted by predators (Caro, 1987; Wolff and Van Horn, 2003). Mothers are slowed down when carrying infants and are less likely to escape predator attacks. Lactating females are therefore more vigilant than non-lactating females and that vigilance was sustained at the cost of feeding time, as the former may possibly have greater long-term fitness benefits (Barrett *et al*., 2006).

To avoid potential energy deficits associated with low food availability, reproductive events, including conception (e.g., baboons: Altmann, 1980), gestation, birth and lactation (e.g., rhesus monkeys *Macaca mulatta*, langur monkeys *Semnopithecus* and vervet monkeys: Lancaster, 1965; Lee, 1987) in primates often correspond with the availability of nutrient-rich foods. Food availability is generally at its highest during the wettest months of the year. The seasonality of vervet monkey reproduction differs depending on environmental conditions. For example, in Amboseli, Kenya, the copulation period of the vervet monkeys corresponds with the dry season and the birth season peaks early during the wet season in November (Struhsaker, 1967b). Similarly, vervet monkeys in the Karoo copulate between April and August (i.e., during the dry season) with births peaking in November and most rain falling from December through March (Sashaw, 2012), resulting in peak lactation falling within the period of high food abundance. Although vervet monkeys are seasonal breeders, 'off-season' breeding can occur, which may lead to peak lactation corresponding with periods of low food

abundance (Lee *et al*., 1986). For example, in Barbados, West Indies, most vervet monkey births occurred within the two months following the month with the least amount of rainfall, well within the dry season (Horrocks, 1986). Similarly, gelada baboons in Ethiopia give birth during the dry season (Dunbar, 1980). Postnatal death as a result of climatic exposure may be highest during the wet season as a result of respiratory infections caused by frequent soakings and sub-zero temperatures, therefore births peaking during the dry season may reduce infant mortality (Dunbar, 1980). Droughts, or other environmental disturbances, may also alter food availability during lactation, which may have knock-on consequences for thermoregulation, protection against predators and milk output, placing the mother's and infant's survival at risk.

Timing of lactation outside of the rainy season, or during a drought, may compromise a mother's ability to manage her body water balance. Lactation significantly increases body water flux, as water is the main component of milk (Kunz *et al*., 1994; Wilde *et al*., 1995). Water scarcity in combination with environmental heat stress may result in a reduced body water volume, as a result of the demand for water to sustain milk production and to aid in evaporative cooling for thermoregulation. If body water is prioritized for milk production, rather than for thermoregulation, then one might expect lactating females in hot environments to experience hyperthermia (Hetem *et al*., 2016). Indeed, environmental heat stress was associated with increased body temperature in primiparous sows during lactation (Williams *et al*., 2013). Lactation also is an exothermic process which releases energy in the form of heat, which may further contribute to a rise in body temperature.

The ‘heat dissipation limitation’ (HDL) theory hypothesizes that the sustained rate of energy expenditure is determined and limited by an animal’s capacity to dissipate excess metabolic heat generated (Speakman and Król, 2010). For example, lactating mice raising offspring in thermoneutral environments were observed to be limited by the capacity to dissipate heat under conditions of high metabolic demands (Król and Speakman, 2003a; Król and Speakman, 2003b; Król *et al*., 2003; Król *et al*., 2007). Speakman (2008) suggested that increased metabolic rate during lactation may result in an increase in body temperature, which can lead to reduced milk production as a result of vasodilation redirecting blood flow away from mammary glands. With a lower milk output associated with increased maternal body temperature, suckling events will presumably increase for infants to obtain sufficient milk. It has been suggested that suckling generates heat (Speakman and Król, 2005), therefore lactating females might cease suckling events earlier if they are faced with hyperthermia which might result in retarded growth in offspring.

Throughout lactation, maternal core body temperature remains ~ 0.5 °C higher than that of nonpregnant female rats (Fewell, 1995). Increased core body temperature during lactation has been suggested to be the result of several mechanisms, including increased metabolic heat production as a result of milk production and greater food intake (Adels and Leon, 1986; Speakman 2008) and altered hormone levels, including corticosterone and progesterone (Stern *et al*., 1973; Adels and Leon, 1986). Increased core body temperature during lactation has been suggested to be a forced thermoregulatory response (i.e., forced hyperthermia) that involves the failure of homeostasis when an animal’s heat load exceeds the animal’s ability to dissipate heat (Gordon, 1983; Eliason and Fewell, 1997). Chronic hyperthermia has been found in several small lactating rodents such as mice (Gamo *et al*., 2013), dwarf hamsters (Scribner and Wynne-Edwards, 1994), Mongolian gerbils (*Meriones unguiculatus*: Weinandy

and Gatterman, 1995) and Sprague-Dawley rats (*Ratus norvegicus*: Fewell, 1995). Whether lactation in free-living non-human primates results in hyperthermia is not known. Although dehydration-induced hyperthermia was evident in baboons deprived of drinking water and exposed to heat (Mitchell *et al*., 2009), there is a lack of data on increased maximum daily body temperatures during the combined stressors of lactation and water deficiency, particularly in primates.

1.3 Implications for thermoregulation

In addition to supporting offspring, mothers need resources in order to maintain their own homeostasis. For mammals, a homeostatic system that requires energy and water is body temperature regulation. Most mammals are homeothermic to some degree (De Ricqlés, 1974; Bakker, 1975; Crompton *et al*., 1978), maintaining their body temperature within a relatively narrow range (usually less than 2 °C variation over 24-h). Homeothermy is maintained through a facilitating process called endothermy (Refinetti and Menaker, 1992; Schmidt-Nielsen, 1997). Homeothermic endothermy is a characteristic of birds and mammals where they maintain a stable body temperature when exposed to different thermal environmental conditions by using internally generated heat, which requires a considerable amount of energy input (Hetem *et al*., 2016). Animals in cold environments need to maintain body core temperature above ambient temperature, which requires oxygen and fuel consumption in order to generate internal heat. Animals in hot environments need to maintain body core temperature below ambient temperature, which requires water for evaporative cooling. Therefore, maintaining body core temperature (i.e., homeothermic endothermy) requires sufficient intake of food and water. Hetem *et al*. (2016) have shown that, amongst regulated homeostatic systems, homeothermy is not prioritized and is only evident in large mammals if they are well nourished and hydrated. For example, if an animal is water-stressed it results in

hyperosmolarity and hypovolemia of body fluids, therefore maintaining body fluid homeostasis is in direct competition with thermal homeostasis in animals that employ evaporative cooling (Cain *et al*., 2006). Maintaining a consistently high body temperature is suggested to increase performance as a result of the high metabolic function and increased efficiency of chemical reactions (Heinrich, 1977; Knies *et al*., 2009). Body temperature control therefore plays an important role in the performance and welfare of endotherms (Angilletta *et al*., 2010). However, the advantages of maintaining a high body temperature must outweigh the substantial water and energy costs required for homeothermic endothermy.

To reduce energetic and water costs of autonomic thermoregulation, animals may employ behavioural adjustments that facilitate heat transfer with the environment. The amount of heat exchanged between an animal and its environment by non-evaporative means is dependent on the temperature difference between the body surface and the environment (Mitchell *et al*., 2018). Heat is exchanged between an animal and its environment to achieve thermal equilibrium by means of dry heat exchange, which includes conduction, convection and radiation, as well as evaporative heat loss (Hammel, 1968). Conductive heat transfer occurs when an animal comes into direct contact with a solid surface. For example, chacma baboons in the Namib Desert throw cool subsurface sand on to their bodies to help them regulate their body temperatures (Brain and Mitchell, 1999). Convective heat transfer depends on the temperature difference between the animal and the surrounding air (Potter *et al*., 2013; Pincebourde *et al*., 2016) or water. Radiant heat exchange encompasses an array of radiant heat sources and sinks in an animal's habitat that include, but are not limited to, direct solar radiation, ground and vegetation thermal radiation and atmospheric thermal radiation. Animals seeking shade will only be able to escape direct solar radiation, as other sources of radiation penetrate the shade (Mitchell *et al*., 2018). Some species make postural adjustments

to reduce the body surface area exposed to direct sunlight in an attempt to minimize heat gained from direct solar radiation at high environmental heat loads (Maloney *et al*., 2005).

When environmental temperature exceeds body temperature, dry heat loss is no longer possible, which leaves evaporative cooling as the primary avenue of heat dissipation (Mitchell *et al*., 2018). Evaporative cooling through panting and sweating facilitates heat dissipation but places a demand on the animal's body water (Hetem *et al*., 2016). Thermoregulation is thus costly in terms of metabolic energy required at low environmental temperatures and in terms of body water required at high environmental temperatures. Maintaining homeothermy might therefore be difficult for an animal to achieve when water and food are scarce.

Reduced energy availability may compromise the ability of mammals to maintain a high body temperature at night, or in the cold. Large mammalian herbivores that are energy deficient exhibit lower than normal body temperatures at night or in the early morning, when the minimum 24-h rhythm of body temperature occurs (Hetem *et al*., 2016). Exposure to cold conditions in the face of poor food availability has been shown to lead to lower than normal body temperatures (i.e., hypothermia) in small and large-bodied mammals (rats *Rattus norvegicus*: Hoshino, 1996; horses *Equus ferus przewalskii*: Arnold *et al*., 2006) including vervet monkeys (Lubbe *et al*., 2014). However, even in warm seasons, 24-h minimum body temperatures may be lower than normal in the face of reduced food availability, as demonstrated for the Arabian oryx (*Oryx leucoryx*: Spalton, 1999; Hetem *et al*., 2010) and Western grey kangaroos (*Macropus fuliginosus*: Maloney *et al*., 2011).

There is a lack of data on thermoregulation of free-living non-human primates, and very little is known about the potential costs of gestation and lactation for thermoregulation. Free-living vervet monkeys in a semi-arid environment regulate body temperature relatively well, despite their small body size (Lubbe *et al*., 2014). However, how vervet monkeys, which are exposed to high daytime temperatures and cold stress at night, are able to balance the demands of thermoregulation and simultaneously balance energetic and water demands of gestation and lactation, is unknown. Vervet monkeys are seasonal breeders with a birth peak in mid- to end spring and lactation occurring in the summer (Sashaw, 2012). In the semi-arid Karoo, an area prone to droughts, vervet monkey mothers may be exposed to poor resource availability in combination with high summer air temperatures during drought conditions. Although Karoo summers are characterised by high daytime air temperatures, which often exceed 40°C, night-time temperatures are known to reach lows of around 5°C during the summer and drop below zero during winter (Low and Rebelo, 1996). Large variation in environmental temperatures and extreme climatic events, such as droughts and snowfall, may compromise the ability of female vervet monkeys to maintain body temperature while simultaneously having to cope with the energetic and water costs associated with reproduction.

1.4 Dissertation aims and hypotheses

During an energetically-costly reproductive period combined with environmental stressors of heat and cold, and reduced food and water availability, might result in resources and energy being directed towards the costly reproductive events and away from other homeostatic systems, such as thermoregulation. With future climate change scenarios characterised by higher ambient temperatures, decreased rainfall and increased frequency of extreme climatic events in South Africa (Engelbrecht *et al*., 2015), thermoregulation during the costly reproductive period might be compromised.

The aim of my dissertation is therefore to investigate the effect of environmental factors such as air temperature and vegetation greenness, as indexed by normalized difference vegetation index (NDVI), and reproductive state (pregnancy, lactating and non-lactating) on the body temperatures of female vervet monkeys in the semi-arid Nama Karoo. Long-term continuous body temperature measurements will allow me to:

1. Investigate the relationship of environmental factors (air temperature and vegetation greenness, as indexed by NDVI) on the body temperatures of females within different reproductive states (pregnancy, lactating and non-lactating). Non-lactating females will act as the control group to which the body temperatures of pregnant and lactating females will be compared. Comparing the body temperatures of reproductively active females to non-lactating females will help identify whether the costs of reproduction are evident through thermoregulatory adjustments in a seasonally variable environment that is prone to droughts.
    - I predict that minimum 24-h body temperature will be lower in pregnant females compared to lactating and non-lactating females because of the gestational hypothermia.
    - I predict that minimum 24-h body temperature of lactating females will be lower than non-lactating females because of a possible energy deficiency as a result of the increased energetic demands of caring for a growing infant, particularly during dry years when food resources are limited.
    - I predict that maximum 24-h body temperature of lactating females will be higher than non-lactating females because of the increased water demands of milk production which may result in maternal water balance being challenged during hot and dry periods.

2. Investigate the relationship between environmental factors (air temperature and vegetation greenness, as indexed by NDVI) and pregnancy progression on body temperature. Pregnancy is associated with a developing foetus that requires mothers to not only consume sufficient nutrients and energy to sustain foetal growth, but also to maintain body temperature within a safe range as heat transfer from the foetus to the mother is crucial to avoid teratogenic effects from damage caused by thermal stress.
    - I predict 24-h mean, minimum and maximum body temperature will decrease with progression of gestation as a result of gestational hypothermia.
    - I predict that pregnant females will reduce the 24-h amplitude of the body temperature rhythm as pregnancy progresses.

3. Investigate the relationship between environmental factors (air temperature and vegetation greenness, as indexed by NDVI) and lactation progression on body temperature. The costs associated with lactation such as milk production and infant care may place the mother under nutritional and water stress if she is unable to obtain sufficient resources from the environment. The added environmental stressors such as high air temperatures during the day, low air temperatures at night and variable food availability, might increase energetic and water stress during lactation.
    - I predict that lactating females will have an increase in the 24-h amplitude of body temperature rhythm over the course of lactation as a result of increased 24-h maximum body temperature because of stress placed on the mother's water balance from milk production and reduced minimum 24-h body temperature because of increased energetic and metabolic costs of caring for a growing infant.
    - I predict that the increase in 24-h amplitude of the body temperature rhythm as lactation progresses will be exaggerated during drought conditions as a result of

energy deficiency and water scarcity.

CHAPTER TWO – STUDY SITE AND METHODS

This chapter aims to describe the study site (geographical location, vegetation and climate), provide detailed information on the environmental conditions during the study period and detailed information on the study subjects. For my study I used a long-term data set on body temperature and behavioural observations of three troops of vervet monkeys inhabiting the Nama-Karoo. In this chapter I provide details on capture and surgical procedures for the implantation of the temperature-sensitive data loggers as well technical details of the data loggers used to measure body temperature in free-ranging vervet monkeys.

The Department of Environmental Affairs and Tourism in Graaff-Reinet issued a research permit for the project (Permit number – CRO 97/10CR) and Samara Private Game Reserve gave permission to work at the field-site (E:32/2011/GR). The capture and surgical procedures outlined in this chapter were approved by the University of the Witwatersrand Animal Ethics Screening Committee (AESC) in 2010 (clearance number AESC 2010/41/04, see appendix) and in 2015 (clearance number AESC 2015/04/14/B, see appendix). My research objectives were added to the original project via a Modification and Extension to the aforementioned ethics application and was approved in May 2017 (see appendix).

2.1 Study species

The vervet monkey (*Chlorocebus pygerythrus*) is an Old-World monkey of the subfamily *Cercopithecinae* (Grubb *et al*., 2003). The vervet monkey was originally classified in the genus *Cercopithecus* which means ‘long-tailed monkey’ (Tappen, 1960), but Groves (2001) placed the vervet monkey within their own genus namely *Chlorocebus* which means ‘green monkey’. However, a more recent review by Skinner and Chimimba (2005) retained the original classification of the vervet monkey as a superspecies within the genus

Cercopithecus. Sexual dimorphism is evident in the vervet monkey with males being heavier and larger in length than females. Adult male vervet monkeys weigh on average 5.5 kg and measure between 420 and 600 mm in length from the top of the head to the tip of the tail, while their female counterparts only weigh around 4.1 kg on average and measure between 300 and 495 mm in length (Skinner and Smithers, 1990). The lifespan of wild vervet monkeys are difficult to determine because of high predation rates, but Fairbanks and McGuire (1986) suggested that the upper limit of the vervet monkey's lifespan in captivity to be between 11 and 12 years as this is the age where serious health problems have been reported.

Vervet monkeys are found throughout southern and east Africa, from Ethiopia, Kenya, Tanzania, Malawi, Mozambique, Botswana to the southernmost part of South Africa (Fig 2.1; Kingdon *et al*., 2008). Vervet monkeys, along with chacma baboons (*Papio ursinus*), are the most widely distributed and densely populated African non-human primate (Jasinska *et al*., 2013; Struhsaker, 1967b) and inhabit tree-rich areas (Turner *et al*., 2016) such as high plains, woodland and savanna regions throughout Africa. Home range size of vervet monkeys is determined by food and water availability and can vary in size between 0.06 to 1.78 km^2 (Struhsaker, 1967a; Harrison, 1983). Although vervet monkeys are territorial animals, they will venture outside their normal home range to neighbouring group home ranges in search of water (Wrangham, 1981). Seasonal and geographical variations in home range size are common (Struhsaker, 1967b; Wrangham, 1981). Pasternak *et al*. (2013) found that vervet troops in the Karoo that have home ranges centered on rivers tend to be larger compared to troops with home ranges further away from rivers.

Vervet monkeys are semi-terrestrial, spending most of their days foraging and feeding on the ground, and semi-arboreal, sleeping in trees at night (Cawthon Lang, 2006). Vervet monkeys are opportunistic omnivores with a diet that consists mostly of parts of various plant species, but they also eat invertebrates, rodents and, occasionally, birds and bird eggs (Cawthon Lang, 2006; Skinner and Chimimba 2005). Vegetative food sources are limited under environmental conditions such as droughts and bush fires, resulting in monkeys relying on other food sources such as insects and rodents.



Figure 2.1: *The vervet monkey distribution range (green area) as of 2008, from the International Union for Conservation of Nature (Kingdon et al., 2008) with the field site, Samara Private Game Reserve, indicated by the red location pin.*

Vervet monkeys live in multiple male/multiple female groups where females tend to remain in the home range they were born in, whilst males will leave their natal troop once sexually mature at about five years old (Cawthon Lang, 2006; Horrocks, 1986). Females reach sexual maturity at approximately three years of age and will give birth to a single offspring for the first time between the ages of three and five years (Turner *et al*., 1997). Multiple births

among vervet monkeys and other small-bodied non-human primates are extremely rare as the energetic cost of parturition and infant rearing may simply be too high (Harris *et al*., 2013). The average gestation period of vervet monkeys is 165 days (Rowell, 1970) and they will nurse their infant for five to six months, after which the infant will start to incorporate invertebrate and vegetative food sources into its diet (Cheney *et al*., 1981). Vervet monkeys are vulnerable to rapidly changing environmental conditions due to them being long-lived animals with slow reproductive cycles and life histories (Lubbe, 2013). Vervet monkeys are especially vulnerable to prolonged periods of drought (Wrangham, 1981, McDougall *et al*., 2010) which makes the Karoo a challenging habitat for such a water-dependent species and an ideal site to investigate the effect of environmental stress on vervet monkeys.

2.2 Study site

The study was conducted at Samara Private Game Reserve, Eastern Cape, South Africa (32°22'S, 24°52'E), located in the semi-arid Nama-Karoo approximately 40 km from Graaff-Reinet (Fig. 2.2). The Nama Karoo is close to the southernly limit of the distribution range of vervet monkeys (Fig 2.1) which offers vervet monkeys narrow bands of suitable habitat along rivers (Pasternak *et al*., 2013). The reserve offers a diverse range of vegetation types with four distinguishable biomes, namely savanna, sub-tropical thicket, grassland and Nama-Karoo (Van Cauter, 2004, Fig. 2.3). The vegetation at Samara is dominated by chaemophytes (dwarf shrubs) and hemicryptophytes (grass) with many deciduous plants (Pasternak *et al*., 2013). The sweet thorn (*Vachellia karroo*) and wolfthorn (*Lycium oxycarpum*) trees dominate the woodland habitat, interspersed with firethorn (*Searsia pyroides)*, broom karee (*Searsia erosa*) and mountain karee (*Searsia lancea*). The woodland habitat ranges in height from 1 - 5 m and has a canopy cover of 70 - 80% (Pasternak *et al*., 2013). Large exotic pepper bark

trees (*Schinus molle*), ranging from 6 – 12 m, are scattered along the riverbank and commonly used as a sleep site by the vervet monkeys (Pasternak *et al*., 2013; Lubbe, 2013).

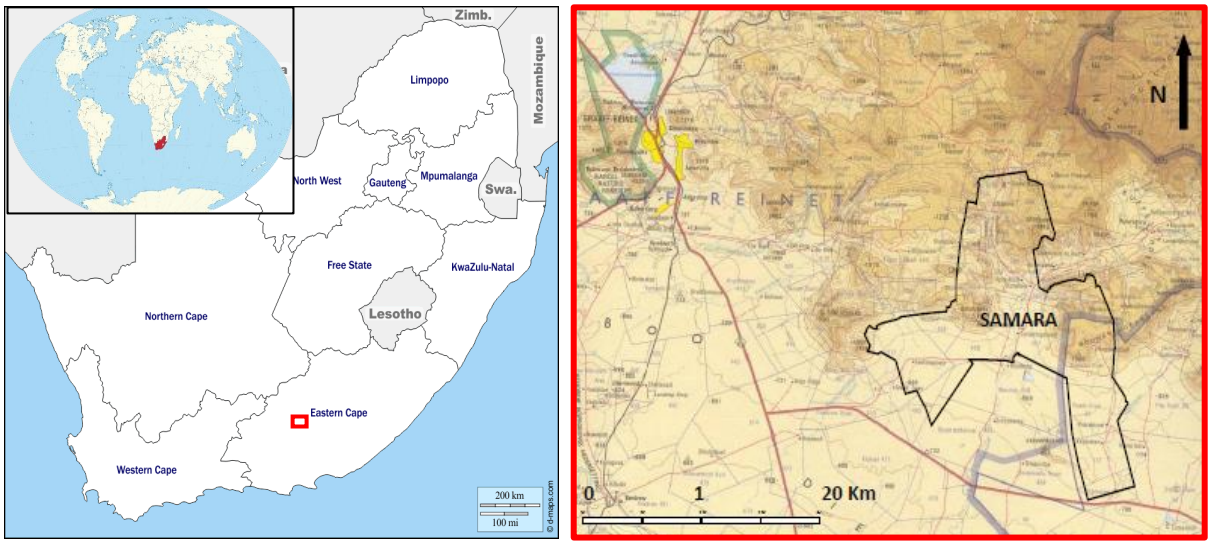

Figure 2.2: *The location of Samara Private Game Reserve in South Africa (left) and the reserve boundary (right). Maps courtesy of South African Geographical Services and reserve boundary GPS data courtesy of A. van Cauter, 2004.*

The Nama-Karoo is characterized by strong seasonality in temperature and rainfall with hot wet summers (December - February) and cold dry winters (June - August) (Desmet and Cowling, 1999b). During the summer, maximum air temperatures can exceed 40 °C and minimum air temperatures often drop below freezing during winter (Palmer and Hoffman, 1997; Lubbe, 2013). Daily air temperatures fluctuated considerably with summer temperatures ranging from 4.3 to 41.9 °C and winter temperatures ranging from -8.7 to 33.9 °C. Large temperature variations of up to 30 °C between day and night within a single 24-h period were common during my study period.

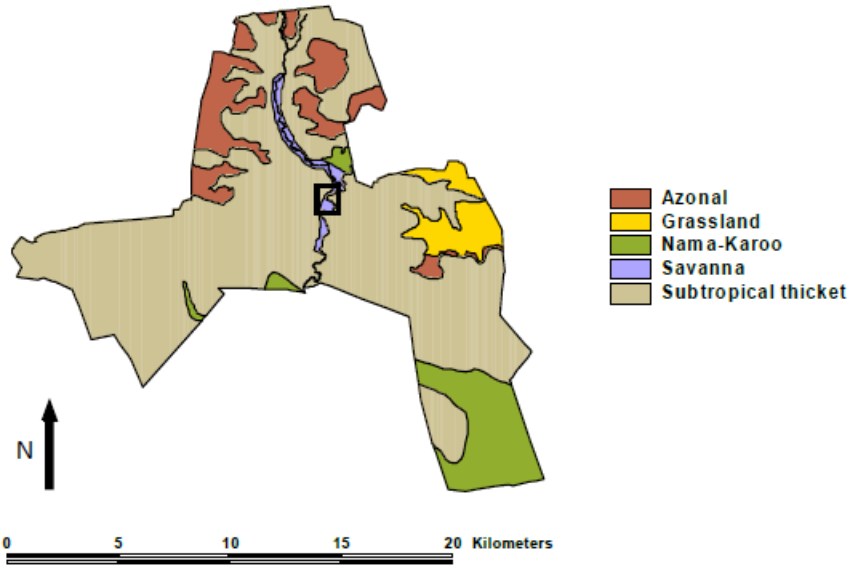

Figure 2.3: *Vegetation types at Samara Private Game Reserve with the location of the study troops home ranges (clear square) centered on the Melk river. Vegetation GPS data courtesy of A. Van Cauter, 2004.*

Droughts are common in the Nama-Karoo and rainfall is highly seasonal. Rainfall in the summer months peak between December and March (Palmer and Hoffman,1997), and varies between 100 and 520 mm per year with a mean annual rainfall of 330 mm (McDougall *et al*., 2010). The home ranges of the vervet monkey troops in my study were centered on the beds of the Melk River that runs through the study site (Fig. 2.5) and provided the monkeys with a natural source of continuously flowing water during the wet season (Sashaw, 2012). For the duration of my study (September 2010 to June 2017) annual rainfall varied greatly (Fig. 2.4) with 2011 and 2014 receiving the most rain. Average annual rainfall for the study period was 291 ± 99 mm (range from 132 mm in 2016 to 433 mm in 2011). Monkeys generally had access to standing water pools in the river during the study period but, the river dried up after the drought of 2016 leaving the vervet monkeys with no standing water during the winter and early summer months of 2016. After the first summer rains in January 2017, the vervet monkeys had access to standing water pools throughout the summer months of January and February of 2017.

