



Diet, activity, and body temperature patterns of ground pangolins in a semi-arid environment

by

Wendy Panaino

545644

Thesis

Submitted in fulfilment of the requirements for the degree

Doctor of Philosophy

in

Animal, Plant, and Environmental Sciences

in the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa

Supervisors

Professor Andrea Fuller

Professor Francesca Parrini

July 2021

DECLARATION

I declare that this research thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any other degree or examination at any other University.

____ *W Panaino* ____

(Signature of Candidate)

____ 19/07/2021 ____

(Submission Date)

ABSTRACT

Climate change is threatening biodiversity globally, with the effects already apparent across various ecosystems. Increases in air temperatures and greater variability in precipitation will reduce primary productivity, with profound effects for arid areas. Climate change affects animals directly by imposing greater heat loads and indirectly by altering the availability of their resources. Temminck's ground pangolin (*Smutsia temminckii*) is a predominantly nocturnal, myrmecophagous (ant- and termite-eating) mammal that inhabits parts of eastern and southern Africa, including the hot and dry southern Kalahari. Studying the responses of pangolins to fluctuations in climate and food availability in a hot and dry environment provides an analogue for the conditions likely to become prevalent elsewhere across the pangolin distribution with climate change. I investigated the behavioural and physiological responses of six pangolins at Tswalu Kalahari Reserve for two years in response to fluctuations in climate and food availability. Each pangolin was fitted with a VHF tracking transmitter and a miniature temperature-sensitive data logger, which recorded core body temperature every 5 minutes. Low and late rainfall during the first year of the study, and the year before that, resulted in lower grass cover and prey abundance compared to in the second year. Pangolins responded to food scarcity by shifting their diet, which was normally dominated by *Crematogaster* ants, to include more *Anoplolepis* ants and *Trinervitermes* termites. Despite shifting their diet, pangolins experienced energy deficits, particularly during winter when prey was least available. The energy deficits resulted in lower than normal 24h minimum body temperatures when prey resources were scarce. When 24h minimum body temperature was low, which was more likely to occur during winter, pangolins emerged from their burrows earlier during the day and shortened their activity period compared to in summer, presumably to offset the metabolic costs of maintaining constant high body temperatures at night. Although the physiological and behavioural plasticity exhibited by the pangolins allowed them to cope with fluctuations in food availability, the extent to which this plasticity will buffer pangolins and other myrmecophages to climate change-induced reductions in food availability in the future is unclear.

To my loving and supportive parents, without whom this incredible journey would not have been possible.

ACKNOWLEDGEMENTS

I would like to thank the Oppenheimer family and Tswalu Kalahari Reserve for the opportunity to conduct my research on one of the most spectacular properties in South Africa. I acknowledge the South African Weather Services for providing me with historical weather data. I also gratefully acknowledge Peter Kamerman for helping me with statistical analyses. I thank Africa Wildlife Tracking for providing me with custom-designed tracking transmitters for pangolins. I also thank the National Research Foundation, Save Pangolins, the Brain Function Research Group, and the Tswalu Foundation for providing funding throughout my PhD degree.

The on-site support provided by the staff of Tswalu and the Tswalu Foundation contributed immensely to the success of the pangolin project. To the guides and trackers of Tswalu, who often spent a lot of time helping me search for new and existing study animals, for which I am incredibly grateful. Through tracking together with you all, I have gained a valuable skill set of my own. To Gus van Dyk, thank you for taking the time to help me come up with practical solutions and for always assisting me, without hesitation, whenever it was needed. More than anything, thank you for sharing your broad ecological knowledge with me. To Prince Ngomane, for always going above and beyond to provide me with assistance when it was needed. Your work ethic is inspiring. Thank you to all the nature conservation students that made for great field assistants each year. In particular, thank you to Tara Naeser for always being up for an adventure and for being my number one cheerleader over the last few years.

To the research teams that were involved in surgery trips to implant pangolins with data loggers, thank you for dedicating your time and energy to ensuring that each trip rolled out smoothly. To our vets, Dr Anna Haw, Dr Jess Briner, and Dr Leith Meyer, thank you for your professionalism and for adding invaluable expertise to the team. I am grateful to Robyn Hetem and Nora Weyer for showing me the ropes early on, and for teaching me how to organize and coordinate a successful research trip.

To my supervisors, Francesca Parrini and Andrea Fuller, thank you for always supporting me and for working so hard to provide me with feedback that allowed me to improve my research and writing skills. Thank you for giving me the freedom and independence to be creative and to grow as a researcher. To Andrea in particular, for taking me under your wing and being an incredible teacher and supporter. Thank you for providing me with so many opportunities to get involved with other research projects beyond my own. So many of my achievements over the last few years, I owe to you.

There is an overwhelming number of individuals that I would like to thank for contributing in various ways throughout this PhD process. I am grateful to Hamish Robertson and Frederic Delsuc for sparking my passion for the world of ants and termites, and for

helping me set up a brilliant reference collection of the ants and termites of Tswalu. The reference collection was a valuable contribution to developing my ant and termite identification skills. To the Dedebeben crew, thank you for the endless laughs and unforgettable memories. Thank you for sharing your research and passion with me over the years.

To Anthony Panaino-Lowney, my rock, you have supported me every step of the way and have been someone I could always turn to for advice and for a good laugh. You are such an inspiration to me, and you have taught me so much throughout the years (except anything requiring coordination). To Norma-Jean Naude and Jethro Dell, I am immensely grateful for your unconditional friendship. Thank you for the many cups of tea and bowls of popcorn that got me through some long nights. You both have shown me that life is always an adventure, even when you are not “prepared”. To Valery Phakoago, it has been such an adventure being able to work with you, and to learn about how you view the world. Thank you for all your help over the last two years, and never with any hesitation. You have been an absolute ray of sunshine, and I thank you for bringing uncontrollable laughter to my life. To Wesley Hattingh and Hiral Naik, for being friends that have been there to support and encourage me without fail. Thank you to Robin Cook, Blair Cowie, and Chris Rankin, for helping me get through the 2020 lockdown with endless banter.

To Roni and Alan Campey, who have both become such a huge part of my life. By living vicariously through me, you have reminded me to appreciate the work I do every day. Your generosity and love have been a special part of my time at Tswalu, even from a distance. I hope to grow up to maintain the passion that you both have for the natural world around you.

To Dylan and Theresa Smith, my family away from home, thank you for being the most kind, generous, and caring people. Thank you for the numerous cups of tea and delicious meals. Theresa, thank you for always making me feel at home in your home and for reminding me to take breaks. Thank you for all the good laughs shared over a glass of wine. Dylan, you have been an incredible mentor to me over the last few years, and I would not be where I am today without your support and encouragement. Thank you for always being willing to help, whether it was just bouncing ideas off you or providing assistance in the field. I am in awe of your vast knowledge and passion for nature. You both have opened my eyes to a world that is full of beauty.

Lastly, I am forever grateful to my family, who have always supported me and encouraged me to explore my passion for the outdoors. Thank you to my parents for giving me the freedom to make my own choices and for providing me with the opportunity to be educated. Thank you for always going above and beyond to help me and provide

me with the tools I needed to be successful. I have dedicated this thesis to you as a token of my gratitude and love.

TABLE OF CONTENTS

Declaration.....	i
Abstract.....	ii
Dedication.....	iii
Acknowledgements.....	iv
Table of contents.....	vii
List of figures.....	x
List of tables.....	xv
 Chapter 1 : Introduction.....	 1
1.1 Pangolins.....	3
1.1.1 General information.....	3
1.1.2 Ecological role of pangolins.....	3
1.1.3 Conservation status and threats.....	5
1.1.4 Temminck's ground pangolin: <i>Smutsia temminckii</i>	5
1.1.4.1 Distribution and habitat.....	6
1.1.4.2 Breeding.....	7
1.1.4.3 Diet.....	8
1.1.4.4 Activity.....	11
1.1.4.5 Metabolism and body temperature.....	12
1.2 Climate change.....	13
1.2.1 Climate change across the pangolin distribution range in Africa.....	14
1.2.2 Potential impacts of climate change on pangolins.....	15
1.2.2.1 Direct impacts.....	16
1.2.2.2 Indirect impacts.....	17
1.3 Potential responses available to pangolins to buffer the effects of climate change.....	21
1.3.1 Range shifts and movement.....	21
1.3.2 Genetic adaptation.....	21
1.3.3 Phenotypic plasticity.....	22
1.3.3.1 Phenology.....	23
1.3.3.2 Body size.....	24
1.3.3.3 Physiology.....	24
1.3.3.4 Behaviour.....	27

1.4	Thesis structure, objectives, and hypotheses.....	31
Chapter 2: Methods and materials.....		33
2.1	Study site and climate.....	34
2.1.1	Study site.....	34
2.1.2	Climate.....	36
2.2	Study animals, implants and data collection.....	37
2.2.1	Ethical clearance and research permits.....	37
2.2.2	Study pangolins and telemetry fitting.....	37
2.2.3	Surgical procedures.....	39
2.2.4	Dietary observations and activity.....	43
2.2.5	Grass cover and prey abundance.....	45
Chapter 3: Ground pangolins in the Kalahari shift their diet in response to resource scarcity.....		46
3.1	Introduction.....	47
3.2	Materials and methods.....	49
3.2.1	Climatic variables.....	49
3.2.2	Grass cover and prey abundance.....	49
3.2.3	Pangolin diet.....	50
3.2.4	Pangolin activity.....	53
3.2.5	Data analyses.....	53
3.2.5.1	Climatic variables.....	53
3.2.5.2	Grass cover	54
3.2.5.3	Prey abundance.....	54
3.2.5.4	Pangolin diet.....	55
3.3	Results.....	57
3.3.1	Climatic variables.....	57
3.3.2	Grass cover.....	59
3.3.3	Prey abundance.....	61
3.3.4	Pangolin diet.....	66
3.3.4.1	Dietary observations and scat contents.....	66
3.3.4.2	Abundance of pangolin prey items.....	69
3.3.4.3	Number of prey items consumed.....	71
3.3.4.4	Estimated energy intake.....	75
3.4	Discussion.....	78
Chapter 4: Seasonal patterns of pangolin activity are influenced by food availability and 24h minimum body temperature.....		87
4.1	Introduction.....	88

4.2	Material and methods.....	89
4.2.1	Climatic variables.....	89
4.2.2	Prey abundance.....	89
4.2.3	Pangolin body temperature.....	90
4.2.4	Pangolin activity.....	90
4.2.5	Data analyses.....	93
4.3	Results.....	95
4.3.1	Climatic variables.....	95
4.3.2	Prey abundance.....	98
4.3.3	Pangolin body temperature.....	98
4.3.4	Pangolin activity.....	98
4.4	Discussion.....	112
Chapter 5: Ground pangolins relax the precision of body temperature regulation when resources are scarce in the Kalahari.....		119
5.1	Introduction.....	120
5.2	Material and methods.....	122
5.2.1	Climatic and seasonal variables.....	122
5.2.2	Prey abundance.....	122
5.2.3	Pangolin activity.....	122
5.2.4	Pangolin body temperature.....	123
5.2.5	Data analyses.....	123
5.3	Results.....	125
5.3.1	Climatic variables.....	125
5.3.2	Prey abundance.....	125
5.3.3	Pangolin activity.....	125
5.3.4	Pangolin body temperature.....	125
5.4	Discussion.....	135
Chapter 6: Conclusion.....		140
6.1	Climate change.....	142
6.2	Implications of climate change for myrmecophagous animals.....	144
6.3	Implications for ecosystem function.....	149
6.4	Research gaps on Temminck's ground pangolin and other myrmecophages.....	150
6.4.1	Thermoregulation.....	150
6.4.2	Ecosystem dynamics.....	152
6.5	Consideration for conservation management.....	153
6.5.1	Habitat degradation.....	153
6.5.2	Ecotourism.....	154

6.5.3	Methods for assessing pangolin welfare.....	155
6.6	Threats beyond the illegal wildlife trade.....	155
	References.....	157
	Appendix	194

LIST OF FIGURES

Figure 1.1: Number of peer-reviewed papers or books published each decade since 1930, with particular reference to Temminck's ground pangolins.....	6
Figure 1.2: Projected change in annual average temperature (°C; left) and rainfall (mm; right) across the pangolin distribution range (black outline) for 2071-2100 compared to 1961-1990. Adapted from Engelbrecht <i>et al.</i> (2015), using the 90 th percentile models under the A2 SRES scenario.....	15
Figure 2.1: Geographical location of Tswalu Kalahari Reserve within South Africa.....	34
Figure 2.2: Satellite image showing the Korannaberg and Lekgaba sections, with boundaries of the reserve (blue) and Lekgaba (yellow).....	35
Figure 2.3: Map of Tswalu vegetation types (adapted from Tokura <i>et al.</i> 2018).....	36
Figure 2.4: Pangolin with a VHF tracking transmitter attached to a dorsolateral scale (<i>top</i>), and a single scale of a pangolin that had died of natural causes, showing the two attachment points of a tracking transmitter (<i>bottom</i>).....	38
Figure 2.5: Miniature temperature-sensitive data logger (before adding the wax coating) implanted into pangolins to record core body temperature.	39
Figure 2.6: Mobile surgical site on the tailgate of a 4 x 4 Hilux vehicle showing the mosquito net covering to prevent insects entering the surgical site at night.....	41
Figure 2.7: Anaesthesia being induced in a pangolin by face mask, before surgery to implant a wax-coated miniature temperature-sensitive data logger.....	42
Figure 2.8: A scattered pangolin faecal sample that was not buried by the pangolin, with an intact sausage-shaped excrement above.....	44
Figure 2.9: A camera trap placed outside a pangolin burrow to detect the time of emergence and return.....	45
Figure 3.1: The 24h mean black globe temperatures at Tswalu for the period October 2015 to October 2017. The gaps in the data occurred due to a failed weather station....	57
Figure 3.2: Seasonal 24h black globe temperatures at Tswalu for the study period, including the seasonal 24h means (mean $\pm$ SD). Autumn only includes March to May 2017, since data for March to May 2016 were not collected due to a failed weather	

station. November 2016 was excluded so that appropriate interannual comparisons could be made with the spring of 2017, since the study period ended in October 2017.....58

Figure 3.3: Total monthly rainfall at Tswalu for three years. The orange dotted lines represent the month with the highest rainfall for the last 16 years (January).....59

Figure 3.4: Average monthly grass cover for the study period (October 2015 to October 2017). Data for grass cover were not collected during March 2017.....60

Figure 3.5: Monthly ant (A) and termite (B) abundance for the two study years (October 2015 to October 2016 and October 2016 to October 2017). Data for March 2017 are not included as transects were not conducted for the month.....62

Figure 3.6: The relationship between the monthly 24h mean black globe temperature and monthly prey abundance. The black dashed line shows the piecewise regression and the breakpoint (where the line changed direction).....63

Figure 3.7: Seasonal and interannual proportions of the prey items in the pangolin diet, including soldier (s) and worker (w) castes where applicable.....68

Figure 3.8: The seasonal and interannual proportions of the three dominant prey items and 'other' ants and termites in the pitfall traps.....69

Figure 3.9: Seasonal and interannual number of prey genera (prey diversity) recorded per pangolin scat sample. The centre line in the boxes represents the median, and the bars represent the minimums and maximums. n = the number of scats collected per season. * Indicates a $p < 0.05$ statistically significant difference between seasons and ** indicates a $p < 0.01$ statistically significant difference between seasons.....71

Figure 3.10: Relationship between the proportion of arboreal prey (*Crematogaster* ants) eaten and the organic content of the scat (A), and the relationship between the proportion of subterranean prey (*Anoplolepis* ants and *trinervitermes* termites combined) eaten and the organic content of the scat (B).....72

Figure 3.11: Seasonal and interannual number of prey items eaten per 24h. Black borders indicate significant differences between years. The centre line in the boxes represents the median, and the bars represent the minimums and maximum number of prey items eaten per 24h. n = the number of scats collected per season. * Indicates a $p < 0.05$ statistically significant difference between seasons and ** indicates a $p < 0.01$ statistically significant difference between seasons.....73

Figure 3.12: The relationship between the number of prey items eaten per day and rainfall three months prior to conducting transects (A), prey abundance (B), and the amount of time pangolins spent active (C). the black dashed lines represent the regression.....	75
Figure 3.13: Seasonal and interannual 24h energy intake from the diet. * indicates statistical significance ($p<0.05$). Black borders indicate significant differences between years. The centre line in the boxes represents the median, and the bars represent the minimums and maximum number of prey items eaten per 24h. n = the number of scats collected per season. * indicates statistical significance between seasons ($p<0.05$).....	76
Figure 3.14: Relationship between energy intake and the proportion of <i>Anoplolepis</i> ants eaten (A), the amount of time that pangolins spent active (B), prey abundance (C), and rainfall three months prior to conducting transects (D). The black dashed line represents the regression.....	78
Figure 4.1: The 24h body temperature patterns of a pangolin, showing the estimated and actual (camera trap data) burrow emergence and return times for two consecutive winter days and two consecutive summer days.....	91
Figure 4.2: Frequency distribution of time of emergence (A) and return (B) data obtained directly from camera traps only (<i>left</i>) and indirectly from 24h body temperature patterns only (<i>right</i>).....	92
Figure 4.3: The relationship between pangolin time of emergence from the burrow and black globe temperature at the time of emergence (A), 24h mean (B), 24h minimum (C), and 24h maximum (D) black globe temperatures. P01 to P10 represent the different study animals	95
Figure 4.4: The 24h mean, 24 minimum, and 24h maximum black globe temperatures at Tswalu for the period October 2015 to October 2017. The gaps in the data occurred due to a failed weather station.....	96
Figure 4.5: Time of sunrise and sunset; closed circles represent time of sunset, open circles represent time of sunrise (A), pangolin time of emergence from the burrow (A), time of return to the burrow (B), and the time spent out of the burrow (C) of six pangolins from October 2015 to October 2017. P01 to P10 represent the different study animals.....	100

Figure 4.6: Seasonal time of emergence of six pangolins across the full study period, expressed as the proportion of observations that occurred per 2h time category.....	102
Figure 4.7: Seasonal and interannual emergence and return times, and the duration of activity of six pangolins for October 2015 to October 2016 (pink) and for October 2016 to October 2017 (blue), expressed as the proportion of observations that occurred per 1h time category.....	105
Figure 4.8: The relationship between pangolin emergence from the burrow and photoperiod (A), prey abundance (B), 24h mean black globe temperature (C), and pangolin 24h minimum body temperature (D). P01 to P10 represent the different study animals	107
Figure 4.9: The relationship between pangolin return to the burrow and photoperiod (A), prey abundance (B), 24h mean black globe temperature (C), and pangolin 24h minimum body temperature (D). P01 to P10 represent the different study animals	108
Figure 4.10: The relationship between the duration of activity and photoperiod (A), prey abundance (B), mean black globe temperature (C), and 24h minimum body temperature (D). P01 to P10 represent the different study animals	110
Figure 4.11: The relationship between pangolin time of emergence and return to the burrow. P01 to P10 represent the different study animals	111
Figure 5.1: Body temperature patterns recorded at 5-minute intervals for six individual pangolins at Tswalu across the study period.....	126
Figure 5.2: Frequency distribution (%) of body temperature averaged across six pangolins for the study period (October 2015 to October 2017).....	127
Figure 5.3: The seasonal and interannual 24h body temperature patterns for two years. The black lines represent the average 24h body temperature across all pangolins across each month in that season. The pink (first study year) and blue (second study year) shaded areas represent the dark phase for each study year.....	128
Figure 5.4: The relationship between pangolin 24h minimum body temperature and photoperiod (A), prey abundance (B) and 24h minimum black globe temperature (C). P01 to P10 represent the different study animals.....	131

Figure 5.5: The relationship between 24h maximum body temperature and photoperiod (A), prey abundance (B) and 24h maximum black globe temperature (C). P01 to P10 represent the different study animals.....	132
Figure 5.6: The relationship between amplitude of the 24h rhythm of body temperature and photoperiod (A), prey abundance (B) and the amplitude of 24h black globe temperature (C). P01 to P10 represent the different study animals.....	134
Figure 5.7: The relationship between pangolin time of emergence from the burrow and 24h maximum body temperature. P01 to P10 represent the different study animals.....	135
Figure 6.1: Daily mean and maximum air temperatures for the period 1993 to 2019 for van Zylsrus (data obtained from the South African Weather Services).....	142
Figure 6.2: Annual rainfall for the period 2001 to 2019. Each year (E.g., 2001) represents rainfall that fell between June of the previous year (E.g., June 2000) and May of the next year (E.g., May 2001).....	143
Figure 6.3: The number of months in which the major rainfall events occurred before (positive numbers) or after (negative numbers) January each year from 2001 to 2019 at Tswalu. The dotted line at zero represents January, the month in which major rainfall events occurred, on average, for the 14 years preceding the study.....	144
Figure 6.4: Mean monthly insects per trap for the period 2014 to 2020, showing seasonal fluctuations (orange dotted line) and the overall decreasing trend (blue solid line) in ant and termite abundance at Tswalu. Data collected during my study (2015 to 2017) were supplemented with data collected by N. Weyer (2014 to 2015) and M. Phakoago (2018 to 2020).....	145

LIST OF TABLES

Table 1.1: List of ant and termite genera recorded in the diet of pangolins across their distribution range and which of six different studies recorded them.....	9
Table 2.1: Study pangolin ID, sex, body mass at the first and last surgery to implant data loggers, and change (Δ) in body mass between the first and last surgery.....	38
Table 2.2: Start and end dates of implantation and removal of body temperature data loggers from six pangolins between October 2015 to October 2017).....	40
Table 3.1: The number of pangolin scat samples collected across the study period, and the number of pangolins that samples were collected from per month (total number of samples = 98, total number of pangolins collected from = 9).....	51
Table 3.2: Multiple linear regression results of the effects of total rainfall three months prior to conducting transects and 24h mean black globe temperature on monthly grass cover, as well as their interactive effects.....	60
Table 3.3: Multiple linear regression results of the effects of rainfall, grass cover, and 24h mean black globe temperature on monthly prey abundance.....	63
Table 3.4: The contribution and occurrence of ant and termite genera in the pitfall traps across the study period. Grey blocks indicate significant differences ($p < 0.05$) between the two study years.....	65
Table 3.5 Percentage contribution of ant and termite prey items to the pangolin diet (mean $\pm$ SD) and percentage occurrence of prey items in scat samples. Grey blocks indicate significant differences ($p < 0.05$) between the two study years.....	67
Table 3.6: Multiple linear regression results of the effects of average monthly rainfall and 24h mean black globe temperature on the abundance of <i>Anoplolepis</i> ants, <i>Crematogaster</i> ants, and <i>Trinervitermes</i> termites in the pitfall traps.....	70
Table 3.7: Multiple linear regression results of the effects of accumulated rainfall three months prior to conducting transects, prey abundance, and the amount of time pangolins spent active on the number of prey items eaten.....	74
Table 3.8: Multiple linear regression results of the effects of accumulated rainfall three months prior to conducting transects, prey abundance, the amount of time that pangolins spent active, and the proportion of <i>Anoplolepis</i> soldier ants consumed on the 24h estimated energy intake by pangolins.....	77

Table 4.1: Seasonal and interannual summary statistics of the 24h mean, 24h minimum, and 24h maximum black globe temperature for two years (mean $\pm$ SD). Red shaded columns show 2015-2016, the warmer year, as indicated by higher 24h mean black globe temperature in all seasons, except autumn, compared to 2016-2017, shaded blue. Grey blocks indicate significant differences between the two years.....	97
Table 4.2: Rayleigh test output using the strength of the Rayleigh statistic to determine whether each pangolin's burrow emergence and return data differed from random.....	99
Table 4.3: Watson two-sample test output for the pangolins with the longest datasets to assess the seasonal and interannual differences in time of emergence and return to the burrow.....	103
Table 4.4: Seasonal and interannual summary statistics of the pangolin burrow emergence and return times, as well as the duration of activity for years (mean $\pm$ SD). Red shaded columns show 2015-2016, the warmer year, compared to 2016-2017, shaded blue. Grey blocks indicate significant differences between the two years.....	104
Table 4.5: Linear mixed model results of the effects of photoperiod, prey abundance, mean black globe temperature, and 24h minimum body temperature on pangolin time of emergence from the burrow.....	106
Table 4.6: Linear mixed model results of the effects of photoperiod, prey abundance, 24h mean black globe temperature, and 24h minimum body temperature on pangolin time of return to the burrow.....	108
Table 4.7: Linear mixed model results of the effects of photoperiod, prey abundance, mean black globe temperature, and 24h minimum body temperature on the amount of time pangolins spent out of their burrows.....	109
Table 4.8: The 24h mean, 24h minimum, 24h maximum black globe temperatures, and the globe temperature at the time of emergence from the burrow when pangolin emerged either before or after 21:50 (mean $\pm$ SD). Grey blocks indicate significant differences between when pangolins emerged from their burrows before 21:50 and when they emerged after 21:50.....	111
Table 5.1: Seasonal and interannual summary statistics of the 24h mean, 24h minimum, 24h maximum, and 24h amplitude of body temperature for two years (mean $\pm$ SD). Pink shaded columns show 2015-2016, the year in which rainfall, grass cover, and prey abundance was low, and the blue shaded columns show 2016-2017, the year in which	

rainfall, grass cover, and prey abundance was high. Grey blocks indicate significant differences between the two years.....129

Table 5.2: Linear mixed model results of the effects of photoperiod, prey abundance, and 24h minimum black globe temperature on pangolin 24h minimum body temperature...130

Table 5.3: Linear mixed model results of the effects of photoperiod, prey abundance, and 24h maximum black globe temperature on pangolin 24h maximum body temperature.....132

Table 5.4: Linear mixed model results of the effects of photoperiod, prey abundance, and the amplitude of the 24h rhythm of black globe temperature on the amplitude of the 24h rhythm of pangolin body temperature.....133

Table 5.5: Linear mixed model results of the effect of pangolin time of emergence from the burrow on their 24h maximum body temperature.....134

Chapter 1

Introduction

Global biodiversity is currently under threat by multiple anthropogenic influences, including habitat degradation and loss, the illegal wildlife trade and climate change (Islam and Rahmani 2011; Bellard *et al.* 2012; 't Sas-Rolfes *et al.* 2019). Climate change models predict that weather events are likely to become more extreme and more unpredictable (Engelbrecht *et al.* 2015; Bathiany *et al.* 2018). Parts of southern Africa are predicted to experience increased heat and aridity with climate change (Engelbrecht *et al.* 2015), with the warming rate exceeding that in many other areas of the world. Despite global efforts to try to understand the effects of climate change on ecosystems and species, there is a paucity of research conducted in the southern hemisphere and in Africa. Very little is known about how most of the mammals in southern Africa might respond to the predicted changes. The southern Kalahari is a hot, semi-arid region within western South Africa, a part of the country that has been identified as a climate change “hot spot” (Giorgi 2006; Diffenbaugh and Giorgi 2012; de Sherbinin 2014). Kalahari organisms, although adapted to hot and dry conditions, are thus likely to be particularly vulnerable to the increased heat and aridity projected with climate change. The ability of organisms inhabiting arid areas to adapt to even more extreme conditions is poorly understood because of the lack of empirical data available.