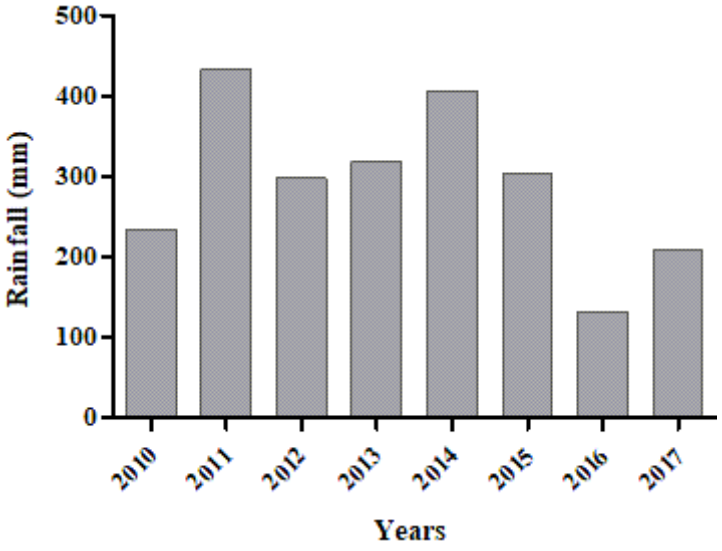

Figure 2.4: *Total annual rainfall for the study period (2010 –2017). Data courtesy of the South African Weather Service from a weather station located at a farm (Klipfontein) approximately 14km from Samara Private Game Reserve.*

Potential predators for the vervet monkeys on our study site included carnivores such as the cheetah (*Acinonyx jubatus*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*), venomous snakes such as puff adders (*Bitis arietans*), boomslang (*Dispholidus typus*) and cape cobra (*Naja nivea*) and birds of prey such as the black eagle (*Ictinaetus malavensis*) and martial eagle (*Polemaetus bellicosus*).

2.3 Study subjects

I used retrospective data from three troops of habituated vervet monkeys that occupied adjacent territories along the Melk River: Riverside Troop (RST), Riverbend Mob (RBM) and Picnic Troop (PT) (Fig. 2.5). These troops have been monitored since September 2008 as part of a long-term study. These monkeys were habituated to human presence with field researchers conducting behavioural observations ten hours a day, five days a week. The monkeys were individually recognizable through facial features and other distinguishing markings.

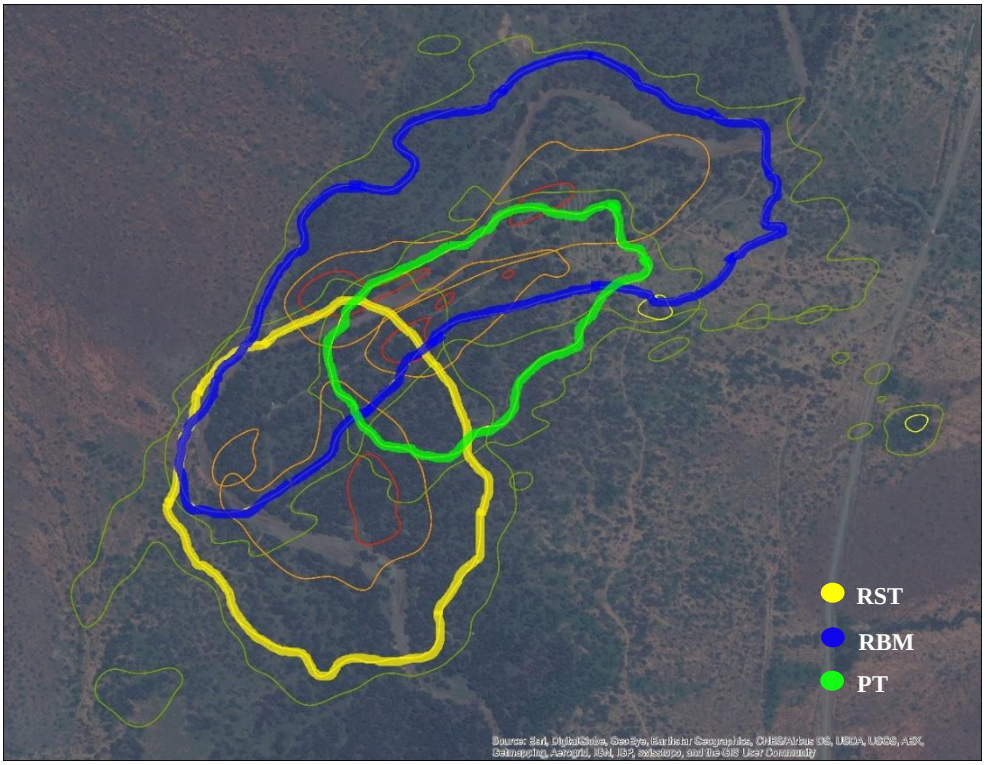

Figure 2.5: *All three troop territories situated along the Melkriver. (RST = Riverside Troop, RBM = Riverbend Mob, PT = Picnic Troop). Image courtesy of M. Dostie.*

Sixty-one monkeys (31 males, 30 females) were implanted over a seven-year period (Table 2.1) with intra-abdominal temperature-sensitive data loggers that recorded body temperature at intervals of 5-minutes. The data loggers were explanted at approximately yearly intervals after implantation to retrieve the recorded body temperature data (Fig. 2.6). The missing data during the period of March 2013 – December 2013 (see Fig. 2.6) was as a result of rhino being released on site and the project being temporarily terminated to ensure the safety of the field researchers. There was no difference between the body temperature profiles of males and non-reproductive females (Fig. 2.7), therefore males were excluded from the analysis allowing the non-reproductive females to act as the control group to which the reproductive females were compared.

Table 2.1: *The number of males and females implanted in each troop (RST = Riverside Troop, RBM = Riverbend Mob and PT = Picnic Troop), the number of births, and average body mass for males (M) and females (F) during the different study cohorts.*

Cohort	Male	Female	Birth	Average male mass (kg) ± SD	Average female mass (kg) ± SD	Troop					
						RST		RBM		PT	
						M	F	M	F	M	F
2010 – 2011	3	6	2	5.10 ± 1.02	3.41 ± 0.45	2	5	1	1		
2011 – 2012	5	8	0	5.52 ± 1.09	3.32 ± 0.54	2	5	3	3		
2012 – 2013	11	11	1	4.69 ± 1.14	3.28 ± 0.41	4	6	5	5	2	
2013 – 2014	14	3	1	4.62 ± 0.55	3.38 ± 0.69	4	1	8	1	2	1
2014 – 2015	10	13	11	5.02 ± 0.30	3.61 ± 0.50	2	4	5	4	3	5
2015 – 2016	9	11	5	5.28 ± 0.19	3.57 ± 0.18	2	4	3	3	4	4
2016 – 2017	9	12	7	5.08 ± 0.32	3.33 ± 0.27	4	5	2	3	3	4

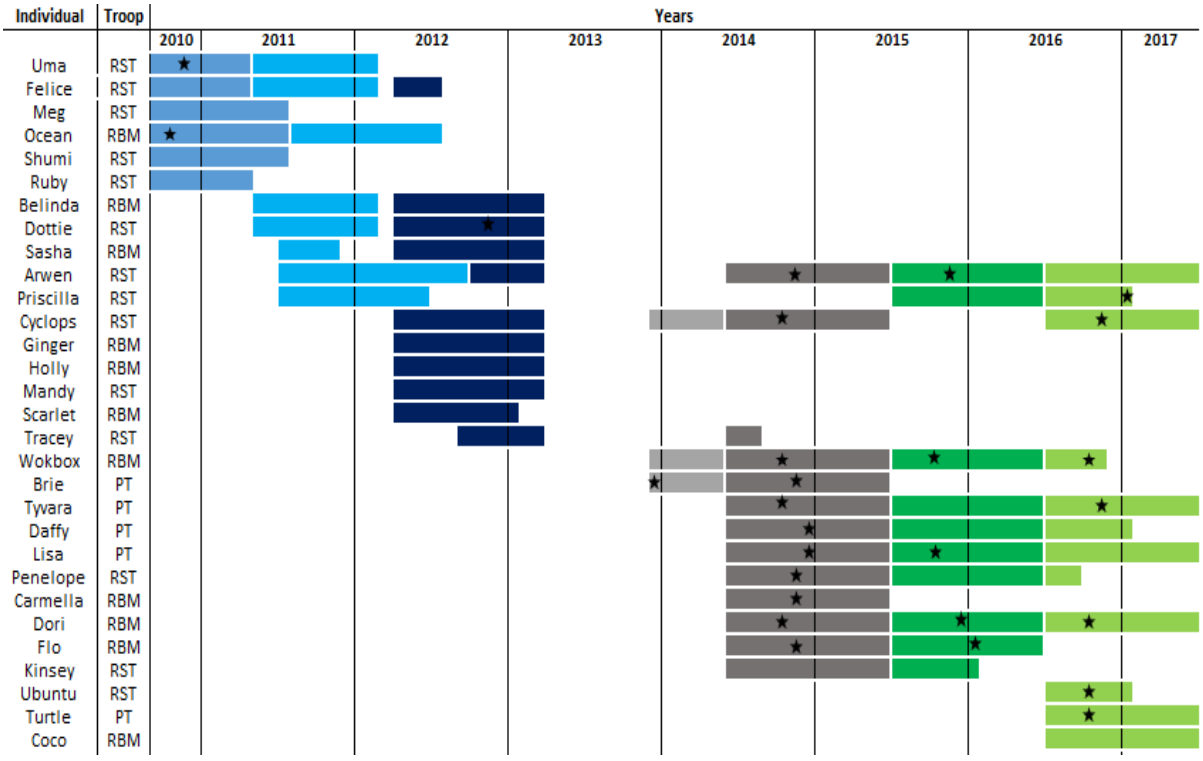

Figure 2.6: *Summary of all 30 female vervet monkeys implanted over a seven-year period. Each colour bar indicates a different cohort. Not every individual implanted in the previous cohort was implanted in the following cohort. Individuals in cohorts with shorter data sets either died or their temperature data logger malfunctioned and stopped recording. Individuals implanted in the 2011-2012 and 2012-2013 cohorts were not all implanted or explanted at the same time. Births are indicated by the black stars.*

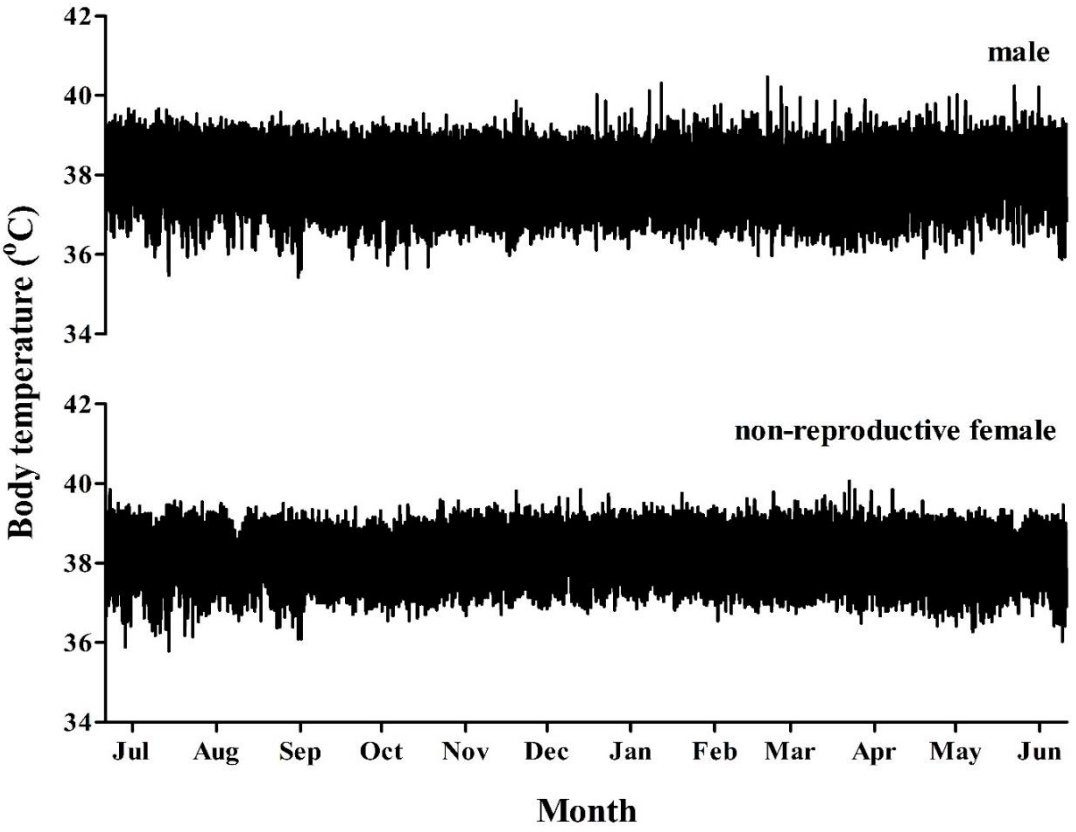

Figure 2.7: *Original 5-minute body temperature of a male and a non-reproductive female exposed to the same environmental conditions over a year (June 2014 – June 2015).*

The study troops had a completely natural diet, previously shown to consist of 26 different plant species with 33.8% of the diet consisting of sweet thorn constituents, 15.3% of the diet consisting of berries from the creeping saltbush (*Atriplex semibaccata*), 7.7% of the diet comprised of insects such as grasshoppers and termites, 6.5% and 5.4% of the diet consisting of wolfthorn (*Lycium oxycarpum*) and pepper (*Schinus molle*) berries respectively, during a non-drought year (Pasternak *et al*., 2013). The proportion of the vervet monkeys' diet that consisted of berries from the creeping saltbush and insects decreased significantly during the winter months (June - August). During the winter months the vervet monkeys diet mainly consisted of sweet thorn constituents and wolfthorn berries (Pasternak *et al*., 2013).

2.4 Surgical procedures

Monkeys were immobilized using darts from a blowpipe (Dan-Inject system, Zoo Blow 1.25, Dan-Inject APS, Børhup, Denmark) containing a ketamine (50 mg, Anaket-V, Bayer (Pty) Ltd., Johannesburg, South Africa) and midazolam (2.5 mg, Dormicum, Roche Products (Pty) Ltd., Johannesburg, South Africa) combination. Once a monkey was recumbent (~ 5 min), it was transported to a temporary surgical facility (Fig. 2.8). Each monkey was weighed (Snowrex Electronic Scale, Clover Scales (Pty) Ltd., Johannesburg, South Africa) as they arrived at the temporary surgical site, allowing us to calculate accurate doses for the long-acting antibiotic (Peni LA Phenix, penicillin: 0.1 ml/kg, Virbac Animal Health, Johannesburg, South Africa) and anti-inflammatory and analgesic (Metacam, Meloxicam 0.3 mg/kg, Boehringer Ingelheim (Pty) Ltd., Johannesburg, South Africa) administered to each individual. Each monkey was maintained under anaesthetic using isoflurane (Isofor, Safe Line Pharmaceuticals (Pty) Ltd., Johannesburg, South Africa) administered in 100 % oxygen through an anaesthetic mask. Isoflurane was administered at 2-3 % in order to induce a level plain of anaesthesia.

Once a monkey was stable, equipment to monitor rectal temperature (Bailey Type T thermocouple, Sensotek Inc., New Jersey, U.S.A), blood pressure (Cardell, Sharn Veterinary Inc., Florida, U.S.A), oxygen saturation (pulse oximeter, Nonin Medical Inc., Michigan, U.S.A) and end tidal CO_2 (Capnograph, Medair, Hudiksvall, Sweden) was connected. A local anaesthetic (xylocaine: 10 mg, Astra Zeneca (Pty) Ltd., Johannesburg, South Africa) was sprayed into the tracheal opening to reduce irritation before intubating with an endotracheal tube. An eye gel (Refresh Optive® Gel Drops) was applied before surgery to keep the eyes moist.



Figure 2.8: *Temporary surgical theatre*

Surgery to implant the temperature-sensitive data loggers was performed by an experienced veterinarian with assistance from a veterinary nurse (Fig. 2.9). Each monkey's vital signs (heart rate, blood pressure, rectal temperature, end tidal CO_2 and blood oxygen saturation) was monitored at 5-minute intervals throughout the surgical procedure. Anaesthesia was maintained during surgery as necessary with 0.5–2 % isoflurane administered in 100 % oxygen through an endotracheal tube. Monkeys were kept warm during surgery using heating pads and heated bean bags. Each monkey was given a drip (Ringers lactate solution, B. Braun Medical Ltd., Northriding, South Africa) throughout surgery in order to replace fluids and provide hydration.

A 100 x 100 mm patch of hair on the ventral abdominal surface of each monkey was shaved and the abdomen sterilized using chlorhexidine gluconate in alcohol (Hibicol, Astra Zeneca (Pty) Ltd., Johannesburg, South Africa). A local anaesthetic (Lignocaine: 40 mg, Bayer (Pty) Ltd., Johannesburg, South Africa) was administered subcutaneously at the incision site before the start of surgery. A 30 mm midline incision was made through the skin and the *linea alba*

to implant or explant the temperature-sensitive data logger. After the implantation or explantation of a data logger, the muscle layers were sutured closed with a single interrupted absorbable suture (Viamac 3/0, Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd., Essex, United Kingdom). Thereafter, the skin was sutured closed with a buried subcutaneous continuous suture (Viamac 2/0, Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd., Essex, United Kingdom) pattern. A single layer of interrupted sutures was also placed on top; these were distraction sutures, to prevent the monkeys from picking at the holding layer of sutures below. The surgical wound was treated with a germicidal wound spray (F10, Health and Hygiene, Johannesburg, South Africa) and tick-grease (mixture of pesticide and Vaseline Petroleum Jelly, Unilever, USA) to prevent external wound infection. Total surgery time was on average 25 minutes. After surgery each monkey was left to recover in a dark cage until fully alert before being released near to where the rest of their troop was situated.



Figure 2.9: *Veterinarian and veterinary nurses preparing an anaesthetized vervet monkey for surgery to implant the temperature-sensitive data logger.*

2.5 Body temperature measurements

The monkeys were re-captured annually for seven years approximately a year after each implantation to retrieve data loggers. The temperature-sensitive data loggers (mlog T1C, Sigma Delta Technologies, Perth, Australia) (Fig. 2.10A) used during the first three cohorts (September 2010 to March 2013) had dimensions of 30 x 25 x 10 mm, a mass of ~ 12 g after being coated with an inert wax (Sasolwax 1276; Sasol, Johannesburg, South Africa), and were set to record body temperature at 5-minute intervals at a resolution of 0.06 °C (Lubbe, 2013). As the technology of biologging advanced, more reliable temperature-sensitive data loggers (DST centi-T, Star-Oddi Ltd., Gardabaer, Iceland; Fig. 2.10B) were used from December 2013 to June 2017. The newer data loggers were cylindrical, measured 15 mm x 45 mm in length, had a mass of ~ 18 g when coated with inert wax, and were set to record body temperature at 5-minute intervals (see example of data in Fig. 2.11) at resolution of 0.03 °C. The data loggers had a temperature range of 5-45 °C. All the loggers were calibrated in an insulated water bath against a high accuracy thermometer (Quat 100, Heraeus, Hanau, Germany). Loggers were calibrated to an accuracy of 0.1 °C between 34 and 42 °C at 2 °C intervals to cover the body temperature range of vervet monkeys. The loggers were dry-sterilized in formaldehyde vapour before implantation.

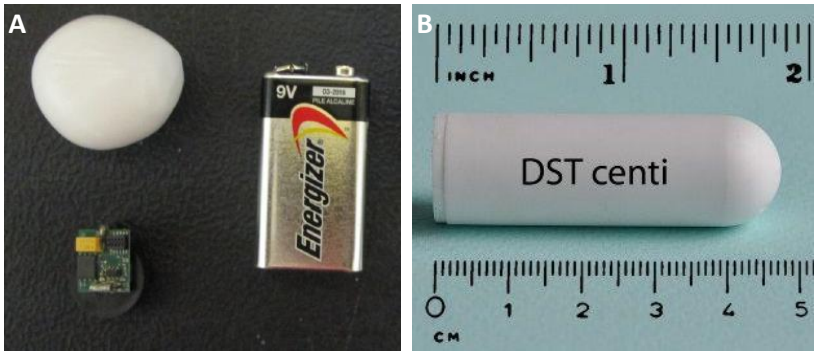

Figure 2.10: *A) Temperature-sensitive data logger (mlog T1C), used from September 2010 to March 2013, uncoated and in inert wax. A 9V battery is used as a size reference (Lubbe, 2013), B) temperature-sensitive data logger (DST centi-T) used from December 2013 to June 2017.*

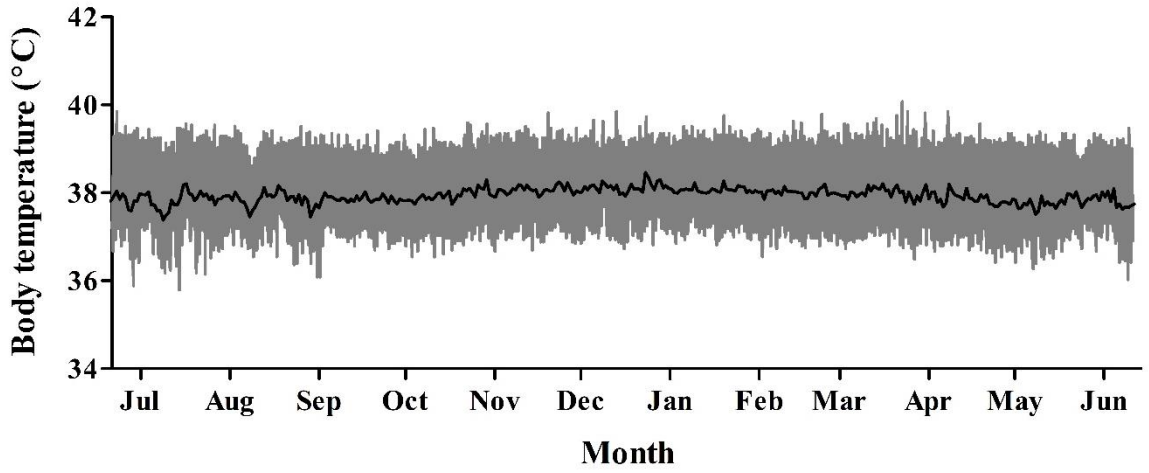

Figure 2.11: *Original 5-minute body temperature (grey) and mean 24-h body temperature (black line) of a non-reproductive female over a year (June 2014 - June 2015).*

2.6 Identifying pregnancies, births and lactation periods

Biologging of body temperature has been determined to be a reliable index of reproductive phenology making it possible to identify reproductive events such as gestation and parturition (Williams *et al*., 2011). The sudden decrease in body temperature followed by a precipitous increase in body temperature on the day of parturition, allowed me to identify the exact time and date of a birth (Fig. 2.12 and Fig. 2.13). Behavioural data were collected by the field researchers and included recordings of events such as pregnancies, births and nursing. Births were sometimes recorded by observers a couple of days after the actual birth. Behavioural data were used in combination with body temperature data to confirm the exact time of birth. Primate births typically occur at night (Jolly, 1973) and the births of the vervet monkeys in my study were no exception (Fig. 2.14).