Climate change affects animals directly by imposing greater heat loads and indirectly by altering the availability of their resources. One species likely to be challenged, particularly in the Kalahari, by direct and indirect effects of climate change is Temminck's ground pangolin (*Smutsia temminckii*). Very little is known about how pangolins respond to changes in climate. There is also very little known about how climate change will impact the insects that pangolins prey on. The fact that pangolins, as myrmecophagous mammals, specialize on ants and termites as prey means that any climate change-induced shifts in these social insects will likely impact pangolins through trophic cascades.

Temminck's ground pangolin is an understudied, medium-sized, African mammal. Its slow life-history makes genetic adaptation unlikely as an adaptive response in the face of rapid climate change. Barriers to movement, fragmented habitats and capture for illicit trade will also make it difficult for ground pangolins to relocate to more suitable habitats. A large proportion of research on the species has explored the illegal wildlife trade (Ingram *et al.* 2018; George *et al.* 2019; Jacobs *et al.* 2019; Ullmann *et al.* 2019), and some research has focused on ecological topics (Swart *et al.* 1999; Pietersen *et al.* 2014b; Pietersen *et al.* 2016), but the impacts of climate change on pangolins have not been explored until now. Indeed, it is unknown whether pangolins can employ phenotypic plasticity to buffer the effects of climate change. Investigating the responses of ground pangolins to climatic variations in an already hot and dry environment in the Kalahari, as an analogue for the conditions likely to become prevalent elsewhere across their distribution in the future, will

provide insights into how pangolins will cope with climate change. I had the opportunity to conduct a comprehensive ecophysiological study on pangolins in the southern Kalahari region of South Africa. This introductory chapter reviews what is currently known about Temminck's ground pangolins to identify research gaps. The chapter also will explore the literature available on the impacts of climate change on mammals, as well as the potential responses available to them, using the pangolin as a model animal.

1.1 PANGOLINS

1.1.1 General information

Pangolins range from 1-33 kg in body mass and are the only extant organisms in the order Pholidota, a sister clade to the Carnivora (Lovegrove 2012; Challender *et al.* 2020). Pangolins are elusive and solitary mammals covered in pale to dark brown coloured keratin scales, which make up 20 to 35% of their body mass (Heath 1992; Pietersen *et al.* 2020, W. Panaino unpublished data). The scales provide defence against predators such as lions (*Panthera leo*), tigers (*Panthera tigris*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and honey badgers (*Mellivora capensis*). Lifespan is unknown for wild pangolins, but rare reports suggest longevity of up to 20 years in captivity (Swart 2013). There are eight extant species of pangolin in the world; four in Asia and four in Africa (Challender *et al.* 2020). The four Asian species are the Chinese pangolin (*Manis pentadactyla*), Sunda pangolin (*Manis javanica*), Philippine pangolin (*Manis culionensis*), and Indian pangolin (*Manis crassicaudata*), and the four African species are the black-bellied pangolin (*Phataginus tetradactyla*), white-bellied pangolin (*Phataginus tricuspis*), giant ground pangolin (*Smutsia gigantea*), and Temminck's ground pangolin (*Smutsia temminckii*).

With the exception of the Chinese pangolin, which is fossorial, the Asian pangolins are semi-arboreal, whereas among the African pangolins, the black-bellied pangolin is strictly arboreal, the white-bellied pangolin is semi-arboreal, and the giant and Temminck's ground pangolins are fossorial (Challender *et al.* 2020). The arboreal species are more slender and have longer tails than do the ground-dwelling species (Wang *et al.* 2016; Challender *et al.* 2020). Pangolins spend most of their time sleeping in burrows, hollowed-out termitaria, small cave-like structures on rocky slopes, or the hollows of trees (Jacobsen *et al.* 1991; Heath 1992; Pietersen *et al.* 2014b). All species emerge from sleeping sites at night to forage, with the exception of the predominantly diurnal, black-bellied pangolin (Gudehus *et al.* 2020).

1.1.2 Ecological role of pangolins

Limited evidence suggests that pangolins play an important role in the ecosystems they inhabit (Challender *et al.* 2020), but further research is required to quantify the ecosystem

services they provide, including the services valued by humans. Understanding their ecological role will allow for a better understanding of the potential impact of their loss in ecosystems, which can inform decision-making regarding their management and investment in their conservation.

Pangolins are myrmecophagous mammals, feeding almost exclusively on ants and termites, including their eggs and larvae (Irshad *et al.* 2015; Pietersen *et al.* 2016). As predators to ants and termites, pangolins presumably act as a population control agent of social insects. It is likely that pangolins impact ant and termite community structure and abundance, but without empirical data to show it, the impacts of pangolins on social insects remain largely unknown. Ants and termites provide services to ecosystems by influencing nutrient cycling, soil structure, seed dispersal, pollination, decomposition, and they act as biological indicators of ecosystem health (Bignell and Eggleton 2000; Del Toro *et al.* 2012). By predating on ants and termites, pangolins could therefore influence ecosystem function through trophic interactions, nutrient cycling, and energy flow.

All pangolin species, except the black-bellied pangolin, are capable of digging burrows for shelter use, and digging in search of subterranean prey (Challender *et al.* 2020). In areas where other burrowing animals, such as armadillos or porcupines coexist, they do not necessarily have to dig their own burrows and often make use of existing ones (Pietersen *et al.* 2020). In areas where pangolins do not typically dig their own burrows, they regularly modify and maintain existing burrows, which can then be used as refuges for other burrowing animals. Digging burrows can contribute to soil turnover, gas exchange, and water infiltration, which in turn can decrease soil runoff and erosion, and increase soil moisture (Fleming *et al.* 2014). For example, in Taiwan, the burrowing activity of Chinese pangolins contributed to a total soil turnover volume of 1.08m³/ha (Chao *et al.* 2020), a volume similar to the soil turnover (1.6m³/ha) created by the foraging activity of the larger Cape porcupines (*Hystrix africaeaustralis*) (Bragg *et al.* 2005).

Pangolins may also facilitate the foraging success of other insect-eating animals. Pangolins do not deplete entire ant or termite colonies while foraging (Pietersen *et al.* 2020), leaving several prey items behind when moving to the next colony. By exposing ant and termite nests, pangolins may provide access to prey for other insect-eating animals. The ecologically similar armadillo (*Orycteropus afer*) provides such a service, whereby the ants and termites exposed by the armadillo during foraging activity are eaten by other animals, such as ant-eating chats (*Myrmecocichla formicivora*) (Taylor and Skinner 2001).

1.1.3 Conservation status and threats

On the IUCN Red List of Threatened Species, the Chinese, Sunda, and Philippine pangolins are listed as critically endangered (Challender *et al.* 2019a, b; Schoppe *et al.* 2019), and the Indian, white-bellied, and giant ground pangolins are listed as endangered (Mahmood *et al.* 2019; Nixon *et al.* 2019; Pietersen *et al.* 2019a). The black-bellied and Temminck's ground pangolins are listed as vulnerable (Ingram *et al.* 2019; Pietersen *et al.* 2019b). All eight pangolin species' population numbers are declining (IUCN 2019), although difficult to assess without data on wild population numbers. All pangolin species were up-listed from Appendix 2 to Appendix 1 by CITES in 2016 (Nash *et al.* 2018), which mean that they are now considered to be threatened with extinction.

The major threat to pangolins is their overexploitation for the illegal wildlife trade (Ingram *et al.* 2018), with pangolins currently considered the most trafficked mammal in the world (Aisher 2016; Challender *et al.* 2020). Their scales and body parts are used for traditional medicine and bushmeat (Boakye *et al.* 2015; Boakye *et al.* 2016). Another threat is electrocution by electrified fences (Beck 2008; Pietersen *et al.* 2014a). As a consequence of their bipedal locomotion and defence mechanism of curling into a ball when threatened (Ganguly 2013), once the belly or face of a pangolin makes contact with an electrified strand, the pangolin curls around the strand, and the result is often fatal (Beck 2008; Pietersen *et al.* 2014a). Road mortalities and habitat destruction are listed as further threats to pangolins (Pietersen *et al.* 2014a). The impacts of climate change have only recently been recognized as a potential, but unexplored threat to pangolins, especially to pangolin species that inhabit arid areas (Pietersen *et al.* 2020). As a consequence of their elusive nature and low population densities (Keeping 2014; Pietersen *et al.* 2014a), it is difficult to study pangolins in the wild, and therefore very little is known about them globally.

1.1.4 Temminck's ground pangolin: *Smutsia temminckii*

Temminck's ground pangolins are the most widespread pangolin species in Africa, and the only pangolin species that occurs in southern and eastern Africa (Pietersen *et al.* 2020). Although they are the most studied of the African pangolin species, very little is known about Temminck's ground pangolins (hereafter pangolins). I conducted a comprehensive search of the available literature pertaining to pangolins using Google Scholar as an online library source (Appendix; Table A1). I conducted the literature search to identify the gaps in the current understanding of the species, and particularly to find any literature that may contribute to the understanding of pangolin responses to climate change. The following key words were used to search for articles or books published in English-language, peer-reviewed formats only (published conference abstracts and policy reports were excluded): *Temminck's ground pangolin*, *ground*

pangolin, *African ground pangolin*, *Manis temminckii*, and *Smutsia temminckii*. The relevant full-text articles and books were reviewed, and additional published research was sourced through reference lists.

The following 11 themes (and number of published sources per theme) were identified in 72 pieces of literature found: population (15; includes status, genetics, densities, occurrence, and monitoring), illegal wildlife trade (12), phylogeny and palaeontology (10), ecology (6; includes home range, behaviour, and relocation), anatomy and physiology (6), culture (5; includes traditional medicine and cultural beliefs), husbandry and farming (4), disease (4), diet (3), biology (1), and broad (6; where three or more themes were identified). There has been a 53 % increase in the amount of research pertaining to pangolins over the past decade compared to the total amount of research published before 2010 (Figure 1.1). The increase in the amount of research published has presumably been in response to the increasing threat imposed on the species by the illegal wildlife trade, although the amount of research has increased across all disciplines. Of 72 pieces of literature published since 1930, only nine related to the ecology or diet of pangolins, and only four were from studies in the arid regions of southern Africa.

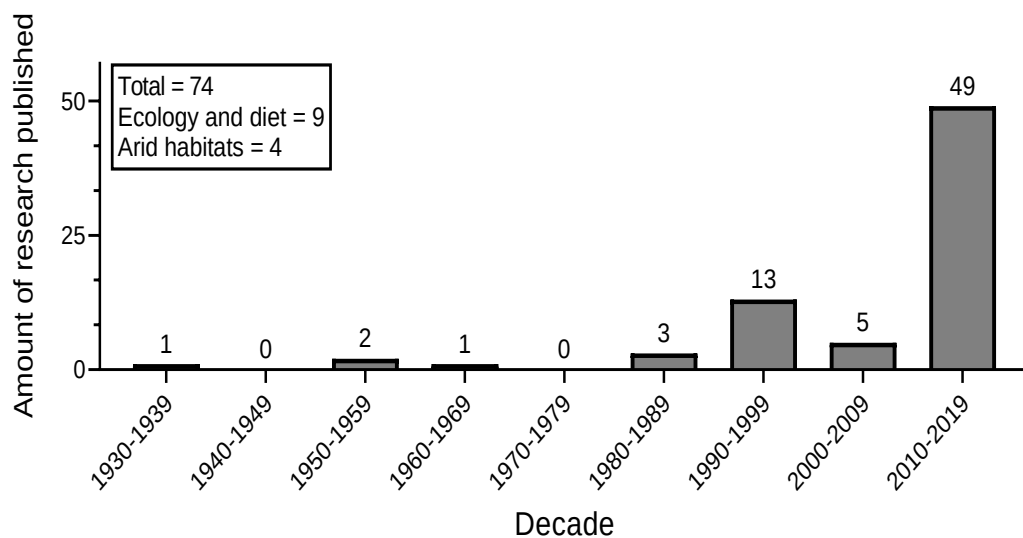


Figure 1.1: Number of peer-reviewed papers or books published each decade since 1930, with particular reference to Temminck's ground pangolins.

1.1.4.1 Distribution and habitat

Pangolins are widely distributed across southern and eastern Africa, inhabiting areas as far south as the northern parts of South Africa, including the southern Kalahari, and as far north as Chad and Sudan (Sweeney 1956; Swart 2013; Pietersen *et al.* 2019; 2020; Hoffman *et al.* 2020; also see Figure 1.2 below). The distribution of the species is not uniform throughout their range and is apparently limited by prey availability and habitat quality (Pietersen *et al.* 2020). Pangolins predominantly occupy semi-arid and mesic

savanna and woodland habitats, where average annual rainfall is 250 -1400 mm and they are excluded from forests and true deserts (Pietersen *et al.* 2019b; 2020). Their habitat also includes well-managed livestock farms, but they are generally excluded from degraded lands such as croplands and human settlements (Pietersen *et al.* 2019b). Within individual home ranges, which span about 6.5 km² in the Kalahari, no habitat selectivity has been observed (Pietersen *et al.* 2014b). However, pangolins exhibited habitat selectivity elsewhere in South Africa, preferring open savanna clearings, mixed tree savanna and calc brack thicket habitats over any others (Swart 1996). Typically, animals in arid areas have larger home ranges than their conspecifics inhabiting areas with higher rainfall (Alcala-Galvin 2013), presumably because higher rainfall results in higher primary productivity and more available resources. Pangolins in the Kalahari are smaller than their conspecifics in higher rainfall areas within South Africa, and smaller animals are expected to have smaller home ranges compared to larger animals (Pietersen *et al.* 2014b). Instead of having smaller or larger home ranges as predicted by body size and habitat, the home ranges of pangolins in the Kalahari were similar to the home ranges of pangolins inhabiting the more mesic, Zimbabwean habitat (Heath and Coulson 1997; Pietersen *et al.* 2014b). Pietersen *et al.* (2014c) speculated that the combined effects of body size and habitat productivity may explain the similar home ranges of pangolins observed across the varying habitats.

1.1.4.2 Breeding

Pangolins are largely solitary mammals, with males and females coming together only during the breeding season (Pietersen *et al.* 2020). Juveniles remain with their mothers only for a few months before being weaned (Swart 2013). Breeding in pangolins is generally considered aseasonal, although seasonal peaks have been recorded in some populations in South Africa (Heath 1992; Swart 2013; Pietersen *et al.* 2020). Gestation length is approximately 140 days (van Ee 1966), and pups are born around September (South African spring) in parts of South Africa, such as in the Transvaal and Kalahari regions (Jacobsen *et al.* 1991; Pietersen *et al.* 2020; W. Panaino personal observations). Pangolins have slow reproductive rates, with female pangolins giving birth to a single pup once per year (Coulson 1989; W. Panaino personal observations), or once every two years (Pietersen *et al.* 2020), although twins have been recorded on rare occasions (Jacobsen *et al.* 1991). Little is known about how the adult female pangolins meet the energetic costs of gestation or lactation. Furthermore, little is known about the dispersal of juvenile pangolins, which is energetically costly (Benoit *et al.* 2019) compared to their non-dispersing adult counterparts.

1.1.4.3 Diet

Pangolins are specialist feeders, using their strong sense of smell and long, sticky tongue to feed selectively on ants and termites (Sweeney 1956; Heath 1992; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen *et al.* 2016). They use their well-adapted forelimbs and powerful claws to dig open subterranean ant and termite nests, nests under the bark of trees, and superficial termitaria (Heath 1992; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen *et al.* 2020). Approximately 16% of their time active above ground is spent feeding, typically by digging shallow holes of up to 10 cm deep to gain access to subterranean prey (Swart *et al.* 1999). Feeding bouts (from a single prey colony) are short (~40 seconds), likely as a consequence of the activation of chemical and physical defenses of ants and termites, which progressively decrease the perceived value of the prey (Swart *et al.* 1999).

Pangolins show selectivity towards specific genera of ants and termites, and typically obtain all of their water from their prey (Swart *et al.* 1999; Pietersen *et al.* 2016). However, they are known to drink free-standing water opportunistically (Pietersen *et al.* 2020). The diet of pangolins has predominantly been assessed using direct behavioural observations and isotope analyses (Sweeney 1956; Jacobsen *et al.* 1991; Swart *et al.* 1999; Pietersen *et al.* 2016). Dietary assessments from six studies have revealed that pangolins, across their distribution range, feed on prey items from 17 ant and 9 termite genera (Table 1.1). Furthermore, pangolins do not tend to target the most abundant prey items. For example, in an area where *Pheidole* were the most abundant ants, they made up less than 1% of the diet, whereas *Anoplolepis* ants were not the most abundant, yet they made up 77% of the diet (by visually observing what they ate; Swart *et al.* 1999).

Isotope analyses alone did not yield positive results for inferring the pangolin diet due to multiple prey and non-prey items sharing similar isotopic values (Pietersen *et al.* 2016). Isotopic analyses were well-suited for estimating stable carbon and nitrogen enrichment values for pangolin organs, but the method was not useful for identifying specific prey items in the diet. Coupling isotopic analyses with behaviour data, however, revealed that Kalahari pangolins preyed on ants from three genera (*Anoplolepis*, *Camponotus*, and *Crematogaster*) and one termite genus (*Trinervitermes*; Pietersen *et al.* 2016).

While behavioural observations may be useful for identifying the predominant prey items in the pangolin diet, the observations alone may not account for additional, less abundant prey species taken in incidentally. Low abundance and unintentional ingestion of some ants and termites may make it difficult to accurately observe the diet, resulting in misrepresented prey items. Collecting and analyzing scat samples can provide a non-invasive, detailed record of an animal's diet (Kelly *et al.* 2012), without the need for an observer. Pangolins typically defecate once per day, excreting a sausage-shaped scat

containing soil, vegetation and the chitinous remains of ants and termites (Jacobsen *et al.* 1991; Heath 1992). Scats are usually buried, which may serve to avoid predator detection or to mark territories (Pietersen *et al.* 2020) but makes it difficult to find and collect the scat. Thus far, only one study has used scats to assess the pangolin diet, but only two samples were collected, and they were collected from a captive individual that was released into the wild (Jacobsen *et al.* 1991), so may not reflect the natural behaviour of the pangolin. There is thus a lack of detailed and accurate data for the diet of free-living pangolins.

Table 1.1: List of ant and termite genera recorded in the diet of pangolins across their distribution range and which of six different studies recorded them.

Genus	Studies recorded
Ants	
<i>Acantholepis</i>	3
<i>Aenictus</i>	5
<i>Anoplolepis</i>	2-6
<i>Camponotus</i>	2-6
<i>Crematogaster</i>	1,3,5,6
<i>Dorylus</i>	5
Formicidae*	1,2
<i>Monomorium</i>	3,5
<i>Myrmica</i>	3-5
<i>Ocymyrmex</i>	5
<i>Paltothyreus</i>	2
<i>Pheidole</i>	3-5
<i>Polyrhachis</i>	3,5
<i>Tapenomia</i>	3
<i>Technomyrmex</i>	3
<i>Tetramorium</i>	5
<i>Xiphomyrmex</i>	3
Termites	
<i>Amitermes</i>	1
<i>Ancistrotermes</i>	1

<i>Hodotermes</i>	5
<i>Macrotermes</i>	1
<i>Microtermes</i>	1
<i>Odontotermes</i>	1,2,3,5
<i>Rhadinotermes</i>	5
Termitidae*	2,3,5
<i>Trinervitermes</i>	2,3,5,6

*Unidentified genus of the ant or termite family. Studies: ¹Sweeney 1956, ²Coulson 1989, ³Jacobsen *et al.* 1991, ⁴Richer *et al.* 1997, ⁵Swart *et al.* 1999, ⁶Pietersen *et al.* 2016.

Although a number of attempts have been made to identify preferred prey species, few studies have assessed seasonal variation in the pangolin diet (Swart *et al.* 1999; Pietersen *et al.* 2016). Seasonality is an environmental constraint that influences food availability, and ultimately the ability for animals to obtain food resources (Storms *et al.* 2008). Understanding seasonal variation of pangolin food resources and how this variation influences their diet may provide information about the ability of pangolins to adapt to seasonal fluctuations in food resources, but it requires long-term data collection. One study that assessed the seasonal variation in the pangolin diet found no seasonal variation (Pietersen *et al.* 2016). Another study did find seasonal variation in the diet, whereby ants from the *Anoplolepis* and *Camponotus* genera and termites from the *Hodotermes* genus were preyed on more during winter compared to summer, and ants from the *Myrmecaria* and *Polyrhachis* genera were preyed on less during winter compared to summer. Clarity on seasonal variation in the pangolin diet, which may be obtained accurately from behavioural observations coupled with scat analyses, is therefore required.

Understanding how much food an animal requires for survival, growth, maintenance, and reproduction can provide information about how that animal copes in its environment, and its ability to adapt to changing environments (Pagano *et al.* 2018). Understanding how much food animals require may also provide insights into the ecological role they play in an ecosystem. As far as I am aware, no attempts have been made to assess how many ants and termites pangolins consume per 24h, or how much energy those ants and termites provide for pangolins. However, one study investigated the 24h energy expenditure by pangolins (see *Body temperature and metabolism* below), which may be useful for comparing daily pangolin energy intake (estimated using scats) with their potential daily expenditure.

1.1.4.4 Activity

The 24h activity patterns of mammals may provide insights about their nutritional status. Some nocturnal mammals switch to diurnal activity when they experience energy deficits as a consequence of low food availability, particularly during winter when the costs of maintaining constant high body temperatures are higher compared to the rest of the year (Guiden and Orrock 2020; van der Vinne *et al.* 2015; Weyer *et al.* 2020). Monitoring the 24h activity patterns of animals may thus provide insights into their ability to cope with fluctuations in climate and food resources but requires long-term data collection.

Pangolins are predominantly nocturnal, but diurnal and crepuscular activity has been reported during cooler months of the year (Coulson 1989; Jacobsen *et al.* 1991; Heath and Coulson 1997; Swart 1996; Pietersen *et al.* 2014b). The onset of activity has been reported to occur between 14:30 and 02:15 (Jacobsen *et al.* 1991; Swart 1996; Heath and Coulson 1997; Pietersen 2013; Pietersen *et al.* 2014b). In a detailed study, the onset of activity occurred between 19:00 and 22:00 for 61% of all observations (n=199; Swart 1996). The duration of above-ground activity previously has been shown not to vary seasonally (Swart 1996; Pietersen *et al.* 2014b) but pangolins have been recorded being active for 1-12 hours, although four studies found that pangolins were predominantly active for 4 to 8 hours (Swart 1996; Heath and Coulson 1997; Pietersen *et al.* 2014b).

Much of the research that has assessed pangolin activity has been short-term, or the research was conducted during an unspecified time of year (Jacobsen *et al.* 1991; Heath and Coulson 1997; Pietersen 2013; Pietersen *et al.* 2014b), providing little information on seasonal variability. Since crepuscular and diurnal activity typically occur during cooler months, and nocturnal activity occurs during warmer months (Swart 1996; Pietersen *et al.* 2014b), it is important to know what time of year the data were collected to ensure that the data are not biased towards any particular seasons. Pangolin activity has been assessed using direct behavioural observations, GPS tags, or radio transmitters (Jacobsen *et al.* 1991; Swart 1996; Heath and Coulson 1997; Pietersen *et al.* 2014b). While GPS and radio transmitter technology work well for estimating the onset of activity (Swart 1996; Pietersen *et al.* 2014b), behavioural observations may affect a pangolin's activity if the animal is aware of the observer's presence (Swart 1996; W. Panaino personal observations). Camera traps provide a non-invasive method for monitoring animal behaviour (Caravaggi *et al.* 2017), but they have never been used to assess pangolin activity patterns.

In addition to being short-term, most studies of pangolin activity have had small sample sizes (less than three pangolins). In one study, although the activity of three pangolins was studied, only one pangolin was monitored for a full year, while the other two were

monitored during winter and spring only (Pietersen 2013). The pooled data may therefore not reflect the true activity periods of pangolins and may be biased towards activity exhibited during the cooler months of the year. Another study, however, studied 18 pangolins for one year (Swart 1996), and it is, until now, the most extensive study on pangolin activity. However, the study took place in a mesic habitat, where the environment receives high rainfall and where pangolin food resources are likely abundant. Availability of food resources is known to impact an animal's 24h activity (Rezende and Bozinovic 2001; Lambert *et al.* 2009). It is therefore expected that pangolins in an arid habitat would behave differently to those in a mesic habitat with more rainfall. There is thus a need to comprehensively assess the activity of pangolins in a more arid habitat. A long-term study on the activity patterns of pangolins will allow me to detect seasonal changes, and to elucidate the role of factors such as photoperiod, environmental temperatures, and food availability in driving their 24h activity.

1.1.4.5 Metabolism and body temperature

The physiology of pangolins is of interest because they have been reported to maintain relatively lower metabolic rates and body temperatures than is expected based on their size (McNab 1984). Pangolin metabolic rates are less than 75% of that expected based on body mass (Speakman 2000; Boyles *et al.* 2019). The discrepancy between metabolic rate and body mass can partly be explained by the metabolically inactive scales (20 – 35% of body mass; Heath 1992; Pietersen *et al.* 2020, W. Panaino unpublished data) of pangolins contributing to the relatively high body mass compared to mammals of similar size (Heath and Hammel 1986). If the mass of the scales were excluded from the total body mass, the metabolic rates of pangolins would be less than 60% of that expected based on body mass. It has also been suggested that the low metabolic rates of pangolins reflect their slow life histories (Boyles *et al.* 2019). Furthermore, low metabolic rates and body temperatures are characteristic of myrmecophagous mammals and are associated with burrowing habits and a diet of ants and termites (McNab 1984; Legendre and Botha-Brink 2018; Boyles *et al.* 2019).

Obtaining detailed information on the pattern of body temperature is useful because mammals without sufficient access to food and water typically exhibit exaggerated 24h body temperature minima and maxima (Yoda *et al.* 2000; Mitchell *et al.* 2002; Wang *et al.* 2006; Angilletta *et al.* 2010; Samara *et al.* 2012; Hetem *et al.* 2016; McKinley *et al.* 2017). The decreased 24h body temperature minima and increased 24h body temperature maxima result in increased amplitudes of the 24h rhythm of body temperature, also known as heterothermy. Increased heterothermy associated with energy and water deficits in mammals may be used as a proxy for the physiological welfare of mammals (Hetem *et al.* 2016) but requires long-term measurements of core body temperature.

The core body temperature of pangolins has only ever been reported for a single free-living individual for 34 days during winter (Pietersen 2013). Core body temperature of the pangolin fluctuated predominantly between 32 and 35 °C (range: 29.5 - 35.4 °C) and was on the lower end of the distribution of body temperatures for mammals (Lovegrove 2012). Body temperature of that pangolin peaked during activity and steadily decreased during the inactive phase (Pietersen 2013). Pietersen (2013) suggested that variation in free-living pangolin body temperature likely occurred as a means of coping with low food availability in an unpredictable environment but he did not assess the effects of food availability on body temperature patterns. Little is known about how free-living pangolins regulate body temperature. In one study, pangolins placed inside a temperature-controlled cabinet and exposed to experimental ambient temperatures of 5 - 35 °C exhibited rectal temperatures that were positively and linearly associated with the experimental temperatures ($r^2=0.71$; Boyles *et al.* 2019). The rectal temperature of pangolins undergoing rehabilitation (after being confiscated from the illegal wildlife trade) has been reported to be 32 – 34 °C (Wicker *et al.* 2020). While data from laboratory conditions and confiscated pangolins are important and have implications for the welfare of pangolins under controlled or stressful, captive conditions, without comparison to free-living pangolins in natural settings there is no reference base for normal body temperatures. Long-term measurements are required to understand how fluctuations in environmental temperatures and food resources affect the body temperature patterns of free-living pangolins.

1.2 CLIMATE CHANGE

Increasing emissions of greenhouse gases, such as CO₂, are the primary cause of global anthropogenic climate change (Mikhaylov *et al.* 2020). Since the 1970's, global average air temperatures have increased by 0.2°C per decade (Solomon *et al.* 2007). Climate change models predict further global temperature increases of up to 4.5°C in the 21st century (Stocker *et al.* 2013). The African continent is strongly impacted by climate change and the impacts on fauna and flora are apparent in various ecosystems (Gitay *et al.* 2002; Hannah *et al.* 2002; Fuller *et al.* 2010; Boyles *et al.* 2011; Hetem *et al.* 2012; Fuller *et al.* 2014; Hetem *et al.* 2014; Pacifici *et al.* 2017). Surface temperatures in parts of Africa have been rising at more than double the global rate (Engelbrecht *et al.* 2015). Limiting future warming in Africa to no more than 1.5°C is crucial because model predictions show that warming above 1.5°C will result in an increased frequency of heat waves (James and Washington 2013; Nangombe *et al.* 2018). Increasing temperatures will impact organisms by imposing greater heat loads on them, thereby increasing their water demands (Brierly and Kingsford 2009; Bloor *et al.* 2010). Furthermore, increasing temperatures will impact the hydrological cycle by reducing soil moisture and surface

water available to organisms through increased evaporation and evapotranspiration (Norby and Luo 2004; Engelbrecht *et al.* 2015).

In addition to increased air and surface temperatures, southern Africa is strongly affected by El Niño-Southern Oscillations (ENSO) through reductions in rainfall, further impacting the hydrological cycle (Hulme *et al.* 2001). Climate change models predict precipitation reductions of between 20 – 30% in the future, particularly for areas that already occur in dry latitudes (Stocker *et al.* 2013). As a consequence of rainfall reductions and temporal shifts in rainfall regimes, the south-western regions of southern Africa will experience more extreme droughts and reductions in primary productivity (Hulme *et al.* 2001; Shongwe *et al.* 2009; Engelbrecht *et al.* 2015).

1.2.1 Climate change across the pangolin distribution range in Africa

Pangolins are distributed widely across southern and eastern Africa (Pietersen *et al.* 2020). Within their distribution range, climate change models predict surface temperature increases of 3-5 °C over the tropics and 4-6 °C over the subtropics (Engelbrecht *et al.* 2015). Warming is predicted right across the pangolin distribution but is expected to be most extreme at the south-western edge of their range (Figure 1.2 *left*). Increased precipitation is expected across most of the pangolin distribution, which includes eastern and central-to-northern Africa, but decreased precipitation is expected in the south-western edge of the distribution, which includes the Kalahari (Figure 1.2 *right*). Even if rainfall remained constant right across the pangolin range, increasing environmental temperatures will increase evaporation and transpiration, which will reduce ground and surface water necessary for organism survival, particularly in the more arid regions (Pereira 2017). Climate projections also include an increased precipitation variability and frequency of heat waves and droughts, but these extreme events are predicted to be most severe for the south-western parts of the pangolin distribution (Shongwe *et al.* 2009; Engelbrecht *et al.* 2015).

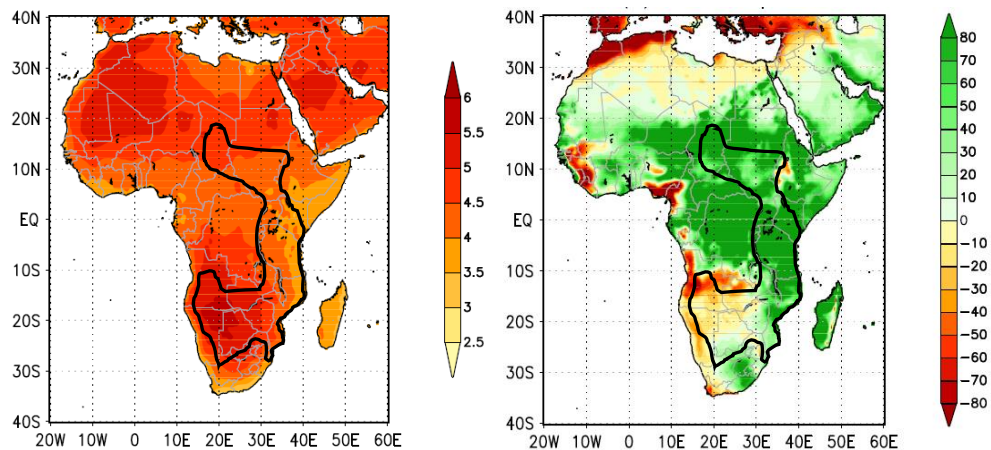


Figure 1.2: Projected change in annual average temperature (°C; left) and rainfall (mm; right) across the pangolin distribution range (black outline) for 2071-2100 compared to 1961-1990. Adapted from Engelbrecht *et al.* (2015), using the 90th percentile models under the A2 SRES scenario.

Increased temperatures and evapotranspiration are predicted to reduce soil moisture (Le Roux *et al.* 2016). In arid and semi-arid systems, water is the primary driver of ecosystem productivity and functioning (Ehleringer *et al.* 1998), and the timing and amount of precipitation determines vegetation dynamics (Martinez and Gilabert 2009). The combined effects of increased warming, reduced soil moisture, and shifts in rainfall regimes will result in extended dry periods and shorter productive periods, effectively causing agricultural drought (Engelbrecht *et al.* 2015; Shongwe *et al.* 2009). Increased frequency of droughts will result in shorter growing seasons, decreased vegetation cover, and can lead to increased soil erosion and land degradation (Martinez and Gilabert 2009; James and Washington 2013). Moreover, increasing atmospheric CO₂ and shorter growing seasons will result in vegetation shifts and changes in land cover, such as the transformation of African grasslands to systems dominated by trees (Higgins and Scheiter 2012; Engelbrecht and Engelbrecht 2016), or the desertification of grasslands (Mirzabaev *et al.* 2020). Habitat degradation and alteration as a consequence of increased CO₂, air and surface temperature, and decreased precipitation will lead to decreased carrying capacity for fauna and flora and will accelerate biodiversity extinction risks (Nic Lughada *et al.* 2020; Raven 2020).

1.2.2 Potential impacts of climate change on pangolins

Pangolins inhabiting the south-western edge of their distribution, including the semi-arid Kalahari, are likely to be most vulnerable under the projected climate change scenarios, since water is so crucial for healthy ecosystem functioning and primary productivity in arid systems (Ehleringer *et al.* 1998; Niang *et al.* 2014; Engelbrecht *et al.* 2015). Although

some efforts have been made to understand their ecology (Sweeney 1956; Coulson 1989; Jacobsen *et al.* 1991; Heath and Coulson 1997; Swart *et al.* 1999; Richer *et al.* 1997; Pietersen *et al.* 2014b; 2016), there has been no attempt to assess the direct and indirect impacts of climate change on pangolins. Increased environmental temperatures, as well as more sporadic and unpredictable rainfall, could impact pangolins directly through increased heat gained from their environment and increased water demands for thermoregulation, and indirectly through the effects on their prey resources.

1.2.2.1 Direct impacts

While diurnal mammals must contend with high environmental heat loads during the day, nocturnal mammals, although they avoid high heat loads, must contend with cold nights. A major route for heat loss in dry environments is via radiation to the clear night sky, which acts as a large heat sink with an effective temperature of between -10 °C and -30 °C (Mitchell *et al.* 2018). As a consequence of that heat sink, the costs of maintaining constant high body temperatures at night are high. Some nocturnal mammals switch to diurnal activity when exposed to low night-time temperatures during winter, a response likely to provide energetic benefits (Warnecke *et al.* 2008; Pagon *et al.* 2013; Guiden and Orrock 2020). By becoming diurnal, otherwise nocturnal mammals reduce the gradient for heat loss to the environment, thereby conserving energy that would otherwise be used for maintaining high body temperatures in the cold (Warnecke *et al.* 2008; van der Vinne *et al.* 2015). Indeed, by switching to diurnal activity during winter, nocturnal white-footed mice (*Peromyscus leucopus*) reduced potential heat loss by 4% (Guiden and Orrock 2020).

Although switching to diurnal activity incurs energetic benefits, exposure to solar radiation and thus, potentially high heat loads, increases water costs. Increased daytime temperatures associated with climate change may result in more scenarios whereby environmental temperature exceeds body temperature. When environmental temperature approaches or exceeds body temperature, the need for evaporative cooling increases, thereby impacting the water balance of animals (Mitchell *et al.* 2018). These increased water demands may lead to dehydration and hyperthermia, which can be fatal, particularly in hot and dry environments (Welbergen *et al.* 2008; Albright *et al.* 2017). Increased evaporation as a consequence of increased environmental temperatures expected with climate change will also reduce the surface water available to mammals (Pereira 2017), which may further compromise their water balance. Nocturnal mammals in arid environments that alter their activity across the diel cycle may need to trade off water balance against energy balance.

Increased air temperatures as a result of climate change will likely benefit nocturnal mammals when they are active at night. The increased air temperatures will reduce the

gradient for dry heat loss to the environment, thereby allowing nocturnal mammals to conserve energy. However, the increased air temperatures will make little difference to the radiant heat sink of the clear night sky. Increasing surface temperatures will also benefit mammals at night, particularly smaller mammals that are close to the ground. In the Sonoran Desert in Arizona, USA, for example, night-time air temperatures during summer were more than 2°C higher 3 cm above the ground compared to 1.5 m above ground (Walsberg 2000). Increased surface and air temperatures close to the ground will therefore further benefit mammals further by reducing the gradient for dry heat loss.

Pangolins are likely to be impacted by increasing environmental temperatures throughout their range. Pangolins are medium-sized mammals, but their relatively smaller size means that they gain and lose heat more rapidly than larger mammals in their environment like antelope. Another disadvantage of smaller size is more rapid dehydration when under a heat load. Pangolins rarely drink free-standing water (Challender *et al.* 2020) but may need to do so more frequently as their water demands increase with increasing environmental temperatures. Unfortunately, not enough is known about pangolin responses to fluctuations in climate and water availability to accurately predict the impacts of climate change on them.

1.2.2.2 Indirect impacts

The indirect impacts of climate change are also important for mammals because of the effects on food availability, habitat, species interactions (predation and competition), and disease (Harley 2011; Cahill *et al.* 2012; Ockendon 2014). Many insects depend on vegetation for survival (Cros *et al.* 1997; Donovan *et al.* 2001; Moll *et al.* 2012; Weyer 2018). Increasing air temperatures resulting in increasing rates of evapotranspiration (Le Roux *et al.* 2016) will reduce soil moisture, groundwater, and surface water necessary for sustainable vegetation growth and insect life (Martinez and Gilabert 2009; Cornelius and Osbrink 2010). Climate-change induced reductions in insect populations will impact the energy balance of animals that depend on these insects as prey resources through trophic disruptions.

Reductions in insects will also impact the hydration status of some myrmecophages because many of them obtain their source of body water from their prey (Green *et al.* 1992; Clark 2005; Pietersen *et al.* 2020; Weyer *et al.* 2020). Without drinking water, animals can obtain water through preformed water in food or through metabolic water production. Insects provide a relatively high preformed water content (Withers *et al.* 2016). Metabolic water is also indirectly dependent on energy intake (Donald and Pannabecker 2015), so a body water imbalance is likely to occur in myrmecophages in the face of reductions in insect populations.

Very little is known about how myrmecophagous mammals respond to shifts in the abundance, activity, and accessibility of their prey. Seasonal and climate change-induced shifts in the abundance and activity of insects are likely to impact both the energy and water balance of myrmecophages. Insect abundance and activity decrease during winter compared to in summer in arid habitats (Barrow and Parr 2008; Davies *et al.* 2015), likely making winter a nutritionally challenging period for myrmecophages. In response to dry conditions, some insects also move deeper underground (Williams and Middleton 2008), likely making them less accessible to myrmecophages. There are, however, some insect species that are well-adapted to high air temperatures and high rates of body water loss in arid habitats (Cloudsley-Thompson 2001; Zachariassen and Pedersen 2002; Silva *et al.* 2018). For example, desert-adapted Saharan silver ants (*Cataglyphis bombycina*) are able to remain active at surface temperatures of up to 70°C (Wehner *et al.* 1992; Shi *et al.* 2015), and tenebrionid desert beetles can tolerate body water losses of more than 80% (Zachariassen and Pedersen 2002). The resilience of such species to harsh environmental conditions presumably means that they remain accessible to their predators. If the prey of various myrmecophages can tolerate increasing environmental temperatures, and remain active close to the surface, then the myrmecophages that depend on them will likely not be as negatively affected by the indirect effects of climate change compared to those that depend on vulnerable prey. Understanding shifts in the abundance, activity, and accessibility of ants and termites over seasons and in response to climate change is crucial for understanding the responses of myrmecophages, such as pangolins, because these fluctuations will likely impact their energy and water balance.

Phenological changes can also influence the relationship between insects and the predators that depend on them. Phenology refers to the timing of seasonal biological events (Visser *et al.* 2010). Changes in the timing of reproduction, first appearances, and migration of organisms are known to occur in response to changes in air temperature and rainfall (Gordo and Sanz 2005; Carey 2009; Bronson 2009). By speeding up their rates of development, rising temperatures have been associated with earlier first appearance events for many insect species (Forrest 2016). For example, first flights by butterflies have advanced by 24 days in response to changes in air temperature and rainfall in California, USA (Forister and Shapiro 2003). When the phenology of herbivorous insects changes more rapidly than the plants they feed on, a trophic mismatch occurs (Gordo and Sanz 2005), impacting the survival of insects and the predators that depend on them (Forrest 2016). Moreover, animals often match the timing of reproduction with the timing of peak resource availability. Matching breeding with peak resource availability provides the young with enough food for growth (Visser *et al.* 2006) and provides pregnant and lactating females with energy to sustain them during the energetically stressful pregnancy and lactation periods (Trebaticka *et al.* 2007). If pangolins match the timing of

reproduction with peak resource availability, and if the phenology of ants and termites changes with climate change, a trophic mismatch could occur that could ultimately impact pangolin performance (defined as the “interface between lower-level morphological and physiological functions and the ecological context in which these traits influence fitness”; John-Adler *et al.* 2009) by impacting offspring survival. Long-term data on temporal changes in vegetation and insect availability are needed to understand whether pangolins will experience shifts in food availability as a consequence of phenological changes resulting from climate change.

Mammals with a specialized diet have a higher probability of experiencing negative impacts of climate change compared to generalist feeders because of their inability to exploit prey resources outside of their preferred selection (Maron *et al.* 2015; Pacifici *et al.* 2017). Specialist feeders may be especially vulnerable if their preferred prey items are not well-adapted to cope with the effects of changing environments. In the Kalahari, the northern harvester termite (*Hodotermes mossambicus*), a species highly dependent on the availability of grass, accounts for ~75% of the aardvark diet and aardvarks do not exploit other prey species in the termite’s absence (Weyer 2018). Lower than normal annual rainfall reduced the availability of grass, which resulted in reduced harvester termite abundance, and was likely responsible for increased aardvark mortalities (Rey *et al.* 2017; Weyer 2018; Weyer *et al.* 2020). It is unknown whether pangolins feed on insect species that are similarly susceptible to changes in the climate, or whether they can shift their diet in if their favoured prey species become less available.

If limitations in insect food abundance occur they may also increase local interspecific and intraspecific competition (Ayala 1970; Moore and Yong 1991; Williams *et al.* 2006). Less abundant insect prey resources with climate change are likely to result in pangolins experiencing increased competition for food from other pangolins in the area or from other insect-eating species such as aardvarks, bat-eared foxes (*Otocyon megalotis*) and aardwolves (*Proteles cristata*). Climate-induced changes in the spatiotemporal distribution of food resources drives habitat selectivity and animal movement into more favourable areas (Maron *et al.* 2015; Dupke *et al.* 2016), further increasing competition. If animals cannot exploit other resources, increased competition for limited food resources will ultimately lead to reduced performance (Irons *et al.* 2007; Roden-Reynolds 2014; Harvey *et al.* 2013) by reducing energy intake, growth, and reproduction (Heesen *et al.* 2013).

Predation risk also may increase with limited food resources arising as a result of climate change (Traill *et al.* 2009). Limited food resources may lead to range expansion for many species to more suitable habitats (also see 1.3.1 *Range shifts and movement*). Range expansion in response to resource abundance can interrupt predator-prey interactions,

introduce new ones (Laws 2017), or can even increase intraguild predation between sympatric species (Pamperin *et al.* 2006). Indeed, the range expansion resulting in increased overlap between two carnivore species likely was the reason for the killing of an arctic fox (*Alopex lagopus*) by a red fox (*Vulpes vulpes*) (Pamperin *et al.* 2006). In cases where animals cannot expand their range (i.e., because of man-made or geographical barriers), they may need to compensate for low resource abundance or quality in their current environment by altering the duration or timing of their foraging activity. Increasing the time spent feeding can increase predation risk (Beauchamp 2009; Hentley *et al.* 2014) by reducing vigilance (Beauchamp 2015) and increasing exposure to predators. Furthermore, by shifting the timing of their foraging activity in response to limited food abundance, animals could be exposed to predators they would otherwise avoid (Metcalf and Steele 2001). Shifts in species interactions are complex, and ultimately, they require an understanding of species responses to changing environments through long-term empirical field data collection.

Climate change is also predicted to increase the outbreak of disease in terrestrial systems by increasing vector reproduction rates and population growth, and by increasing parasite development rates and periods of infectivity (Harvell *et al.* 2002; Purse *et al.* 2006). Although range shifts and migration allow animals to escape potential pathogens, they also can advance the spread of infectious diseases and introduce novel diseases to hosts without immunity to those novel pathogens (Harvell *et al.* 2009; Altizer *et al.* 2011). Animals that cannot shift their range (because of man-made or geographical barriers) may face greater exposure to local pathogens as a result of climate change. Climate change has been linked to biodiversity losses as a consequence of reduced defence against pathogens induced by environmental stressors (Kiesecker *et al.* 2001; Cahill *et al.* 2012). For example, El Niño-induced increases in temperature variability resulted in increased susceptibility to fungal diseases in *Atelopus* amphibians (Rohr and Raffel 2010). Additionally, suppression of host immunity likely caused by stress of the rutting season, hunting season, and unusually high air temperatures is believed to be the underlying mechanism triggering fatality in musk ox (*Ovibos moschatus*) in Norway (Ytrehus *et al.* 2008). Pangolins are known to have poor immunity, and are thus highly susceptible to infection and disease, especially when they are stressed (Choo *et al.* 2016; Wicker *et al.* 2020). Pangolins that have been exposed to starvation, dehydration, and extreme environmental temperatures, from being held captive in the illegal wildlife trade chains, regularly suffer from infections such as pneumonia, secondary to stress-related immune suppression (Wicker *et al.* 2020). Understanding the direct and indirect impacts of climate change on pangolins will allow us to better predict their responses to infection and disease, and better conserve this already vulnerable species.