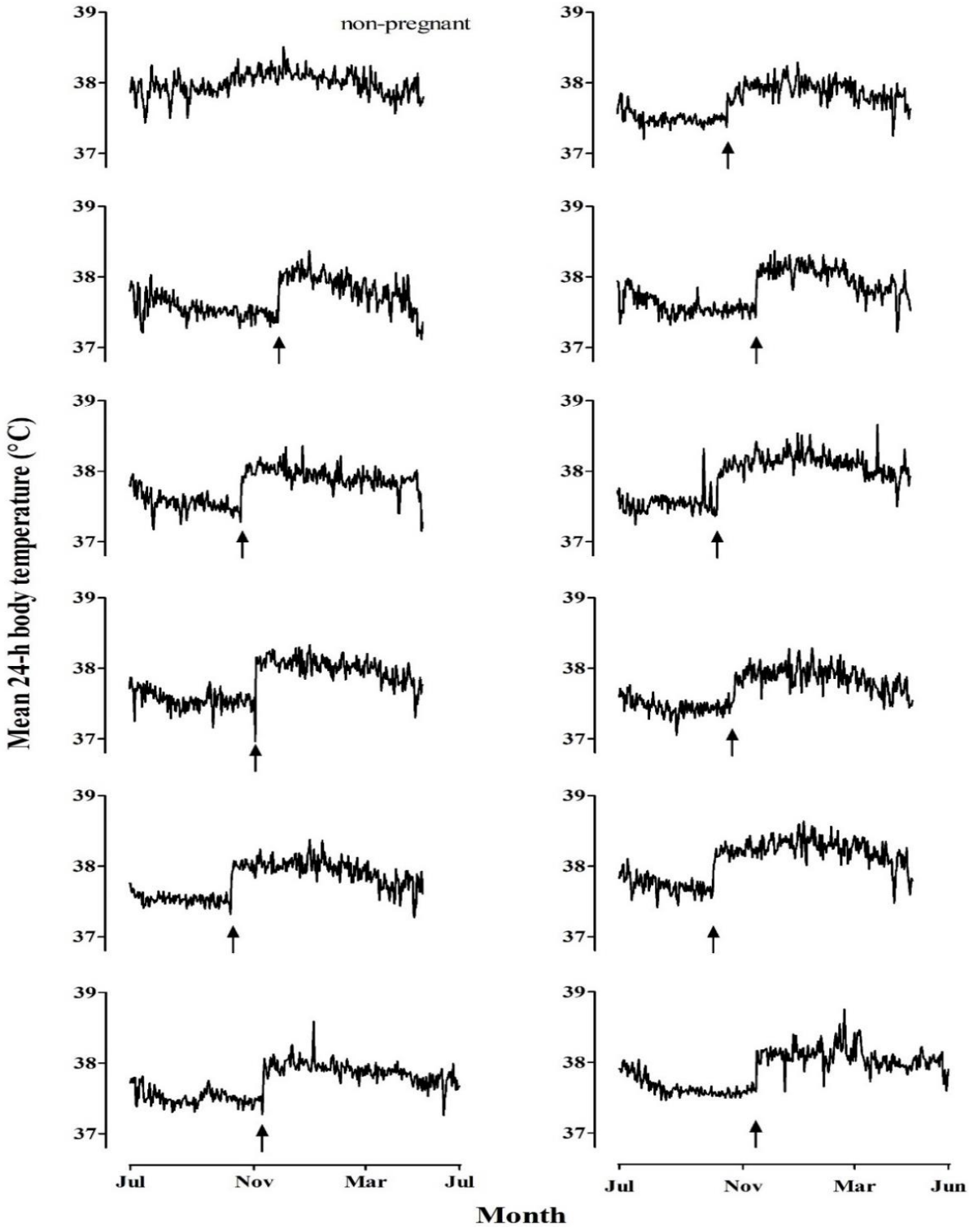

Figure 2.12: *Mean 24-h body temperature of 12 females (1 non-pregnant female and 11 pregnant females) July 2014 – July 2015. Birth is indicated by the black arrows. The abrupt increase in body temperature on the day of parturition is evident.*

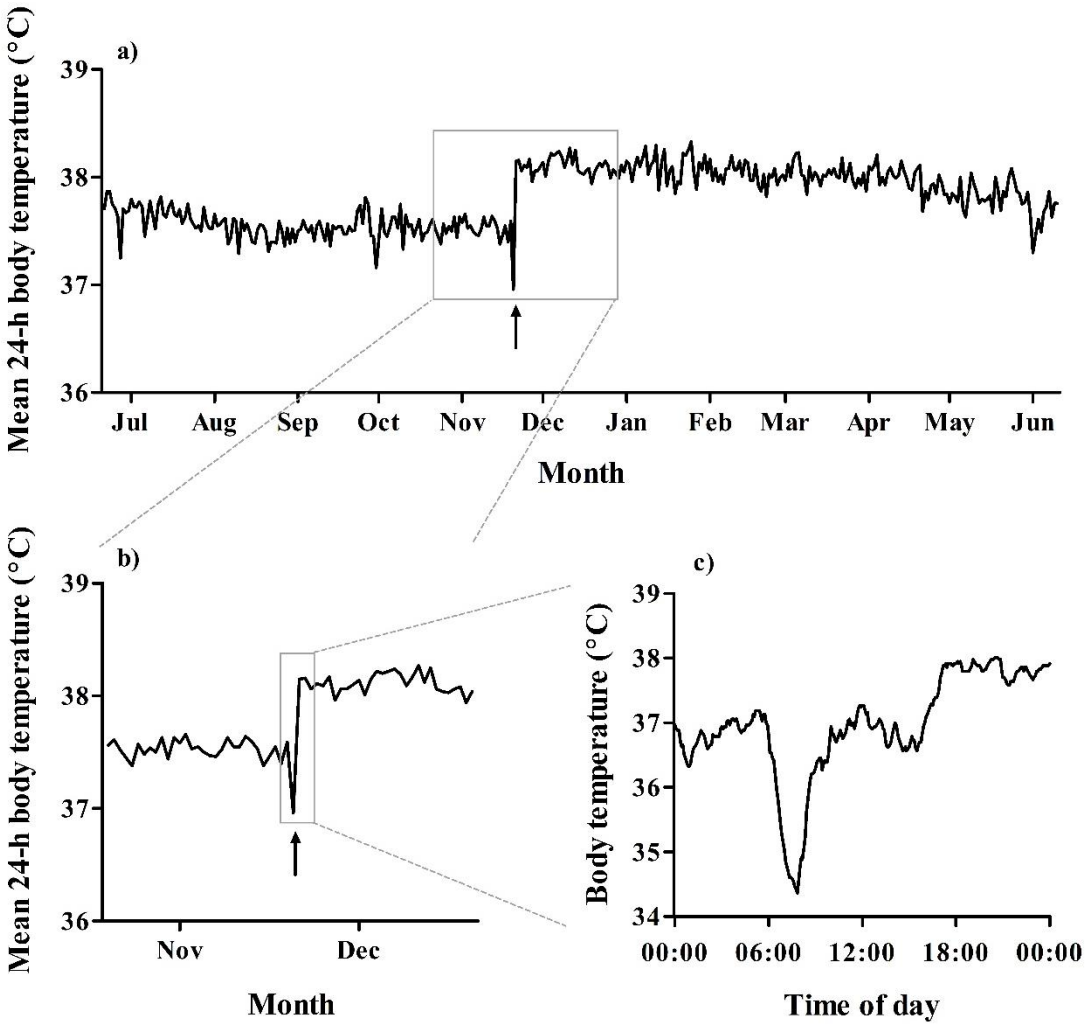

Figure 2.13: *a) Mean 24-h body temperature of a pregnant female over 12-months, b) mean 24-h body temperature before and after birth (indicated by the black arrow), c) 5-minute body temperature on the day of birth.*

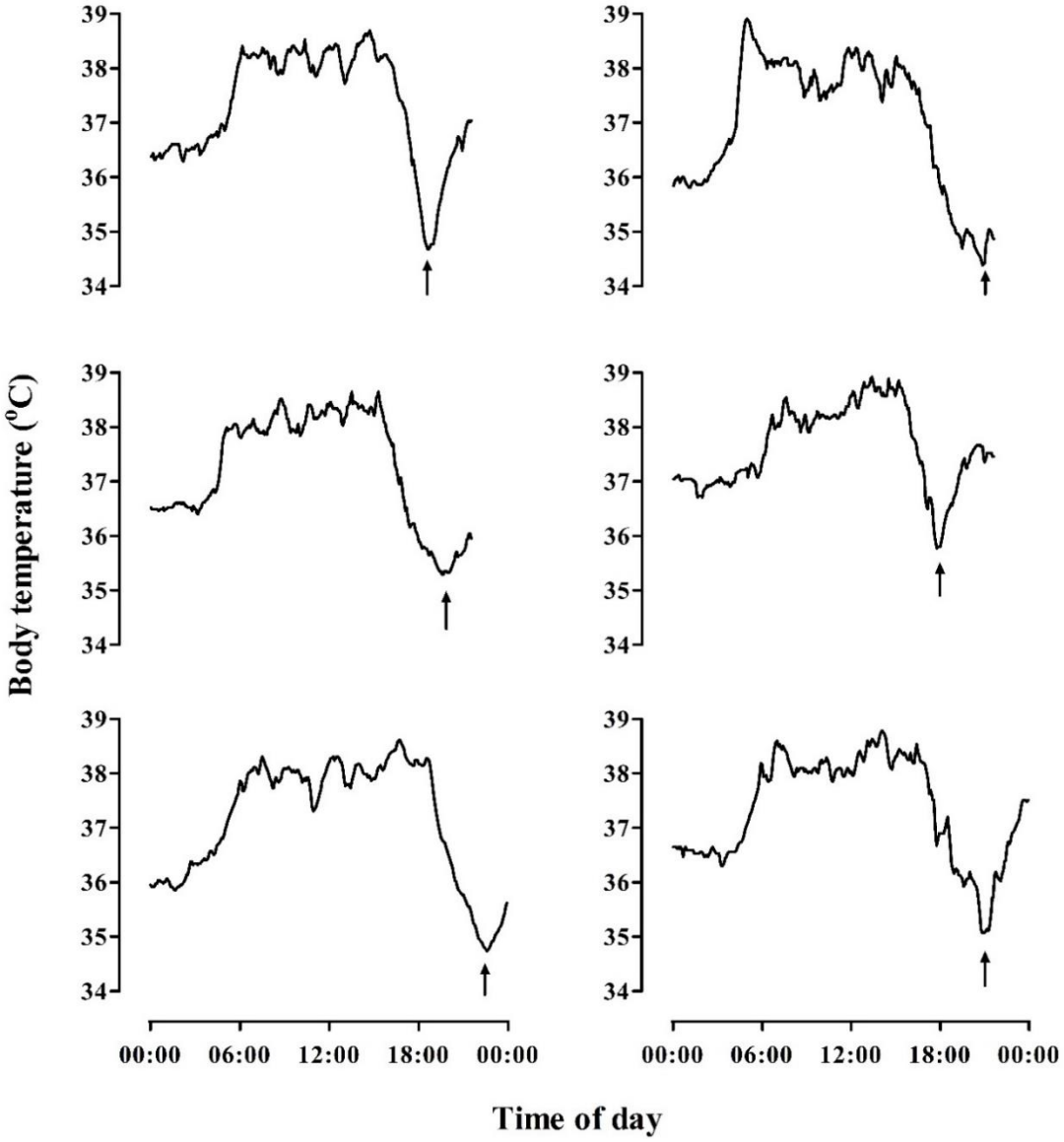

Figure 2.14: *5-minute body temperature of six pregnant females on the day of parturition. Births are indicated by the black arrows. It is evident that births typically occurred at night.*

Vervet monkeys have a gestation period of approximately 157-168 days (Rowell, 1970; Hess *et al*., 1979; Seier *et al*., 2000). An estimation date of when a female fell pregnant was calculated by counting back 165 days from the date of birth (Fig. 2.15). The lactation period was identified as the period immediately after birth up until the last nursing event recorded by the field researchers (Fig.2.15).

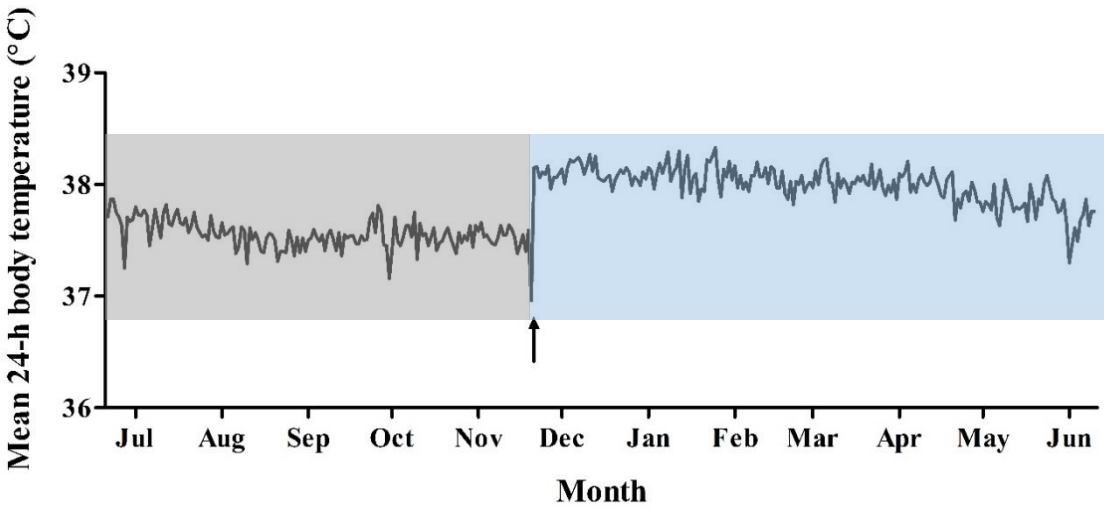

Figure 2.15: *Mean 24-h body temperature of a pregnant female over a 12-month period with pregnancy (grey) and the lactation period (blue) indicated by the shaded blocks. Birth is indicated by the black arrow.*

2.7 Environmental measurements

A weather station (Hobo U30, Onset Computer Corporation, Pocasset, USA) placed on the reserve measured black globe temperature, air temperature, solar radiation, wind speed and relative humidity at 30-minute intervals, malfunctioned multiple times throughout the study period. Therefore, air temperatures for my analyses were obtained from the South African Weather Services weather station in Graaff-Reinet, approximately 40 km from Samara Private Game Reserve.

Remotely sensed normalized difference vegetation index (NDVI) at Samara, calculated by M. Dostie, was used as a proxy for food availability. NDVI is a satellite-derived measure of vegetation 'greenness' (Reed *et al*., 1994) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument. The MODIS vegetation indices are produced in 16-day composites. The NDVI values range between -1 and +1 with water registering less than 0, bare soils registering between 0 and 0.1 and vegetation registering between 0.1 and 1

(Weiss *et al*., 2001). As vegetation grows and the photosynthetic activity of the plants within an area increases the corresponding NDVI values increase. The NDVI values decrease as vegetation dies and the plants start to lose their photosynthetic activity or 'greenness'.

2.8 Data analysis

The 24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude of the body temperature rhythm were calculated from the original 5-minute measures of the body temperature for each of the monkeys. The 24-h minimum, 24-h maximum, 24-h mean and 24-h range of the air temperature were also calculated from the original hourly measurements recorded by the weather station. I ran a series of generalized linear mixed-effects models (GLMM) to investigate the relationship between:

1. Environmental factors (air temperature and NDVI values) and reproductive events (pregnancy, lactation and non-lactation) on the body temperature profile (Fig. 2.16).
2. Environmental factors (air temperature and NDVI values) and pregnancy progression (in days) on the body temperature profile (Fig. 2.17).
3. Environmental factors (air temperature and NDVI values) and lactation progression (in days) on the body temperature profile (Fig. 2.18).

I ran four GLMM's for each of the above three categories by entering each of the different body temperature profile measures (24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude) as dependent variables in separate models (Fig. 2.16, 2.17 and 2.18), therefore a total of 12 GLMM's were run. I entered reproductive progression/status (lactating, non-lactating and pregnant), NDVI and air temperature (24-h minimum, 24-maximum, 24-h mean and 24-h range) as independent variables, with body mass as a control variable in each model. As air temperature drops at night, I expect to see a coinciding decline in the monkey's

body temperature. The same principle will apply for the high daytime temperatures which, I expect, will coincide with an increase in 24-h maximum body temperature. Therefore, I matched the air temperature measures (24-h mean, 24-h minimum, 24-h maximum and 24-h range) with the corresponding body temperature measures (24-h mean, 24-h minimum, 24-h maximum and 24-h amplitude), for example I looked at the relationship between 24-h minimum air temperature and 24-h minimum body temperature, and again between 24-h maximum air temperature and 24-h maximum body temperature. I tested for collinearity between air temperature and NDVI within my models and found no correlation between the two variables which allowed me to have them both present in my models.

Model selection was performed using Akaike's information criteria (AIC) to determine the best model fit for all variables, including entering troop as a nested effect or a control variable. Based on model selection and the area of focus (i.e., reproductive status, pregnancy progression and lactation progression), the measured variables (i.e., air temperature and vegetation greenness, as indexed by NDVI) that yielded the best model fit to test the effect of drought on body temperature, were entered into their respective models. The decision was made to enter monkey I.D nested within troop as a random factor based on the better model fit. The family was entered as Gaussian with a log link as the data fit a Gaussian distribution. All statistical analyses were conducted using the package 'lme4' in RStudio Version 1.1.456®. Statistical significance was set at $P < 0.05$.

```
# Models to investigate the relationship of reproductive status (RS) on body temperature
RSmin_mod <- glmer(Min_BT ~ Status + Min_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                   family = gaussian(link = "log"), data = GLMM_RS)

RSmax_mod <- glmer(Max_BT ~ Status + Max_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                   family = gaussian(link = "log"), data = GLMM_RS)

RSmean_mod <- glmer(Mean_BT ~ Status + Mean_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                    family = gaussian(link = "log"), data = GLMM_RS)

RSamp_mod <- glmer(BT_amp ~ Status + AT_amp + NDVI + BM + (1 | Troop:Monkey_ID),
                   family = gaussian(link = "log"), data = GLMM_RS)
```

Figure 2.16: *Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h minimum air temperature (Min_AT), 24-h maximum air temperature (Max_AT), 24-h mean air temperature (Mean_AT) and 24-h range of air temperature (AT_amp), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and reproductive status (pregnancy, lactation and non-lactation) on 24-h minimum body temperature (Min_BT), 24-h maximum body temperature (Max_BT), 24-h mean body temperature (Mean_BT) and 24-h amplitude of body temperature rhythm (BT_amp) while controlling for body mass (BM). Monkey ID nested within troop was entered as a random factor. The family was entered as Gaussian with a log link as the data fit a Gaussian distribution.*

```
# Models to investigate the relationship of pregnancy progression on body temperature
Pmin_mod <- glmer(Min_BT ~ Pregnant + Min_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Pregnant)

Pmax_mod <- glmer(Max_BT ~ Pregnant + Max_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Pregnant)

Pmean_mod <- glmer(Mean_BT ~ Pregnant + Mean_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                   family = gaussian(link = "log"), data = GLMM_Pregnant)

Pamp_mod <- glmer(BT_amp ~ Pregnant + AT_amp + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Pregnant)
```

Figure 2.17: *Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h minimum air temperature (Min_AT), 24-h maximum air temperature (Max_AT), 24-h mean air temperature (Mean_AT) and 24-h range of air temperature (AT_amp), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and pregnancy progression on 24-h minimum body temperature (Min_BT), 24-h maximum body temperature (Max_BT), 24-h mean body temperature (Mean_BT) and 24-h amplitude of body temperature rhythm (BT_amp) while controlling for body mass (BM). Monkey ID nested within troop was entered as a random factor. The family was entered as Gaussian with a log link as the data fit a Gaussian distribution.*

```
# Models to investigate the relationship of lactation on body temperature
Lmin_mod <- glmer(Min_BT ~ Lactate + Min_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Lactate)

Lmax_mod <- glmer(Max_BT ~ Lactate + Max_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Lactate)

Lmean_mod <- glmer(Mean_BT ~ Lactate + Mean_AT + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Lactate)

Lamp_mod <- glmer(BT_amp ~ Lactate + AT_amp + NDVI + BM + (1 | Troop:Monkey_ID),
                  family = gaussian(link = "log"), data = GLMM_Lactate)
```

Figure 2.18: *Generalized linear mixed effects models (GLMM) to investigate the relationship of 24-h minimum air temperature (Min_AT), 24-h maximum air temperature (Max_AT), 24-h mean air temperature (Mean_AT) and 24-h range of air temperature (AT_amp), vegetation greenness, as indexed by normalized difference vegetation index (NDVI) and progression of lactation on 24-h minimum body temperature (Min_BT), 24-h maximum body temperature (Max_BT), 24-h mean body temperature (Mean_BT) and 24-h amplitude of body temperature rhythm (BT_amp) while controlling for body mass (BM). Monkey ID nested within troop was entered as a random factor. The family was entered as Gaussian with a log link as the data fit a Gaussian distribution.*

CHAPTER THREE – RESULTS

3.1 Environmental conditions during the study period

There was an annual seasonal variability in air temperature during the study period where June – August were the coldest winter months and December – February were the warmest summer months (Fig. 3.1a). There was interannual variability in the warm and cold months where December 2012 – February 2013 experienced a decline in air temperature similar to colder winter temperatures (Fig. 3.1a). For the duration of the study, the summer months had a mean air temperature (±SD) of 22.9 ± 1.0 °C while the winter months had a mean air temperature (±SD) of 11.3 ± 1.1 °C. Maximum 24-h air temperatures exceeded 40 °C every summer during the study period except for the summer of 2012 - 2013. A total of 281 days of winter during the study period experienced minimum 24-h air temperatures of below zero. On the hottest day during the study period (December 2015) maximum 24-h air temperatures reached a high of 42.3 °C and during the coldest day of the study period (July 2014) a minimum 24-h air temperature of -8.7 °C was recorded. Large 24-h air-temperature fluctuations were recorded with 246 days during the study period experiencing 24-h air temperature ranges of 25-33 °C, with the largest 24-h air temperature range recorded during September 2013.

For the duration of the study (September 2010 to June 2017) the average annual rainfall was 291 ± 99 mm per year and total annual rainfall during the study period ranged from 132 mm to 433 mm (Fig. 3.1). Rain fell predominantly in the summer months peaking between December and March while the winter months were drier months. Drought conditions were experienced in 2016 with a total annual rainfall of only 132 mm rain received that year. There was a significant correlation ($r^2 = 0.245$, $n = 79$, $p = <0.0001$) between vegetation greenness

indexed by normalized difference vegetation index (NDVI) and the previous month's rainfall. Vegetation greenness increased approximately one month after rainfall events (Fig. 3.1b).

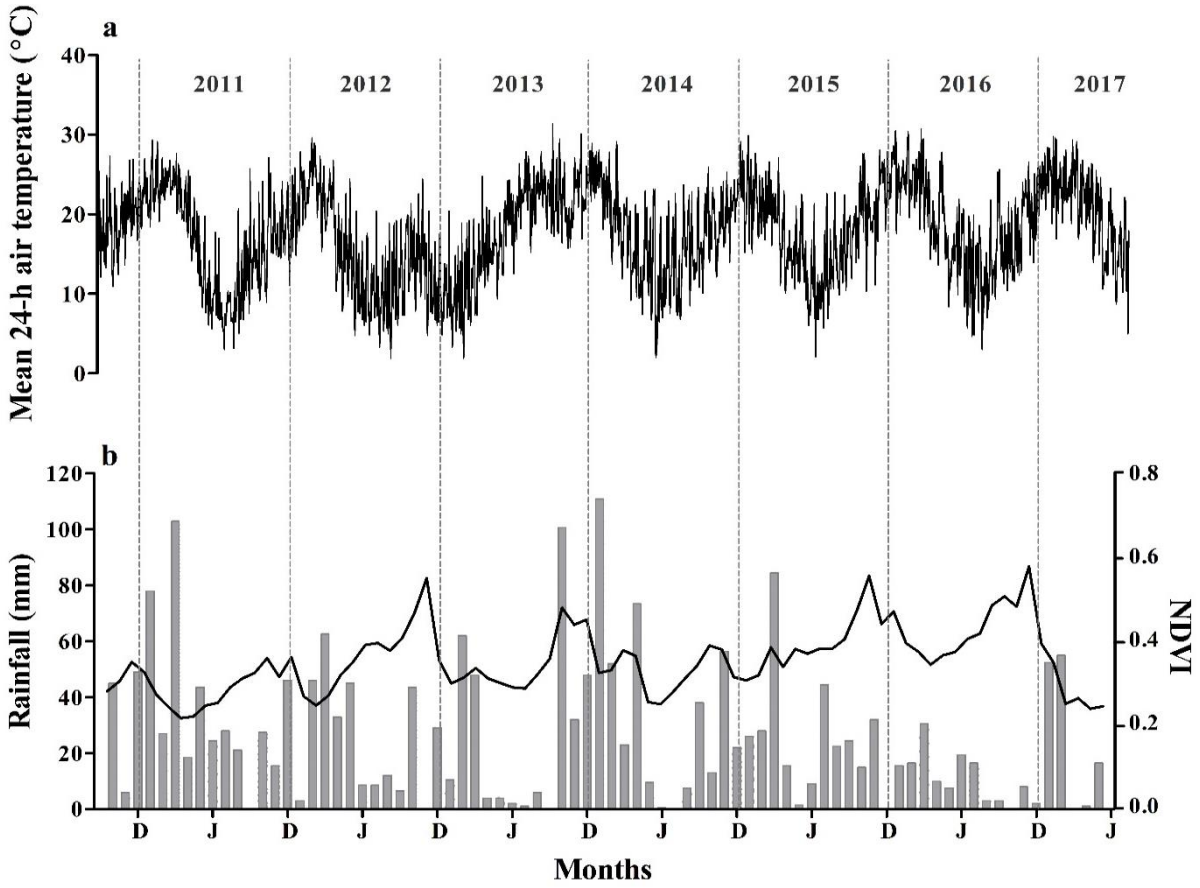

Figure 3.1: *Cumulative monthly rainfall (grey bars), mean monthly vegetation greenness as indexed by normalized difference vegetation index (NDVI) values (black line) and mean 24-h air temperatures for the duration of the study period (September 2010 to June 2017).*

3.2 Reproductive status

The vervet monkeys in my study population showed a clear nychthemeral rhythm of body temperature, irrespective of reproductive status, with body temperature lowest in the early morning and highest near midday. The body temperature profile during reproduction differed from that of non-reproductive females which, combined with behavioural observations, allowed me to define the different reproductive states (Fig. 3.2). There was a lowering in mean 24-h body temperature during pregnancy followed by a precipitous increase in body temperature on the day of parturition which initiated the lactation period (Fig. 3.2b). A total

of 27 births were recorded for implanted females during the study period (September 2010 to June 2017). The number of births varied between years with the most births occurring in 2014 (11 births) and only one birth in both 2012 and 2013 cohorts. Only one birth was recorded in 2013 because we mostly implanted males as the majority of the females were already pregnant when we were scheduled to implant the biologgers and we did not want to risk any surgical complications on pregnant females. There were no births recorded in 2011 from the implanted females which is most likely related to drought conditions experienced the year before and females possibly not having regained their optimal physical condition to resume cycling. All the births for the study period occurred between the months of October and January with 74% of the births occurring in late spring (October and November). The timing of the majority of the births coincided with favourable environmental conditions with high vegetation greenness and mean air temperature ranging from 15-20 °C (Fig. 3.1). There were only two births in mid-summer in the month of January of 2016 and 2017, respectively where air temperatures reached highs of 30 °C.

Based on behavioural observations made by field researchers that included nursing events, lactation lasted on average 157 ± 75 days with the exception in cases where the infant died during the lactation process. Lactation generally occurred during the warmer summer months where environmental conditions were characterized by high air temperatures, high rainfall and vegetative greenness, and was terminated before the dry winter months. There was interannual variability in the lactation period for females who raised their young to independence, where females who lactated during normal years lactated on average 22 days longer than females who lactated during warm-dry conditions. A total of 16 infants were raised to independence and 11 infants died within six months after birth. In cases of infant

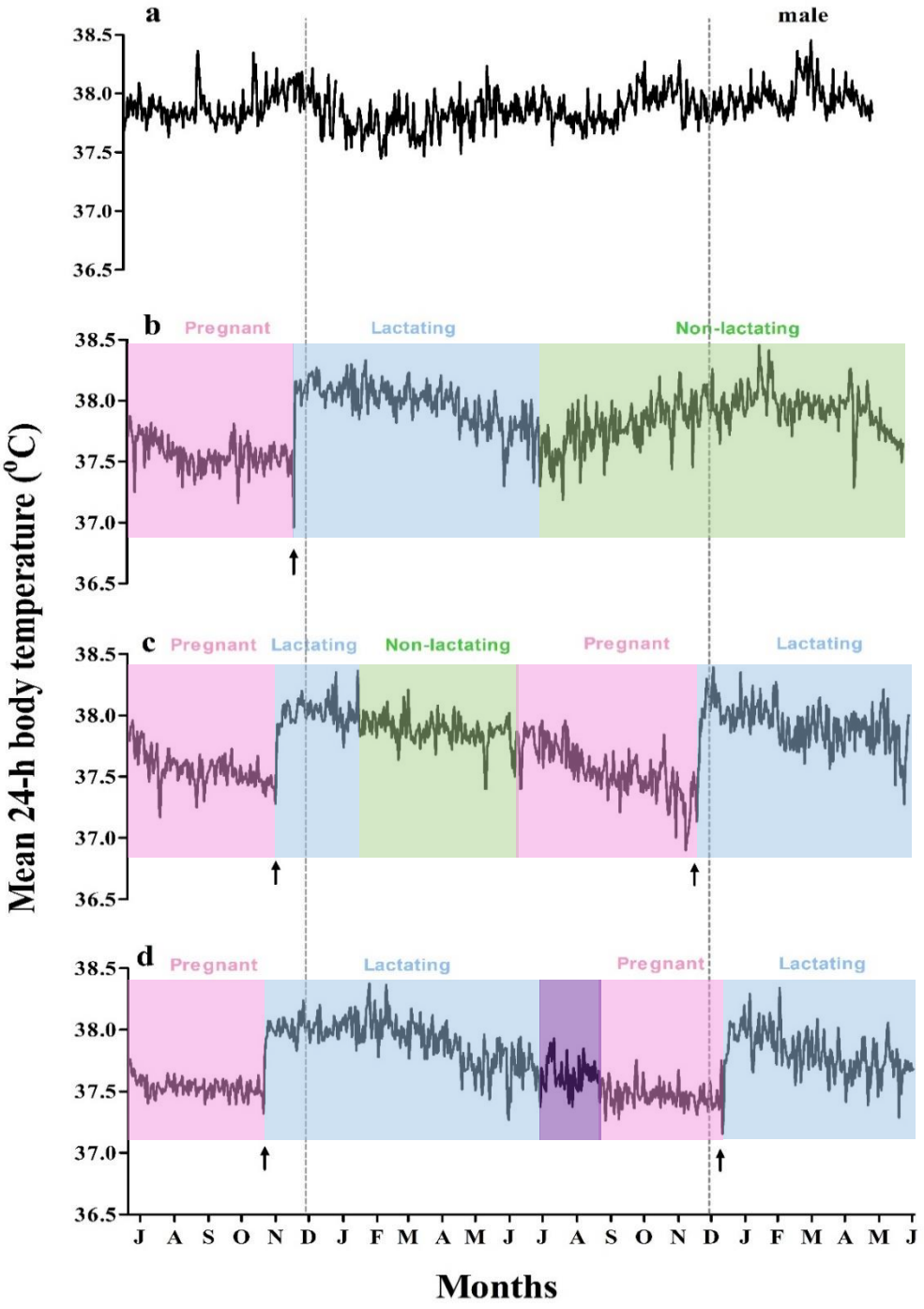

Figure 3.2: *Mean 24-h body temperatures of four individuals, (a) non-reproductive individual (male), (b) female who gave birth once over a period of two years and had a complete lactation period (203 days), (c) female who gave birth twice over a period of two years and had a shorter lactation period (53 days) due to the death of the infant and a (d) female who gave birth twice over a period of two years where lactation and pregnancy overlapped (indicated by the purple block). Births are indicated by the black arrows.*

deaths, females were likely to fall pregnant the following year (e.g. Fig. 3.2c). There was evidence of a female falling pregnant while still lactating during both normal environmental and drought conditions (e.g. Fig. 3.2d).