1.3 POTENTIAL RESPONSES AVAILABLE TO PANGOLINS TO BUFFER THE EFFECTS OF CLIMATE CHANGE

1.3.1 *Range shifts and movement*

As a consequence of reduced quality or quantity of food resources associated with climate change, range shifts may occur towards more favourable habitats (Owen-Smith and Ogutu 2012; Shah *et al.* 2012). Animal movements are likely to occur in arid environments where the unpredictable nature of rainfall, which drives vegetation growth and ultimately food productivity, places pressure on animals to search for more favourable habitats (Owen-Smith and Ogutu 2012). Although pangolins are relatively small, bipedal, and non-migratory mammals, they can cover large areas within their habitats. Juveniles in the Kalahari have been reported to move up to 49 km in 8 months (Pietersen *et al.* 2014b). Although movement to another area may provide animals with more suitable habitats, it also may increase interspecific competition, expose pangolins to novel levels of predation, and risk the spread of disease between local populations (Harvell *et al.* 2002; Williams *et al.* 2006; Traill *et al.* 2009). Man-made barriers such as electrified fences and roads, and geographical barriers, however, may limit movements of many species under the predicted climate change scenarios. Indeed, during drought conditions in the Kalahari, fences prevented wildebeest migrations towards more favourable habitat and resulted in mass declines in their population (Owen-Smith and Ogutu 2012). As a consequence of their defence mechanism of rolling into a ball when threatened, pangolins are susceptible to electrocution on electrified fences (Beck 2008; Pietersen *et al.* 2020), so not only will they not be able to move out of some areas but they may succumb in an attempt to do so. Fragmented habitats, a lack of safe corridors, and a lack of suitable habitat are likely already to limit range shifts of pangolins. Pangolins therefore will need to rely on alternative mechanisms to buffer the effects of climate change.

1.3.2 *Genetic adaptation*

One such mechanism is adaption through changes in the genetic composition of the population. Through range shifts, new genetics may be introduced into local populations, which can increase genetic variation and improve the population's chances of adapting to changing environments (Garant *et al.* 2007). Alternatively, some individuals with specific traits within a population may be favoured. Microevolution is another form of genetic adaptation that may allow animals to buffer the effects of climate change (Hetem *et al.* 2014). Microevolution entails a process in which genotypes that improve performance in the face of changing environmental conditions are selected for and genotypes that reduce performance decline in frequency (Visser 2008). However, the potential for a species to buffer climate change will depend on the alleles already present in the population.

A morphological trait, which is determined by a specific genetic code, that could allow animals to buffer the effects of changing environments is coat colour (Hetem *et al.* 2009). For example, a decrease in the proportion of dark-coloured Soay sheep (*Ovis aries*) has been observed in response to increasing temperatures in the United Kingdom (Maloney *et al.* 2009). Whereas dark coat colour may have been advantageous in the past for absorbing solar radiation to offset metabolic costs of heat production during cold conditions, there will be less benefit in a warming future. Lighter coat colour reduced the absorption of solar radiation in springboks (*Antidorcas marsupialis*) in the Karoo, South Africa, thereby reducing their solar heat load during summer compared to darker coat colours, potentially offering an advantage to the white morph of springbok in facing climate change (Hetem *et al.* 2009).

Microevolution is most likely to occur in short-lived species with fast generation times rather than in long-lived species with slow life histories (Reznick and Ghalambor 2001; Yoshida *et al.* 2003). However, examples do exist where relatively long-lived species, such as the Canadian lynx (*Lynx canadensis*), which has a maximum lifespan of 16 years (Kolbe and Squires 2006), have increased genetic differentiation between populations (Row *et al.* 2014). The lynx genetic differentiation is predicted to increase in response to future climatic divergence without any physical landscape changes. It is unclear whether species with slow life histories, such as pangolins, will also be able to genetically adapt and whether these adaptations will occur quickly enough in response to rapidly changing climate. Species with slow life histories (species with a long life span and low reproductive output) are less likely to have their populations recover if they do decline, and are thus prone to extinction if they cannot adapt in other ways (Gomulkiewicz and Holt 1995; Berteaux *et al.* 2004; Rondinini and Visconti 2015). Whether heritable changes that occur through epigenetic processes can buffer mammals against some of the consequences of climate change is not known (Fuller *et al.* 2016). Although genetic changes may partially explain some responses of mammals to changing environments, these responses often are more strongly attributed to phenotypic plasticity (Réale *et al.* 2003). Like many long-lived animals (Fuller *et al.* 2016), pangolins will likely need to rely on phenotypic plasticity if they are to survive in the future.

1.3.3 Phenotypic plasticity

Phenotypic plasticity refers to environmentally induced variation in phenotypes from a single, existing genotype (DeWitt and Scheiner 2004). Organisms may employ plastic responses to changes in their environment through changes in their morphology, physiology, and behaviour (Miner *et al.* 2005). Unlike genetic adaptation, phenotypic plasticity is an effective means of adaptation to rapidly changing environments because it can occur within the lifespan of a single individual (Charmantier *et al.* 2008) rather than its

future generations. However, the extent to which phenotypic plasticity will buffer organisms against the direct and indirect effects of climate change is poorly understood.

1.3.3.1 Phenology

As indicated above (1.2.2.2 Indirect impacts) phenology refers to the timing of seasonal biological events, such as breeding (Visser *et al.* 2010). Seasonal breeding in many mammals is triggered by changes in their energy balance as a consequence of changes in food availability (Bronson 2009). When changes in their environment occur, animals can shift the timing of their breeding to match the timing of peak food availability to promote performance through survival of adults and their offspring (Visser *et al.* 2006, 2010). Indeed, over a period of 10 years in Canada, red squirrels (*Tamiasciurus hudsonicus*) advanced the timing of their breeding by 18 days in response to increasing spring temperatures and food availability (Réale *et al.* 2003). However, in some cases, like when food abundance is low, animals will delay breeding to promote individual adult survival, but in doing so they produce fewer offspring. For example, Antarctic fur seals (*Arctocephalus gazella*) do not breed during years of low food availability, thereby increasing the chances of survival of adults and ultimately increasing their performance (Forcada *et al.* 2008). However, by delaying breeding and producing fewer offspring, the capacity for genetic adaptation is limited compared to when animals have shorter generation times (Forcada *et al.* 2008).

For long-lived mammals, photoperiod, which will not shift with climate change, is usually the driver for seasonal breeding (Bronson 2009). If increasing temperatures result in earlier plant growing seasons and earlier food abundance peaks, mismatches will occur between the birth of young and peak resource availability if animal breeding date is fixed. Mismatches between birthing time and peak food availability may lead to reductions in energy intake and thus reductions in the growth rates of young during early development (Saalfeld *et al.* 2019). These mismatches will ultimately reduce the performance and survival of animals, especially those with fixed breeding seasons, such as when photoperiod is the breeding stimulus. For example, a 4°C warming in West Greenland has advanced the growing season of plants, but caribou (*Rangifer tarandus*) breeding has not advanced in synchrony with plant growth because their breeding is timed by photoperiod, resulting in increased mortality of caribou calves (Post and Forchhammer 2008). There is a plethora of evidence documenting climate-induced phenological changes and mismatches in animals in the Northern Hemisphere (Burthe *et al.* 2011; Mills *et al.* 2013; Reed *et al.* 2013; Plard *et al.* 2014; Sheriff *et al.* 2015), but little is known about phenological shifts of animals in the Southern Hemisphere. The difficulties associated with studying pangolins in the wild, and their breeding in particular, makes it

difficult to assess the proximate causes of any potential phenological changes that might occur with climate change.

1.3.3.2 *Body size*

Body mass declines, attributed to reduced food availability, reduced foraging time, and high air temperatures, have been observed in many species facing climate change (Gardner *et al.* 2011; Mason *et al.* 2014). In line with Bergmann's rule, small body sizes evolve in warm environments (Bergmann 1847). Small body size is considered advantageous because it favours heat loss as a consequence of the relatively large surface area to volume ratio of small animals (Gardner *et al.* 2011). However, smaller animals also will gain heat more rapidly in hot environments compared to larger animals, and the demand for evaporative cooling will increase as air temperatures exceed body temperatures more frequently (Mitchell *et al.* 2018). Small animals are more susceptible to dehydration and hyperthermia when exposed to high radiant heat loads compared to larger animals (McKechnie and Wolf 2010; Fuller *et al.* 2016).

Small body size also reflects poor growth in animals. In the Kalahari, meerkat (*Suricata suricatta*) pup body mass has declined over the last 20 years in response to increased air temperatures, likely as a consequence of decreased water content of their prey or because of the increased water and energy costs associated with thermoregulation (Van de Ven *et al.* 2020). Pangolins in the Kalahari are smaller than their conspecifics in higher rainfall habitats, likely because of the low productivity and thus low prey availability in the Kalahari compared to mesic regions (Pietersen *et al.* 2014c). Currently, there are no data on changing trends in body mass for pangolins, although it will likely be difficult to assess in the wild in many regions given their rare and elusive habits, resulting in infrequent encounters in nature. The increasing confiscations of pangolins from the illegal wildlife trade by law enforcement perhaps presents an opportunity for body mass measurements to be collected over the long-term and should be explored further.

1.3.3.3 *Physiology*

Animals in hot and dry environments will need to rely on physiological and behavioural plasticity if they are to survive in a warming world. When water is readily available, animals can use evaporative cooling mechanisms to regulate body temperature in hot environments (Jessen 2001a; Robertshaw 2006). In hydrated animals, evaporative cooling typically increases as body temperature increases during exposure to heat stress (Collier *et al.* 2002; Cain III *et al.* 2006; Robertshaw 2006; Bernabucci *et al.* 2010), and sometimes even before the increases in body temperature (Mitchell *et al.* 2018). However, as drinking or prey water become increasingly limited with climate change, animals will need to exhibit plasticity in their ability to conserve body water to avoid

dehydration. Dehydration compromises physiological function and can be fatal (Angilletta *et al.* 2010). Small mammals will be particularly prone to dehydration as a consequence of their large surface area to volume ratio (Degen 2012; Alagaili *et al.* 2020).

Adaptations available to some animals when water is limited include the reduction of water loss in urine and faeces (Cain III *et al.* 2006; Ostrowski *et al.* 2006). Dehydration can stimulate the alteration of kidney function through the slowing of glomerular filtration rate and can be used to increase water absorption (Kamili *et al.* 2013). Glomerular filtration rate in water-deprived dromedary camels (*Camelus dromedarius*), for example, decreased by 20% compared to hydrated animals (Kamili *et al.* 2013). Through increased water absorption in the kidneys, water stress induces a decrease in urine output and higher urine concentration (Ostrowski *et al.* 2006; Schwimmer and Haim 2009; Degen 2012). In addition to alterations in urine production, water stress induces the production of dry faeces through increased water reabsorption in the gastrointestinal tract (Jaber *et al.* 2013; Chedid *et al.* 2014). Indeed, dehydrated Arabian oryx (*Oryx leucoryx*) increased urine concentration, reduced urine volume by 40% and reduced faecal water content by 5%, thereby allowing the animals to conserve 550 g of water per day (Ostrowski *et al.* 2006).

Perhaps a more common response to water deprivation in mammals is the reduction of panting or sweating rate, which are important avenues for evaporative heat loss, especially in hot and dry environments (Alamer and Al-hozab 2004; Robertshaw 2006; McKinley *et al.* 2017). Reducing the rate of evaporation at a given body temperature or increasing the threshold at which panting or sweating is initiated can reduce evaporative water loss (Schwimmer and Haim 2009). For example, in a hot environment, dehydrated eland (*Taurotragus oryx*) delayed panting and sweating until threshold skin temperature was higher than the threshold skin temperature of hydrated eland, thereby conserving water (Finch and Robertshaw 1979). It is unknown whether pangolins use panting to regulate body temperature, but it is possible, since an increased breathing rate was observed in Chinese pangolins (*Manis pentadactyla*) when air temperatures rose above 32 °C (Heath and Hammel 1986).

Because pangolins lack sweat glands (Hyman and Wake 1992; Feldhamer *et al.* 2007), they will not be able to regulate water conservation through inhibited or delayed sweating. One advantage of not having sweat glands in a hot and dry environment, though, is that the body surface temperature will increase in the absence of evaporative cooling. Increased body surface temperature will decrease the thermal gradient between the body surface and the hot environment, thereby reducing the gradient for dry heat gain and reducing the potential for evaporative cooling (Jessen *et al.* 1998). Water can, however, diffuse through the skin via insensible water loss, and may be a significant contributor to

temperature regulation in the absence of sweat glands (Dmitrieva and Burg 2011; Nicolaus *et al.* 2016). Elephants, for example, do not have sweat glands and can lose water through the skin via diffusion, which can then be evaporated to regulate body temperature (Dunkin *et al.* 2013). In hot environments, where water (drinking and dietary) is limited, cutaneous water loss can be reduced through modifications of the integument. For example, some desert birds acclimated to high temperatures alter the lipid composition of their stratum corneum, which reduces cutaneous water loss, thereby conserving water (Haugen *et al.* 2003).

Selective brain cooling is another example of a mechanism available to some mammals that reduces evaporative water loss and conserves water (Hetem *et al.* 2010; Hetem *et al.* 2014; Fuller *et al.* 2016). Selective brain cooling is the capacity to reduce brain temperature below arterial blood temperature (Mitchell *et al.* 2002) and is supported by a well-developed carotid rete structure in the brain that is present in some animals such as artiodactyls (Fuller *et al.* 2016). The thin walls and large surface area of rete vessels allows for rapid heat exchange from arterial blood leading to the brain to the cool venous blood exiting the nasal mucosa, an extracranial surface where evaporation occurs (Jessen 2001b; Caputa 2004). The heat exchange results in hypothalamic temperature that is lower than arterial blood temperature (Maloney *et al.* 2007). Thermoreceptors in the hypothalamus are responsible for evaporative cooling regulation (Nagashima 2006), and by reducing hypothalamic temperature, evaporative cooling can be reduced, thereby conserving water (Jessen 2001b). For example, water deprived Dorper sheep (*Ovis aries*) exposed to heat were able to save ~60 % of their daily water intake by employing selective brain cooling for half of the day (Strauss *et al.* 2015).

The reduction of evaporative cooling in hot and dry environments suggests that animals favour osmoregulation over the maintenance of homeothermy when water is limited (Hetem *et al.* 2016). When water-deprived, animals exhibit increased heterothermy through increases in daily maximum body temperatures (Angilletta *et al.* 2010; Samara *et al.* 2012; McKinley *et al.* 2017). For example, during hot months, Arabian oryx exhibited increased 24-h maximum body temperature in response to reduced water availability compared to in cooler months when water was readily available (Hetem *et al.* 2010). In addition to conserving water, an advantage of allowing body temperature to increase is that the thermal gradient between the body and the environment is reduced, thereby reducing dry heat gain. Despite that advantage, dehydration-induced hyperthermia places animals closer to heat illness and death (Terrien *et al.* 2011). For large mammals, the heat gained during the day can be dissipated at night. Indeed, Arabian oryx allowed body temperature to increase during the day, and then dissipated the heat by non-evaporative means during the night when air temperature was lower than body temperature, thereby conserving water (Ostrowski *et al.* 2003; Hetem *et al.* 2010). Pangolins are predominantly

nocturnal and usually will not be exposed to the high solar heat loads that diurnal animals face. Whether there is any change in 24h maximum body temperatures in response to limited water availability for pangolins is unknown.

Not only will limited water pose challenges to mammalian thermoregulation, but food energy intake will also be compromised with climate change and can alter patterns of body temperature. Food energy is required to maintain constant high body temperature in mammals. In contrast to dehydration-induced hyperthermia, animals may experience hypothermic-heterothermy through decreased 24h minimum body temperatures when food energy is limited (Yoda *et al.* 2000; Wang *et al.* 2006; Hetem *et al.* 2016). Indeed, when food deprived, Comisana sheep (*Ovis aries*) and Maltese goats (*Capra aegagrus hircus*) experienced decreased 24h minimum body temperatures (Piccione *et al.* 2002). A common response to limited food energy availability is to decrease metabolic rate (Wang *et al.* 2006). Indeed, Alpine ibex (*Capra ibex ibex*) reduced energy expenditure during food shortage during winter by reducing metabolism by 60% (as indicated by reduced heart rate) compared to in summer (Signer *et al.* 2011). Although the energy conservation resulting from a lower metabolic rate and body temperature initially may be adaptive, prolonged negative energy balance can lead to deterioration in body condition in mammals, which can be fatal (Jagoe *et al.* 2003; Weyer 2018; Weyer *et al.* 2020). Nevertheless, animals that can employ physiological plasticity to conserve energy during periods of limited food scarcity will likely cope better compared to animals that cannot employ such plasticity.

Some animals also can alter the gastrointestinal tract to compensate for limited food availability. Red deer (*Cervus elaphus*), for example, can improve nutrient absorption from their food in the gastrointestinal tract to compensate for reduced abundance and quality of their forage during winter (Arnold *et al.* 2015). Furthermore, some animals may reduce their digesta passage rate or increase retention time, allowing for increased nutrient absorption (Kadzere *et al.* 2002). It is unknown whether this acclimatization to reductions or unpredictability of food resources, likely to become more prevalent with climate change, will sufficiently buffer mammals against these environmental changes.

1.3.3.4 Behaviour

Behavioural adjustments can reduce thermoregulatory costs and are therefore likely to be used to buffer the effects of climate change (Huey and Tewksbury 2009; Fey *et al.* 2019). The use of microclimates is one such example. By using thermally stable refuges, animals can avoid the hottest or coldest periods of the day, thereby reducing the water and energy costs associated with thermoregulation (Pike and Mitchell 2012). The use of refuges during summer allows for an increased thermal gradient between the body and the burrow environment compared to the outside, facilitating heat loss inside the refuge.

Diurnally active Cape ground squirrels (*Xerus inauris*) were able to lower their body temperature by 1-2 °C during the day by shuttling in and out of burrows during summer (Fick *et al.*, 2009). Furthermore, a humid burrow may reduce water loss compared to dry outside conditions (Bulova 2002; Baldo *et al.* 2015), because the smaller water vapour pressure gradient between the body and the humid burrow environment reduces evaporative water loss (Burda *et al.* 2007). Humid burrows used by Point Reyes mountain beavers (*Aplodontia rufa phaea*) likely helped reduce evaporative water loss compared to other non-burrowing mammals in the same habitat (Crocker *et al.* 2007).

For large mammals that cannot make use of relatively small refuges, the reliance on shade may increase when environmental temperatures increase. In hot environments, shade use can reduce exposure to solar radiation during the day by 80% (Dawson and Brown 1970). Arabian oryx avoided solar radiation by resting in shade in the morning, even before air temperature exceeded body temperature, and remained there until the evening (Ostrowski *et al.* 2003). Shade does not completely eliminate radiant heat load, since reflected radiation also contributes to heat load (Mitchell *et al.* 2018), but it may help animals prevent excessive increases in body temperature and reduce the need for evaporative cooling. Although pangolins are primarily nocturnal, if they become diurnal during winter, increasing winter daytime temperatures predicted with climate change may increase the need for shade-seeking behaviour during and between foraging bouts.

The opportunities for animals to seek shade may change as a result of changes to vegetation resulting from climate change. Although increased atmospheric carbon dioxide is likely to increase bush encroachment in some areas (Ward 2005), climate change may alter landscapes through reduced abundance of shade-providing trees in other areas (van Mantgem *et al.* 2009; Nagendra and Gopal 2010). Where shade-seeking behaviour is not possible, some animals can use orientation behaviour to regulate heat gain from the environment and reduce water loss (Norris and Kunz 2012). During cold conditions, animals can orientate the large surface of the body perpendicular to incoming solar radiation to facilitate heat gain. In contrast to perpendicular orientation, animals can orientate themselves parallel to solar radiation to minimize the surface area exposed to solar radiation, thereby reducing heat gain. Indeed, by orientating themselves parallel to solar radiation in a semi-arid savannah, black wildebeest (*Conochaetes gnou*) were able to reduce radiant heat absorption by 30%, and the orientation behaviour occurred more frequently when water was not readily available (Maloney *et al.* 2005).

Animals can also adjust their body posture to alter heat exchange with their environment (Terrien *et al.* 2011). In cold environments, ball-like postures can reduce heat loss to the environment by reducing the body surface area exposed to the environment and reducing tissue conductance. Indeed, black-and-gold howling monkeys (*Alouatta caraya*) used

ball-like or curled postures frequently while resting during cold conditions (Bicca-Marques and Calegario-Marques 1998). In hot environments, animals can facilitate heat dissipation by resting in a stretched-out position or in a position that maximizes body surface area exposed to the environment, so long as they are not exposed to solar radiation. Indeed, pigs spent more time lying laterally on the cool floor with increasing room temperatures to allow for effective heat dissipation compared to cooler air temperatures (Huynh *et al.* 2005). Pangolins appear to exhibit postural changes through curling behaviour during cold conditions and by laying on their backs during hot conditions (Heath and Hammel 1986; Jacobsen *et al.* 1991), but little is known about how these behaviours contribute to their thermoregulation.

Additional behaviours have been observed in pangolins that could potentially facilitate heat loss. One pangolin was observed urinating onto its belly on a hot day, which presumably improved heat loss via evaporative cooling (Jacobsen *et al.* 1991). In a similar way, kangaroos are able to lick their forearms to regulate body temperature through cutaneous evaporative heat loss (Dawson *et al.* 2000). Mud bathing is another behaviour that increases heat loss via evaporative cooling in animals such as African (*Loxodonta Africana*) and Asian (*Elephas maximus*) elephants (Dunkin *et al.* 2013). Although mud bathing in pangolins apparently plays a role in reducing parasite load and masking scent (Pietersen *et al.* 2020), it also may play a role in thermoregulation.

Animals must trade off behavioural thermoregulation with behaviours such as foraging and drinking time, anti-predation behaviours, and breeding opportunities (Mole *et al.* 2009; Cunningham *et al.* 2015). When surface temperatures increased in Darwin, Australia, male fiddler crabs (*Uca mjoebergi*) that retreated to underground burrows to escape the heat did not display to females and thus lost mating opportunities (Munguia *et al.* 2017). Vervet monkeys (*Chlorocebus pygerythrus*) increased resting time at high air temperatures but did so at the expense of feeding time (McFarland *et al.* 2014). There are various ways therefore in which the prioritization of behavioural thermoregulation may ultimately lead to reduced performance (Cunningham *et al.* 2015).

Some animals can compensate for reduced foraging time during the day and avoid high heat loads by shifting their activity across the 24h diel cycle (Levy *et al.* 2019). For example, Arabian oryx reduced their proportion of diurnal activity to less than 30% during hot months compared to the rest of the year, when diurnal activity was usually more than 50% (Hetem *et al.* 2012a). By becoming nocturnal or crepuscular, especially when water is limited, animals can avoid the solar heat load of the day and reduce the need for evaporative cooling, although this activity shift may come with the increased risk of predation (Hetem *et al.* 2012a; Selebatso *et al.* 2017; Mitchell *et al.* 2018). Some animals can employ a behavioural response that reduces both the costs of thermoregulation and

predation. In the Kalahari, blue wildebeest (*Connochaetes taurinus*) were able to avoid high heat loads by restricting activity to the cooler parts of the day (i.e., increased crepuscular activity) while reducing predation pressure by decreasing their activity at night (Selebatso *et al.* 2017).

In contrast to experiencing high heat stress during summer, animals also face cold stress during winter. In seasonal environments, winter is typically associated with food shortages (Humphries *et al.* 2003; Giroud *et al.* 2008; Signer *et al.* 2011). Animals must therefore contend with limited energy availability in addition to cold stress during winter. Some animals can increase the amount of time spent foraging to compensate for food shortages (Podolski *et al.* 2013), whereas many nocturnal animals switch to diurnal activity during winter in response to food shortages (Warnecke *et al.* 2008; Pagon *et al.* 2013; Guiden and Orrock 2020; Weyer *et al.* 2020). For example, in response to reductions in prey availability, Geoffroy's cats (*Leopardus geoffroyi*) increased diurnal activity compared to when prey was abundant (Pereira. 2010). Diurnal activity can offset the need for metabolic heat production, thereby conserving energy (Walsberg and Wolf 1995; Warnecke *et al.* 2008; van der Vinne *et al.* 2015).

An additional behaviour that can be employed by usually nocturnal mammals to conserve energy when food abundance is low is basking during the day. Basking allows animals to use solar radiation to passively warm the body (Brown and Downs 2007; Terrien *et al.* 2011), in the same way that diurnal activity would do. Aardvarks in the Kalahari switched to diurnal behaviour during winter when resources declined, and were often observed basking during this time, likely allowing them to conserve energy (Rey *et al.* 2017; Weyer 2018). Basking in otherwise nocturnal mammals may incur some costs such as increased exposure to predators. Basking mammals can reduce this predation risk by basking close to refuges to allow for fast retreat in the event of a predation attempt (Pavey and Geiser 2008). Climate-induced food limitations may also occur during summer in many areas in the future since rainfall is closely linked with food availability (Dean and Milton 2001). Little is known about how pangolins modify their behaviour in response to changing climatic variables and resources in their environment, largely as a consequence of the lack of research on the species in the wild.

1.4 THESIS STRUCTURE, OBJECTIVES AND HYPOTHESES

Chapter 2: To describe all key methods and materials relevant to all data chapters.

Chapter 2 describes the general methodological approach, with additional details, including those for data analysis, in each of the following results chapters:

Chapter 3: To investigate the seasonal and interannual variation in the pangolin diet in response to fluctuations in climate and prey abundance.

Understanding the dietary shifts of pangolins in response to resource availability can provide important information about how they may cope with environmental change. I therefore first identified the food resources available to pangolins in the Kalahari and the factors that influenced fluctuations in ants and termites. I predicted that increases in environmental temperature and decreased rainfall, and hence decreased primary productivity (grass cover), would result in decreased ant and termite abundance. I then quantified the pangolin diet using behavioural observations and faecal samples. I predicted that pangolins would shift their dietary preferences to include a wider diversity of prey taxa during periods of resource scarcity, such as during winter, resulting in seasonal shifts in the diet. Lastly, I identified the factors that were associated with pangolin food intake. I predicted that prey abundance and the amount of time spent foraging would most strongly affect the amount of food consumed and that the amount of food consumed, and specific prey selection would most strongly affect energy intake.

Chapter 4: To investigate pangolin 24h activity responses to fluctuations in climate and prey abundance.

Understanding the role of climate and food resources in driving the 24h activity pattern of pangolins is crucial for predicting the future responses of pangolins to climate change. I therefore aimed to identify the key factors associated with pangolin 24h activity in the Kalahari. I predicted that pangolins would be predominantly nocturnal throughout the year, but that they would increase diurnal activity during winter. I also predicted that the main driver for the onset of pangolin activity (emergence from the burrow) would be food availability, particularly when it was cold. Based on previous reports (Swart 1996; Heath and Coulson 1997; Pietersen *et al.* 2014b), I predicted that pangolins would be active above ground for about four to eight hours each day to forage, and that the duration of activity would increase during winter in response to food shortages. Because I expected the duration of activity to vary seasonally, I predicted that the relationship between the time of emergence and return to the burrow would not be linearly related. I also predicted that the increase in diurnal activity during winter would be particularly pronounced in the study year in which there was below-average rainfall in summer.

Chapter 5: To investigate the effects of changes in prey resources on the 24h body temperature patterns of pangolins.

I investigated the long-term body temperature patterns of free-living pangolins to understand how fluctuations in prey resources influence the precision of body temperature regulation. I predicted that pangolin body temperature would be lower than for most other placental mammals, but pangolins would regulate body temperature within a narrow 24h range when food resources were abundant. When food resources were scarcer, I predicted that pangolins would exhibit increased heterothermy as indicated by decreased 24h minimum temperatures, and possibly also increased 24h maximum body temperatures given that they obtain water primarily from their diet. Because diurnally emerging pangolins could be exposed to high heat loads, particularly as a result of high solar radiation, I predicted that the 24h maximum body temperature would increase as a function of the time of emergence. In other words, when pangolins emerged from their burrows earlier during the day, I predicted that their 24h maximum body temperature would be higher compared to when they emerged later during the day.

Chapter 6: Thesis synthesis and conclusion

In Chapter 6, I provide a comprehensive synthesis of the potential responses of myrmecophagous mammals to global climate change using my findings of the responses of pangolins to fluctuations in climate and prey resources in a hot and dry environment.

Chapter 2

Methods and materials

This chapter describes the general methodological approach, with additional details, including those for data analysis, in each results chapter (Chapters 3 to 5).

2.1 STUDY SITE AND CLIMATE

2.1.1 Study site

The study took place at Tswalu Kalahari Reserve (27°13'S, 22°26'E), a private reserve situated in the southern Kalahari region of South Africa (Figure 2.1). The reserve is approximately 114 000 ha in size and is divided into two sections: Korannaberg and Lekgaba (Figure 2.2). The smaller portion of the reserve, Lekgaba, is inhabited by lions (*Panthera leo*), whereas the larger portion, Korannaberg is not inhabited by lions and is where my study was conducted. Although lions are absent from Korannaberg, other predators such as cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), and leopards (*Panthera pardus*) inhabit the area. Ant- and termite-eating (myrmecophagous) mammalian species that inhabit the reserve include the aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*), bat-eared fox (*Otocyon megalotis*), and pangolin (*Smutsia temminckii*).

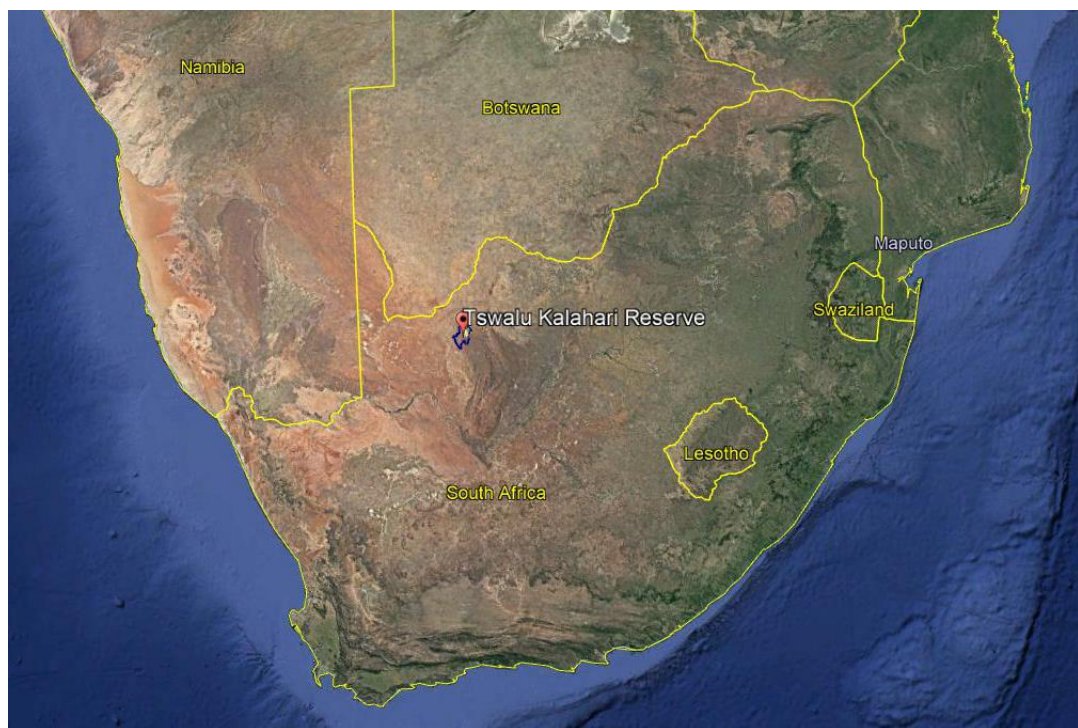


Figure 2.1: Geographical location of Tswalu Kalahari Reserve within South Africa

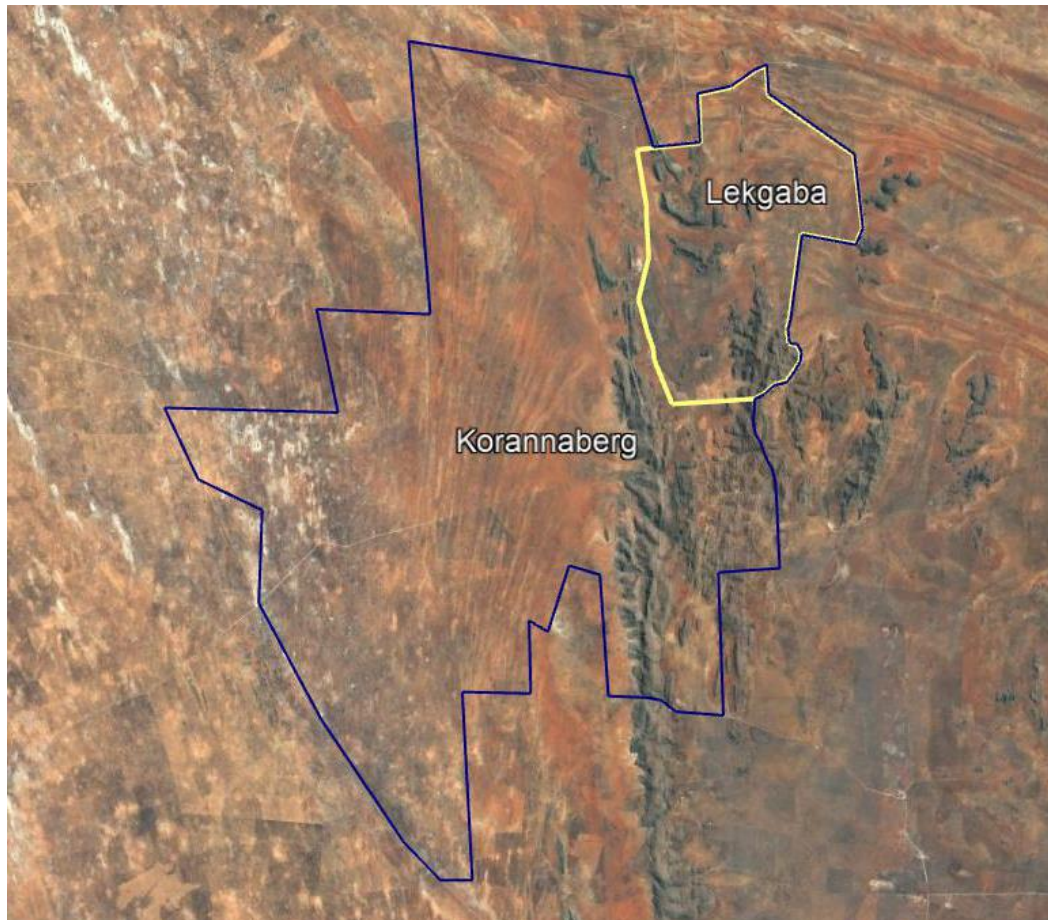


Figure 2.2: Satellite image showing the Korannaberg and Lekgaba sections, with boundaries of the reserve (blue) and Lekgaba (yellow).

The reserve comprises of sandy plains, dunes that run parallel to one another, and rocky mountains towards the eastern boundaries (Davis *et al.* 2010). The reserve is predominantly characterised by five vegetation types, namely Koranna-Langeberg Mountain Bushveld, Gordonia Duneveld, Gordonia Plains Shrubveld, Olifantshoek Plains Thornveld, and Kathu Bushveld (Tokura *et al.* 2018, Figure 2.3). Study pangolins roamed freely throughout the reserve but were most prevalent in the Gordonia Duneveld and Gordonia Plains Shrubveld vegetation types.

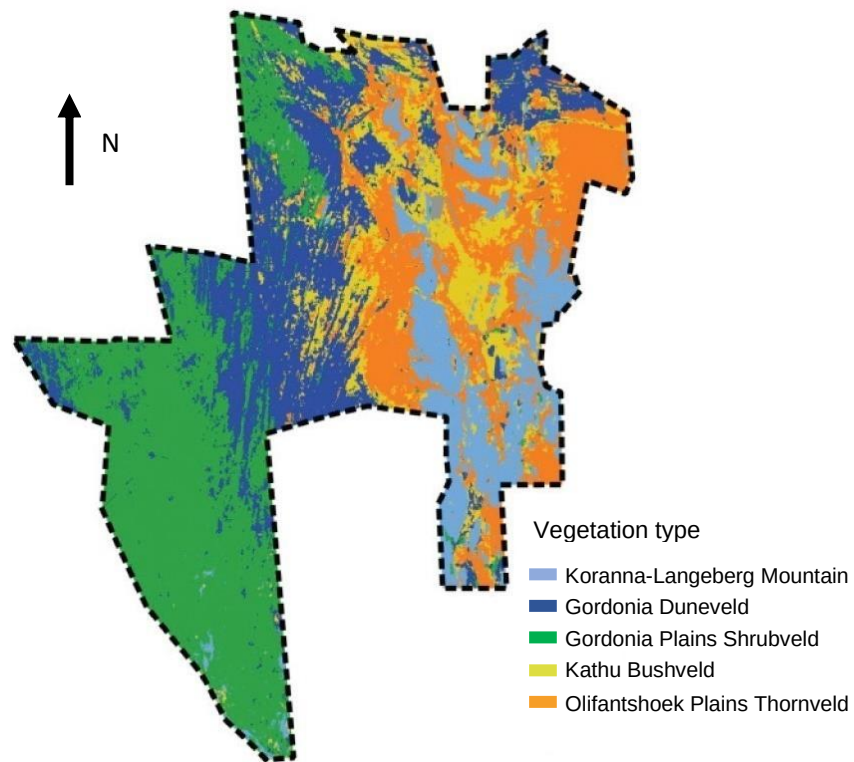


Figure 2.3: Map of Tswalu vegetation types (adapted from Tokura *et al.* 2018).

2.1.2 Climate

Tswalu is a semi-arid savannah, where rainfall is highly variable, with a mean annual rainfall of about 360 mm $\pm$ 170 mm (Tokura *et al.* 2018). The region is characterised by wet summers (December to February), with the majority of rainfall events occurring in December and January, and dry winters (June to August). Air temperatures at the nearest town of van Zylsrus, situated 60 km from Tswalu, range between an absolute minimum of -6.6 °C in winter and an absolute maximum of 42.5 °C in summer (van Rooyen and van Rooyen 2017). In January, the mean daily minimum air temperature in van Zylsrus is 19.0 °C and the mean daily maximum air temperature is 35.6 °C, while in July the mean daily minimum air temperature is 0.6 °C and the mean daily maximum air temperature is 21.7 °C (van Rooyen and van Rooyen 2017).

For the purposes of my study, a weather station measuring black globe temperature at 30-minute intervals was placed on the reserve, approximately 10 km from the area where tagged pangolins ranged. The weather station could not be placed within the pangolin range because wildlife such as baboons and buffalos moved freely in the area and were likely to damage the weather station. Our research team had previously shown that environmental temperatures were similar across the pangolin range (N. Weyer

unpublished data). Black globe temperature was measured by inserting a temperature-sensitive probe (HOBO Temperature/Relative Humidity/2 External Channel Data Logger, Onset Computer Corporation, Massachusetts, USA) into a 150 mm copper globe spray-painted matte black. Black globe temperature was used because it incorporates the effects of solar radiation and wind speed, thus providing a more accurate indication of the heat load experienced by animals than air temperature alone (Buffington *et al.* 1981; Mader *et al.* 2006; Hetem *et al.* 2007). Daily rainfall data were obtained for the period January 2001 to October 2017 from 32 rain gauges distributed across Tswalu, overlapping with the ranges of pangolins at Tswalu.

2.2 STUDY ANIMALS, IMPLANTS AND DATA COLLECTION

2.2.1 Ethical clearance and research permits

The research conducted at Tswalu in fulfilment of my PhD degree was approved by the Tswalu Foundation. Ethical clearance was obtained from the Animal Research Ethics Committee, University of the Witwatersrand (clearance number 2015/04/16B). Provincial permits to conduct research in the Northern Cape were obtained from the Northern Cape Nature Conservation (FAUNA 1075/2015, FAUNA 1076/2015, FAUNA 1345/2017, FAUNA 1346/2017).

2.2.2 Study pangolins and telemetry fitting

Between April 2015 and March 2017, Tswalu staff opportunistically located or tracked (by identifying tracks crossing sandy roads and following them to the pangolin or its burrow) six free-living adult pangolins (three male and three female, 6.5 – 9.4 kg, Table 2.1) and fitted them with Very High Frequency (VHF) tracking transmitters (~90 g, Africa Wildlife Tracking, Pretoria, South Africa). A seventh pangolin was tagged with a tracking transmitter, but the transmitter fell off three months into the study and the pangolin could not be located subsequently.

Once a pangolin was located it was moved to an open area on the ground within 5 m to attach the tracking transmitter. Pangolins typically curled into a ball when handled, making the attachment of tracking transmitter possible without requiring anaesthetic drugs. A dorsolateral scale was identified, and two 3 mm holes were drilled into the non-vascularized portion of a single scale for attachment of the transmitter with two 3 mm bolts (Figure 2.4). A strip of a material belt or animal tracking collar material was placed under the scale before drilling holes to prevent injury to the animal while drilling. The entire procedure took less than 10 minutes. Once the tracking transmitter was secured, the pangolin was allowed to roam freely. All pangolins were located on the subsequent days after the procedure and there were no apparent ill effects from the procedure.

Table 2.1: Study pangolin ID, sex, body mass at the first and last surgery to implant data loggers, and change (Δ) in body mass between the first and last surgery.

Pangolin ID	Sex	Start body mass (kg)	End body mass (kg)	Δ body mass (kg)
P01	Female	8.7	8.4	- 0.3
P02	Female	7.0	8.2	+ 1.2
P04	Male	7.5	7.1	- 0.4
P05	Male	6.5	6.3	- 0.2
P09	Male	9.4	9.8	+ 0.4
P10	Female	7.7	7.3	- 0.4



Figure 2.4: Pangolin with a VHF tracking transmitter attached to a dorsolateral scale (*top*), and a single scale of a pangolin that had died of natural causes, showing the two attachment points of a tracking transmitter (*bottom*).

2.2.3 Surgical procedures

Each pangolin was implanted with a miniature temperature-sensitive data logger (DST milli-T, ± 20 g, Star Oddi, Gardabaer, Iceland), which recorded core body temperature at 5-minute intervals. Pangolins were located and tagged with tracking transmitters at different dates, resulting in variability in body temperature sampling durations across individuals (Table 2.2). Each data logger was coated in inert wax (Sasolwax 1276, Sasol (Pty) Ltd., Sandton, South Africa). I calibrated the temperature data loggers at hourly intervals before implantation against a highly accurate thermometer (Quat 100, Heraeus, Germany) in a water bath over a range of 26 °C to 42 °C, and I re-calibrated them the same way after removal from animals. Star Oddi data loggers are known to drift by $\pm$ one minute per month, therefore appropriate adjustments were made by shifting the data by five minutes every five months. There was no drift in the temperature calibration and the data loggers were accurate to at least 0.1 °C. After the data loggers were calibrated, they were sterilized by placing them into instant sterilant (F10 sterilant, F10 Health and Hygiene (Pty) Ltd., South Africa) until surgery to implant them.



Figure 2.5: Miniature temperature-sensitive data logger (before adding the wax coating) implanted into pangolins to record core body temperature.

Table 2.2: Start and end dates of implantation and removal of body temperature data loggers from six pangolins between October 2015 to October 2017) .

	J	F	M	A	M	J	J	A	S	O	N	D
2015												
P01												
P02												
P04												
P05												
P09												
P10												
2016												
P01												
P02												
P04												
P05												
P09												
P10												
2017												
P01												
P02												
P04												
P05												
P09												
P10												

On the day of surgery, I located a pangolin at its burrow in the morning using VHF telemetry. The surgical team returned at night and waited at the surgical site while I waited at the burrow in the dark, quietly, from a distance of 15-20 m away to avoid disturbing the pangolin and delaying its emergence. When the pangolin emerged, the noise generated by the scales rubbing against each other or against vegetation allowed me to detect its movement. On windy nights, when I could not detect emergence because of noise generated by the environment, I used the telemetry to detect emergence, with a conspicuous change in the signal strength indicating movement of the pangolin. I then

waited another 10 minutes to allow the pangolin to move away from the burrow before locating it with the telemetry. The pangolin was then captured (picked up) and placed into a Perspex box (55 cm x 40 cm x 30 cm). The pangolin was carried 100 m – 800 m to a mobile surgical site (the tailgate of a 4x4 Toyota Hilux double cab vehicle with a canopy). A table was placed next to the vehicle for sterilized surgical equipment. A mosquito net was placed over the back of the vehicle, covering the surgical site to prevent any insects being attracted to the lights around the surgical site used during night-time surgeries (Figure 2.6).



Figure 2.6: Mobile surgical site on the tailgate of a 4 x 4 Hilux vehicle showing the mosquito net covering to prevent insects entering the surgical site at night.

A veterinarian experienced with data logger implants into wild mammals administered anaesthetic drugs (1-6% isoflurane in oxygen, ISOFOR, SafeLine Pharmaceuticals (Pty) Ltd., Johannesburg, South Africa) through a 1.5 cm hole in the Perspex box. Once the pangolin was unconscious, we sexed it by looking at the external genitalia, and then weighed it in the Perspex box on a scale (MICRO SW 30, 40 kg capacity, 1 g division, Associated Scale Corporation, Johannesburg, South Africa), subtracting the mass of the box afterwards. Pangolin anaesthesia was maintained using a face mask (Figure 2.7) with isoflurane in oxygen (1–6% as needed). We cleaned a 15 x 15 cm patch on the abdomen of the pangolin and sterilized the area using antiseptic solutions (Hibitane, chlorhexidine: 5 %, and Hibicol, chlorhexidine gluconate: 0.5 % in spirit, F10 Health and Hygiene (Pty) Ltd., Roodepoort, South Africa). A local anaesthetic (lignocaine hydrochloride, 1-2 ml, Animal Health Division, Bayer HealthCare (Pty) Ltd., Kempton Park, South Africa) was injected subcutaneously into the sterilized site on the lower abdomen along the *linea alba* where the incision was to be made.



Figure 2.7: Anaesthesia being induced in a pangolin by face mask, before surgery to implant a wax-coated miniature temperature-sensitive data logger.

A 15 mm incision was made and the miniature temperature-sensitive data logger was inserted retroperitoneally and tethered to the midline with 2/0 non-absorbent Nylon suture material (Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd., Essex, UK) to prevent the logger from drifting. Subcutaneous stitching of the *linea alba* was performed with 4/0 absorbable suture material (Viamac (USP), Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd., Essex, UK), followed by 2/0 absorbable vicryl suture material (Viamac (USP), Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd., Essex, UK) to close the skin. A non-steroidal anti-inflammatory (Metacam®, meloxicam, 5 mg/ml, 0.1 ml/kg, Boehringer Ingelheim Pharmaceuticals (Pty) Ltd., Johannesburg, South Africa) and a long-acting antibiotic (PeniLA, 0.1 ml/kg, penicillin, VIRBAC RSA (Pty) Ltd., Johannesburg, South Africa) were injected subcutaneously. Wound spray (Necrospray, oxytetracycline hydrochloride: 40 mg, gentian violet: 4 mg, Animal Health Division, Bayer HealthCare (Pty) Ltd., Kempton Park, South Africa) and tick grease (chlorfenvinphos: 0.3 %, SWAVET RSA (Pty) Ltd., Johannesburg, South Africa) were applied to the wound site once suturing was completed.

Immobilization was reversed by removing the face mask and allowing the pangolin to breathe natural air. Pangolins were returned to the site of capture, where an observer and a veterinarian ensured a smooth recovery by standing quietly at a distance of 10 – 15 m away without using a flashlight, thereby allowing the animal to walk off unaware of human presence. Once the animal was walking normally (with a steady gait), the observer and veterinarian left the area. The methods used to explant data loggers from the pangolins were similar to those used to implant them. The VHF tracking transmitters were left on the

pangolins for at least one week after the explant surgeries before removing them, to ensure that the animals recovered fully.

2.2.4 Dietary observations and activity

Pangolins roamed freely throughout the study period and were tracked at least once per week for dietary observations. Pangolins were tracked during their active phase using telemetry (R-1000 VHF receiver, range 148-152 MHz, Africa Wildlife Tracking, Pretoria, South Africa, and Three-Element Folding Yagi Antenna, range 148-152 MHz, Sirtrack Ltd., Havelock North, New Zealand). A pangolin was followed and observed from a distance of 5 to 15 m, usually with a torch, with negligible interference to natural behaviour. A red filter over the torch light was not used since pangolins do not navigate or avoid predators using their sight, and therefore a normal LED torch light was used. Nevertheless, I avoided shining the torch directly into the pangolins' eyes. Pangolin behaviours (walking, digging, resting, feeding, or other) were recorded using a continuous sampling method. Each pangolin was monitored for a minimum of one hour during its active phase to record foraging behaviours. During observations early on during the study, after each feeding bout and once the pangolin moved off, the prey items that it was feeding on were collected and stored in 90% ethanol for later identification. Live specimens were only collected at the beginning of the study because I did not observe pangolins preying on any additional unidentified prey items later during the study that would have required identifying.