Minimum 24-h body temperature differed with the reproductive status of the female vervet monkeys (see Table 3.1), with pregnant females having the lowest minimum 24-h body temperature compared to lactating and non-lactating females. Lactating females displayed higher minimum 24-h body temperature than non-lactating females (Fig. 3.3a). Minimum 24-h body temperature of females were positively associated with vegetation greenness, as indexed by NDVI, and minimum 24-h air temperature (Table 3.1). Not only was minimum 24-h body temperature lowest during pregnancy, maximum 24-h body temperature in pregnant females were also lower than lactating and non-lactating females. There was no significant difference in maximum 24-h body temperature between lactating and non-lactating females (Fig. 3.3b). Maximum 24-h body temperature of females was high when maximum 24-h air temperature was high and vegetation greenness was low (Table 3.1).

Mean 24-h body temperature differed with the reproductive status of the females (Fig. 3.2 and Table 3.1). There was a clear period of gestational hypothermia in pregnant females where mean 24-h body temperature was significantly lower during pregnancy compared to lactating and non-lactating females which is a result of the decreased minimum and maximum 24-h body temperatures during pregnancy (Fig. 3.3c). Lactating females had higher mean 24-h body temperatures than non-lactating females as a result of the higher minimum 24-h body temperature and no change in maximum 24-h body temperature (Fig. 3.3c). Mean 24-h body temperature of females was high when environmental air temperature was high and vegetation was green (Table 3.1).

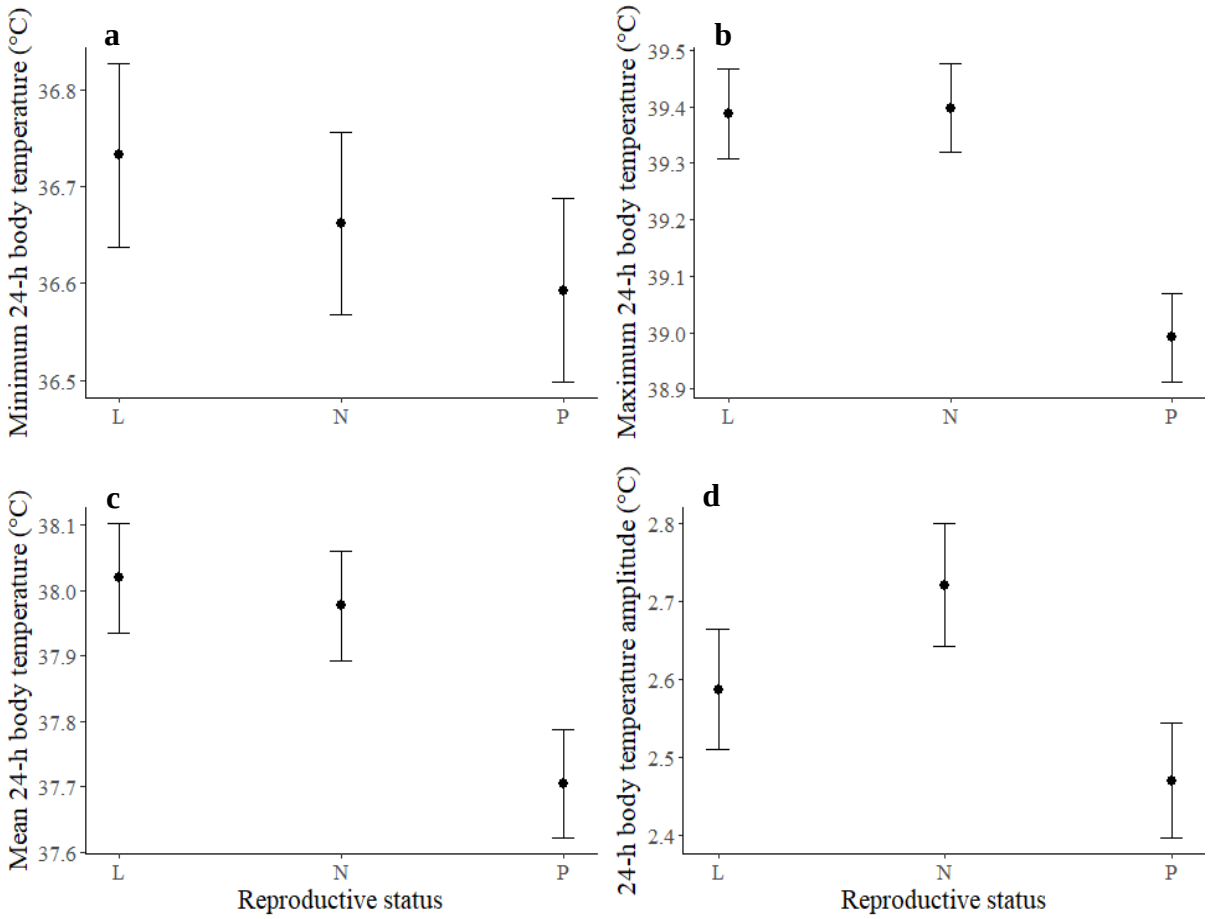

***Figure** 3.3: Generalized linear mixed-effects model (GLMM) marginal effects of reproductive status (lactating = L, non-lactating = N and pregnant = P) on minimum 24-h body temperature (a), maximum 24-h body temperature (b), mean 24-h body temperature (c) and 24-h amplitude of body temperature rhythm (d), while controlling for air temperature (24-h minimum (a), 24-h maximum (b), 24-h mean (c) and 24-h range (d)), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and body mass.*

Pregnant females had a lower 24-h amplitude of body temperature rhythm than lactating and non-lactating females (Fig. 3.3d). The decrease in maximum 24-h body temperature was more pronounced than the lowered minimum 24-h body temperature in pregnant females such that the 24-h amplitude of body temperature rhythm was narrowed during pregnancy. Lactating females had a lower 24-h amplitude of body temperature rhythm than did non-lactating females as a result of the higher minimum 24-h body temperature in lactating females compared to non-lactating females. The 24-h amplitude of body temperature rhythm

of females were particularly high when 24-h range of air temperature was high and vegetation greenness was low (Table 3.1).

Table 3.1: *Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a) (24-h minimum, 24-h maximum, 24-h mean and 24-h range), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and reproductive status (L= lactating, N= non-lactating and P = pregnant) with 24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude of body temperature (T_b) rhythm of 30 female vervet monkeys over the duration of the study period (September 2010- June 2017). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor. Pregnancy (P) was the reference category to which lactating and non-lactating females were compared to. (N = 17284).*

Dependent	***Independent***	***Estimate ± SE***	***t***	***p***
24-h minimum T_b	L vs P	-0.0038 ± 0.0003	-13.22	< 0.0001
	N vs P	-0.0019 ± 0.0003	-6.15	< 0.0001
	24-h minimum T_a	0.0008 ± 0.0000	54.87	< 0.0001
	NDVI	0.0243 ± 0.0011	21.42	< 0.0001
	Body mass	0.0031 ± 0.0004	7.72	< 0.0001
	Intercept	3.5770 ± 0.0020	1764.16	< 0.0001
24-h maximum T_b	L vs P	-0.0101 ± 0.0002	-50.09	< 0.0001
	N vs P	-0.0104 ± 0.0002	-47.84	< 0.0001
	24-h maximum T_a	0.0002 ± 0.0000	18.23	< 0.0001
	NDVI	-0.0041 ± 0.0008	-5.06	< 0.0001
	Body mass	0.0004 ± 0.0003	1.49	0.136
	Intercept	3.6690 ± 0.0015	2390.52	< 0.0001
24-h mean T_b	L vs P	-0.0083 ± 0.0002	-50.71	< 0.0001
	N vs P	-0.0072 ± 0.0002	-41.16	< 0.0001
	24-h mean T_a	0.0005 ± 0.0000	58.57	< 0.0001
	NDVI	0.0069 ± 0.0007	10.50	< 0.0001
	Body mass	0.0014 ± 0.0002	6.16	< 0.0001
	Intercept	3.6210 ± 0.0023	1592.25	< 0.0001
24-h amplitude of T_b	L vs P	-0.0465 ± 0.0047	-9.91	< 0.0001
	N vs P	-0.0967 ± 0.0051	-18.88	< 0.0001
	24-h range of T_a	0.0050 ± 0.0003	19.08	< 0.0001
	NDVI	-0.2003 ± 0.0187	-10.70	< 0.0001
	Body mass	-0.0372 ± 0.0070	-5.31	< 0.0001
	Intercept	3.5750 ± 0.0019	1839.67	< 0.0001

3.3 Progression of pregnancy

The lowered mean 24-h body temperature experienced during pregnancy was not a result of an immediate and precipitous drop in body temperature when the female fell pregnant, but rather a progressive decline in mean 24-h body temperature as pregnancy progressed (Fig. 3.4 and Fig.3.5c). To assess the progressive decline in body temperature associated with gestational hypothermia, I ran a series of generalized linear mixed-effects models (GLMMs) to assess 24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude of body temperature rhythm during pregnancy.

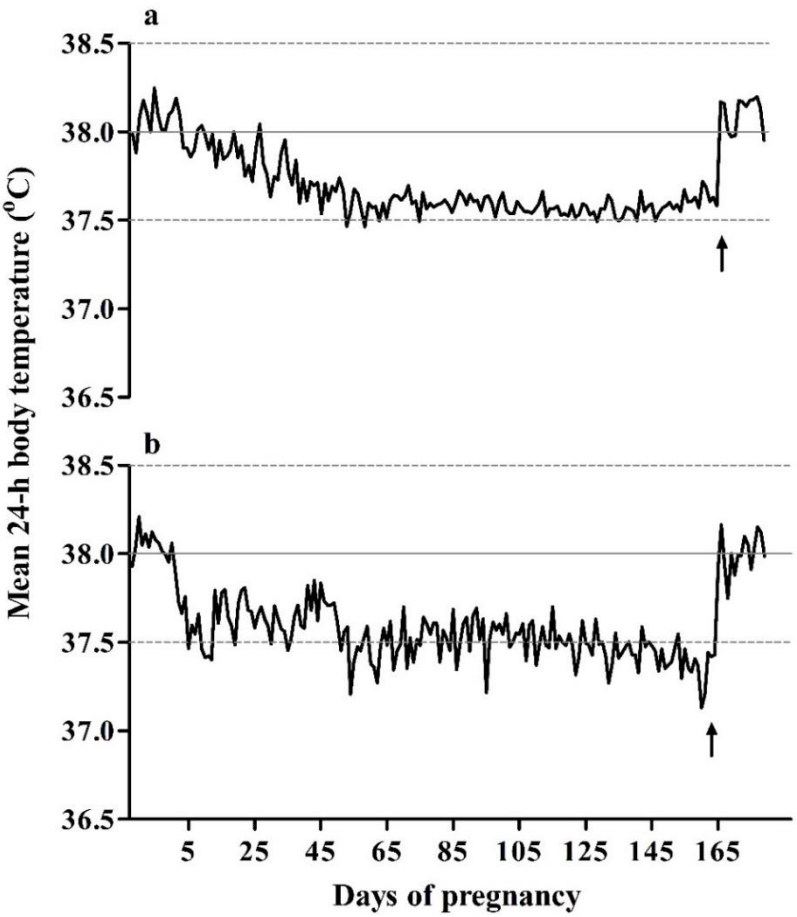

Figure 3.4: *Mean 24-h body temperature of two females during pregnancy leading up to the birth (indicated by the black arrows). Female in (a) was pregnant during a normal year while female in (b) was pregnant during cold and dry environmental conditions. The horizontal solid grey line at 38 °C indicate the mean body temperature of non-reproductive vervet monkeys, ± SD indicated by the grey dotted lines at 37.5 and 38.5 °C.*

The progressive decline in mean 24-h body temperature during pregnancy was a result of a decrease in minimum and maximum 24-h body temperatures. Minimum 24-h body temperature decreased as pregnancy progressed and was on average 1.8 °C lower at the end of pregnancy (Fig. 3.5a). The decline in minimum 24-h body temperature that was associated with pregnancy progression would have initially coincided with a colder period and progressed into a warm period when vegetation was green as the majority of monkeys gave birth in late spring. Despite these favourable environmental conditions, minimum 24-h body temperature of pregnant females remained low during the warm period so that the decline in minimum 24-h body temperature was independent of ambient temperature and vegetation greenness (Table 3.2). Minimum 24-h body temperature was positively associated with minimum 24-h air temperature but negatively associated with vegetation greenness as indexed by NDVI (Table 3.2). Despite later stages of pregnancy being associated with warm environmental conditions, maximum 24-h body temperature also decreased by 0.4 °C, on average, during pregnancy (Fig. 3.5b). Maximum 24-h body temperature was independent of maximum 24-h air temperature but was negatively associated with vegetation greenness (Table 3.2).

The lowering of 24-h minimum and 24-h maximum body temperature with the progression of pregnancy resulted in a lowering of mean 24-h body temperature that was independent of mean 24-h air temperature and vegetation greenness (Table 3.3). Females who were pregnant during drought conditions experienced cold environmental air temperatures and low vegetation greenness. Mean 24-h body temperature was particularly low in females who were pregnant during the cold-dry period where food was scarce (Fig.3.4b).

The decline in minimum and maximum 24-h body temperatures occurred at a similar magnitude which did not affect the 24-h amplitude of body temperature rhythm as the days of pregnancy progressed (Fig. 3.5d). There was a positive relationship between 24-h amplitude of body temperature rhythm of pregnant females and 24-h range of air temperature and 24-h amplitude of body temperature rhythm was high when vegetation greenness was high (Table 3.2).

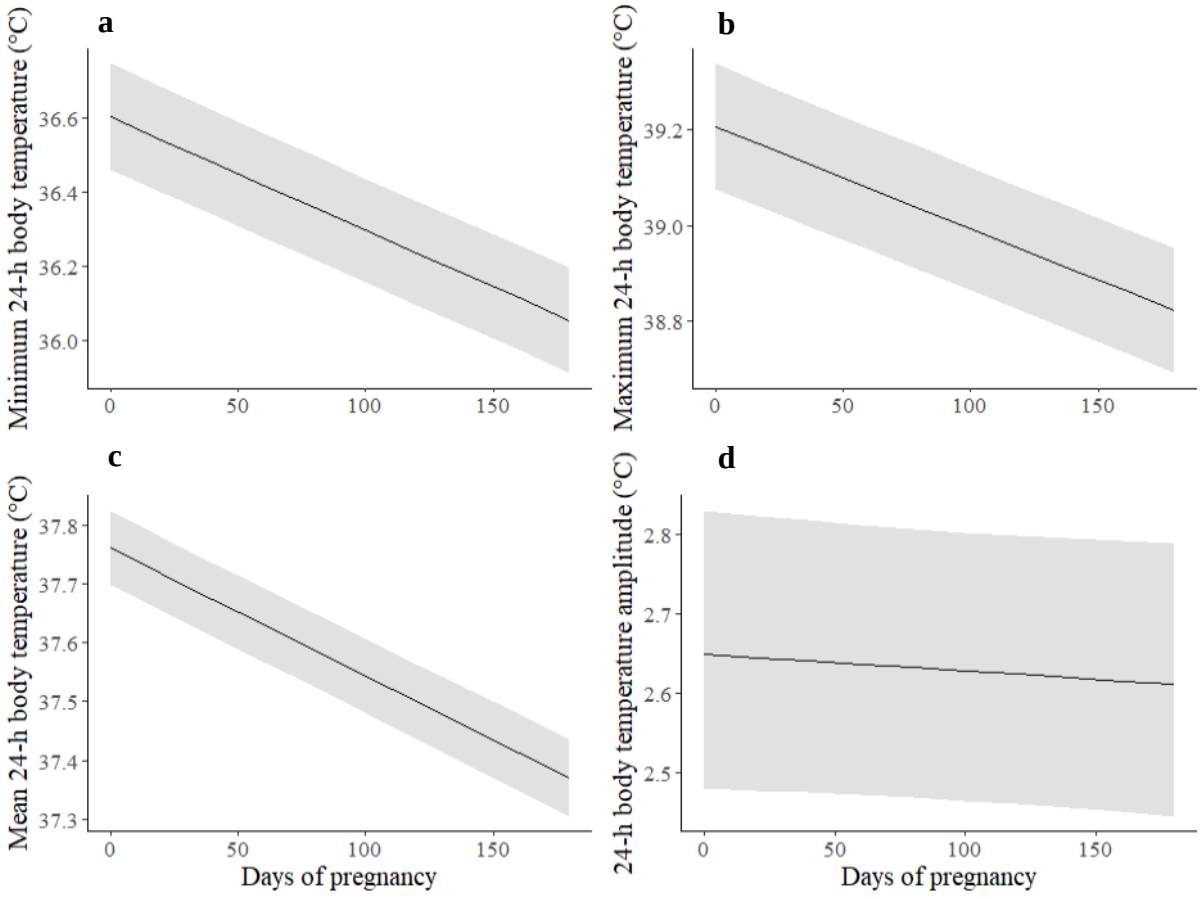

Figure 3.5: *Generalized linear mixed-effects model (GLMM) marginal effects of pregnancy progression in days (with 95% CI) on minimum 24-h body temperature (a), maximum 24-h body temperature (b), mean 24-h body temperature (c) and 24-h amplitude of body temperature rhythm (d) while controlling for air temperature (24-h minimum (a), 24-h maximum (b), 24-h mean (c) and 24-h range (d)), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and body mass.*

Table 3.2: *Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a) (24-h minimum, 24-h maximum, 24-h mean and 24-h range), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and progression of days of pregnancy with 24-h mean, 24-h minimum, 24-h maximum and 24-h amplitude of body temperature (T_b) rhythm of 17 pregnant female vervet monkeys over the duration of the study period (September 2010- June 2017). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor (N = 3078).*

Dependent	***Independent***	***Estimate ± SE***	***t***	***p***
24-h minimum T_b	Days of pregnancy	-0.0001 ± 0.0000	-18.59	< 0.0001
	24-h minimum T_a	0.0005 ± 0.0000	17.96	< 0.0001
	NDVI	-0.0436 ± 0.0048	-9.19	< 0.0001
	Body mass	0.0067 ± 0.0017	3.85	< 0.001
	Intercept	3.5870 ± 0.0067	538.12	< 0.0001
24-h maximum T_b	Days of pregnancy	-0.0001 ± 0.0000	-14.72	< 0.0001
	24-h maximum T_a	0.0000 ± 0.0000	0.38	0.704
	NDVI	-0.0152 ± 0.0039	-3.94	< 0.0001
	Body mass	0.0061 ± 0.0015	4.16	< 0.0001
	Intercept	3.6520 ± 0.0056	646.87	< 0.0001
24-h mean T_b	Days of pregnancy	-0.0001 ± 0.0000	-25.88	< 0.0001
	24-h mean T_a	0.0002 ± 0.0000	12.09	< 0.0001
	NDVI	-0.0216 ± 0.0021	-10.22	< 0.0001
	Body mass	0.0050 ± 0.0009	5.65	< 0.0001
	Intercept	3.6180 ± 0.0033	1089.06	< 0.0001
24-h amplitude of T_b	Days of pregnancy	-0.0001 ± 0.0001	-0.94	0.348
	24-h range of T_a	0.0044 ± 0.0005	8.77	< 0.0001
	NDVI	0.3154 ± 0.0997	3.16	< 0.01
	Body mass	-0.0108 ± 0.0336	-0.32	0.748
	Intercept	0.8359 ± 0.1292	6.47	< 0.0001

3.4 Days of lactation

The lactation period was initiated immediately following the precipitous increase in body temperature on the day of parturition. I ran a series of generalized linear mixed-effects models (GLMM) to assess whether there were similar progressive changes in the 24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude of body temperature rhythm, compared to pregnancy progression, as the days of lactation progress and the nutritional and energetic demands of the lactating female increases as the result of a growing infant. Although the lactation period occurred during the warmer summer months where environmental temperatures were high and rainfall peaked, which resulted in an increase in vegetation greenness, as indexed by NDVI, mean 24-h body temperature was independent of lactation progression (Fig. 3.6c) but was high when environmental air temperatures and vegetation greenness was high (Table 3.3).

Minimum 24-h body temperature was also independent of days of lactation (Fig. 3.6a) but was positively associated with minimum 24-h air temperature and vegetation greenness (Table 3.3). Maximum 24-h body temperature increased slightly by 0.2 °C as days of lactation progressed (Fig. 3.6b) and was particularly high when maximum 24-h air temperature was high and vegetation greenness was low (Table 3.3). The progressive increase in maximum 24-h body temperature throughout lactation resulted in a progressive increase in 24-h amplitude of body temperature rhythm during lactation (Fig. 3.6d) but the effect was small with only 0.1 °C increase between the start and the end of lactation. The 24-h amplitude of body temperature rhythm was particularly high when 24-h range of air temperature was high and vegetation greenness was low (Table 3.3).

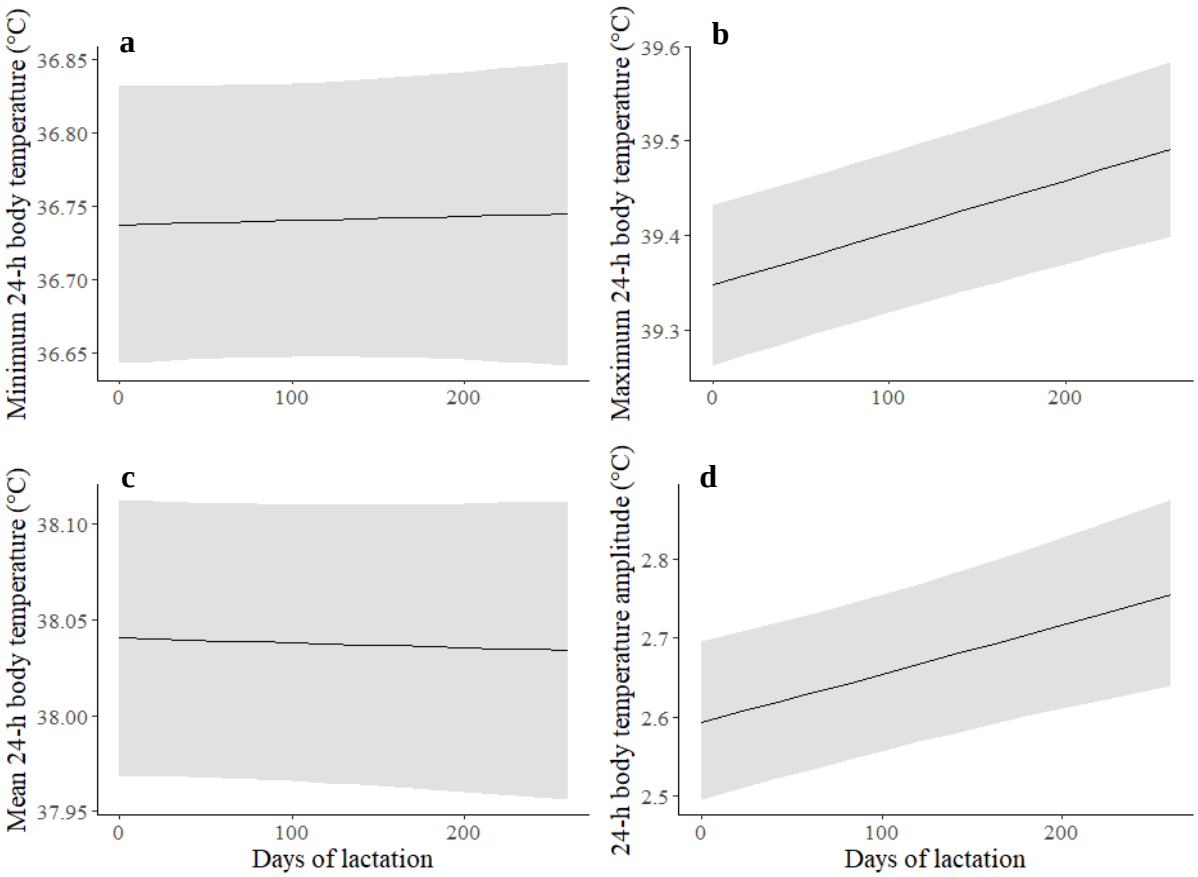

Figure 3.6: *Generalized linear mixed-effects model (GLMM) marginal effects of lactation progression in days (with 95% CI) on a) minimum 24-h body temperature, b) maximum 24-h body temperature, c) mean 24-h body temperature and d) 24-h amplitude of body temperature rhythm while controlling for air temperature (24-h minimum (a), 24-h maximum (b), 24-h mean (c) and 24-h range (d)), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and body mass.*

Maximum 24-h body temperature of females who lactated during normal environmental conditions (Fig.3.7a) were less variable compared to females who lactated during drought conditions. Females who lactated during drought conditions where environmental air temperatures were high and rainfall was particularly low, resulting in low vegetation greenness and limited access to drinking water, had higher maximum 24-h body temperatures (Fig. 3.7b and Fig.3.7c) than females lactating during normal environmental conditions (Fig. 3.7a). After rain fell approximately 90 days after the start of the lactation process, resulting in

an increase in food and water availability, maximum 24-h body temperature decreased significantly (Fig. 3.7b and Fig. 3.7c).

Table 3.3: *Result of the generalized linear mixed-effects model (GLMM) investigating the relationship of air temperature (T_a) (24-h minimum, 24-h maximum, 24-h mean and 24-h range), vegetation greenness as indexed by normalized difference vegetation index (NDVI) and the progression of the lactation period on 24-h minimum, 24-h maximum, 24-h mean and 24-h amplitude of body temperature (T_b) rhythm of 17 female vervet monkeys over the duration of the study period (September 2010- June 2016). Body mass was included as a control variable and individual monkey ID, nested within troop, was included as a random factor (N = 3930).*

Independent	***Dependent***	***Estimate ± SE***	***t***	***p***
24-h minimum T_b	Days of lactation	0.0000 ± 0.0000	0.24	0.815
	24-h minimum T_a	0.0005 ± 0.0000	14.74	< 0.0001
	NDVI	0.0164 ± 0.0022	7.33	< 0.0001
	Body mass	0.0003 ± 0.0007	0.44	0.661
	Intercept	3.5910 ± 0.0030	1192.56	< 0.0001
24-h maximum T_b	Days of lactation	0.0000 ± 0.0000	5.64	< 0.0001
	24-h maximum T_a	0.0003 ± 0.0000	12.40	< 0.0001
	NDVI	-0.0065 ± 0.0016	-4.09	< 0.0001
	Body mass	0.0009 ± 0.0005	1.74	0.082
	Intercept	3.6640 ± 0.0024	1542.25	< 0.0001
24-h mean T_b	Days of lactation	-0.0000 ± 0.0000	-0.33	0.741
	24-h mean T_a	0.0005 ± 0.0000	21.57	< 0.0001
	NDVI	0.0045 ± 0.0012	3.72	< 0.001
	Body mass	0.0006 ± 0.0004	1.57	0.117
	Intercept	3.6250 ± 0.0019	1920.10	< 0.0001
24-h amplitude of T_b	Days of lactation	0.0002 ± 0.0001	3.75	< 0.001
	24-h range of T_a	0.0053 ± 0.0005	10.31	< 0.0001
	NDVI	-0.2807 ± 0.0442	-6.35	< 0.0001
	Body mass	0.0159 ± 0.0136	1.17	0.241
	Intercept	0.8966 ± 0.0540	16.61	< 0.0001

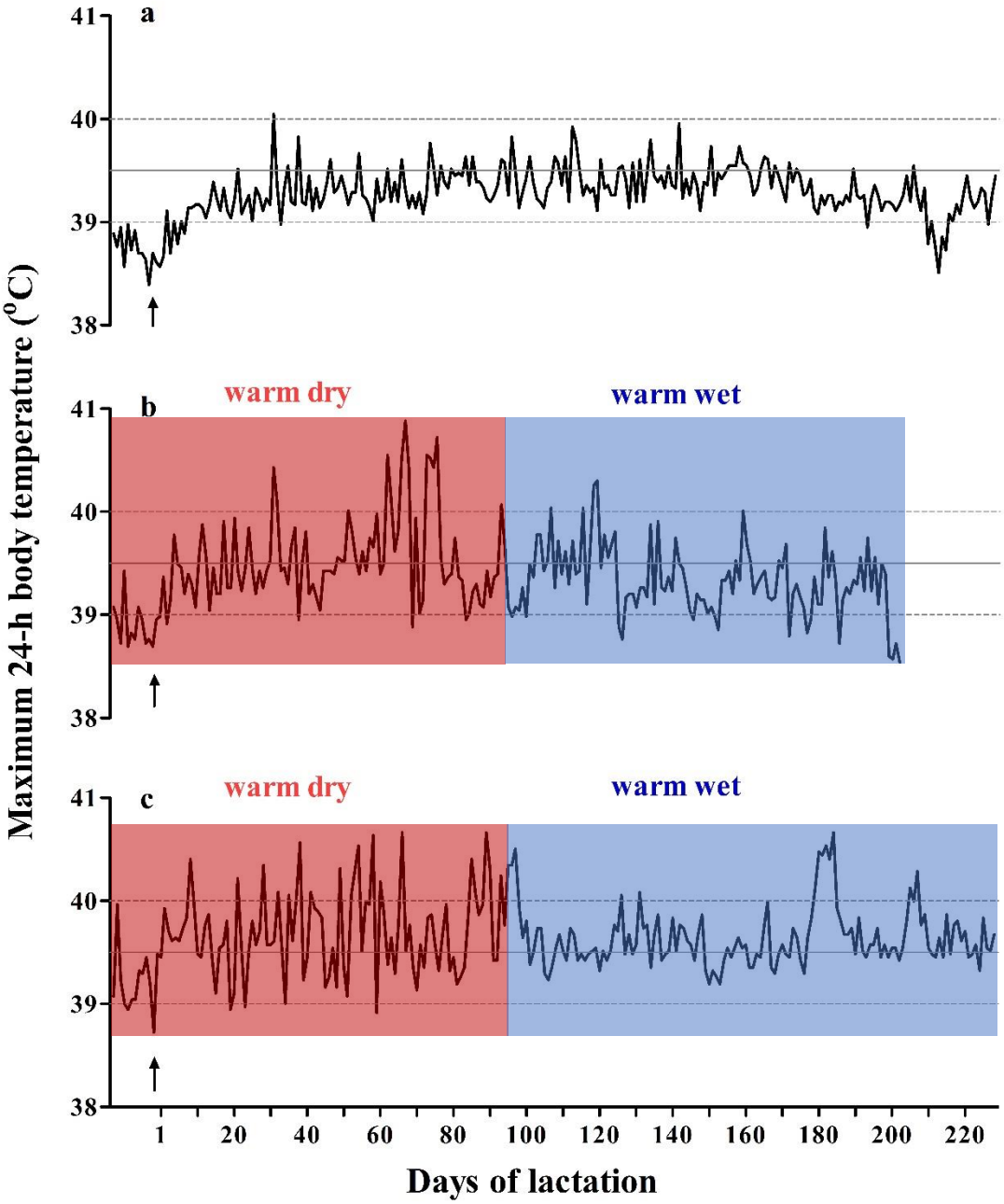

Figure 3.7: *Maximum 24-h body temperature of three females from different cohorts during the lactation period starting immediately after birth (indicated by the black arrows). Female in (a) is from the 2014-2015 cohort where the lactation period coincided with favourable environmental conditions. Females in (b) and (c) are from the 2016-2017 cohort where the first three months of lactation (red block) coincided with dry and warm environmental conditions with mean Ta of 23.0 ± 3.5 °C. Rain fell during the fourth month of lactation which was the start of the warm-wet period (blue block) with mean Ta of 19.5 ± 4.9 °C. The solid grey horizontal line at 39.5 °C indicates the average maximum body temperature of non-reproductive vervet monkeys, ± SD indicated by the grey dotted lines at 39 and 40 °C.*

CHAPTER FOUR – DISCUSSION

I have provided the first characterization of body temperature patterns during pregnancy and lactation in free-living vervet monkeys. Body temperature differed with the reproductive status of the female vervet monkeys. As shown previously (Lubbe *et al*., 2014), vervet monkeys displayed a clear nychthemeral rhythm of body temperature, where body temperature was lowest in the early morning and highest near midday. Mean 24-h body temperature of non-lactating females was on average 37.9 ± 0.3 °C.

In comparison to non-lactating females, pregnant females had a mean 24-h body temperature of 37.6 ± 0.2 °C, approximately 0.3 °C lower than non-lactating females. Earlier stages of pregnancy (first trimester) coincided with cold-dry winter conditions while later stages of pregnancy (second and third trimester) stretched into early to mid-spring and coincided with warm-wet conditions as the first rains generally fell in mid spring. Despite the relative benign environmental conditions near the end of pregnancy, minimum 24-h body temperature and maximum 24-h body temperature were lower at the end of pregnancy than at the start of pregnancy. The lower 24-h minimum body temperature and 24-h maximum body temperature with pregnancy progression resulted in a progressive decline of mean 24-h body temperature as pregnancy progressed that was on average 0.4 °C lower at the end of pregnancy compared to the start of pregnancy. Although minimum 24-h body temperature was lower on colder days, the progressive decline in mean 24-h body temperature with pregnancy was independent of air temperature and coincided with a period when air temperature would have increased during spring. The first rains generally fell during late pregnancy resulting in an increase in vegetation greenness, as indexed by normalized difference vegetation index (NDVI), however, the progressive decline in mean 24-h body temperature was independent of NDVI. The progressive decline in mean 24-h body temperature is likely to reflect

gestational hypothermia, which is a regulated decrease in body temperature during pregnancy (Wilson and Stricker, 1979; Eliason and Fewell, 1997).

Gestational hypothermia was resolved at birth as body temperature displayed a precipitous increase on the day of parturition. Lactating females had a mean 24-h body temperature of 38.0 ± 0.3 °C, approximately 0.1 °C higher than non-lactating females. In contrast with my predictions that lactating females would have lower than normal minimum 24-h body temperatures and higher than normal maximum 24-h body temperatures, lactating females had higher minimum 24-h body temperatures, but similar maximum 24-h body temperatures compared to non-lactating females. Therefore, lactating females had a narrower 24-h amplitude of their body temperature rhythm compared to non-lactating females and thus maintained better homeothermy than non-lactating females.

Although 24-h mean body temperature and 24-h minimum body temperature of lactating females were higher compared to non-lactating females, lactating females maintained that higher 24-h mean body temperature and 24-h minimum body temperature over the course of lactation likely because lactation occurred during the warm-wet summer months where environmental temperatures were high and food and water sources were generally adequate. It appears that the vervet monkeys were able to increase energy intake to compensate for increased energy demands during lactation. They also would have faced warmer environments at night over the summer, reducing the energetic demand for maintaining homeothermy. However, there was an increase in 24-h amplitude of body temperature rhythm as lactation progressed, primarily as a result of increased maximum 24-h body temperature. The increase in maximum 24-h body temperatures was particularly evident in the dry year when no drinking water was available when the river was dry. Increased water intake is

necessary for evaporative cooling when environmental temperature exceeds body temperature of an endotherm (Hetem *et al*., 2016). Insufficient water intake as a result of drought conditions, or excessive water loss as a result of evaporative cooling, results in an increase in maximum 24-h body temperature of mammals during heat exposure (Jessen *et al.*, 1998; Mitchell *et al*., 2009; Hetem *et al*., 2012). With already high water demands of evaporative cooling during dry-hot periods, water demands are exacerbated during the lactation period as water is the main component of milk (Kunz *et al*., 1994; Wilde *et al*., 1995). Water demand of lactation is likely to increase as the infant grows (Altmann & Samuels, 1992). In most years the vervet monkeys appeared to have compensated for the water demands of lactation by drinking more water, but in the dry year, when there was little to no access to surface water, female water balance may have been compromised as lactation progressed.

As far as I am aware, my study is the first to show long-term (seven years) body temperature patterns for any mammal, and the first to document body temperature during reproductive events such as pregnancy, birth and lactation in free-living primates. Despite the insights my study provided into body temperature patterns during reproduction, I appreciate that my study is not without some shortfalls. My conclusions regarding drought and lactation must remain tentative because there was only one drought year, with only five vervet monkeys lactating during that period. Not all the individuals who were implanted in one year were recaptured the following year, resulting in incomplete data sets where pregnancies and births could have occurred and added to my sample size and duration of data for reproductive females. Despite this limitation, the data set presented is extensive in terms of time scale and number of individuals analysed for any mammal and it has provided new valuable insights into body temperature patterns in reproducing female mammals. Those insights may have been

enhanced if we could have had a measure of hormonal profiles and body condition of both mothers and their infants. Such measurements may have allowed us to better assess the nutritional status of the animals, to document events such as ovulation and miscarriage, and to investigate the mechanisms of gestational hypothermia.

Body mass measurements of mothers and infants also may have helped to identify a possible relationship between the mother's body condition during the nutritionally expensive lactation period where a rapidly growing infant would require more milk as lactation progressed and the energetic costs of carrying a growing infant, increases. An advantage of my study, however, was that the vervet monkeys were not handled or followed closely for sampling, allowing us to assess patterns of body temperature in naturally living animals.

The vervet monkeys, however, were habituated to the presence of human observers as part of a long-term study of their behavioural ecology. Unfortunately, the overall study aims required that behavioural observations for the seven-year study period not be focused specifically on reproductive females, but rather that scan sampling of all individuals within the troop be conducted. During the first year of my study, a greater focus was placed on reproductive females (Sashaw, 2012), but these detailed time budgets were unsustainable over the seven-year period. Continuous behavioural observations of all females to obtain detailed records from conception to lactation would have been too labour-intensive but might have added valuable information to the reproductive timeline of the individuals, accurate time budgets and changes in activity for pregnant and lactating females. Although scan sampling of all the females within the three troops over the seven-year study period, in combination with the reproductive histories of each female, can be used to determine activity budgets and changes in activity of reproductive females, focal sampling would have given a more accurate

measure of activity budgets (Gilby *et al*., 2010). Without these observations we do not know whether pregnant females prioritized certain activities above others to cope with the nutritional demands of a developing foetus, or whether lactating females increased their foraging time to compensate for increased energy demands of feeding a growing infant. Despite these limitations, my study was the first to show long-term body temperature patterns during reproductive events such as pregnancy, birth and lactation. The extensive data set gives us an insight into how vervet monkeys, inhabiting a semi-arid environment characterized by droughts and fluctuating environmental temperatures, cope with competing demands of different homeostatic processes while also having to deal with harsh environmental conditions. My study is also the first to show gestational hypothermia in free-living non-human primates.

4.1 Gestational hypothermia

As shown for other species (see Table 4.1), including humans (Lindqvist *et al*., 2003), vervet monkeys displayed a continuous decline in mean body temperature as pregnancy progressed. This continuous decline in mean body temperature during gestation has been termed 'gestational hypothermia' (Kozak, 1997). The magnitude of the reduced maternal body temperature during gestation in my pregnant females (0.4 °C) was similar to that observed in small mammals such as Arctic ground squirrels (Williams *et al*., 2011) and rats (Cairns *et al*., 2005), which had an average decrease in mean body temperature of 0.5 °C over the course of gestation. Similar decreases in core body temperature of 0.5 °C have been recorded in pregnant women from 29 to 36 weeks of gestation (Lindqvist *et al*., 2003). Bigger decreases of 0.8 to 1.4 °C in mean body temperature were evident during gestation in larger mammals such as African lions (Trethowan *et al*., 2016) and sheep (Laburn *et al*., 1992). Larger mammals have a decreased thermal conductance as a result of their reduced surface area-to-

volume ratio. Therefore, larger mammals have a larger thermal inertia as a result of their relatively small surface area through which they can either lose or gain heat from the environment (Hayssen and Lacey, 1985). Indeed, in 17 species of large mammalian herbivores, minimum and maximum body core temperature decreased with body mass (Hetem *et al*., 2016).

Foetal body temperature has been reported to be 0.3 – 0.5 °C higher than maternal body temperature in all species studied to date, including humans, during the later stages of pregnancy (Assali and Westin, 1962; Wood and Beard, 1964; Hart and Faber, 1965; Gilbert *et al*., 1985; Laburn *et al*., 1992; Laburn *et al*., 2002, Faurie *et al*., 2004). The increased foetal body temperature is a result of increased metabolic activity and foetal cell division which generates heat and elevates foetal body temperature (Laburn *et al*., 1992). Cell division is temperature dependent and has been found to be impaired and inhibited at temperatures higher than 40 °C (López-Sáez et al., 1966; Rieder and Maiato, 2004). Developing foetuses are vulnerable to damage caused by intrauterine hyperthermia (Laburn, 1996), particularly damage to the central nervous system during early pregnancy as a result of delayed cell proliferation (Edwards, 1986) and growth retardation during later stages of pregnancy as a result of cell death (Dreiling *et al*., 1991). The foetus's vulnerability to the teratogenic effects of thermal stress suggests gestational hypothermia may possibly be a protective mechanism as it allows a bigger safety margin before damaging hyperthermia occurs (Benson and Morris, 1971). The feto-maternal temperature gradient ensures that the foetus is thermally protected, however, if the mother becomes heat stressed as a result of environmental heat load or febrile infection the foetus may be at risk of teratogenic effects of thermal stress (Edwards, 2006). While the feto-maternal temperature gradient can be maintained with a

Table 4.1: *Average decrease in mean body temperature (T_b) (gestational hypothermia) and average decrease in the 24-h amplitude of the T_b rhythm (improved homeothermy) during pregnancy, as well as living conditions of the animals, and the method through which body temperature was measured.*

Species	24-h body temperature (T_b)		Living conditions	Method of T_b measurement	Reference
	Average decrease in mean T_b (°C)	Average decrease in amplitude of T_b (°C)			
Rats *Rattus*	0.8	-	Laboratory	Rectal thermocouple	Cairns *et al*., 2005
	1.0	-	Laboratory	Abdominal logger	Eliason and Fewell, 1997
	0.3	0.2	Laboratory	Abdominal logger	Kittrell and Satinoff, 1988
	1.0	-	Laboratory	Subcutaneous logger	Bu and Lephart, 2005
Mice *Mus musculus*	1.0	1.1	Laboratory	Abdominal logger	Gamo *et al*., 2013
	0.5	0.1	Laboratory	Abdominal logger	Wharfe *et al*., 2016
Hamster *Phodopus campbelli*	-	0.5	Laboratory	Abdominal logger	Scribner and Wynne-Edwards, 1994
Echidna *Tachyglossidae*	-	0.6	Free-living	Implanted logger (location unknown)	Nicol and Andersen, 2006
Arctic ground squirrel *Urocitellus parryii*	0.5 – 1.0	-	Free-living	Abdominal loggers	Williams *et al*., 2011
Rabbits *Oryctolagus cuniculus*	0.7	-	Laboratory	Rectal thermocouple	Naccarato and Hunter, 1983

Table 4.1: *Continued*

Species	24-h body temperature		Living conditions	Method of T_b measured	Reference
	Average decrease in 24-h T_b (°C)	Average decrease in amplitude of T_b (°C)			
Dogs *Canis lupus familiaris*	1.4	-	Laboratory	Rectal thermocouple	Concannon and Hansel, 1977
Sheep *Ovis aries*	0.8	-	Laboratory	Abdominal logger	Laburn *et al*., 1992
Lion *Panthera leo*	1.3	0.6	Free-living	Abdominal logger	Trethowan *et al*., 2016
Brown bear *Ursus arctos arctos*	0.4	0.1	Free-living	Abdominal logger	Friebe *et al*., 2014
	0.4	-	Laboratory	Abdominal logger	Hissa, 1997
Black bear *Ursus thibetanus japonicus*	0.7	-	Captivity	Rectal thermocouple	Shimozuru *et al*., 2013
Killer whale *Orcinus orca*	0.8	-	Captivity	Rectal thermocouple	Katsumata *et al*., 2006
Human *Homo sapiens*	0.4	-	Free-living	Tympanic thermometer	Hartgill *et al*., 2011
	0.5	-	Free-living	Tympanic thermometer	Lindqvist *et al*., 2003

- = not investigated

steady and slow rise in maternal body temperature (Schröder and Power, 1994), a sudden and rapid rise or fall in maternal body temperature will result in a smaller gradient during heat stress and a larger gradient during cold stress (Laburn *et al*., 1992). With a smaller feto-maternal temperature gradient during heat stress, the rate of heat transfer from the foetus to the mother might be reduced, placing the foetus at risk of damage from hyperthermia.

There may be other benefits of a lower maternal body temperature during gestation than only the reduced risk of hyperthermia for the foetus. Towards the end of pregnancy, foetal growth and the rate of foetal metabolic processes are at their highest, which requires high levels of oxygen. The reduced maternal body temperature during gestation has been proposed to be an oxygen-conserving mechanism by reducing heat-producing metabolic processes of both the mother and the foetus, which protects the foetus from hypoxia (Busto *et al*., 1987; Fewell, 1995; Kozak, 1997). A reduced maternal body temperature has also been found to cause a leftward shift in the oxyhaemoglobin dissociation curve, which result in increased oxygen saturation (Kozak, 1997). Neuronal injury in hypoxic conditions has been found to be reduced under mild hypothermia, which further contributes to the proposed idea that gestational hypothermia may be a neuroprotective mechanism in situations where foetal oxygen is limited (Nishio *et al*., 2000).

Given the benefits of a lower maternal body temperature during gestation, it is not surprising to find that it is a well-regulated response. In near-term pregnant rats raised in a thermocline, pregnant and non-pregnant females preferred similar environmental temperatures, indicating reduced maternal body temperature to be a regulated response rather than the female's inability to increase and maintain a higher body temperature (Eliason and Fewell, 1997). Similarly, pregnant rats showed a lowering of the threshold temperature at which cooling

mechanisms such as salivary evaporative cooling and skin vasodilation are activated, indicating that pregnant rats actively defended a lower body temperature (Wilson and Stricker, 1979). This actively controlled gestational hypothermia must therefore have an advantage, as described previously. Pregnant vervet monkeys may have actively reduced body temperature during pregnancy by seeking cooler microclimates or enhancing evaporative cooling during periods when they had access to surface drinking water. Pregnant vervet monkeys could also have used other mechanisms that are less costly than evaporative cooling, for example increasing peripheral vasodilation at low environmental temperatures. Unfortunately, we don't know whether pregnant vervet monkeys used autonomic or behavioural means to lower body temperature. Autonomic mechanisms were likely employed to reduce maternal body temperature as mothers would need to be active and heat-exposed when feeding, travelling with the troop and engaging in social behaviours.

In addition to a progressive decline in maternal body temperature during gestation, a narrowing of the amplitude of the 24-h body temperature rhythm (i.e., improved homeothermy) has also been found in pregnant females (Table 4.1). Small mammals, such as rats (Kittrell and Satinoff, 1988), hamsters (Scribner and Wynne-Edwards, 1994) and echidnas (*Tachyglossus aculeatus*: Nicol and Andersen, 2006), as well as large mammals, such as the African lion (Trethowan *et al*., 2016) and brown bears (Friebe *et al*., 2014) have been reported to display narrowing of the amplitude of the 24-h body temperature rhythm towards the end of gestation. It is proposed that the decreased amplitude of the maternal body temperature rhythm during gestation is a result of the increased body mass as gestation progresses (Refinetti, 1999). The proficiency with which an animal can store and dissipate heat has been found to be associated with body mass in non-pregnant animals, where an increase in body mass resulted in a decrease in amplitude of body temperature (Aschoff,

1982; Mortola and Lanthier, 2004). Based on Aschoff (1982) and Mortola and Lanthier's (2004) findings, one could infer that the same principle applies to pregnant females who gain body mass during gestation as the result of foetal growth.

However, more recent studies, where the metrics of these comparative analyses were more refined, found no interspecies relationship between body mass and the amplitude of body temperature rhythm in small (Refinetti, 1999) and large mammals (Hetem *et al*., 2016). Refinetti (1999) found that interspecies differences in amplitude of body temperature rhythm in small mammals were not a function of surface area (i.e., body size) but rather related to diurnality, where diurnal species had a greater amplitude in body temperature rhythm than did nocturnal species, and habitat, where species in tropical and desert habitats had a greater amplitude of the body temperature rhythm than did species in temperate habitats. Similarly, no relationship was found between body mass and amplitude of the body core temperature rhythm in large mammals; the amplitude in the 24-h body core temperature rhythm was similar for a 21-kg springbok, a 44-kg goat, a 56-kg blesbok, a 160-kg lion and a 3000-kg savanna elephant (Fuller *et al*., 2016; Hetem *et al*., 2016). Similarly, a meta-analysis of body temperature measurements under laboratory conditions showed no change in amplitude of body temperature rhythm of 57 mammals ranging from 15 kg to 5000 kg in mass (Mortola and Lanthier, 2004). The meta-analyses may be confounded by timing of activity and habitat, yet within a species there may be a relationship between small and large individuals.

The relationship between body mass and thermal conductance is inversely proportional, and an increase in body mass will result in a decrease in the thermal conductance of an animal (Hayssen and Lacy, 1985; Snyder and Nestler, 1990). Therefore, a larger body should be able to better regulate body temperature with less variability (i.e., narrower amplitude of body

temperature rhythm). It is therefore possible that if larger individuals maintain a tighter amplitude of the body temperature rhythm compared to smaller individuals, similar responses (i.e., tighter amplitude of the body temperature rhythm) could be observed during pregnancy.

Contrary to the literature and the findings of previous studies, my pregnant females tightly regulated body temperature compared to lactating and non-lactating females but did not display a narrowing of 24-h amplitude of body temperature rhythm as gestation progressed and body mass increased as a result of foetal growth. Minimum 24-h body temperature of pregnant females decreased by ~ 0.5 °C and maximum body temperature decreased in parallel, by ~ 0.4 °C as pregnancy progressed, which resulted in the amplitude of body temperature rhythm remaining unchanged as pregnancy progressed. The absence of improved homeothermy in my pregnant females, as gestation progressed, might have been the result of various environmental factors and possibly social behaviours having an effect on body temperature. My females were free-ranging and faced high heat loads during the day as a result of solar radiation, and high heat loss at night to clear skies. It may not have been possible for them to reduce the amplitude of body temperature any further as pregnancy progressed. Improved homeothermy in other small mammals such as rats and hamsters has been found only under laboratory conditions. Although improved homeothermy has been recorded in large free-ranging mammals such as lions (Trethowan *et al*., 2016), body size (i.e., small or large) might be an important factor determining the absence or presence of reduced amplitude of body temperature in free-living mammals.