Faecal samples were collected throughout the study period to further identify pangolin prey items. Pangolins typically defaecated once per night, by digging a small (10 x 5 cm) hole in the soil (although not always), dropping the sausage-shaped excrement in the hole. They then dragged their tail over the faecal matter, thereby burying it under the soil or scattering it along the ground (Figure 2.8), often making it difficult to detect or collect. When pangolins occasionally defaecated inside their burrows, or under dense shrubs, the faeces were more difficult to detect or collect. Additional samples were opportunistically collected from non-study pangolins while walking around at Tswalu. By using telemetry to determine the location of study pangolins, I could confirm that the additional faecal samples collected were not from study pangolins if they were fresh (less than 48h old, as indicated by soft faeces) and more than 4km away from the study pangolins. If a pangolin could not be followed for the full active phase after a defaecation event, their tracks were followed the next day, where possible, to confirm that no more defaecation events had occurred. Only fresh faecal samples were collected. If the faecal samples were hard and dry, they could not be aged and were thus not collected. Faecal samples were stored in resealable plastic packets (Glad Products Company, California, USA), and frozen for later analyses. A reference collection of Tswalu ants and termites obtained from Dr Frederic

Delsuc (Montpellier University) and Dr Hamish Robertson (Iziko South African Museum) was used, along with a guidebook on the ants of southern Africa (Slingsby 2017) to identify ants and termites to genus level. More details on the methods used to assess the pangolin diet are provided in Chapter 3.



Figure 2.8: A scattered pangolin faecal sample that was not buried by the pangolin, with an intact sausage-shaped excrement above.

Pangolins were also tracked in the mornings at least once per week during their inactive phase using telemetry to locate their burrows to place camera traps (MMS wireless scouting camera, LTL-6210MC HD series, Ltl Acorn, Shenzhen, China) about 0.5-1.5 m outside the burrow (Figure 2.9) to assess time of emergence and return. Camera traps did not always trigger for emergence or return events, and pangolins did not always return to the same burrow, thus the camera traps could not always detect time of emergence and return. Therefore data for time of emergence and return were supplemented with data extracted from 24h body temperature patterns, indicated by a conspicuous change in body temperature around the onset of activity or return to the burrow (validated by matching 201 times of emergence and 65 times of return obtained from camera traps with 24h body temperature records). Where there was uncertainty associated with small changes in body temperature, emergence and return times were not estimated. More details are provided in Chapter 4.



Figure 2.9: A camera trap placed outside a pangolin burrow to detect the time of emergence and return.

2.2.5 Grass cover and prey abundance

A total of 30 permanent 50 m long transects were selected randomly across the reserve where pangolins had been previously detected (predominantly in the *Gordonia* Duneveld vegetation type). Vegetation was assessed once a month across the study period by visually estimating the percentage of grass covering the ground in a 2 m² quadrat every 10 m along each transect, for a total of 150 quadrats across the 30 transects. Prey abundance was recorded once a month using pitfall traps (50 ml Falcon® Centrifuge Tubes, 27 mm diameter, Corning Inc., Massachusetts, USA) placed five metres apart along the same 30 transects, for a total of 10 pitfall traps per transect, a method similar to that used previously as a proxy for prey abundance (Swart *et al.* 1999, Pietersen 2013). Traps were placed in the ground, with the opening of the trap level with the ground surface. Each tube contained 20-30 ml antifreeze and water solution (100 ml commercial glycerol-based antifreeze: 1 L water). All traps remained in the ground for four days. More details are provided in Chapter 3.

Chapter 3

**Ground pangolins in the Kalahari
shift their diet in response to
resource scarcity**

3.1 INTRODUCTION

In addition to increased air temperatures and surface evapotranspiration, climate change models predict changes in the amount and timing of rainfall, particularly in areas that already occur in dry latitudes, such as the Kalahari region of southern Africa (Mphale *et al.* 2014; Stocker *et al.* 2013; Engelbrecht *et al.* 2015; Le Roux *et al.* 2016). Increased heat, as well as more sporadic and unpredictable rainfall, will impact mammals directly through increased heat gain from their environment, which will increase their water demands for thermoregulation (Fuller *et al.* 2016; Mitchell *et al.* 2018). Climate change may also impact mammals indirectly through the effects of reduced primary productivity on their food resources (Cahill *et al.* 2013; Schleuning *et al.* 2016). Increasing air temperatures and increasing evapotranspiration associated with climate change (Le Roux *et al.* 2016) will result in reduced soil moisture, ground water and surface water, which are key resources for vegetation and the insects that depend on vegetation for survival (Botes *et al.* 2006; Cornelius and Osbrink 2010; 2011; Moll *et al.* 2012). Indeed, increased heat and aridity in arid environments has been linked to shifts in the abundance, accessibility, and activity of insects such as ants and termites (Barrow and Parr 2008; Williams and Middleton 2008; Davies *et al.* 2015; Weyer *et al.* 2020), which will affect the energy balance of the animals that depend on them.

In arid environments, winter, the dry season, is an energetically challenging period for some mammals because metabolic and thermoregulatory demands are high, and their prey resources become less available (Williams *et al.* 1997; Humphries *et al.* 2004). Ants and termites are an important resource for many animals (Chakravorty *et al.* 2016). The challenges associated with winter for insect-eating mammals in arid environments may be particularly pronounced following a summer of below-average rainfall because of the close link between rainfall and vegetation and insect availability (Dean and Milton 2001; Weyer *et al.* 2020). Myrmecophagous (feeding on ants and termites) mammals must overcome the challenge of reduced insect prey resources by balancing energy intake with energy expenditure to ensure survival.

According to the optimal foraging theory, when foraging, animals typically behave in such a way that increases their energy intake (Baumont *et al.* 2000; Turesson *et al.* 2002). Several factors influence animal daily energy intake, including availability and accessibility of food resources, foraging time, and prey selection (Kondoh 2003; Daunt *et al.* 2006; Ross *et al.* 2010). When food resources decline, animals may increase foraging duration to increase food energy intake (Shaffer *et al.* 2001), but doing so simultaneously increases their energy expenditure, or they may reduce foraging time and therefore the cost of foraging by exploiting larger or more profitable food resources (Bergman *et al.* 2001). While some animals may become more selective when food resources decline

(Folks *et al.* 2014), the optimal foraging theory predicts that animals should expand their dietary niche breadth or shift their dietary preferences (Stephens and Krebs 1986; Svanback and Bolnik 2007; Donazar *et al.* 2010). For example, during winter, the aardwolf (*Proteles cristata*) shifted its diet from the preferred *Trinervitermes* termites, which became less available, to *Hodotermes* termites (Williams *et al.* 1997). Bat-eared foxes (*Otocyon megalotis*) increased their termite intake as well as the diversity of prey in their diet in winter when their preferred food (bluebush fruits) became less available (Klare *et al.* 2011). By shifting the diet when prey resources decline during winter, animals may reduce the costs of foraging for their preferred but less available prey.

Similar to seasonal changes, a climate change-induced decline in food resources, such as the food scarcity resulting from increased air temperatures and droughts, also may drive some animals to shift their diet (Puig *et al.* 2010). For example, some mixed-feeder ungulates switch to foraging more on trees and shrubs when their preferred grasses become less available during drought conditions (Abraham *et al.* 2019). However, if animals cannot shift their diet in response to resource scarcity, the results can be fatal (Rey *et al.* 2017; Vafidis *et al.* 2019). For example, armadillos (*Oryzomys azer*) that fed preferentially on *Hodotermes* termites did not shift their diet during the winter following a summer drought when resources declined, but instead starved, with some animals succumbing (Weyer *et al.* 2020).

Pangolins are strictly myrmecophagous mammals, feeding selectively on a diet of ants and termites, the composition of which may or may not vary seasonally (Swart *et al.* 1999; Pietersen *et al.* 2016). Pangolins have been recorded eating prey from 17 ant genera and 9 termite genera, and they do not necessarily prey on the most abundant species (Sweeney 1956; Coulson 1989; Jacobsen *et al.* 1991; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen *et al.* 2016). For example, in an area where *Pheidole* were the most abundant ants, they made up less than 1% of the diet, whereas *Anoplolepis* ants were not the most abundant, yet made up 77% of the diet (Swart *et al.* 1999). Data on the seasonal variation in the diet are contradictory across regions occupied by pangolins (Swart *et al.* 1999; Pietersen *et al.* 2016), indicating that seasonal dietary shifts may vary across the ground pangolin distribution. The pangolin diet has previously been assessed by examining the stomach contents of museum specimens (Coulson 1989), or through behavioural observations of released or free-living pangolins (Sweeney 1956; Jacobsen *et al.* 1991; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen *et al.* 2016). However, observations alone may exclude incidental intake of less abundant species. Also, by observing an insect-eating animal's feeding, one cannot quantify how much food is ingested by the animal. Animal faeces can be used to obtain a more detailed account of the diet (Kelly *et al.* 2012) and are better suited to account for incidental prey intake by pangolins, as well as to quantify how much food they consume for daily maintenance.

Understanding the dietary shifts of pangolins in response to resource availability can provide important information about how they may cope with environmental change. I therefore first identified the food resources available to pangolins in the Kalahari and the factors that influenced fluctuations in ants and termites. I predicted that increases in environmental temperature and decreased rainfall, and hence decreased primary productivity (grass cover), would result in decreased ant and termite abundance. I then quantified the pangolin diet using behavioural observations and faecal samples. I predicted that pangolins would shift their dietary preferences to include a wider diversity of prey taxa during periods of resource scarcity, such as during winter, resulting in seasonal shifts in the diet. Lastly, I identified the factors that were associated with pangolin food intake. I predicted that prey abundance and the amount of time spent foraging would affect the amount of food consumed and that the amount of time spent foraging, and specific prey selection would affect energy intake.

3.2 MATERIAL AND METHODS

3.2.1 Climatic variables

A weather station measuring black globe temperature at 30-minute intervals was placed approximately 10 km from the area where study pangolins ranged. A weather station could not be placed in the pangolin range because of damage by wildlife such as baboons and buffalos. However, our research team had previously shown that weather was similar across the range of pangolins (N. Weyer unpublished data). Black globe temperature was measured by inserting a temperature-sensitive probe into a 150 mm black globe (see Chapter 2 for details). Daily rainfall data were obtained for the period January 2001 to October 2017 from 32 rain gauges spread across Tswalu, since pangolins were distributed widely across the reserve, roamed large areas across the reserve, and their ranges overlapped with multiple rain gauges.

3.2.2 Grass cover and prey abundance

A total of 30 permanent 50 m long transects were selected randomly across the reserve where pangolins had been previously detected (in grass- and shrub-dominated areas in the dune fields) and the transects were orientated in random directions. A comparison of four methods for estimating grass cover indicated that a visual estimation method used by both experienced and inexperienced observers yielded the same results as using a more objective method, making the visual estimation method sufficiently accurate (Murphy and Lodge 2002). Grass cover was estimated by assigning individual grass clumps (where one or more grass shoots meet at the same base) a percentage value of one to three. A percentage of one was assigned when a clump comprised of only one grass shoot, a percentage of two was assigned when the clump comprised of two to ten

grass shoots, and a percentage of three was assigned when the clumped comprised of eleven to thirty grass shoots. The total added value of all clumps counted was used as the percentage grass cover for each quadrat. Therefore, vegetation was assessed once a month for the entire study period (October 2015 to October 2017; excluding March 2017) by visually estimating the percentage of grass covering the ground in a 2 m² quadrat every 10 m along each transect, for a total of 150 quadrats across the 30 transects. Prey abundance was recorded once a month using pitfall traps (50 ml Falcon® Centrifuge Tubes, 27 mm diameter, Corning Inc., Massachusetts, USA) placed five metres apart along the same 30 transects, for a total of 10 pitfall traps per transect, a method similar to that used previously (Swart *et al.* 1999, Pietersen 2013). Traps were placed in the ground, with the opening of the trap level with the ground surface. Each tube contained 20-30 ml antifreeze and water solution (100 ml commercial glycerol-based antifreeze: 1 L water). All traps remained in the ground for four days. The number of ants that fell into the traps each month was counted and used as a proxy for prey abundance. All other insects, except ants and termites, falling into the traps were discarded and excluded from analyses.

3.2.3 Pangolin diet

Six free-living Temminck's ground pangolins tagged with VHF tracking transmitters were tracked once per week across the study period (October 2015 to October 2017) to observe what they were feeding on and to collect faecal samples. Additionally, scats from at least three other pangolins (not tagged with tracking transmitters) were collected (20% of all scats collected) from areas close (<7 km) to where the tagged pangolins ranged. Since the additional scats were always collected in the same areas each time, they were assumed to be from the same three individuals, but this may be a limitation in the study. Scats collected from unidentified pangolins were only collected if they were fresh and if the location of a known pangolin in the same area was determined within three nights before the scat was found to ensure that the scat did not belong to the known pangolin. A total of 98 scats were therefore collected from nine pangolins and were pooled together for analyses since the diets of the four pangolins with the highest number of scats collected did not differ from one another (Table 3.1). Pangolins typically defaecated once per night, by digging a small (10 x 5 cm) hole in the soil, dropping the sausage-shaped excrement in the hole, and then dragging the tail over the faecal matter, thereby burying it under the soil or scattering it along the ground, often making it difficult to detect or collect. Pangolins also occasionally defaecated inside their burrows, making faecal collection impossible in those instances. Additional samples were opportunistically collected from non-study pangolins while walking around at Tswalu. If a pangolin could not be followed for the full active phase after a defaecation event, their tracks were followed the next day, where possible, to confirm that no more defaecation events had occurred. Only fresh

(less than 48h old, as indicated by soft faeces) faecal samples were collected. If the faecal samples were hard and dry, they could not be aged and were thus not collected.

Table 3.1: The number of pangolin scat samples collected across the study period, and the number of pangolins that samples were collected from per month (total number of samples = 98, total number of pangolins collected from = 9).

Month	J	F	M	A	M	J	J	A	S	O	N	D
2015												
No. of samples										0	4	1
No. of pangolins										0	2	1
2016												
No. of samples	3	1	3	1	9	2	3	17	7	3	4	0
No. of pangolins	2	1	1	1	3	2	2	5	2	2	3	0
2017												
No. of samples	6	3	4	1	6	2	2	2	8	6		
No. of pangolins	3	2	3	1	2	1	1	1	2	1		

Faecal samples were stored in resealable plastic packets (Glad Products Company, California, USA), and frozen for later analyses. At the start of analyses, faecal samples were thawed, then dried in the open plastic packets naturally outside until each sample reached constant mass. Each sample was weighed on a digital pocket scale (Jewelry Pocket Balance 3000 g/0.1 g, Yongkang Zhengya Weighing Apparatus Factory, Zhejiang, China) and placed into a bucket with 2 L water where they disintegrated naturally to allow the inorganic material (sand) to separate from the buoyant, chitinous body parts of ants and termites. Organic material was collected while in the bucket of water with a tea strainer (Lion Brand®, 0.5 x 0.5 mm, Bombay Tea Strainers Manufacturing, Mumbai, India), placed into a Tupperware container with no lid, but under 2 x 2 mm wire mesh (to avoid the samples being destroyed by birds and flies), and allowed to dry naturally until constant mass. Since each faecal sample contained thousands of insect remains, in order to determine the appropriate subsample mass to be used for further analyses, 0.1 to 0.8 g samples were extracted from three faecal samples and the number of ant and

termite heads were counted and identified under a microscope. Subsamples of 0.3 to 0.8 g returned similar values to each other, and therefore 0.3 g (0.30 to 0.34 g, 0.8 – 6.3 % of organic material) subsamples were used for further analyses. A reference collection of Tswalu ants and termites obtained from Dr Frederic Delsuc (Montpellier University) and Dr Hamish Robertson (Iziko South African Museum) was used, along with a guidebook on the ants of southern Africa (Slingsby 2017) to identify ants and termites to genus level.

Pangolins were tracked and located at least once a week for observations of their diet. The pangolin was observed at varying stages of its activity phase, usually with a torch, from a distance of 5 to 15 m so as to not interfere with normal behaviour. Pangolin behaviours (walking, digging, resting, feeding, or other) were recorded using a continuous sampling method. Pangolins were monitored for a minimum of one hour during their active phase to record behaviours. During observations early on during the study, after a foraging bout, and once the pangolin moved off, the prey items that it was feeding on were collected and stored in 90% ethanol for later identification. During later observations, once the pangolin moved off from a foraging bout, the prey items eaten were visually identified and recorded since no new unidentified prey items were observed being eaten by pangolins.

Through behavioural observations, and confirmed with early faecal sample analyses, the three dominant prey items in the pangolin's diet were identified. Live specimens of each dominant prey item (*Crematogaster* ants, *Anoplolepis steingroeveri* ants, and *Trinervitermes trinervoides* termites) were collected throughout the year and frozen for later analyses. Previously, our team found that the energy content (in kJ) of aardvark prey items (*Hodotermes*, *Anoplolepis*, and *Trinervitermes*) did not change throughout the year (N. Weyer, unpublished observations), therefore all samples collected throughout the year were pooled together for each genus for energy content analyses. The number of individual ants and termites from each genus collected was counted and the soldier and worker castes were separated where possible. Prey items were thawed and then dried until constant mass. Bomb calorimetry (Cal2K Calorimeter System, Digital Data Systems (Pty) Ltd. Randburg, South Africa) was used to quantify the energy of the dominant prey genera (including soldier and worker castes separately where possible). For each prey genus, 4 to 12 samples (0.5 g, dry mass) were bombed, and the energy value returned by the calorimeter was divided by the number of individuals in the sample to obtain an energy value per individual ant or termite. A Benzoic acid tablet (0.5 g, DDS Calorimeters, Randburg, South Africa) was used as a standard to calibrate the calorimeter.

3.2.4 Pangolin activity

Pangolins were tracked in the mornings during their inactive phase using telemetry (see Chapter 2 for details) to locate their burrows, and camera traps were placed outside the burrows to assess time of emergence and return for the six pangolins. Camera traps did not always trigger for emergence or return events, and pangolins did not always return to the same burrow, thus the camera traps could not always detect time of emergence and return. Therefore, time of emergence and return data obtained from camera traps were supplemented with data extracted from the 24h body temperature patterns of pangolins which shows a detectable change when pangolins are either emerging or burrowing (see Chapter 4 for details). The duration of above ground activity could then be estimated from the time of emergence and return data obtained from the camera traps and body temperature records.

3.2.5 Data analyses

Data analyses were conducted in GraphPad software (version 8.00; GraphPad Prism, 2021) for all analyses in this chapter. For all models, Akaike Information Criterion (AIC) was used to determine the best model (model selection is presented in the appendix), and residuals were examined to assess the accuracy of the models. For all models, correlation matrices were created to assess the relationships between variables, and where collinearity between variables was >0.7 (Dormann *et al.* 2013), one of the related variables was removed from the model. For models that did not involve individual pangolins, interactive effects were included, and AIC modelling was used to determine whether the model with or without interactive effects was the most accurate, and that model was then used. For models involving individual pangolins, interactive effects were not tested since the small sample size of pangolins did not provide the statistical power necessary for testing interactive effects.

3.2.5.1 Climatic variables

The 24h mean, 24h minimum, and 24h maximum black globe temperatures were determined for each day across the study period. Since the 24h minimum and 24h maximum black globe temperatures were linearly related in the same way to the 24h mean black globe temperature (24h minimum globe temperature vs 24h mean globe temperature: $r^2=0.828$, slope=0.928, $p<0.0001$; 24h maximum globe temperature vs 24h mean globe temperature: $r^2=0.815$, slope=0.990, $p<0.0001$), only the 24h mean was used in analyses. Seasonal means were calculated by averaging the 24h mean for summer (December to February), autumn (March to May), winter (June to August), and spring (September to November).

Total monthly rainfall was calculated by averaging total rainfall across all 32 rain gauges for each month for the period November 2014 to October 2017. The mean annual rainfall occurring between June and May (to include all summer rainfall events, which may occur across years from December to February) was averaged for a 16-year period (2001 to 2017) at Tswalu to compare rainfall during the study period to the long-term annual mean. The mean month with the highest rainfall was calculated for the 16-year period by assigning each month a number and averaging the month numbers that coincided with the highest monthly rainfall each year to determine whether rainfall during the study period fell earlier or later than usual. Rainfall data from one year before the study period was included in further analyses where rainfall is concerned because it is known that rainfall from the preceding months and even the preceding years can impact insect abundance and vegetation composition in arid ecosystems (Ridley and Raihani 2007; Reichmann *et al.* 2013; Dudney *et al.* 2017).

3.2.5.2 Grass cover

The monthly mean grass cover (%) was calculated by averaging the estimated grass cover per transect and then averaging grass cover across all transects per month. Multiple linear regression was used to assess the effects of rainfall and 24h mean black globe temperature on monthly grass cover where rainfall and globe temperature were the explanatory variables and grass cover was the response variable. AIC modelling was used to determine whether the accumulated rainfall that fell during the month of transects, or the accumulated rainfall that fell four, three, two or one month prior to conducting transects was best suited to use in the model. Interactive effects between 24h black globe temperature and rainfall on grass cover were also tested.

3.2.5.3 Prey abundance

To calculate the percentage contribution of each ant and termite genus in the pitfall traps per year, the monthly ant and termite counts were combined for each genus across each study year and then their proportions were calculated in relation to the total number of ants and termites in each genus. To calculate the percentage occurrence of ants and termites in the pitfall traps, the number of times each genus occurred per transect (the ten pitfalls per transect were combined) was counted and divided by the total number of transects sampled across each study year. To calculate prey abundance, the ants counted from the pitfalls were totalled per transect and divided by the number of traps retrieved from the transect to calculate the number of ants per trap per transect. The number of ants per trap per transect was then averaged across all transects to calculate mean monthly prey abundance. Interquartile range analyses were used to identify prey abundance outliers (more than $\pm 3SD$ beyond the mean) since some transects

occasionally yielded unusually high numbers of ants per trap, and the outliers were then excluded.

Multiple linear regression analyses were used to assess the effects of grass cover, rainfall, and 24h mean black globe temperature on prey abundance, and AIC modelling was used to determine which rainfall variable (accumulated rainfall that fell during the month of transects, or the accumulated rainfall that fell four, three, two or one month prior to conducting transects) was best suited to the model. The relationship between prey abundance and 24h black globe temperature was not linear, and therefore a piecewise regression was used to assess the relationship before and after a breakpoint. A search was conducted to determine the breakpoint by running the model using various breakpoints between 24 and 29 °C, and then comparing the models for the best fit using AIC to identify the breakpoint. To assess whether the abundance of the main pangolin prey items was influenced by rainfall and environmental temperature, multiple linear regression was used, where average monthly rainfall and 24h mean black globe temperature were the explanatory variables, and the percentage contributions of each main prey item were the response variables. Interactive effects between 24h black globe temperature and rainfall on the abundance of the main prey items was also tested.

3.2.5.4 Pangolin diet

The percentage contribution of each prey item to the diet was calculated by dividing the number of individuals representing each genus counted per scat subsample by the total number of prey items counted in the subsample and multiplying that by 100. The mean monthly prey contribution was then averaged for each month to account for the variation in the number of scat samples collected throughout the year. The percentage occurrence of each prey item in the diet was calculated by counting the number of scat samples that each genus occurred in, dividing it by the total number of scat samples analysed, and multiplying it by 100.

The percentage organic matter was calculated per scat by dividing the dry organic portion of the scat by the whole dried scat (including inorganic matter). To assess whether preying on a specific genus influenced the amount of organic matter ingested by pangolins, simple linear regression was used, where the prey genus (*Crematogaster*, *Anoplolepis*, or *Trinervitermes*) was the explanatory variable, and percentage organic matter was the response variable. Since both *Anoplolepis* ants and *Trinervitermes* termites are subterranean insects (Adam *et al.* 2008; Picker *et al.* 2012), the two genera were pooled together for analysis of the relationship between prey items eaten and organic matter ingested. Since *Crematogaster* ants are arboreal (Tschinkel 2002), these ants were separately analysed in relation to percentage organic matter using simple linear regression.

Prey diversity was calculated by counting the number of different genera recorded in each scat and was averaged per month. Brown-Forsythe ANOVA tests were conducted to assess whether seasonal and interannual differences occurred in the diversity of prey targeted, and Dunnett's multiple comparisons tests were used to identify where those differences occurred.

The number of prey items per gram organic matter was extrapolated to a number of prey items consumed per 24h by multiplying the number of prey items per gram by the total dry organic scat mass per scat sample. Multiple linear regression analyses were used to assess the effects of environmental temperature, rainfall, prey abundance, and pangolin activity on the number of prey items eaten by pangolins per 24h. Individual pangolins could not be used as a random factor for the multiple linear regression because in certain cases scats were collected from unknown individuals, which was a limitation in my study.