4.2 Lactation

Although gestational hypothermia has been documented in several species, very few studies have investigated body temperature patterns during lactation (e.g., Eliason and Fewell, 1997;

Williams *et al*., 2013). In general, the lactating females in my study population were able to maintain body temperature remarkably well despite the reported high energetic costs of lactation. Vervet monkeys likely compensated for high energetic demands of lactation by increasing food intake. Lactating females in our population were found to spend more time foraging than were non-lactating females, presumably increasing their food intake (Sashaw, 2012). Increases in food intake during lactation have been observed in several species (Wade and Schneider, 1992; Speakman & McQueenie, 1996; Bartness, 1997; Scantlebury *et al*., 2000; Johnson *et al*., 2001), including primates such as yellow baboons (*Papio cynocephalus*: Altman, 1980), gelada baboons (*Theropithecus gelada*: Dunbar and Dunbar, 1988) and Hanuman langurs (*Presbytis entellus*: Koenig *et al*., 1997). Food intake of lactating female striped hamsters (*Phodopus sungorus*) were further enhanced in cold conditions compared to those lactating in warmer environments (Zhao, 2010). As lactation in my study population coincided with the warm-rainy season and an increase in vegetation greenness, the lactating females likely had access to sufficient high-quality food sources such as sweet thorn constituents (i.e., leaves, flowers, seeds and gum of the tree) that are abundant in the vervet monkey's home ranges (Pasternak *et al*., 2013). Lactating vervet monkeys in our population were not only found to increase foraging time but also prioritized selection of forage with high nutrient content (Sashaw, 2012). Similarly, lactating female chimpanzees had a higher percentage of fruit intake in their diet than did cycling females (Murray *et al*., 2009), which increased their nutrient intake above that of cycling females.

In conditions where food resources are insufficient to meet increased energy requirements with lactation, females may resort to using their own energy stores, resulting in a decrease in body mass, as reported in several rodent studies (Rogowitz, 1996; Speakman and McQueenie, 1996; Zhang and Wang, 2006; Zhao, 2010). Female olive baboons (*Papio*

anubis) also lost body mass during lactation and weighed 7% less than cycling females (Bercovitch, 1987). Although we did not measure body mass changes throughout lactation, the high minimum 24-h body temperature during lactation suggests that lactating vervet monkeys in my study were not energy deficient, even in dry years. If females were energy-deficient, we would expect the minimum 24-h body temperature to be lower than normal (i.e., lower than minimum 24-h body temperature of non-lactating females), as seen in other mammals experiencing energy-deficiency (Hetem *et al*., 2016).

The high energetic costs for lactation are likely to be exacerbated for those species that carry their young. In Callitrichidae primates, infant-carrying imposes high energetic costs, which increase as the body mass of the growing infant increases (Altmann, 1980; Tardif, 1997). Poor physical condition has been observed in female cotton-top tamarins that were carrying their infants (Sánchez *et al*., 1999). Again, the high minimum 24-h body temperature displayed by the lactating vervet monkeys in my study population suggest that they may have met the additional cost of carrying an infant while also meeting the energetic cost of milk production.

In addition to the energetic costs associated with lactation, lactating females must maintain homeothermy. Despite lactation coinciding with the warm summer months, lactating vervet monkeys in my study population still face cold stress at night during the summer, as the gradient for heat loss to the usually clear night sky is high, and air temperatures at night are still, on average, 27 °C below body temperature. Low night-time temperatures correspond with a low in the nychthemeral rhythm of body temperature, which reaches a low during the early morning hours (Lubbe, 2013). Mothers are in constant contact with their infant during the first two months of infant life, similar to the contact obtained through huddling behaviour,

which might also have contributed to lactating females maintaining minimum 24-h body temperature during cold exposure at night or early in the morning.

Primates exposed to cold environments have been found to adopt behavioural mechanisms, such as sunbathing and huddling, which play an important role in thermoregulation (Hanya, 2004). Sunbathing and huddling have been found to significantly increase skin temperature in Japanese macaques (*Macaca fuscata*) which indicate that these thermoregulatory behaviours can help conserve energy in cold environments (Hanya *et al*., 2007). Similarly, ruffed lemurs (*Varecia variegata variegata*) and vervet monkeys, employ sunbathing as a behavioural strategy to cope with cold (Morland, 1993; Cramer *et al*., 2012). Huddling, as a thermoregulatory behaviour, mediates thermal conductance by increasing the surface area of the body in contact with a warm body and decreasing the surface area of the body exposed to low environment temperatures (Gordon, 1985; Stelzner, 1988). Behavioural adjustments have been shown to aid thermoregulation during thermal stress in several observational studies of free-ranging primates. Chimpanzees (*Pan troglodytes*) and chacma baboons (*Papio ursinus*) used caves to shelter them from the wind (Barrett *et al*., 2004; Pruetz, 2007). Postural adjustments (e.g., sunbathing and hunching) and social behaviours (e.g., huddling) are associated with colder environmental conditions and are suggested to aid in thermoregulation in non-human primates such as colobine monkeys (*Colobus polykomos*: Da Silva, 1993), yellow baboons (*Papio cynocephalus*: Pochron, 2000), hamadryas baboons (*Papio hamadryas*: Brent *et al*., 2003), Japanese macaques (*Macaca fuscata*: Hanya *et al*., 2007) and collared lemurs (*Eulemur collaris*: Donati *et al*., 2011). Social behaviours such as huddling may have helped lactating female vervet monkeys to reduce heat loss to the environment and therefore, reduce the fall in body temperature during the cold summer nights.

In addition to heat loss at night, lactating vervet monkeys need to cope with high daytime

environmental heat loads in summer. High energetic costs of lactation and carrying an infant, combined with close body contact (i.e., huddling) with an infant during the hot summer months may limit a lactating female's ability to dissipate heat. Indeed, it has been argued that lactating mammals struggle to dissipate heat (Speakman and Król, 2010). The 'heat dissipation limitation (HDL)' theory suggest lactating mammals are limited in their capacity to dissipate heat under increased metabolic demands (Speakman and Król, 2010). Speakman and Król (2010) found evidence for the HDL theory by showing that mice that raised their offspring in thermoneutral conditions (30 °C) were apparently limited in their capacity to dissipate heat, as was evident from their reduced food intake, low reproductive output and reduced milk energy output compared to mice raising offspring at 21 °C and 8 °C (Król and Speakman, 2003a; Król and Speakman, 2003b). Reduced resting metabolic rate in mice that raised their offspring at 8 °C and 21 °C compared to mice that raised their offspring at thermoneutrality, further supports the HDL theory (Król *et al*., 2003). Despite what the HDL theory suggests with regards to lactating females being limited in their capacity to dissipate heat (Speakman and Król, 2010), lactating vervet monkeys in my study population appeared to be able to cope with the water and energy costs associated with lactation and infant carrying. Despite the added thermal stress from lactating during the hot summer months, lactating vervet monkeys in my study population efficiently dissipated heat, as shown by their maximum 24-h body temperatures being no different to non-lactating females.

Lactating females may achieve that heat balance through several mechanisms. One proposal is that they impose physiological energy-sparing mechanisms such as suppressing thermogenesis in brown adipose tissue (BAT). After ingesting food, BAT generates heat by increasing metabolic rate that converts food energy to heat (Cannon and Nedergaard, 2004). During lactation, thermogenic activity of BAT is reduced (Trayhurn and Richard, 1985;

Andrews *et al*., 1986; Wade *et al*., 1986; Nizielski *et al*., 1993; Speakman, 2008). Reduced BAT thermogenesis may allow available energy to be directed towards milk production rather than thermoregulation (Trayhurn *et al*., 1982). Reducing BAT thermogenesis can prevent hyperthermia from heat generated through milk production and food breakdown (Król and Speakman, 2003a). BAT thermogenic activity might have been suppressed in lactating vervet monkeys to allow for excess heat generated from milk production and food breakdown to be dissipated and therefore, being able to maintain maximum 24-h body temperature.

Although maximum 24-h body temperature was not different between lactating and non-lactating females, there was a slight but significant increase in maximum 24-h body temperature as lactation progressed. During the first month of infant life, infants spend 88% of their time in ventral contact with the mother and are still solely dependent on their mother for nutrition, which results in mothers not only being placed under nutritional stress but also energetic stress by having to carry around a highly precocial infant (Sashaw, 2012). Species with highly precocial young, such as the vervet monkey, have diluted milk with a lower fat content compared to species that give birth to altricial young (Shad, 1963) and therefore needs to replace water lost through milk production (Kunz *et al*., 1994; Wilde *et al*., 1995). Lactating females also need to replace water lost through evaporative cooling during hot environmental conditions. Primates make use of several autonomic and behavioural mechanisms to help them cope with heat stress, including sweating (Stitt and Hardy, 1971; Nakayama *et al*., 1971; Elizondo, 1977), panting (Hiley, 1976) and sticking out their tongues to aid evaporative cooling (Campos and Fedigan, 2009). However, if access to water is limited in a hot environment, lactating females may be unable to dissipate the heat generated through milk production and sucking and could potentially contribute to maternal

hyperthermia (Speakman and Król, 2005).

Hyperthermia was observed in water-deprived baboons exposed to similarly high environmental temperatures as my vervet monkeys (Mitchell *et al*., 2009). The absence of hyperthermia in these baboons when they had *ad libitium* access to drinking water in the heat suggests that access to surface water is crucial for thermoregulation (i.e., evaporative cooling) during heat stress. When environmental temperatures are higher than an animal's body temperature, evaporative cooling is the only mechanism available to the animal to dissipate heat (Hetem *et al*., 2016). If an animal has inadequate water intake or excessive body water loss, maintaining homeostasis of bodily fluids competes with maintaining thermal homeostasis through evaporative cooling (Cain *et al*., 2006). The rate of evaporative water loss has been found to be reduced when large mammals become dehydrated (Nijland and Baker, 1992; Jessen *et al*., 1998). Reduced rate of evaporative water loss in combination with heat exposure has been found to result in an increase in maximum body temperature under laboratory conditions (Jessen *et al*., 1998; Mitchell *et al*., 2009). Increases in maximum 24-h body core temperature have also been recorded in free-living mammals when they were water-stressed and exposed to heat (Hetem *et al*., 2010; Hetem *et al*., 2012).

The lactating females in my study population had access to drinking water for the majority of the study period, except for the drought year in June 2016 – June 2017 when Picnic Troop (PT) and Riverbend Mob (RBM) did not have access to drinking water for approximately 61 non-consecutive days and Riverside Troop (RST) for approximately 23 non-consecutive days out of the year. During these drought conditions, which were associated with scarce food and water, the increase in maximum 24-h body temperature of lactating females as lactation progressed, was exacerbated. As body water reserves diminish, mammals prioritize body

water conservation over thermoregulation (Hetem *et al*., 2016). The progressive increase in maximum 24-h body temperature of lactating females may reflect body water reserves being allocated to lactation rather than thermoregulation.

Body temperature of lactating vervet monkeys rarely exceeded 41 °C and never reached 42 °C. Despite the slight progressive increase in maximum 24-h body temperature as lactation progressed, the absence of hyperthermia in the lactating vervet monkeys in my study population suggest that, in addition to evaporative cooling, lactating females used other means to thermoregulate during possible heat and water stress. In hot environments where water scarcity might compromise the body water balance of lactating females, there are also behavioural mechanisms that primates employ to help them cope with the combination of heat stress and water scarcity, such as adjusting body posture (Stelzner and Hausfater, 1986; Bicca-Marques and Calegaro-Marques, 1998; Pochron, 2000), choosing cooler microclimates (Stelzner, 1988; Barrett *et al*. 2004; Hill, 2006), sand bathing (Brain and Mitchell, 1999; Field, 2008) and changing activity and time budgets (Stelzner, 1988; Sashaw, 2012).

To reduce the risk of maternal hyperthermia during lactation in dry and hot environmental conditions, lactating females may employ energy-sparing mechanisms, such as adjusting activity levels by spending more time on less energetically costly activities. Lactating female primates have been found to adjust their activity budgets. For example, vervet monkey mothers move and feed less during the first month of the infant's life while increasing their time spent resting and socializing (Sashaw, 2012), suggesting that mothers are either recovering from giving birth or they are employing an energy-sparing strategy. At the age of two months, vervet infants become more mobile and supplement milk consumption with their own food intake, but still rely heavily on their mother's milk for nutrition (Sashaw, 2012).

Growing offspring require increasingly more energy to sustain their increased metabolic requirements, which results in increased nutritional costs for lactating females (Lee, 1996; Cameron, 1998). The increased energetic costs placed on the mother having to take care of a more mobile infant as well as the increased nutritional costs of having to feed a growing infant result in lactating females spending more time foraging compared to non-lactating females during months two to five of infant life (Sashaw, 2012). At month six, vervet monkey infants are 95% nutritionally independent of their mother, which allows the mother to reduce milk production with less frequent nursing bouts (Fairbanks, 1990; Sashaw, 2012). Between months five to six, vervet monkey mothers select higher-quality dietary items without further increasing their time spent foraging, compared to the time lactating females spent foraging at infant age two to five months (Sashaw, 2012), which can be interpreted as an energy-sparing strategy.

4.3 Consequences of climate change for reproduction

Although reproductive female vervet monkeys in my study appear to have employed autonomic and behavioural mechanisms to cope with high environmental heat loads, water scarcity, cold exposure and poor food availability, climate change may compromise a female's ability to cope with the energetically costly reproductive period during the exacerbated seasonal environmental conditions predicted under future climate change scenarios.

Over the next few decades, climate change scenarios predict a mean environmental temperature increase of 1-3 °C in the Karoo, extended summer environmental conditions, a decrease of 5-10 % in mean annual rainfall, an increase in aridity and an increase in the frequency of extreme climate events such as droughts (Rutherford *et al*., 1999; van Jaarsveld

and Chown, 2001; Midgley *et al*., 2001; Hoffman *et al.,* 2009; Engelbrecht *et al*., 2015). Such changes are likely to have a significant impact on the survival and distribution of species (Erasmus *et al*., 2002; Hoffman *et al*., 2009; Korstjens *et al*., 2010). The primary environmental stressors for the Karoo and other semi-arid regions in South Africa are likely to be increased heat stress and water scarcity. Rainfall and climate have been shown to be important determinants of vegetation patterns in southern Africa (Tucker *et al*., 1985; Nicholson *et al*., 1990; Desmet and Cowling, 1999a). Food availability and quality also are significantly correlated with rainfall in various sub-Saharan sites (Barton *et al*., 1992). With future climate change scenarios predicting decreased rainfall and increased environmental temperatures, vegetation availability and quality will therefore be negatively impacted. Increasing environmental temperature combined with reduced water (Boyles *et al*., 2012; Hetem *et al*., 2016) and food availability (Humphries *et al*., 2003; Hetem *et al*., 2016) have been shown to significantly influence body temperature patterns in mammals. Reduced food and water availability in the face of climate change with the added environmental stress of higher environmental temperatures will presumably make homeothermy more difficult to maintain, especially during the costly reproductive period.

As the most energetically costly reproductive period, the timing of lactation in relation to favourable environmental conditions is important. Sashaw (2012) showed that the infant vervet monkeys in my study population started feeding independently at the age of two months but were still heavily dependent on their mother's milk for nutrition until their fifth month. In my study population, births occurred in mid- to late spring (October - December) which meant that early lactation when the infants are solely dependent on their mother's milk coincided with the warmer summer months (December - February) when rainfall was high. Plant biomass has been found to be positively correlated with rainfall in the previous two

months (Dunbar *et al*., 2002). Similarly, rainfall was positively correlated with vegetation greenness, as indexed by normalized difference vegetation index (NDVI), during the study period at my study site. During previous studies conducted at Samara Private Game Reserve, nutrient quality was found to be significantly correlated with rainfall (Sashaw, 2012). With rainfall peaking in the summer months when infants are solely dependent on their mother's milk, mothers had access to food to help balance the energetic costs of lactation.

Although reproductive events such as conception, gestation, birth and lactation in primates has been found to coincide with the availability of nutrient-rich foods (Lancaster, 1965; Altmann, 1980; Lee, 1987), climate change may disrupt that relationship. Species are already experiencing climate-induced phenological mismatches, a term defined as "any differential impact of climatic variability on two species, such as predator and prey (or two areas, such as winter or summer ground), may affect the dynamics through a switch from matching to mismatching the environmental conditions" (Stenseth and Mysterud, 2002). Changes in species phenology as a result of climate change may disrupt or alter time-sensitive events such as migration and breeding, which may alter reproduction rates and species survival (Miller-Rushing *et al*., 2010). Climate-induced phenological mismatches have been recorded in European great tits (*Parus major*) where the peak in their main food source, caterpillars, occurred much earlier than the great tits' egg-laying dates, which resulted in chicks hatching after the caterpillar peak, leaving them with little to no available food and a poor chance of survival (Reed *et al*., 2013).

In most mammals, regulation of reproductive physiology is under photoperiod regulation, such that day length regulates and times ovulation and reproductive behaviour (Goldman, 1999). If environmental conditions in the Karoo were to change according to the climate

change predictions (i.e., an increase in air temperature and decrease in rainfall), the birth season of vervet monkeys will still be in spring without any change in photoperiod, but future spring conditions will be far harsher with hot and dry environmental conditions. This seasonal-reproductive mismatch may result in lactating mothers not being able to obtain the necessary nutrients from their environment or sufficient water intake required to sustain milk production or thermoregulation, which will jeopardize both the mother and the infant's survival.

CHAPTER FIVE – CONCLUSION

My study has shown that reproductive female vervet monkeys in the semi-arid Nama Karoo coped well with an array of environmental stressors, from extreme cold during gestation to high heat loads during lactation, and varying food and water availability. During pregnancy, female vervet monkeys displayed gestational hypothermia characterised by a well-regulated reduction in body temperature. Contrary to my initial hypotheses, throughout the demanding reproductive periods of pregnancy and lactation, female vervet monkeys maintained their body temperature within narrow limits, similar to those when females were not pregnant or lactating. The 24-h amplitude of body temperature rhythm of vervet monkeys was highest, as a result of both an increased 24-h maximum and decreased 24-h minimum body temperature, during the drought year when vegetation greenness, as indexed by NDVI, was lowest. However, average 24-h amplitude of body temperature rhythm was generally less than 3 °C, irrespective of reproductive state or environmental conditions. It is plausible that pregnant and lactating vervet monkey females in my study coped well with the energetic costs of reproduction and an array of environmental stressors because they had access to the sweet thorn (*Vachellia karoo*) trees that provided food and water (i.e., water content in food) throughout the dry season (Pasternak *et al*., 2013). Indeed, the high density of sweet thorn trees within the riparian woodland may have allowed vervet monkey to colonize semi-arid Karoo habitats (Pasternak *et al*., 2013).

Resource availability is predicted to be the primary environmental stressor experienced in the Karoo and other semi-arid regions in South Africa as a result of climate change. Future climate change scenarios predict that the seasonal characteristics of the Karoo will be exacerbated with higher ambient temperatures, decreased rainfall and more frequent droughts

(Rutherford *et al*., 1999; van Jaarsveld and Chown, 2001; Midgley *et al*., 2001; Hoffman *et al*., 2009; Engelbrecht *et al*., 2015), which may make homeothermy more difficult to maintain during the costly reproductive period.

Climate change is likely to affect vegetative food sources through changes in plant structure, physiology, distribution and competition as a result of increased ambient temperatures and increased levels of CO_2 (Pritchard *et al*., 1999). Indeed, changes in plant life as a result of increasing ambient temperatures result in changes in vegetation composition and structure with the most evident changes found in the northern hemisphere as well as in southern America, the Indo-Pacific region, New Zealand, Australia and southern Africa (Nolan *et al*., 2018). While the climate-induced changes to vegetation specific to the vervet monkey's diet in the semi-arid Nama Karoo is not yet clear, the sweet thorn tree (*Vachellia karroo*) and its constituents that make up a high percentage of the vervet monkey's diet, may thrive under high levels of CO_2 (Esler *et al*., 2006) and is remarkably resistant to drought (Barnes *et al*., 1996). However, food with high energy content, such as the saltbush (*Antriplex semibaccata*) and *Lycium oxycarpum* berries, and *Lycium cinereum* and *Grewia robusta* flowers, that makes up ~ 28.93 % of the vervet monkeys' diet at the study site (Pasternak, 2011), on which lactating females likely depend, may decline.Other sources of food of the vervet monkey, such as termites may also benefit from warming temperatures. Crop damage as a result of termites have been reported to be higher during dry periods compared to periods of regular rainfall (Logan *et al*., 1990), with increased termite damage to crops reported in African countries such as Uganda and Zambia (Sekamatte and Okwakol 2007; Sileshi *et al*., 2009), suggesting that certain termite species are flourishing under warmer environmental temperatures. However, reduced termite accessibility in the Kalahari have been reported because of decreased soil moisture as a result of reduced rainfall, which may have resulted in

termites moving deeper underground and thus negatively affecting the survival of the ant and termite dependent species, the aardvark (*Orycteropus afer*: Rey *et al*., 2017). The inconsistencies in literature on termite distribution in warmer and dryer environments may be as a result of different species of termites responding differently to changing environments. To better understand how vervet monkeys will be impacted by climate change, we need a better understanding of all the components within an ecological cascade. If, for example, climate change is to negatively impact both vegetative and insect food sources of vervet monkeys, then we might expect pregnant and lactating vervet monkeys to be subjected to periods of limited forage more frequently as climate change progresses.

Successful reproduction and survival depend on the availability of resources, thus reproductive events generally coincide with periods of resource availability (Lancaster, 1965; Altmann, 1980; Lee, 1987; Butynski, 1988; Di Bitetti and Janson, 2000). Since climate change is likely to affect the timing of resource availability (Durant *et al*., 2007), reproductive events may increasingly coincide with periods of limited food and water availability, which poses an imperative question, can animals shift the timing of their reproductive cycles to match the shift in timing of resource availability? A survey conducted of 677 plant and animal species has shown that 62% of these species have shifted their phenology in response to a warming climate (Parmesan and Yohe, 2003), but these phenological shifts may not always be in synchrony with shifts in resources. For example, whereas great tits (*Parus major*) in Oxford shifted their breeding time to be in complete synchrony with the peak in caterpillar abundance (Cresswell and McCleery, 2003), great tits in the Netherlands were able to shift their breeding time earlier but not enough to synchronize with the peak availability of the main food source, caterpillars (Visser *et al*., 1998). Climate-induced phenological mismatches may have severe consequences, including loss of

biodiversity (Stenseth and Mysterud, 2002; Visser *et al*., 2004). While some species might be able to shift their reproduction, other species may be limited in their phenological flexibility. For example, African wild dogs (*Lycaon pictus*) that reared their pups during periods of cooler environmental temperatures had higher reproductive success compared to when pups were reared during periods of high ambient temperatures (Rabaiotti and Woodroffe, 2019). Since these wild dogs are already breeding at the coolest time of year, they may have little scope to change their phenology to maintain reproductive success as climates warm. Therefore, it is important to know the extent to which an animal can adapt to environmental changes if we wish to predict future species distribution and survival.

Animals have the capacity to adapt to changing environments either by micro-evolution through a heritable change in the allele frequencies within a population, or by phenotypic plasticity through which a single genotype gives rise to multiple phenotypes under different environmental conditions (Garland and Kelly, 2006; Fuller *et al*., 2010). The mechanism by which a species will adapt to changing environments (i.e., either by micro-evolution or phenotypic plasticity) depends on the rate and the extent of the environmental changes and the life-history traits of a species (Gienapp *et al*., 2007). The rapid rate of climate change will surpass the rate of evolution of adaptive heritable traits in long-lived species with slow reproduction and long generation times, such as the vervet monkey. Therefore, phenotypic plasticity is the only response available to long-lived species to adapt to climate change (Fuller *et al*., 2010). Phenotypic plasticity includes acclimation, acclimatization and learning (Garland and Kelly, 2006), which are rapid adaptive responses to rapid environmental changes.

Current bioclimatic envelope models assume that the current environmental conditions under

which a species persist, reflects that species' niche (Chown and Gaston, 2008) and use that assumption to predict future species distribution. These models are limited in that they do not account for the potential for species to adapt to changing environments (Chown and Gaston, 2008). If we are to determine the physiological mechanisms available to animals to help them cope with environmental stressors and to predict future species distribution and survival, long-term studies of free-living animals in their natural habitat are crucial. Long-term studies identifying mechanisms of physiological plasticity by monitoring physiological parameters (e.g., body temperature, heart rate and activity) and direct fitness (e.g., growth, reproduction and survival), are necessary to determine the energetic implications of those mechanisms in response to changing environmental conditions. Such studies identifying mechanisms of physiological plasticity in response to changing environments to maintain physical wellbeing, fall within the field of "conservation physiology" (Wikelski and Cooke, 2006). The information obtained on the physiological plasticity of a species to cope with environmental stress has been widely used to implement conservation strategies and policies (Wikelski and Cooke, 2006; Cook and O'Connor, 2010).

Non-invasive methods can be used to provide insights on the physiological functioning and behaviour of free-living mammals in changing environments. For example, measures of body condition, achievable through photogrammetry (De Bruyn *et al*., 2009; Fearnbach *et al*., 2018) or body condition scoring using camera traps (Pérez-Flores *et al*., 2016; Prosser *et al*., 2016), may detect a loss of body condition as a result of disease or energy-deficiency when resource availability is limited. Completing hormonal profiles for female mammals, which is achievable through faecal sampling (Ishikawa *et al*., 2002), would allow for monitoring and identifying timing of ovulation, miscarriages and the nutritional status of female mammals (Nunez-Hernandez *et al*., 1992) without the need for immobilization. The nutritional status of

an animals provides valuable information into the nutrient intake of an animal and therefore provides a measure of whether or not an animal is coping energetically with an array of stressors whether it be environmental (e.g., thermal stress and poor resource availability) or physiological (e.g., reproduction). Scan and focal sampling of behaviour is another non-invasive method that can be used to investigate thermoregulatory behaviour (e.g., sunbathing, huddling and sand bathing) and to determine activity budgets, which can provide insight into time budgets in relation to environmental conditions (e.g., increased feeding time as a result of poor resource availability or increased resting time during periods of high environmental temperatures).

However, the information obtained through biologging pertaining to a species' ability to cope with changing environments is invaluable and provides insights that are unachievable through non-invasive monitoring. Physiological data (e.g., body temperature, heart rate and activity) of free-living animals is now relatively easy to obtain with the use of biologging technology (Rutz and Hays, 2009). Measures of energetic expenditure, such as monitoring heart rate, can be used as a proxy for metabolic rate (Signer *et al*., 2011), which can help us to better understand the energetic implications of reproduction during harsh environmental conditions. Measuring physiological parameters in free-living animals thus provides information on the level of flexibility (i.e., physiological plasticity) of that animal within their habitat, information not obtainable under captive or laboratory conditions.