Estimated 24h energy intake from the pangolin diet was calculated using the equation (adapted from Weyer 2018):

$$E_{24h} = \sum_{i=1}^n (proportion_i * E_i) * PI * m_{scats} * n_{scats} * AE$$

Where E_{24h} = dietary energy intake (kJ per pangolin per 24h);

PI = prey items (no. per gram dry scat mass);

$proportion_i$ = proportion of item i in the diet;

E_i = energy content of i (kJ per individual);

m_{scats} = organic scat mass (g);

n_{scats} = defecations per night (no. per pangolin per 24h)

AE = assimilation efficiency (proportion of 1)

An assimilation efficiency of 0.65 was used, a value that has been reported for other myrmecophagous mammals (Williams *et al.* 1997; Cooper and Withers 2004). Since only dominant prey items were bombed during calorimetry and included in the equation, 24h energy intake values were slightly underestimated since the calculations did not account for any additional incidental intake of other species. Multiple linear regression analyses were used to assess the effects of prey abundance, environmental temperature, pangolin activity, and rainfall on the 24h energy intake by pangolin.

3.3 RESULTS

3.3.1 Climatic variables

The 24h mean black globe temperatures fluctuated throughout the year (Figure 3.1), with the globe temperature reaching an absolute maximum of 50.4 °C during the summer (December to February) and a minimum of -5.1 °C during the winter (June to August).

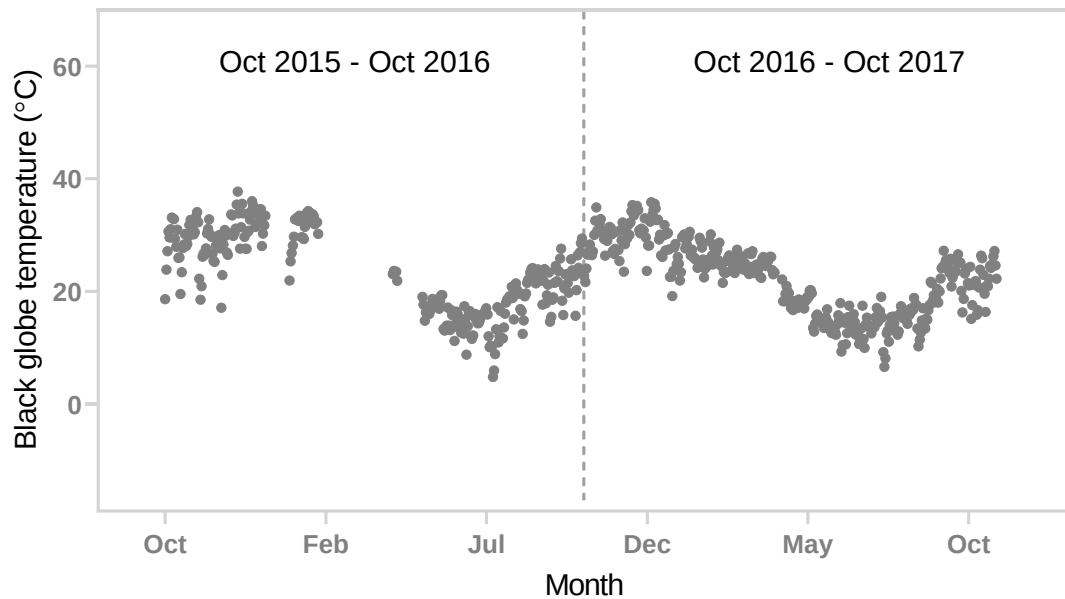


Figure 3.1: The 24h mean black globe temperatures at Tswalu for the period October 2015 to October 2017. The gaps in the data occurred due to a failed weather station.

The 24h mean black globe temperatures during the summer (31.8 ± 2.8 °C) and winter (15.7 ± 3.7 °C) of the first study year (October 2015 to October 2016) were higher compared to the summer (27.9 ± 3.7 °C) and winter (14.5 ± 2.7 °C) of second study year (October 2016 to October 2017), with no other interannual differences (Figure 3.2).

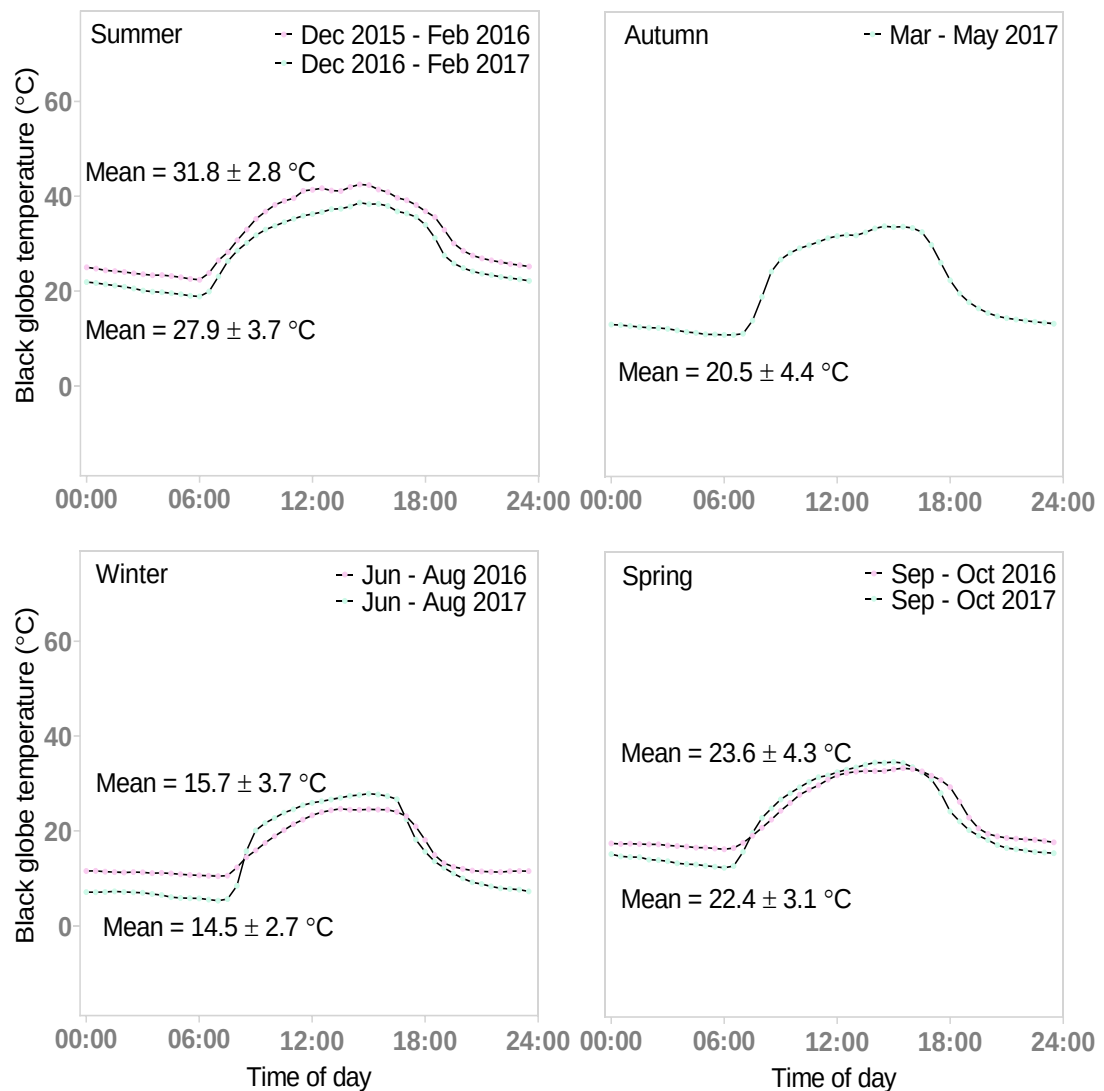


Figure 3.2: Seasonal 24h black globe temperatures at Tswalu for the study period, including the seasonal 24h means (mean $\pm$ SD). Autumn only includes March to May 2017, since data for March to May 2016 were not collected due to a failed weather station. November 2016 was excluded so that appropriate interannual comparisons could be made with the spring of 2017, since the study period ended in October 2017.

In the first study year (October 2015 to October 2016), rainfall was 278 mm, while in the second study year (October 2016 to October 2017) rainfall was 370 mm. In the year preceding the study (October 2014 to October 2015) rainfall was only 214 mm. Total annual rainfall was therefore ~20% lower during the first study year and ~9% higher during the second study year compared to the annual average rainfall for the last 16 years at Tswalu (period: 2001 to 2017, average annual rainfall = 340 mm). In the first study year, the month with the highest rainfall was April (104 mm) while in the second

study year it was January (214 mm) (Figure 3.3). Historically, over the past 16 years at Tswalu, the month with the highest rainfall was January. Rainfall was therefore lower in the first year, and the greatest amount of rainfall occurred later than normal.

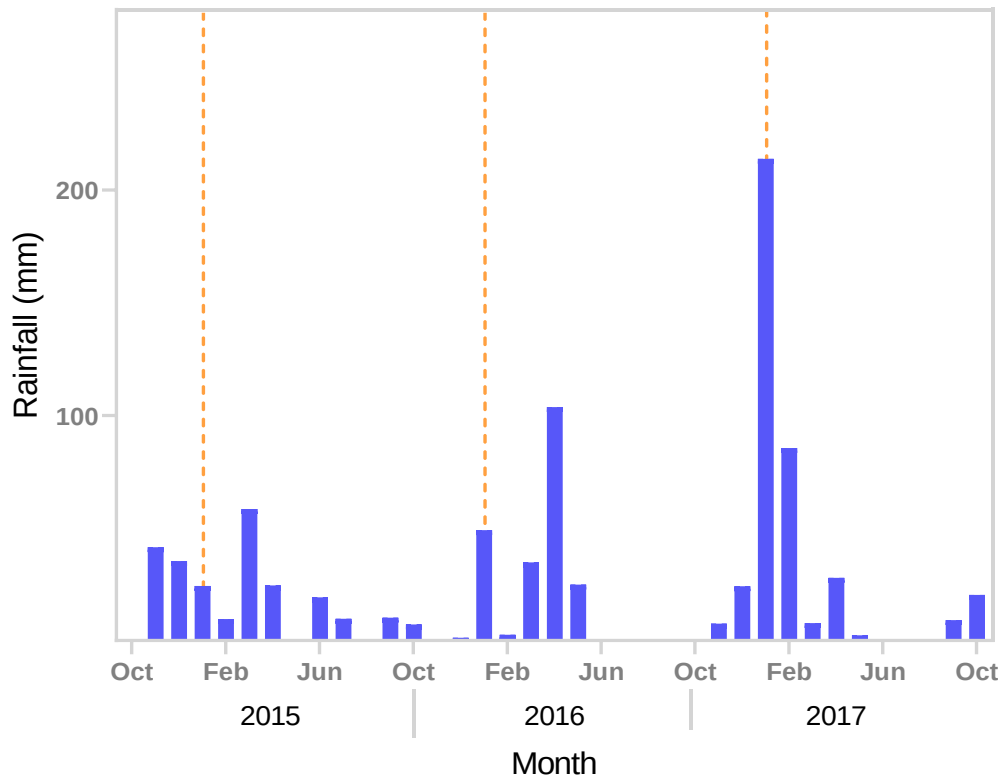


Figure 3.3: Total monthly rainfall at Tswalu for three years (year preceding the study: October 2014 to October 2015; study year 1: October 2015 to October 2016; study year 2: October 2016 to October 2017). The orange dotted lines represent the month with the highest rainfall for the last 16 years (January).

3.3.2 Grass cover

Grass cover was lower in the first study year than in the second (Figure 3.4). Grass cover was lowest during the first study year in December 2015 (~8 %) and was highest during the second study year in February 2017 (~35 %). AIC modelling revealed that the effects of accumulated rainfall three months prior to conducting transects on grass cover produced the most accurate model, with a 90.99% probability that the model was correct, compared to rainfall that fell during the months in which transects were conducted or accumulated rainfall that fell four, two, and one month prior to conducting transects (Appendix; Table A2). Rainfall three months prior was thus used in the multiple linear regression model. AIC modelling further revealed that the model including interactive effects between rainfall and black globe temperature was the most accurate, with a 98.96% probability that the model was correct (Appendix; Table A3). Multiple linear regression analyses revealed that the grass cover was predicted by accumulated rainfall three months prior to conducting

transects and by 24h mean black globe temperature, as well as by the interactive effects of rainfall and globe temperature (Table 3.2). In other words, when the accumulated rainfall in the preceding three months was high, and when environmental temperature was high, grass cover was high.

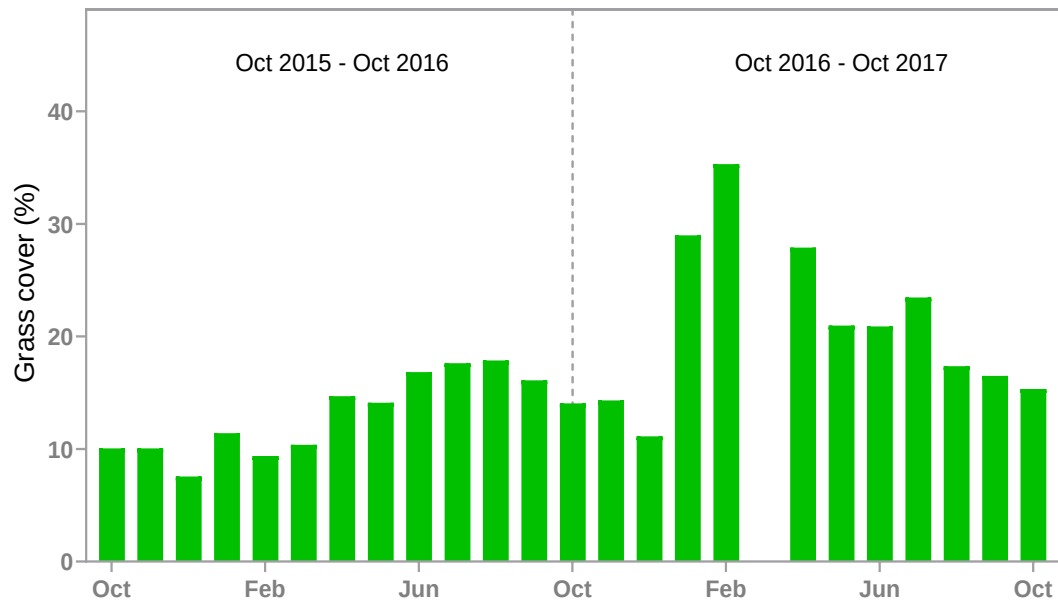


Figure 3.4: Average monthly grass cover for the study period (October 2015 to October 2017). Data for grass cover were not collected during March 2017.

Table 3.2: Multiple linear regression results of the effects of total rainfall three months prior to conducting transects and 24h mean black globe temperature on monthly grass cover, as well as their interactive effects.

Variable	$\beta \pm SE$	t	95% CI	p
<i>Grass cover</i>				
Intercept	33.34 ± 5.12	6.52	22.59 to 44.09	<0.01
Rainfall 3 months prior	-0.19 ± 0.06	2.97	-0.32 to -0.05	<0.01
24h mean black globe temperature	-0.78 ± 0.20	3.84	-1.21 to -0.36	<0.01
Rainfall*globe temperature	$0.01 \pm <0.01$	3.71	<0.01 to 0.02	<0.01

3.3.3 Prey abundance

Monthly ant abundance varied seasonally across the study period (ANOVA, $F_{(7,347)} = 33.9$, $p < 0.0001$; Figure 3.5A) and was highest during summer (20.2 ± 13.0 ants per trap) and spring (25.9 ± 20.9 ants per trap), and lowest during autumn (7.4 ± 6.0 ants per trap) and winter (9.2 ± 10.5 ants per trap). Termite abundance only varied seasonally during the first study year (October 2015-October 2016), but not during the second year (October 2016-October 2017), and was highest during summer (1.1 ± 1.5 termites per trap) and lowest during autumn (0.4 ± 0.9 termites per trap) and winter (0.4 ± 1.3 termites per trap; ANOVA, $F_{(7,167)} = 5.7$, $p < 0.0001$; Figure 3.5B). Ant abundance did not differ between years for summer ($t = 1.78$, d.f. = 157, $p > 0.05$) and spring ($t = 0.42$, d.f. = 139, $p > 0.05$) but was significantly higher during the autumn (11.1 ± 6.8 ants per trap) and winter (15.7 ± 12.3 ants per trap) of the second study year compared to in the autumn (4.7 ± 3.3 ants per trap) and winter (4.0 ± 4.2 ants per trap) of first study year. Termite abundance did not differ between years for autumn ($t = 0.83$, d.f. = 90, $p > 0.05$), winter ($t = 1.69$, d.f. = 112, $p > 0.05$), and spring ($t = 1.21$, d.f. = 67, $p > 0.05$), but was significantly higher during the summer of the first study year (1.1 ± 1.5 termites per trap) compared to the summer of the second study year (0.1 ± 0.2 termites per trap). Since the number of termites that fell into the pitfall traps was negligible, termites were excluded from further prey abundance analyses.

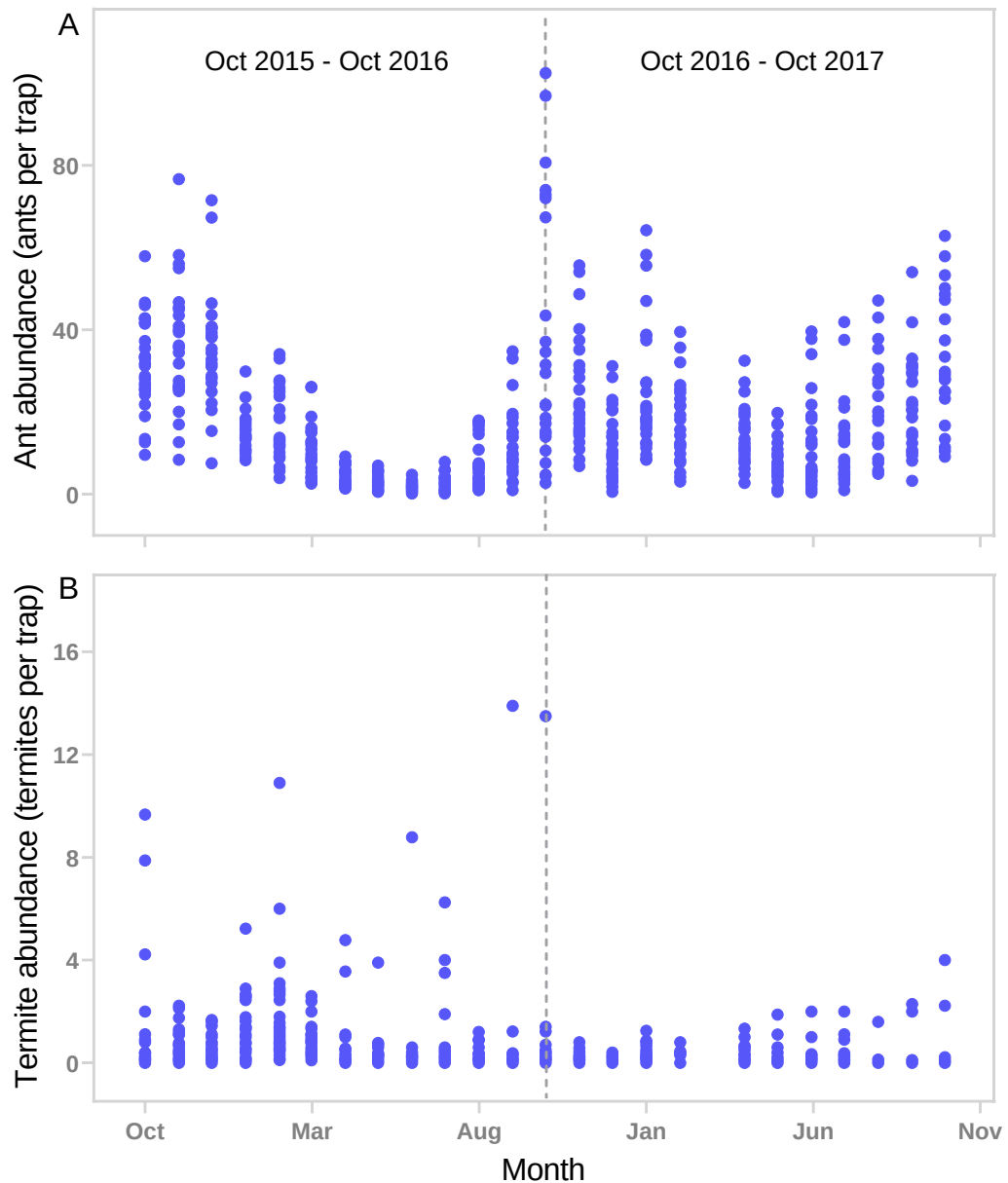


Figure 3.5: Monthly ant (A) and termite (B) abundance for the two study years (October 2015 to October 2016 and October 2016 to October 2017). Data for March 2017 are not included as transects were not conducted for the month.

Multiple linear regression revealed that mean monthly prey abundance was positively associated with 24h mean black globe temperature, but not with rainfall or grass cover (Table 3.3). Interactive effects were excluded because AIC modelling revealed that the model without interactive effects was the most accurate, with a 99.44% probability of the model being correct (Appendix; Table A4). Piecewise regression (AIC modelling; Appendix; Table A5) revealed that prey abundance was only positively associated with 24h mean black globe temperature below 27 °C ($r^2=0.233$, slope=1.736), and above 27 °C the relationship was negative (slope=-1.655) (Figure 3.6). In other words, when daily

mean environmental temperatures were below ~27 °C, prey abundance was high when environmental temperatures were high, but when daily mean environmental temperatures exceeded ~27 °C, prey abundance decreased as a function of environmental temperature.

Table 3.3: Multiple linear regression results of the effects of rainfall, grass cover, and 24h mean black globe temperature on monthly prey abundance.

Variable	$\beta \pm SE$	t	95% CI	p
<i>Prey abundance</i>				
Intercept	-4.70 ± 10.48	0.45	-26.73 to 17.33	0.66
Rainfall 3 months prior	-0.06 ± 0.03	2.05	-0.11 to <0.01	0.06
Grass cover	0.34 ± 0.36	0.96	-0.41 to 1.09	0.35
24h mean black globe temperature	0.91 ± 0.31	2.90	0.25 to 1.56	<0.05

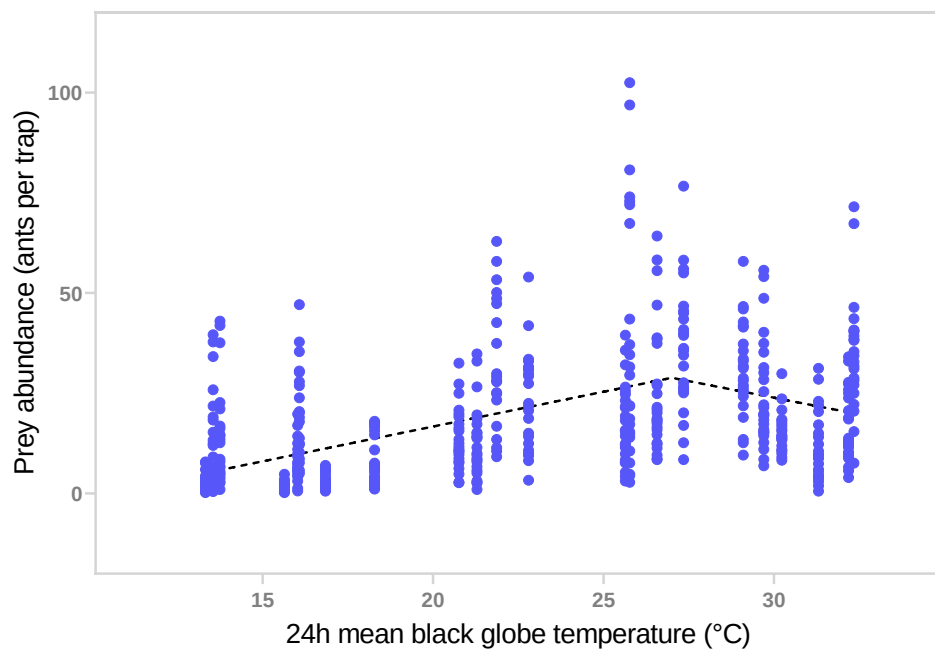


Figure 3.6: The relationship between the monthly 24h mean black globe temperature and monthly prey abundance. The black dashed line shows the piecewise regression and breakpoint (where the line changes direction).