Remotely measured body temperature through biologging not only provides information on the wellbeing of mammals in their natural habitat, it can also provide information on an animal's reproductive fitness. Maintaining a relatively narrow amplitude of 24-h body temperature rhythm (i.e., homeothermy) is associated with increased performance which

results in a net-fitness gain (Boyles *et al*., 2011). Therefore, imprecise thermoregulation may be a valuable indicator of various stressors an animal might be experiencing (e.g., environmental, physiological or social) and provide some insight into how well the animal is coping with these stressors. Imprecise thermoregulation as an indicator can be used as a tool to implement successful conservation strategies by identifying species in specific priority areas whose survival may be at risk in the face of changing environments. Indeed, the amplitude of the 24-h body temperature rhythm in wild rabbits (*Oryctolagus cuniculus*) prior to the breeding season have been reported to be inversely correlated with the number of pregnancies in the following months, while the minimum 24-h body temperature was positively correlated with the number of pregnancies (Maloney *et al*., 2017). The prediction of reproductive output prior to the breeding season from measures of core body temperature rhythm, suggest that body temperature patterns could provide a preemptive index of individual fitness in any given environment.

Physiological mechanisms are likely to be similar within groups of taxa (Blomberg *et al*., 2003), therefore the physiological, environmental and fitness interaction of an animal only has to be estimated for select individual representatives of many taxa, and not for all species (Chown and Gaston, 2008). Such studies fall within the field of "macrophysiology", which has recently been defined as "the investigation of variation in physiological traits over large geographical and temporal scales and the ecological implications of this variation" (Chown *et al*. 2004). By understanding the mechanistic basis of an animal's physiologic plasticity in response to changing environmental conditions as a result of climate change, and the ecological implications thereof, successful conservation strategies can be implemented to reduce the high rates of biodiversity loss predicted under climate change.

REFERENCES

Adels, L. E. and Leon, M. (1986). Thermal control of mother-young contact in Norway rats: factors mediating the chronic elevation of maternal temperature. *Physiology & Behavior*, 36(1), pp. 183–196.

Altmann, J. (1980). *Baboon mothers and infants*. Cambridge, UK: Harvard University Press.

Altmann, J. and Samuels, A. (1992). Costs of maternal care: infant-carrying in baboons. *Behavioral Ecology and Sociobiology*, 29(6), pp. 391-398.

Andrews, J. F., Richard, D., Jennings, G. and Trayhurn, P. (1986). Brown adipose tissue thermogenesis during pregnancy in mice. *Annals of Nutrition and Metabolism*, 30(2), pp. 87-93.

Angilletta, M. J., Cooper, B. S., Schuler, M. S. and Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience*, 2, pp. 861-881.

Archie, E. A., Altmann, J. and Alberts, S. C. (2014). Cost of reproduction in long-lived female primate: injury risk and wound healing. *Behavioral Ecology and Sociobiology*, 68(7), pp. 1183-1193.

Arnold, W., Ruf, T. and Kuntz, R. (2006). Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) II. Energy expenditure. *Journal of Experimental Biology*, 209, pp. 4566–4573.

Arnold, G. W., Wallace, S. R. and Maller, R. A. (1979). Some factors involved in natural weaning process in sheep. *Applied Animal Ethology*, 5, pp. 43-50.

Asakura, H. (2004). Fetal and neonatal thermoregulation. *Journal of Nippon Medical School*, 71(6), pp. 360-370.

Aschoff, J. (1982). The circadian rhythm of body temperature as a function of body size, In: Taylor, C. R., Johansen, K. and Bolis, L. ed. *Companion to Animal Physiology*, Cambridge, UK: Cambridge University Press, pp. 173-188.

Assali, N. S. and Westin, B. (1962). Effects of hypothermia on uterine circulation and on the fetus. *Proceedings of the Society for Experimental Biology and Medicine*, 109(3), pp. 485–488.

Bakker, R. T. (1975). Experimental and fossil evidence for the evolution of tetrapod bioenergetics, In: Gates, D. M. and Schmerl, R. B. ed. *Perspectives of Biophysical Ecology*, New York, USA: Springer-Verlag, pp. 365-399.

Barnes, R. D., Filer, D. L. and Milton, S. J. (1996) *Acacia karroo*: Monograph and annotated bibliography. Tropical Forestry Papers No. 32. Oxford Forestry Institute.

Barrett, L., Gaynor, D., Rendall, D., Mitchell, D. and Henzi, S. P. (2004). Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *Journal of Human Evolution*, 46(2), pp. 215-222.

Barrett, L., Halliday, J. and Henzi, P. (2006). The ecology of motherhood: the structuring of lactation costs by chacma baboons. *Journal of Animal Ecology*, 75(4), pp. 875-886.

Bartness, T. J. (1997). Food hoarding is increased by pregnancy, lactation, and food deprivation in Siberian hamsters. *American Journal of Physiology*, 272, Part 2, pp. R118-R125.

Barton, R. A. (1989). *Foraging strategies, diet and competition in olive baboons*, PhD Thesis, University of St. Andrews, United Kingdom.

Barton, R. A., Whitten, A., Strum, S. C., Byrne, R. W. and Simpson, A. J. (1992). Habitat use and resource availability in baboons. *Animal Behaviour*, 43(5), pp. 831–844.

Benson, G. K. and Morris, L. R. (1971). Foetal growth and lactation in rats exposed to high temperatures during pregnancy. *Journal of Reproduction and Fertility*, 27(3), pp. 369–384.

Bercovitch, F. B. (1987). Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *American Journal of Primatology*, 12(2), pp. 189-195.

Bicca-Marques, J. C. and Calegaro-Marques, C. (1998). Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology*, 106(4), pp. 533–546.

Blomberg, S. P., Garland, T. and Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Journal of Evolution*, 57(4), pp. 717-745.

Boyles, J. G., Seebacher, F., Smit, B. and McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*, 51(5), pp. 676-690.

Boyles, J. G., Smit, B. and McKechnie, A. E. (2012). Variation in body temperature is related to ambient temperature but not experimental manipulation of insulation in two small endotherms with different thermoregulatory patterns. *Journal of Zoology*, 287(3), pp. 224-232.

Brain, C. and Mitchell, D. (1999). Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *International Journal of Primatology*, 20(4), pp. 585–598.

Brent, L., Koban, T., Evans, S. (2003). The influence of temperature on the behavior of captive mother-infant baboons. *Behaviour*, 140(2), pp. 209-224.

Brody, S. (1945). *Bioenergetics and growth; with special reference to the efficiency complex in domestic animals*. Oxford, England: Reinhold.

Bu, L. H. and Lephart, E. D. (2005). Effect of dietary phytoestrogens on core body temperature during the estrous cycle and pregnancy. *Brain Research Bulletin*, 65(3), pp. 219-223.

Busto, R., Dietrich, W. D., Globus, M. Y., Valdes, I., Scheinberg, P., and Ginsberg, M. D. (1987). Small differences in intraischemic brain temperature critically determine the extent of ischemic neuronal injury. *Journal of Cerebral Blood Flow and Metabolism*, 7(6), pp. 729–738.

Butynski, T. M. (1988). Geunon birth seasons and correlates with rainfall and food, In: A. Gautier-Hion, F. Bourlière, J. P. Gautier and Kingdon, J. ed. *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge, UK: Cambridge University Press, pp. 284-322.

Cain, J. W., Krausman, P. R., Rosenstock, S. S. and Turner, J. C. (2006). Mechanisms of thermoregulation and water balance in desert ungulates. *Wildlife Society Bulletin*, 34(3), pp. 570–581.

Cairns, M. J., Burns, P., Di Nicolantonio, R., McKinley, M. J. and Mathai, M. L. (2005). Influence of brain angiotensin on thermoregulation and hydromineral balance during pregnancy in rats. *Journal of Applied Physiology*, 98(5), pp. 1813-1819.

Cameron, E. Z. (1998). Is suckling behaviour a useful predictor of milk intake? *Animal Behaviour*, 56(3), pp. 521-532.

Campos, F. A. and Fedigan, L. M. (2009) Behavioural adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *American Journal of Physical Anthropology*, 138(1), pp. 101–111.

Cannon, B. and Nedergaard, J. (2004). Brown adipose tissue: function and physiological significance. *Physiological Reviews*, 84(1), pp. 277-359.

Caro, T. M. (1987). Cheetah mothers' vigilance: looking out for prey or predators? *Behavioural Ecology and Sociobiology*, 20(5), pp. 351-361.

Cawthon Lang, K. A. (2006). Primate Factsheets: Vervet (*Chlorocebus*) Taxonomy, Morphology, & Ecology. Primate Info Net. Retrieved 2018/09/13.

Charnov, E. L. (1993). *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford, UK: Oxford University Press

Cheney, D. L., Lee, P. C. and Seyfarth, R. M. (1981). Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. *Behavioural Ecology and Sociobiology*, 9(2), pp. 153-161.

Chown, S. L. and Gaston, K. J. (2008). Macrophysiology for a changing world. *Proceedings of the Royal Society B: Biological Sciences*, 275(1642), pp. 1469-1478.

Chown S. L., Gaston, K. J. and Robinson, D. (2004). Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology*, 18(2), pp. 159–167.

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton, USA: Princeton University Press.

Clutton-Brock, T. H., Albon, S. D. and Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, 337, pp. 260-262.

Concannon, P. W. and Hansel, W. (1977). Prostaglandin F2α induced luteolysis, hypothermia, and abortions in beagle bitches. *Prostaglandins*, 13(3), pp. 533-542.

Cooke, S. J. and O'Connor, C. M. (2010). Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters*, 3(3), pp. 159-166.

Cramer, J., Grobler, J. P., Freimer, N. and Turner, T. R. (2012). Sunbathing: a behavioural response to seasonal climatic change among South African vervet monkeys (*Chlorocebus aethiops*). *African Primates*, 7(2), pp. 230-237.

Cresswell, W. and McCleery, R. (2003). How great tits maintain synchronization of their hatch with date food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, 72(2), pp. 356–66.

Crompton, A. W., Taylor, C. R. and Jagger, J. A. (1978). Evolution of homeothermy in mammals. *Nature*, 272, pp. 333-336.

Da Silva, G. L. (1993). Postural changes and behavioural thermoregulation in *Colobus pofykomos*: the effect of climate and diet. *African Journal of Ecology*, 31(3), pp. 226-241.

De Bruyn, P. J. N., Bester, M. N., Carlinin, A. R. and Oosthuizen, W. C. (2009). How to weigh and elephant seal with one finger: a simple three-dimensional photogrammetric application. *Aquatic Biology*, 5, pp. 31-39.

De Ricqlés, A. J. (1974). Evolution of endothermy: Histological Evidence. *Evolutionary Theory*, 1, pp. 51-80.

Desmet, P. G. and Cowling, R. M. (1999a). Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Plant Ecology*, 142(1-2), pp. 23-33.

Desmet, P. G. and Cowling, R. M. (1999b). The climate of the Karoo – A functional approach, In: Dean, W. R. J. and Milton, S. J. ed. *The Karoo. Ecological Patterns and Processes*, Cambridge, UK: Cambridge University Press, pp. 3-16

Di Bitetti, M. S. and Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in neotropical primates. *American Journal of Primatology*, 50(2), pp. 109-130.

Donati, G., Ricci, E., Baldi, N., Morelli, V. and Borgognini-Tarli, S. M. (2011). Behavioural thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic and dietary-related factors. *American Journal of Physical Anthropology*, 144(3), pp. 355-364.

Dreiling, C. E., Carman, F. S. and Brown, D. E. (1991). Maternal endocrine and fetal metabolic responses to heat stress. *Journal of Dairy Science*, 74(1), pp. 312-327.

DuFour, D. L. and Sauther, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, 14(5), pp. 584-602.

Dunbar, R. I. M. (1980). Demographic and life history variables of a population of gelada baboons (*Theropithecus gelada*). *Journal of Animal Ecology*, 49(2), pp. 485-506.

Dunbar, R. I. M. (1988). *Primate social systems*. London: Chapman and Hall.

Dunbar, R. I. M. and Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, 36(4), pp. 970-980.

Dunbar, R. I. M., Hannah-Steward, L. and Dunbar, P. (2002). Forage quality and cost of lactation for female gelada baboons. *Animal Behaviour*, 64(5), pp. 801-805.

Durant, J. M., Hjermann, D. Ø., Ottersen, G. and Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33(3), pp. 271-283.

Edwards, M. J. (1986). Hyperthermia as a teratogen: A review of experimental studies and their clinical significance. *Teratogenesis, Carcinogenesis and Mutagenesis*, 6(6), pp. 563-582.

Edwards, M. J. (2006). Review: Hyperthermia and fever during pregnancy. *Birth Defects Research, Part A, Clinical and Molecular Teratology*, 76(7), pp. 507-516.

Eliason, H. L. and Fewell, J. E. (1997). Thermoregulatory control during pregnancy and lactation in rats. *Journal of Applied Physiology*, 83(3), pp. 837-844.

Elizondo, R. (1977). Temperature regulation in primates. *International Review of Physiology*, 15, pp. 71–118.

Emlen, J. M. (1966). The role of time and energy in food preference. *The American Naturalist*, 100(916), pp. 611-617.

Engelbrecht, F., Adegoke, J., Bopape, M., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M. and Ichoku, C. (2015). Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, 10, pp. 1-16.

Erasmus, B. F. N., Van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. and Wessels, K. J. (2002). Vulnerability of South African animal taxa to climate change. *Global Change Biology*, 8(7), pp. 679-693.

Esler, K. J., Milton, S. J. and Dean, W. R. J. (2006). *Karoo Veld – Ecology and Management*. Briza Press, Pretoria.

Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, 40(3), pp. 553-562.

Fairbanks, L. A. and McGuire, M. T. (1986). Age, reproductive value, and dominance-related behaviour in vervet monkey females: cross-generational influences on social relationships and reproduction. *Animal Behaviour*, 34(6), pp. 1710-1721.

Fairbanks, L. A. and McGuire, M. T. (1995). Maternal condition and the quality of maternal care in vervet monkeys. *Behaviour*, 132(9-10), pp. 733-754.

Farmer, C. G. (2000). Parental care: the key to understanding endothermy and the other convergent features in birds and mammals. *The American Naturalist*, 155(3), pp. 326-334.

Farmer, C. G. (2003). Reproduction: the adaptive significance of endothermy. *The American Naturalist*, 162(6), pp. 826-840.

Faurie, A. S., Mitchell, D. and Laburn, H. (2001). Feto-maternal relationships in goats during heat and cold exposure. *Experimental Physiology*, 86(2), pp. 199-204.

Fearnbach, H., Durban, J. W., Ellifrit, D. K. and Balcomb, K. C. (2018). Using aerial photogrammetry to detect changes in body condition of endangered southern resident killer whales. *Endangered Species Research*, 35, pp. 175-180.

Fewell, J. E. (1995). Body temperature regulation in rats in near term of pregnancy. *Canadian Journal of Physiology and Pharmacology*, 73(3), pp. 364-368.

Field, M. Y. (2008). So hot you can fry a monkey: behavioral thermoregulation in human-commensal white-fronted capuchins (*Cebus albifrons*). *American Journal of Physical Anthropology*, 46, pp. 95–96.

Friebe, A., Evans, A. L., Arnemo, J. M., Blanc, S., Brunberg, S., Fleissner, G. and Swenson, J. E. (2014). Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. *PLoS ONE,* 9, e101410.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R. S., Mitchell, D. and Maloney, S. K. (2010). Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, 83(5), pp. 713-720.

Fuller, A., Mitchell, D., Maloney, S. K. and Hetem, R. S. (2016). Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. *Climate Change Responses*, 3(10), pp. 1-19.

Gamo, Y., Bernard, A., Mitchell, S. E., Hambly, C., Jothery, A. A., Vaanholt, L. M., Król, E. and Speakman, J. R. (2013). Limits to sustained energy intake. XVI. Body temperature and physical activity of female mice during pregnancy. *The Journal of Experimental Biology*, 216(12), pp. 2328-2338.

Garland T. Jr., and Kelly, S.A. (2006). Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology*, 209(12), pp. 2344–2361.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. and Merilä, J. (2007). Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, 17(1), pp. 167-178.

Gilbert, R. D., Schroder, H., Kawamura, T., Dale. P. S. and Power, G. G. (1985). Heat transfer pathways between fetal lamb and ewe. *Journal of Applied Physiology*, 59(2), pp. 634-638.

Gilby, I. C., Pokempner, A. A. and Wrangham, R. W. (2010). A direct comparison of scan and focal sampling methods for measuring wild chimpanzee feeding behaviour. *International Journal of Primatology,* 81(5), pp. 254-264.

Glittleman, J. L. and Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *Integrative and Comparative Biology,* 28(3), pp. 863-875.

Goldizen, A. W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-backed tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20(2), pp. 99-109.

Gordon, C. J. (1983). A review of terms for regulated vs. forced neurochemical-induced changes in body temperature. *Life Sciences,* 32(12), pp. 1285–1295.

Gordon, C. J. (1985). Relationship between autonomic and behavioural thermoregulation in the mouse. *Physiology and Behavior,* 34(5), pp. 687-690.

Groves, C. (2001). Why taxanomic stability is a bad idea, or why are there so few species of primates (or are there?). *Evolutionary Anthropology,* 10(6), pp. 192-198.

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., and Struhsaker, T. (2003). Assessment of the diversity of African primates. *International Journal of Primatology,* 24(6), pp. 1301-1357.

Guedes, D., Young, R. J. and Strier, K. B. (2008). Energetic costs of reproduction in female northern muriquis, *Brachyteles hypoxanthus* (Primates: *Platyrrinhi: Atelidae*). *Revista Brasileira de Zoologia,* 25(4), pp. 587-593.

Hammel, H. T. (1968). Regulation of internal body temperature. *Annual Review of Physiology*, 30, pp. 641-695.

Hanya, G. (2004). Seasonal variations in the activity budget of *Japanese macaques* in the coniferous forest of Yakushime: effect of food and temperature. *American Journal of Primatology*, 63(3), pp. 165-177.

Hanya, G., Kiyono, M. and Hayaishi, S. (2007). Behavioural thermoregulation of wild *Japanese macaques*: comparisons between two sub-populations. *American Journal of Primatology,* 69(7), pp. 802-815.

Harris, R. A., Tardif, S. D., Vinar, T., Wildman, D. E., Ruthford, J., Rogers, J. N., Worley, K. C. and Aagaard, K. M. (2013). Evolutionary genetics and implications of small size and twinning in callitrichine primates. *Proceedings of the National Academy of Sciences*, 111(4), pp. 1467-1472.

Harrison, M. J. S. (1983). Patterns of range use by the Green Monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. *Folia Primatologica*, 41, pp. 157–179.

Hart, F. M. and Faber, J. J. (1965). Fetal and maternal temperatures in rabbits. *Journal of Applied Physiology*, 20(4), pp. 737-741.

Hartgill, T. W., Bergersen, T. K. and Pirhonen, J. P. (2011). Core body temperature and the thermoneutral zone: a longitudinal study of normal human pregnancy. *Acta Physiologica*, 201(4), pp. 467-474.

Hauser, M. D. (1993). Do vervet monkey infants cry wolf? *Animal Behaviour*, 45(6), pp. 1242-1244.

Hayssen, V. (1993). Emperical and theoretical constraints on the evolution of lactation. *Journal of Dairy Science*, 76(10), pp. 3213-3233.

Hayssen, V. and Lacy, R. C. (1985). Basal metabolic rates in mammals: taxonomic differences and the allometry of BMR and body mass. *Comparative Biochemistry and Physiology, Part A, Comparative Physiology*, 81(4), pp. 741-754.

Heasley, J. E. (1983). Energy allocation in response to reduced food intake in pregnant and lactating laboratory mice. *Acta Theriologica*, 28, pp. 55-71.

Heinrich, B. (1977). Why have some animals evolved to regulate a high body temperature? *The American Naturalist*, 111(980), pp. 623-640.

Hess, D. L., Hendrickx, A. G. and Stabenfeldt, G. H. (1979). Reproductive and hormonal patterns in the African green monkey (*cercopithecus aethiops*). *Journal of Medical Primatology*, 8(5), pp. 273–281.

Hetem, R. S., Strauss, W. M., Fick, L. G., Maloney, S. K., Meyer, L. C. R., Shobrak, M., Fuller, A. and Mitchell, D. (2010). Variation in the daily rhythm of body temperature of free-living Arabian oryx (*Oryx leucoryx*): does water limitation drive heterothermy? *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology*, 180(7), pp. 1111–1119.

Hetem, R. S., Strauss, W. M., Fick, L. G., Maloney, S. K., Meyer, L. C. R., Shobrak, M., Fuller, A. and Mitchell, D. (2012). Does size matter? Comparison of body temperature and activity of free-living Arabian oryx (*Oryx leucoryx*) and the smaller Arabian sand gazelle (*Gazella subgutturosa marica*) in the Saudi desert. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, 182(3), pp. 437–449.

Hetem, R. S., Maloney, S. K., Fuller, A. and Mitchell, D. (2016). Heterothermy in large mammals: inevitable or implemented? *Biological Reviews of the Cambridge Philosophical Society*, 91(1), pp. 187-205.

Hiley, P. G. (1976). The thermoregulatory responses of the galago (*Galago crassicaudatus*), the baboon (*Papio cynocephalus*) and the chimpanzee (*Pan satyrus*) to heat stress. *The Journal of Physiology*, 254, pp. 657–671.

Hill, R. A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology*, 129(2), pp. 242–249.

Hinde, K., Power, M. L. and Oftedal, O. T. (2009). Rhesus macaque milk: magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology*, 138(2), pp. 148-157.

Hissa, R. (1997). Physiology of the European brown bear (*Ursus arctos arctos*). *Annales Zoologici Fennici*, 34(4), pp. 267-287.

Hoffman, M. T., Carrick, P. J., Gillson, L. and West, A. G. (2009). Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science*, 105(1-2), pp. 54-60.

Horrocks, J. A. (1986). Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaeus*) in Barbados, West Indies. *International Journal of Primatology*, 7(1), pp. 31-47.

Hoshino, K. (1996). Food deprivation and hypothermia in desynchronized sleep deprived rats. *Brazilian Journal of Medical and Biological Research*, 29(1), pp. 41-46.

Humphries, M. M., Kramer, D. L. and Thomas, D. W. (2003). The role of energy availability in mammalian hibernation: an experimental test in free-ranging eastern chipmunks. *Physiological and Biochemical Zoology*, 76(2), pp. 180-186.

Ishikawa, A., Kikuchi, S., Katagiri, S., Sakamoto, H. and Takahashi, Y. (2002). Efficiency of fecal steroid hormone measurement for assessing reproductive function in the Hokkaido brown bear (*Ursus arctos yesoensis*). *The Japanese Journal of Veterinary Research*, 50(1), pp. 17-27.

Jasinska, A. J., Scmitt, C. A., Service, S. K., Cantor, R. M., Dewar, K., Jentsch, J. D., Kaplan, J. R., Turner, T. R., Warren, W. C., Weinstock, G. M., Woods, R. P. and Freimer, N. B. (2013). Systems biology of the vervet monkey. *Institute of Laboratory Animal Resources Journal*, 54(2), pp. 122-143.

Jessen, C., Dmi'el, R., Choshniak, I., Ezra, D. and Kuhnen, G. (1998). Effects of dehydration and rehydration on body temperatures in the black Bedouin goat. *Pfl¨ugers Archiv - European Journal of Physiology*, 436(5), pp. 659–666.

Johnson, M. S., Thompson, S. C. and Speakman, J. R. (2001). Limits to sustained energy intake. I. Lactation in the laboratory mouse *Mus musculus*. *Journal of Experimental Biology*, 204(11), pp. 1925-1935.

Jolly, A. (1973). Primate birth hour. *International Zoo Yearbook*, 13(1), pp. 391-397.

Katsumata, E., Jaroenporn, S., Katsumata, H., Konno, S., Maeda, Y., Watanabe, G. and Taya, K. (2006). Body temperature and circulating progesterone levels before and after parturition in killer whales (*Orcinus orca*). *The Journal of Reproduction and Development*, 52(1), pp. 65-71.

Kenyatta, C.G. (1995). *Ecological and social constraints on maternal investment strategies*, PhD Thesis, University of London, United Kingdom.

Kingdon, J., Gippoliti, S., Butynski, T. M. and De Yong, Y. (2008). *Cholorocebus pygerythrus. The IUCN Red List of Threatened Species 2008: eT136271A4267738.*

Kittrell, E. M. W. and Satinoff, E. (1988). Diurnal rhythms of body temperature, drinking and activity of reproductive cycles. *Physiology and Behavior*, 42(5), pp. 477-484.

Knies, J. L., Kingsolver, J. G. and Burch, C. L. (2009). Hotter is better and broader: thermal sensitivity of fitness in a population of bacteriophages. *The American Naturalist*, 173(4), pp. 419-430.

Koenig, A., Borries, C., Chalise, M. K. and Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology*, 243(2), pp. 215-235.

Korstjens, A. H., Lehmann, J. and Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, 79(2), pp. 361-374.

Kozak, W. (1997). Regulated decreases in body temperature, In: Mackowiak, P.A. ed. *Fever: Basic Mechanisms and Management*, Philadelphia,USA: Lippincott-Raven, pp. 467-478.

Koteja, P. (2004). The evolution of concepts on the evolution of endothermy in birds and mammals. *Physiological and Biochemical Zoology*, 77(6), pp. 1043-1050.

Król, E. and Speakman, J. R. (2003a). Limits to sustained energy intake. VI. Energetics of lactation in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, 206(23), pp. 4255-4266.

Król, E. and Speakman, J. R. (2003b). Limits to sustained energy intake. VII. Milk energy output in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, 206(23), pp. 4267-4281.

Król, E., Johnson, M. S. and Speakman, J. R. (2003). Limits to sustained energy intake. VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. *Journal of Experimental Biology*, 206(23), pp. 4283-4291.

Król, E., Murphy, M. and Speakman, J. R. (2007). Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. *Journal of Experimental Biology*, 210(23), pp. 4233-4243.

Kunz, T. H., Oftedal, O. T., Robson, S. K., Kretzmann, M. B. and Kirk, C. (1994). Changes in milk composition in three species of insectivorous bats. *Journal of Comparative Physiology B, Biochemical, Systematic, and Environmental Physiology*, 164(7), pp. 543–551.

Künkele, J. (2000). Energetics of gestation relative to lactation in a precocial rodent, the guinea pig (*Cavia porcellus*). *Journal of Zoology*, 250(4), pp. 533-539.

Laburn, H. P. (1996) How does the fetus cope with thermal challenges? *Physiology*, 11(2), pp. 96–100.

Laburn, H. P., Faurie, A. S., Goelst, K. and Mitchell, D. (2002). Effects of fetal and maternal body temperatures of exposure of pregnant ewes to heat, cold and exercise. *Journal of Applied Physiology*, 92(2), pp. 802-808.

Laburn, H. P., Mitchell, D. and Goelst, K. (1992). Fetal and maternal body temperatures measured by radiotelemetry in near-term sheep during thermal stress. *Journal of Applied Physiology*, 72(3), pp. 894-900.

Lancaster, J. B. (1965). The annual reproductive cycle in monkeys and apes, In: Devore, I. ed. *Primate Behavior*, New York, USA: Holt, Rinehart and Winston, pp. 487-513.

Lausen, C. L. and Barclay, R. M. R. (2003). Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *Journal of Zoology*, 260(3), pp. 235-244.

Lee, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. *Primates*, 25(1), pp. 36-47.

Lee, P. C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of Zoology*, 213(3), pp. 409-422.

Lee, P. C. (1996). The meaning of weaning: growth, lactation and life history. *Evolutionary Anthropology*, 5(3), pp. 87-98.

Lee, P. C., Brennan, E. J., Else, J. G. and Altman, J. (1986). Ecology and behaviour of vervet monkeys in a tourist lodge habitat, In: Else, J. and Lee, P. ed. *Primate Ecology and Conservation*, Cambridge, UK: Cambridge University Press, pp. 229-235.

Lee, P. C. and Hauser, M. D. (1998). Long-term consequences of change in territory quality on feeding and reproductive strategies of vervet monkeys. *Journal of Animal Ecology*, 67, pp. 347-358.

Levesque, D. L. and Lovegrove, B. G. (2014). Increased homeothermy during reproduction in a basal placental mammal. *Journal of Experimental Biology*, 217(9), pp. 1535–1542.

Lindqvist, P. G., Marsal, K., Merlo, J. and Pirhonen, J. P. (2003). Thermal response to submaximal exercise before, during and after pregnancy: a longitudinal study. *The Journal of Maternal-Fetal and Neonatal Medicine*, 13(3), pp. 152-156.

Lindstedt, S. L. and Boyce, M. S. (1985). Seasonality, fasting, endurance, and body size in mammals. *The American Naturalist*, 125(6), pp. 878.

Logan, J. W. M, Cowie, R. W. and Wood, T. G. (1990). Termite (*Isoptera*) control in agriculture and forestry by nonchemical methods: a review. *Bulletin of Entomological Research*, 80(3), pp. 309-330.

López-Sáez, J. F., Giménez-Martin, G. and González-Fernández, A. (1966). Duration of the cell division cycle and its dependence on temperature. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 75(3), pp. 591–600.

Loudon, A. S. I., McNeilly, A. S. and Milne, J. A. (1983). Nutrition and lactational control of fertility in red deer. *Nature*, 302(5904), pp. 145-147.

Loudon, A. S. I. and Racey, P. A. (1987), *Reproductive energetics in mammals*. Oxford, UK: Claredon Press.

Low, A. B. and Rebelo, A. G. (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Lubbe, A. (2013). *Thermoregulatory plasticity in free-ranging vervet monkeys (Chlorocebus pygerythrus)*, MSc Dissertation, University of the Witwatersrand, Johannesburg, South Africa.

Lubbe, A., Hetem, R. S., MacFarland, R., Barrett, L., Henzi, P. S., Mitchell, D., *et al*. (2014). Thermoregulatory plasticity in free-ranging vervet monkeys, *Chlorocebus pygerythrus*.

Journal of Comparative Physiology B, Biochemical, Systemic and Environmental Physiology, 184(6), pp. 799–809.

Lycett, J. E., Henzi, P. and Barret, L. (1998). Maternal investment in mountain baboons and the hypothesis of reduced care. *Behavioral Ecology and Sociobiology*, 42(1), pp. 49-56.

MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), pp. 603-609.

Maloney, S. K., Fuller, A., Meyer, L. C., Kamerman, P. R., Mitchell, G. and Mitchell, D. (2011). Minimum daily core body temperature in western grey kangaroos decreases as summer advances: a seasonal pattern, or a direct response to water, heat or energy supply? *Journal of Experimental Biology*, 214 (11), pp. 1813-1820.

Maloney, S. K., Marsh, M. K., McLeod, S. R. and Fuller, A. (2017). Heterothermy is associated with reduced fitness in wild rabbits. *Biology Letters*, 13(12).

Maloney, S. K., Moss, G., and Mitchell, D. (2005). Orientation to solar radiation in wildebeest (C*onnochaetes gnou*). *Journal of Comparative Physiology Part A, Neuroethology, Sensory, Neural and Behavioural Physiology*, 191(11), pp. 1065-1077.

Martin, R. D. (1995). Phylogenetic aspects of primate reproduction: The context of advanced maternal care, In: Pryce, C., Martin, R. and Skuse, D. ed. *Motherhood in Human and Non-human Primates*, Basel, Switzerland: Karger, pp. 16-26

Mattingly, D. K. and P. A. McClure. (1982). Energetics of reproduction in large-littered cotton rats (*Sigmodon hispidis*). *Ecology*, 63(1), pp. 183-195.

McClure, P. A. (1987). The energetics of reproduction and life histories of cricetine rodents (*Neotoma floridana* and *Sigmodon hispidus*), In: Loudon, A. S. I. and Racey, P. A. ed. *Reproductive Energetics in Mammals*, Zoological Society of London, Oxford, UK: Claredon Press, pp. 241-258.

McDougall, P., Forshaw, N., Barrett, L. and Henzi, S. P. (2010). Leaving home: Responses to water depletion by vervet monkeys. *Journal of Arid Environments*, 74(8), pp. 924-927.

Menard, N. and Vallet, D. (1993). Population dynamics of *Macaca sylvanus* in Algeria: an 8-year study. *American Journal of Primatology*, 30(2), pp. 101-118.

Midgley, G., Rutherford, M. and Bond, W. J. (2001). *The heat is on … impacts of climate change on plant diversity in South Africa*. National Botanic Institute, Cape Town, South Africa.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), pp. 3177-3186.

Mitchell, D., Fuller, A. and Maloney, S. K. (2009). Homeothermy and primate bipedalism: is water shortage or solar radiation the main threat to baboon (*Papio hamadryas*) homeothermy? *Journal of Human Evolution*, 56(5), pp. 439–446.

Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M. and Fuller, A. (2018). Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. *Journal of Animal Ecology*, 87(4), pp. 956-973.

Morland, H. S. (1993). Seasonal behavioural variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*), In: Kappeler, P. M. and Ganzhorn, J. U. ed. *Lemur Social Systems and their Ecological Basis*, New York, USA: Plenum Press, pp. 193-204

Mortola, J. P. and Lanthier, C. (2004). Scaling the amplitudes of circadian pattern of resting oxygen consumption, body temperature and heart rate in mammals. *Comparative Biochemistry and Physiology, Part A, Molecular and Integrative Physiology*, 139(1), pp. 83-95.

Mover, H., Hellwing, S. and Ar, A. (1988). Energetic Cost of Gestation in the White-Toothed Shrew *Crocidura russula monacha* (*Soricidae, Insectivora*). *Physiological Zoology*, 61(1), pp. 17-25.

Murray, C. M., Lonsdorf, E. V., Eberly, L. E. and Pusey, A. (2009). Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology*, 20(6), pp. 1211-1216.

Muruthi, P., Altmann, J., and Altmann, S. (1991). Resource base, parity, and reproductive condition affect females feeding time and nutrient intake within and between groups of a baboon population. *Oecologia*, 87(4), pp. 467-472.

Naccarato, E. F. and Hunter, W. S. (1983). Brain and deep abdominal temperatures during induced fever in pregnant rabbits. *The American Journal of Physiology*, 245(3), pp. R421-R425.

Nakayama, T., Hori, T., Nagasaka, T., Tokura, H. and Tadaki, E. (1971). Thermal and metabolic at temperatures of 5 - 38 degrees C. *Journal of Applied Physiology*, 31(3), pp. 332–337.

Nicholson, S. E., Davenport, M. L., and Malo, A. R. (1990). A comparison of the vegetation response to rainfall in the Sahel and East Africa, using the normalised difference vegetation index from NOAA A VHRR. *Climatic Change*, 17(2-3), pp. 209-241.

Nicol, S. and Andersen, N. A. (2006). Body temperature as an indicator of egg-laying in the echidna, *Tachyglossus aculeatus*. *Journal of Thermal Biology*, 31(6), pp. 483-490.

Nicolson, N. (1982). *Weaning and the development of independence in olive baboons*, PhD Thesis, Maastricht University, Maastricht, Netherlands.

Nijland, M. J. and Baker, M. A. (1992). Effects of hydration state on exercise thermoregulation in goats. *The American Journal of Physiology - Regulatory, Integrative and Comparative Physiology*, 263(2), pp. R201–R205.

Nishio, S., Yunoki, M., Chen, Z. F., Anzivino, M. J. and Lee, K. S. (2000). Ischemic tolerance in the rat neocortex following hypothermic preconditioning. *Journal of Neurosurgery*, 93(5), pp. 845–851.

Nizielski, S. E., Billington, C. J. and Levine, A. S. (1993). BAT thermogenic activity and capacity are reduced during lactation in ground squirrels. *The American Journal of Physiology - Regulatory, Integrative and Comparative Physiology*, 33(2), pp. R16-R21.

Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P., Betancourt, J., Binney, H. *et al*. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(6405), pp. 920-923.

Nunez-Hernandez, G., Holechek, J. L., Arthun, D., Tembo, A., Wallace, J. D., Galyean, M. L., Cardenas, M. and Valdez, R. (1992). Evaluation of fecal indicators for assessing energy and nitrogen status of cattle and goats. *Journal of Range Management*, 45(2), pp. 143-147.

Oftedal, O. T. (1985). Pregnancy and lactation, In: Hudson, R. J. and White, R. G. ed. *Bioenergetics of Wild Herbivores*, Florida, USA: CRC Press, pp.215-238

Palmer, A. R., and Hoffman, M.T. (1997). Vegetation of Southern Africa, In: Cowling R. M., Richardson, D. M. and Pierce, S. M. ed. *Nama Karoo*, Cambridge, UK: Cambridge University Press, pp. 167-186.

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, pp. 37–42.

Pasternak, G. (2011). *Environmental effects on group structure and vigilance in vervet monkeys*, MSc Thesis, University of Lethbridge, Alberta, Canada.

Pasternak, G., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L. and Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland**.** *Koedoe*, 55, Article 1078.

Pérez-Flores, J., Calmé, S. and Reyna-Hurtado, R. (2016). Scoring body condition in wild baird's tapir (*Tapirus bairdii*) using camera traps and opportunistic photographic material. *Tropical Conservation Science*, pp. 1-12.

Pianka, E. R. (1970). On r- and K-selection. *The American Naturalist*, 104(940), pp. 592–597.

Pincebourde, S., Murdock, C. C., Vickers, M., and Sears, M. W. (2016). Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology*, 56(1), pp. 45-61.

Pochron, S. T. (2000). Sun avoidance in the yellow baboons (*Papio cynocephalus cynocephalus*) of Ruaha National Park, Tanzania. Variations with season, behaviour and weather. *International Journal of Biometeorology*, 44(3), pp. 141-147.

Potter, K. A, Woods, H. A., and Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19(10), pp. 2932-2939.

Pritchard, S. G., Rogers, H. H., Prior, S. A. and Peterson, C. M. (1999). Elevated CO_2 and plant structure: a review. *Global Change Biology*, 5(7), pp. 807-837.

Prosser, N. S., Gardner, P. C., Smith, J. A., Goon Ee Wern, J., Ambu, L. N. and Goossens, B. (2016). Body condition scoring of Bornean banteng in logged forests. *BMC Zoology*, 1(1), pp. 8

Pruetz, J. D. (2007). Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behaviour. *Primates*, 48(4), pp. 316-319.

Rabaiotti, D. and Woodroffe, R. (2019). Coping with climate change: limited behavioural responses to hot weather in a tropical carnivore. *Oecologia*, 189(3), pp. 587-599.

Racey, P. A. (1982). Ecology of bat reproduction, In Kunz, T. H. ed. *Ecology of bats*, New York, USA: Plenum Press, pp. 57-104.

Reed, B. C., Brown, J. F., Vanderzee, D., Loveland, T. S, Merchant, J. W., and Ohlen, D.O. (1994). Measuring phonological variability from satellite imagery. *Journal of Vegetation Science,* 5(5), pp. 703-714.

Reed, T. C., Grøtan, V., Jenouvrier, S., Sæther, B. and Visser, M. E. (2013). Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340(6131), pp. 488-491.

Refinetti, R. (1999). Amplitude of the daily rhythm of body temperature in eleven mammal species. *Journal of Thermal Biology*, 24(5-6), pp. 477-481.

Refinetti, R. and Menaker, M. (1992). The circadian rhythm of body temperature. *Physiology and Behavior*, 51(3), pp. 613-637.

Rey, B., Fuller, A., Mitchell, D., Meyer, L., and Hetem, R. S. (2017). Drought-induced starvation of aardvarks in the Kalahari: an indirect effect of climate change. *Biology letters*, 13(7).

Rieder, C. L. and Maiato, H. (2004). Stuck in division or passing through: what happens when cells cannot satisfy the spindle assembly checkpoint. *Developmental Cell*, 7(5), pp. 637-651.

Roberts, S. B., Cole, T. J. and Coward, W. A. (1985). Lactational performance in relation to energy intake in the baboon. *The American Journal of Clinical Nutrition*, 41(6), pp. 1270-1276.

Rogowitz, G. L. (1996). Trade-offs in energy allocation during lactation. *American Zoologist*, 36(2), pp. 197-204.

Rousham, E. K., Clarke, P. E. and Gross, H. (2006). Significant changes in physical activity among pregnant women in the UK as assessed by accelerometry and self-reported activity. *European Journal of Clinical Nutrition*, 60(3), pp. 393-400.

Rowe, C. L. (2008). "The calamity of so long life": life histories, contaminants, and potential emerging threats to long-lived vertebrates. *BioScience*, 58(7), pp. 623-631.

Rowell, T. E. (1970). Reproductive cycles of two *Cercopithecus* monkeys. *Journal of Reproduction and Fertility*, 22(2), pp. 321-338.

Rutherford, M.C., Midgley, G.F., Bond, W.J., Powrie, L.W., Roberts, R. and Allsopp, J. (1999). *Plant biodiversity: Vulnerability and adaptation assessment. South African country study on Climate Change*. National Botanical Institute, Cape Town, South Africa.

Rutz, C. and Hays, G. C. (2009). New frontiers in biologging science. *Biology Letters*, 5(3), pp. 289-292.

Sainmont, J., Andersen, K. H., Varpe, Ø. and Visser, A. W. (2014). Capital versus income breeding in a seasonal environment. *The American Naturalist*, 184(4), pp. 466-476.

Sánchez, S., Peláez, F., Gil-Bürmann, C. and Kaumanns, W. (1999). Cost of infant-carrying in cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 48(2), 99-111.

Sashaw, J. J. H. (2012). *Maternal strategies in vervet monkeys*, MSc Thesis, University of Lethbridge, Alberta, Canada.

Sauther, M. L. (1994). Changes in the use of wild plant foods in free–ranging ringtailed lemurs during lactation and pregnancy: Some implications for hominid foraging strategies, In: Etkin, N. L. ed. *Eating on the Wild Side: The Pharmacologic, Ecologic, and Social Implications of Using Noncultigens*, Tucson, Arizona, USA: University of Arizona Press, pp. 240-246.

Scantlebury, M., Butterwick, R. and Speakman, J. R. (2000). Energetics of lactation in domestic dogs (*Canis familiaris*) breeds of two sizes. *Comparative Biochemistry and Physiology, Part A, Molecular and Integrative Physiology*, 125(2), pp. 197-210.

Schmidt-Nielsen, K. (1997). *Animal Physiology: Adaptation and environment*, Cambridge, UK: Cambridge University Press.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369- 404.

Schröder, H. J. and Power, G. G. (1994). Increase of fetal arterial blood temperature by reduction of umbilical blood flow in chronically instrumented fetal sheep. *Pflügers Archiv - European Journal of Physiology*, 427(1-2), pp. 190-192.

Scribner, S. J. and Wynne-Edwards, K. E. (1994). Disruption of body temperature and behaviour rhythms during reproduction in dwarf hamsters. *Physiology and Behavior*, 55(2), pp. 361-369.

Seier, J. V., van der Horst, G., de Kock, M. and Chwalisz, K. (2000). The detection and monitoring of early pregnancy in the vervet monkey (*cercopithecus aethiops*) with the use of ultrasound and correlation with reproductive steroid hormones. *Journal of Medical Primatology*, 29(2), pp. 70–75.

Sekamatte, M. B. and Okwakol, M. J. N. (2007). The present knowledge on soil pests and pathogens in Uganda. *African Journal of Ecology*, 45(s2), pp. 9-19.

Shad, D. M. B. (1963). The composition of the milk of wild animals. *International Zoo Yearbook*, 4(1), pp. 333.

Shimozuru, M., Iibuchi, R., Yoshimoto, T., Nagashima, A., Tanaka, J. and Tsubota, T. (2013). Pregnancy during hibernation in Japanese black bears: effects on body temperature and blood biochemical profiles. *Journal of Mammalogy*, 94(3), pp. 618-627.

Signer, C., Ruf, T. and Arnold, W. (2011). Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Functional Ecology*, 25, pp. 537-547.

Sileshi, G. W., Nyeko, P., Nkunika, P. O. Y., Sekamatte, B. M., Akinnifesi, F. K. and Ajayi, O. C. (2009). Integrating ethno-ecological and scientific knowledge of termites for sustainable termite management and human welfare in Africa. *Ecology and Society*, 14(1), Article 48.

Skinner, J. D. and Chimimba, C. T. (2005). *The mammals of the southern African subregion* (3rd ed.), Cambridge, UK: Cambridge University Press.

Skinner, J. D. and Smithers, R. H. N. (1990). *The mammals of the southern African subregion* (2nd ed.), Pretoria, South Africa: University of Pretoria.

Snyder, G. K. and Nestler, J. R. (1990). Relationships between body temperature, thermal conductance, Q10 and energy metabolism during daily torpor and hibernation in rodents. *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology*, 159(6), pp. 667–675.

Spalton, J. A. (1999). The food supply of Arabian oryx (*Oryx leucoryx*) in the desert of Oman. *Journal of Zoology*, 248(4), pp. 433–441.

Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1490), pp. 375-398.

Speakman, J. R. and Król, E. (2005). Limits to sustained energy intake. IX. A review of hypotheses. *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology*, 175(6), pp. 375-394.

Speakman, J. R. and Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, 79(4), pp. 726-746.

Speakman, J. R. and McQueenie, J. (1996). Limits to sustained metabolic rate: the link between food intake, basal metabolic rate and morphology in reproducing mice (*Mus musculus). Physiological Zoology*, 69(4), pp. 746-769.

Stearns, S. C. (1989). Trade-offs in life history evolution. *Functional Ecology*, 3(3), pp. 259-268.

Stearns, S. C. (1992). *The Evolution of Life Histories.* Oxford, UK: Oxford University Press.

Stelzner, J. K. (1988). Thermal effects on movement patterns of yellow baboons. *Primates*, 29(1), pp. 91-105.

Stelzner, J. K. and Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow baboons. *Primates*, 27(4), pp. 449–463.

Stenseth, N. C. and Mysterud, A. (2002). Climate, changing phenology, and other life history traits: nonlinearity and match/mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America*, 99(21), pp. 13379–13381.

Stern, J. M., Goldman, L. and Levine, S. (1973). Pituitary-adrenal responsiveness during lactation in rats. *Neuroendocrinology*, 12(3), pp. 179–191.

Stitt, J. T. and Hardy, J. D. (1971) Thermoregulation in the squirrel monkey (*Saimiri sciureus*). *Journal of Applied Physiology*, 31(1), pp. 48–54.

Strier, K. B. (1987). Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology*, 13(4), pp. 385-395.

Strier, K. B. (1993). Growing up in a patrifocal society: sex differences in the special relation of immature muriquis, In: Pereira, M. E. and Fairbanks, L. A. ed. *Juvenile Primates: Life History, Development and Behaviour*, New York, USA: Oxford University Press, pp. 138-147.

Struhsaker, T. T. (1967a). Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, 29(2), pp. 83-121.

Struhsaker, T. T. (1967b). Ecology of the vervet monkey (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, 48(6), pp. 891-904.

Takahashi, H. (2002). Female reproductive parameters and fruit availability: factors determining onset of estrus in Japanese macaques. *American Journal of Primatology*, 57(3), pp. 141-153.

Tappen, N. C. (1960). Problems of distribution and adaptation of the African monkeys. *Current Anthropology*, 1(2), pp. 91-120.

Tardif, S. D. (1997). The bioenergetics of parental behaviour and evolution of alloparental care in marmosets and tamarins, In: Solomon, N. G. and French, J. A. ed. *Cooperative Breeding Mammals*, Cambridge, UK: Cambridge University Press, pp. 11-33.

Trayhurn, P., Douglas, J. B. and McGuckin, M. M. (1982). Brown adipose tissue thermogenesis is suppressed during lactation in mice. *Nature*, 298, pp. 59-69.

Trayhurn, P and Richard, D. (1985). Brown adipose tissue and the energetics of pregnancy and lactation in rodents. *Biochemical Society Transactions*, 13(5), pp. 826-828.

Trethowan, P. D., Hart, T., Loveridge, A. J., Haw, A., Fuller, A. and Macdonald, D. W. (2016). Improved homeothermy and hypothermia in African lions during gestation. *Biology Letters*, 12(11).

Trivers, R. (1972). Parental investment and sexual selection, In: Campbell, B. ed. *Sexual Selection and the Descent of Man*, Aldine, USA: Chicago, pp. 1871-1971.

Tucker, C. J., Townshend, C. O., and Goff, T. E. (1985). African land-cover classification using satellites data. *Science*, 227(4685), pp. 369-257.

Turner, T. R., Anapol, F. and Jolly, C. J. (1997). Growth, development and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology*, 103(1), pp. 19-35.

Turner, T. R., Coetzer, W. G., Schmitt, C. A., Lorenz, J. G., Freimer, N. B., and Grobler, J. P. (2016). Localized population divergence of vervet monkeys (*Chlorocebus* spp.) in South Africa: evidence from mtDNA. *American Journal of Physical Anthropology*, 159(1), pp. 17-30.

Van Cauter, A. (2004). *Developing and testing models of mammal community structure in the easten Karoo*, MSc thesis. Nelson Mandela Metropolitan University, South Africa.

Van Jaarsveld, A. S. and Chown, S. L. (2001). Climate change and its impacts in South Africa. *Trends in Ecology and Evolution*, 16(1), pp. 13-14.

Visser, M. E., Both, C. and Lambrechts, M. M. (2004) Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research*, 35, pp. 89–110.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. and Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, 265(1408), pp. 1867–1870.

Wade, G. N., Jennings, G. and Trayhurn, P. (1986). Energy balance and brown adipose tissue thermogenesis during pregnancy in Syrian hamsters. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 19(5), pp. R845-R850.

Wade, G. N. and Schneider, J. E. (1992). Metabolic fuels and reproduction in female mammals. *Neuroscience and Biobehavioural Reviews*, 16(2), pp. 235-272.

Weinandy, R. and Gatterman, R. (1995). Measurement of physiological parameters and activity in a Mongolian gerbil during gravidity and lactation with an implanted transmitter. *Physiology and Behavior*, 58(4), pp. 811-814.

Weiss, E., Marsh, S. E., and Pfirman, E. S., (2001). Application of NOAA-AVHRR NDVI time-series data to assess changes in Saudi Arabia's rangelands. *International Journal of Remote Sensing*, 22(6), pp. 1005-1027.

Wharfe, M. D., Wyrwoll, C. S., Waddell, B. J. and Mark, P. J. (2016). Pregnancy suppresses the daily rhythmicity of core body temperature and adipose metabolic gene expression in the mouse. *Endocrinology*, 157(9), pp. 3320-3331.

Wikelski, M. and Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology and Evolution*, 21(1), pp. 38-46.

Wilde, C. J., Kerr, M. A., Knight, C. H. and Racey, P. A. (1995). Lactation in vespertilionid females. *Symposium of the Zoological Society of London*, 67, pp. 139–149.

Williams, A. M., Safranski, T. J., Spiers, D. E., Eichen, P. A., Coate, E. A. and Lucy, M. C. (2013). Effects of controlled heat stress during late gestation, lactation and after weaning on thermoregulation, metabolism, and reproduction of primiparous sows. *Journal of Animal Science*, 91(6), pp. 2700-2714.

Williams, C. T., Sheriff, M. J., Schmutz, J. A., Kohl, F., Tøien, Ø., Buck, C. L. and Barnes, B. M. (2011). Data logging of body temperatures provides precise information on phenology of reproductive events in a free-living arctic hibernator. *Journal of Comparative Physiology Part B, Biochemical, Systemic, and Environmental Physiology*, 181(8), pp. 1101-1109.

Wilson, N. E. and Stricker, E. M. (1979). Thermal homeostasis in pregnant rats during heat stress. *Journal of Comparative and Physiological Psychology*, 93(3), pp. 585–594.

Wolff, J. O. and Van Horn, T. (2003). Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology*, 81(2), pp. 266-271.

Wood, C. and Beard, R. W. (1964). Temperature of the human foetus. *The Journal of Obstetrics and Gynaecology of the British Commonwealth*, 71, pp. 768-769.
Wrangham, R.W. (1981). Drinking competition in vervet monkeys. *Animal Behaviour*, 29(3), pp. 904-910.

Wright, P. C. (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*, In: Small, M. F. ed. *Female Primates: Studies by Women Primatologists*, New York, USA: A.R. Liss, pp. 59-75.

Zhang, X. Y. and Wang, D. H. (2006). Energy metabolism, thermogenesis and body mass regulation in Brandt's voles (*Lasiopodomys brandtii*) during cold acclimation and rewarming. *Hormones and Behavior*, 50(1), pp. 61-69.

Zhao, Z. J. (2011). Energy budget during lactation in striped hamsters at different ambient temperatures. *Journal of Experimental Biology*, 214, pp. 988-995.