Overall, 17 ant and 6 termite genera were recorded in the pitfall traps across the study period (Table 3.4). Ants contributed the most (96.5 %) to the pitfall contents and occurred in 100% of the transects, whereas termites only contributed 3.5 % and occurred in less than half of the transects. Of all the ant genera sampled in the pitfalls, *Monomorium* was the greatest contributor to the trap contents, followed by *Pheidole*, *Tetramorium*, *Tapinolepis* and *Anoplolepis*. Despite being the greatest contributor to the pitfalls, *Monomorium* did not occur in the transects the most often. Instead, *Pheidole* occurred in the transects more often than any other ant, followed by *Monomorium*, *Tapinolepis*, and *Tetramorium*. Despite its low contribution to the trap contents (~7%), *Anoplolepis* occurred in almost half (~48 %) of the transects. Of all the termite genera sampled, *Hodotermes* was the greatest contributor to the trap contents, followed by *Trinervitermes*. However, *Trinervitermes* occurred in the transects more often than did *Hodotermes*.

Of all the ant genera, *Monomorium* ($t=7.3$, d.f.=516, $p<0.0001$) and *Tetramorium* ($t=3.0$, d.f.=548, $p<0.01$) contributed significantly more to the pitfall contents during the second study year compared to the first study year, whereas *Pheidole* ($t=3.7$, d.f.=590, $p<0.001$), *Tapinolepis* ($t=6.9$, d.f.=504, $p<0.0001$), and *Ocymyrmex* ($t=3.8$, d.f.=577, $p<0.001$) contributed significantly more to the pitfall contents during the first year compared to the second year. Of all the termite genera, *Hodotermes* ($t=4.3$, d.f.=374, $p<0.0001$) and *Trinervitermes* ($t=4.6$, d.f.=343, $p<0.0001$) contributed significantly more to the pitfall contents during the first study year compared to the second study year.

Table 3.4: The contribution and occurrence of ant and termite genera in the pitfall traps across the study period. Grey blocks indicate significant differences ($p < 0.05$) between the two study years.

Genus	% Contribution		Mean	% Occurrence		Overall
	2015-2016	2016-2017		2015-2016	2016-2017	
Ants			96.5			100
<i>Monomorium</i>	22.1 ± 11.6	37.4 ± 16.9	29.8 ± 16.2	82.3	92.1	86.9
<i>Pheidole</i>	28.7 ± 11.1	20.9 ± 10.5	24.8 ± 11.3	92.4	91.4	91.9
<i>Tetramorium</i>	11.1 ± 6.1	15.8 ± 10.3	13.4 ± 8.6	78.5	86.3	82.2
<i>Tapinolepis</i>	15.2 ± 7.5	7.8 ± 4.9	11.5 ± 7.3	82.9	80.6	81.8
<i>Anoplolepis</i>	6.0 ± 3.8	7.9 ± 6.7	6.9 ± 5.4	38.0	59.4	48.0
<i>Ocymyrmex</i>	6.2 ± 5.6	4.1 ± 2.6	5.1 ± 4.4	69.0	75.9	72.2
<i>Lepisiota</i>	2.6 ± 1.6	2.1 ± 1.6	2.3 ± 1.6	45.6	37.8	41.9
<i>Camponotus</i>	1.3 ± 1.4	1.4 ± 0.9	1.3 ± 1.1	38.3	45.7	41.8
<i>Tapinoma</i>	0.5 ± 0.5	0.8 ± 1.6	0.7 ± 1.2	20.3	14.4	17.6
<i>Crematogaster</i>	0.4 ± 0.4	0.5 ± 0.9	0.5 ± 0.7	12.0	11.5	11.8
<i>Plagirolepis</i>	0.1 ± 0.3	0.04 ± 0.1	0.1 ± 0.2	6.0	5.4	5.7
<i>Tetraponera</i>	0.1 ± 0.1	0.02 ± 0.04	0.05 ± 0.1	4.7	1.4	3.2
<i>Messor</i>	0.1 ± 0.1	<0.01 ± 0.01	0.03 ± 0.1	1.9	1.1	1.5
<i>Cataulacus</i>	0.01 ± 0.01	<0.01 ± 0.01	<0.01 ± 0.01	0.9	1.1	1.0
<i>Anochetus</i>	0.01 ± 0.03	<0.01 ± 0.01	0.01 ± 0.02	1.3	0.4	0.8
<i>Ophthalmopane</i>	<0.01 ± <0.01	<0.01 ± 0.01	<0.01 ± <0.01	0.3	0.4	0.3
<i>Dorylus</i>	<0.01 ± <0.01	0	<0.01 ± <0.01	0.2	0	0.1
Termites			3.5			48.8
<i>Hodotermes</i>	3.5 ± 2.5	0.7 ± 0.8	2.1 ± 2.3	35.1	20.9	28.5
<i>Trinervitermes</i>	2.1 ± 2.8	0.4 ± 0.2	1.3 ± 2.1	38.9	21.2	30.6
<i>Odontotermes</i>	0.1 ± 0.3	0.01 ± 0.02	0.07 ± 0.2	1.6	0.7	1.2
<i>Psammotermes</i>	0.1 ± 0.1	0.1 ± 0.3	0.08 ± 0.2	2.2	1.1	1.7
Termitidae	0.02 ± 0.04	<0.01 ± 0.01	0.01 ± 0.03	1.6	0.4	1.0
<i>Allodontotermes</i>	<0.01 ± 0.01	<0.01 ± 0.02	<0.01 ± 0.01	0.3	0.4	0.3

3.3.4 Pangolin diet

3.3.4.1 Dietary observations and scat contents

From observations of 603 foraging bouts, pangolins were observed eating three prey genera, namely *Crematogaster* (unidentified species) ants, *Anoplolepis steingroeveri* ants, and *Trinervitermes trinervoides* termites. On three occasions, *Camponotus fulvopilosus* was recorded. The scats revealed that the overall pangolin diet comprised of 86% ants and 14% termites in terms of the proportion of prey items occurring in the scats. The scats also revealed that ants from ten genera and termites from three genera were recorded in the diet and confirmed that the three dominant prey genera were *Crematogaster*, *Anoplolepis*, and *Trinervitermes* (Table 3.5). The diet comprised of $50.2 \pm 24.3\%$ *Crematogaster* ants, $31.2 \pm 24.0\%$ *Anoplolepis* ants (soldier cast $6.4 \pm 4.3\%$, worker cast $24.9 \pm 20.5\%$), and $11.9 \pm 10.2\%$ *Trinervitermes* termites (soldier cast $5.7 \pm 5.5\%$, worker cast $6.2 \pm 5.5\%$). Additional ants and termites, classed as 'other', accounted for $6.4 \pm 5.3\%$ of the diet, and included ants from the *Camponotus*, *Lepisiota*, *Monomorium*, *Ocymyrmex*, *Pheidole*, *Tapinolepis*, *Tetramorium*, and *Tetraponera* genera, and termites from the *Psammotermes* and *Hodotermes* genera. *Crematogaster* ants were present in 97.1% of the scat samples, *Anoplolepis* ants in 92.2%, and *Trinervitermes* termites in 92.2% of scat samples (Table 3.5). Despite *Crematogaster*, *Anoplolepis*, and *Trinervitermes* dominating the diet, these three prey items were not the most abundant ants and termites at Tswalu (see Table 3.3). Although *Camponotus* ants did not contribute much to the pangolin diet ($3.0 \pm 2.9\%$) or the contents of the pitfall traps (1.1%), the genus appeared in 80.4% of all scat samples, and in 42.0% of the transects.

Overall, there was interannual variation in the pangolin diet, with pangolins feeding on significantly more *Trinervitermes* termites ($t=3.6$, d.f.=10, $p<0.01$) and fewer *Camponotus* ants ($t=4.7$, d.f.=10, $p<0.001$) during the first study year compared to during the second study year (Table 3.5), with no other overall interannual differences.

Table 3.5 Percentage contribution of ant and termite prey items to the pangolin diet (mean $\pm$ SD) and percentage occurrence of prey items in scat samples. Grey blocks indicate significant differences ($p < 0.05$) between the two study years.

Genus	% Contribution			% Occurrence		
	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean
Ants						
<i>Crematogaster</i>	48.3 $\pm$ 28.1	52.2 $\pm$ 20.5	50.2 $\pm$ 24.3	94.2	100.0	97.1
<i>Anoplolepis</i>	27.9 $\pm$ 28.6	34.9 $\pm$ 19.3	31.2 $\pm$ 24.0	86.5	98.0	92.2
<i>Camponotus</i>	1.4 $\pm$ 1.2	4.7 $\pm$ 3.1	3.0 $\pm$ 2.8	76.9	84.0	80.4
<i>Tetramorium</i>	2.7 $\pm$ 4.6	0.7 $\pm$ 0.9	1.7 $\pm$ 3.5	25.0	32.0	28.4
<i>Pheidole</i>	1.9 $\pm$ 4.7	0.4 $\pm$ 0.5	1.2 $\pm$ 3.4	40.4	28.0	34.3
<i>Tetraponera</i>	0.4 $\pm$ 1.0	0.2 $\pm$ 0.4	0.3 $\pm$ 0.8	9.6	8.0	8.8
<i>Tapinolepis</i>	0.1 $\pm$ 0.1	0.2 $\pm$ 0.3	0.1 $\pm$ 0.2	5.8	22.0	13.7
<i>Lepisiota</i>	0	0.02 $\pm$ 0.08	0.01 $\pm$ 0.06	0	2.0	1.0
<i>Monomorium</i>	0	0.01 $\pm$ 0.02	<0.01 $\pm$ 0.01	0	4.0	2.0
<i>Ocymyrmex</i>	0	<0.01 $\pm$ <0.01	<0.01 $\pm$ <0.01	0	<0.01 $\pm$ 0.01	<0.01 $\pm$ <0.01
Termites						
<i>Trinervitermes</i>	17.1 $\pm$ 10.5	6.2 $\pm$ 8.2	11.9 $\pm$ 10.2	96.2	88.0	92.2
<i>Hodotermes</i>	0.7 $\pm$ 0.2	0.01 $\pm$ 0.3	0.05 $\pm$ 0.1	3.8	4.0	3.9
<i>Psammotermes</i>	0.01 $\pm$ 0.2	0.01 $\pm$ 0.03	0.01 $\pm$ 0.03	1.9	6.0	3.9

Seasonally, pangolins fed on fewer *Crematogaster* ants during winter compared to the rest of the year during the first study year (ANOVA, $F_{(7,69)}=4.8$, $p < 0.001$; Figure 3.7). Interannually, during the first study year, pangolins fed on more *Crematogaster* ants during summer and on fewer *Crematogaster* ants during the spring compared to that of the second year. Seasonally, pangolins fed on more *Anoplolepis* ants (soldiers and workers combined) during winter compared to summer and autumn during the first study

year (ANOVA, $F_{(7,67)}=3.6$, $p<0.01$). Interannually, pangolins fed on fewer soldier and worker *Anoplolepis* ants during the summer and autumn of the first study year compared to in the second study year. Seasonally, during the first year, pangolins fed on more *Trinervitermes* termites during winter compared to summer, and during the second year they fed on more *Trinervitermes* termites during winter compared to autumn and summer (ANOVA, $F_{(7,43)}=8.1$, $p<0.0001$). Interannually, pangolins fed on more *Trinervitermes* termites (soldiers and workers combined since their proportions in the diet did not differ) during the autumn, winter, and spring of the first year compared to that of the second year.

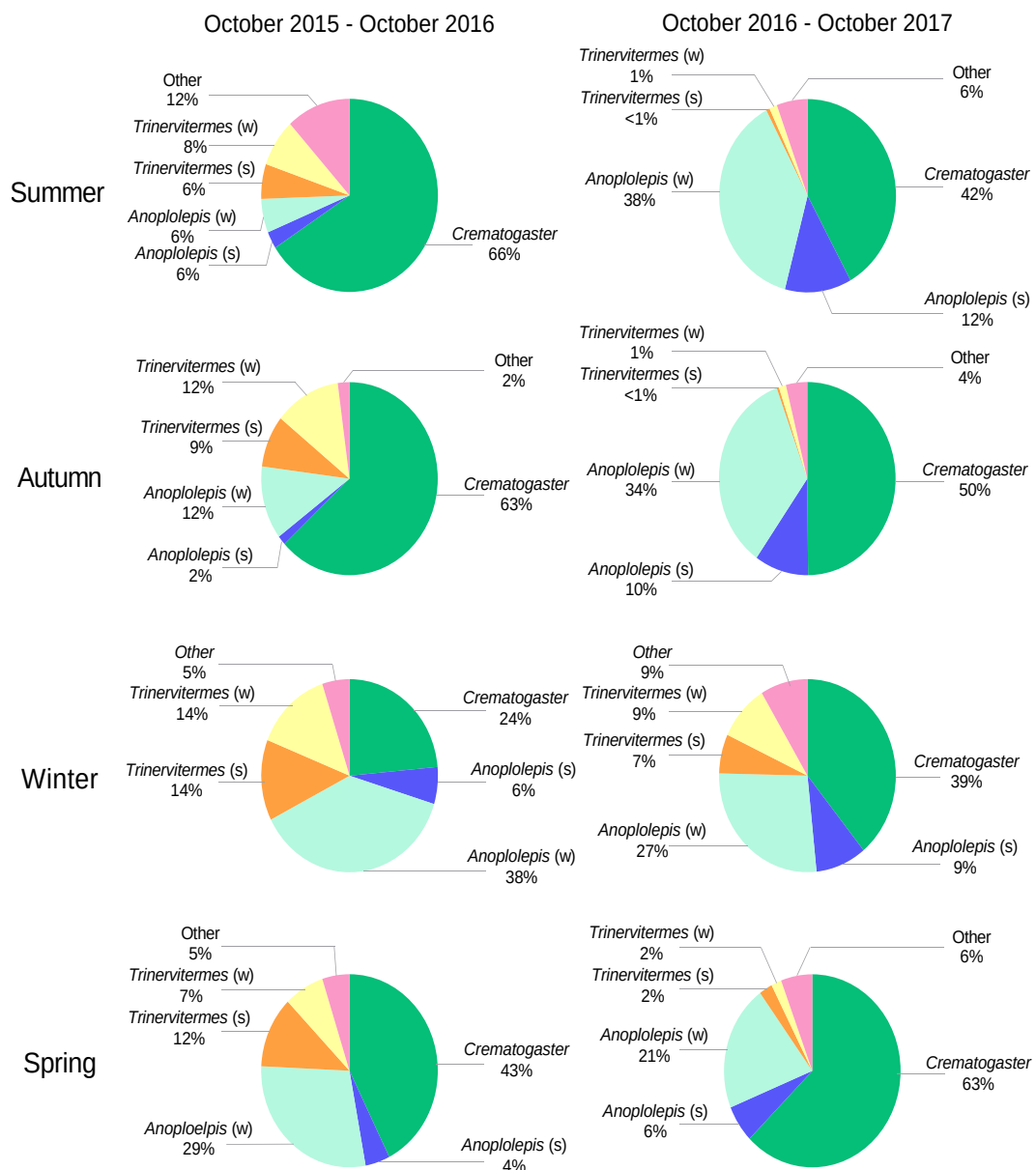


Figure 3.7: Seasonal and interannual proportions of the prey items in the pangolin diet, including soldier (s) and worker (w) castes where applicable.

3.3.4.2 Abundance of pangolin prey items

Of the dominant prey items in the diet, the abundance of *Crematogaster* ants in the pitfall traps did not vary seasonally nor interannually (ANOVA, $F_{(7,65)}=1.1$, $p>0.05$; Figure 3.8). However, during the first study year, the abundance of *Trinervitermes* termites in the pitfall traps was highest during the summer and autumn and lowest during spring (ANOVA, $F_{(7,196)}=8.1$, $p<0.0001$), but did not vary during the second study year. Interannually, *Trinervitermes* termites were more abundant during the summer and autumn of the first year compared to the second year. The abundance of *Anoplolepis* ants did not vary significantly throughout the first year but was highest during the summer and autumn and lowest during the winter and spring of the second year (ANOVA, $F_{(7,328)}=5.6$, $p<0.0001$). Interannually, *Anoplolepis* ants were more abundant during the second summer compared to in the first summer and more abundant during the first winter compared to in the second winter.

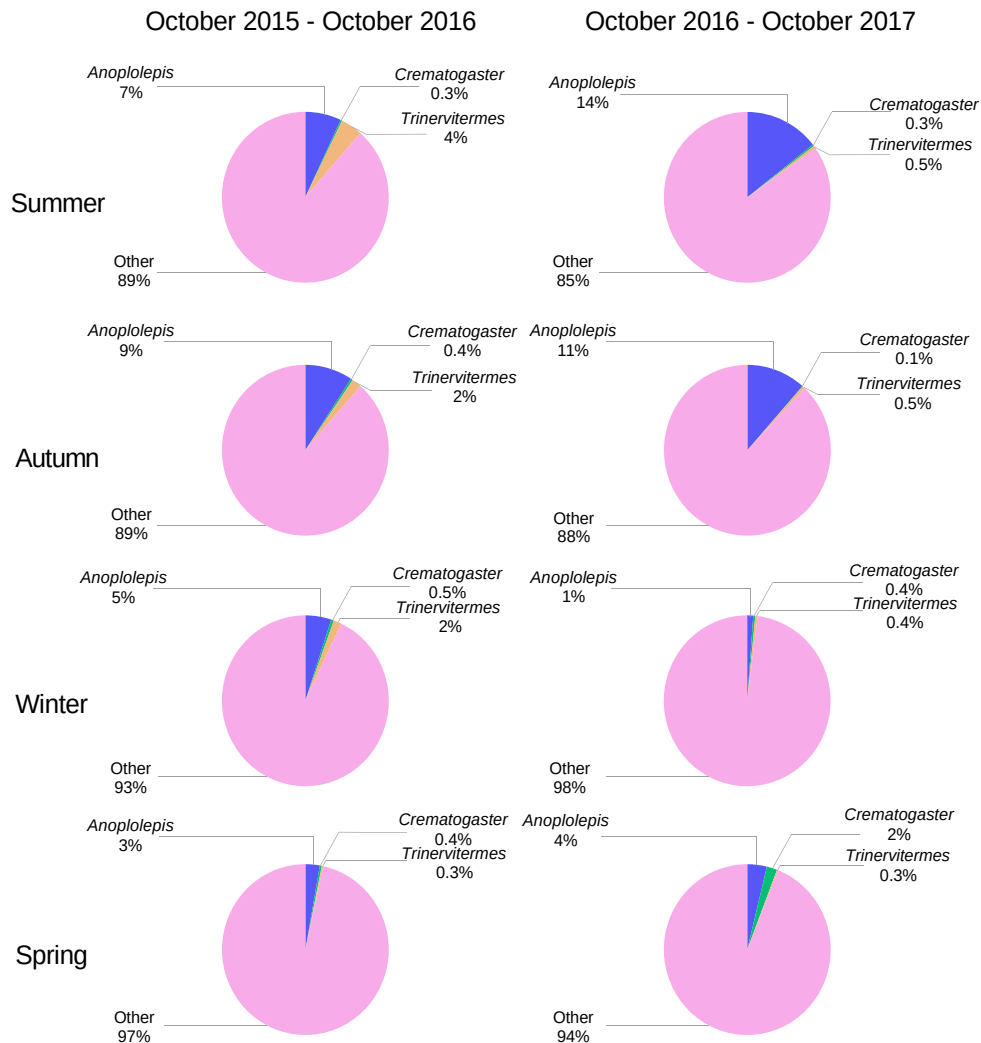


Figure 3.8: The seasonal and interannual proportions of the three dominant prey items and 'other' ants and termites in the pitfall traps.

Multiple linear regression revealed that, of the three dominant prey items in the pangolin diet, the proportion of *Anoplolepis* ants in the pitfall traps was positively associated with average monthly rainfall and not with 24h mean black globe temperature, and that the proportions of *Crematogaster* ants and *Trinervitermes* termites were not associated with average monthly rainfall or with 24h mean black globe temperature (Table 3.6). In other words, when monthly rainfall increased, the abundance of *Anoplolepis* ants increased in the pitfall traps but rainfall did not affect the abundance of *Crematogaster* ants and *Trinervitermes* termites.

Table 3.6: Multiple linear regression results of the effects of average monthly rainfall and 24h mean black globe temperature on the abundance of *Anoplolepis* ants, *Crematogaster* ants, and *Trinervitermes* termites in the pitfall traps.

Variable	$\beta \pm SE$	t	95% CI	p
<i>Anoplolepis</i> contribution				
Intercept	0.04 ± 0.03	1.12	-0.03 to 0.10	0.28
Rainfall	$7.97 \times 10^{-4} \pm 1.93 \times 10^{-4}$	4.12	3.92×10^{-4} to 1.20×10^{-3}	<0.01
24h mean black globe temperature	$5.88 \times 10^{-4} \pm 1.40 \times 10^{-3}$	0.42	-2.35×10^{-3} to 3.52×10^{-3}	0.68
<i>Crematogaster</i> contribution				
Intercept	$2.47 \times 10^{-3} \pm 5.30 \times 10^{-3}$	0.47	-8.62×10^{-3} to 0.01	0.65
Rainfall	$-3.55 \times 10^{-5} \pm 3.17 \times 10^{-5}$	1.12	-1.02×10^{-4} to 3.08×10^{-5}	0.28
24h mean black globe temperature	$1.42 \times 10^{-4} \pm 2.30 \times 10^{-4}$	0.62	-3.39×10^{-4} to 6.22×10^{-4}	0.54
<i>Trinervitermes</i> contribution				
Intercept	$-7.80 \times 10^{-3} \pm 0.02$	0.46	-0.04 to 0.03	0.65
Rainfall	$-8.26 \times 10^{-5} \pm 1.01 \times 10^{-4}$	0.82	-2.94×10^{-4} to 1.29×10^{-4}	0.42
24h mean black globe temperature	$9.64 \times 10^{-4} \pm 7.32 \times 10^{-4}$	1.32	-5.67×10^{-4} to 2.50×10^{-3}	0.20

3.3.4.3 Number of prey items consumed

The average number of prey genera recorded in each scat was 5 ± 1 genera. The diversity of prey items recorded per scat varied during the second study year, but not during the first study year, with pangolins preying on more genera during the summer of the first year compared to any other season (ANOVA, $F_{(7,31)}=2.3$, $p<0.05$; Figure 3.9). There was no interannual variation in the diversity of prey items eaten.

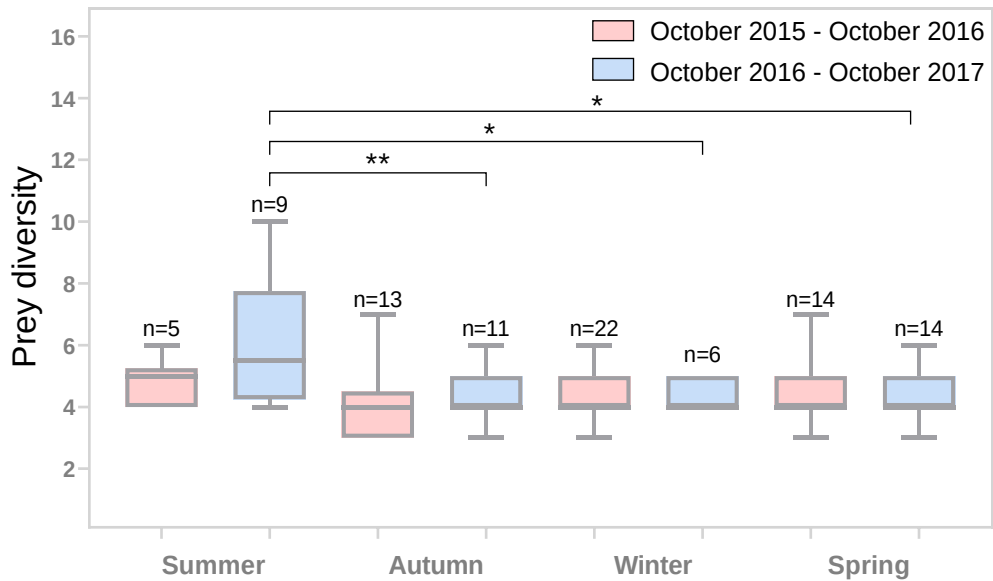


Figure 3.9: Seasonal and interannual number of prey genera (prey diversity) recorded in pangolin scats. The centre line in the boxes represents the median, and the bars represent the minimums and maximums. n = the number of scats collected per season. * Indicates a $p<0.05$ statistically significant difference between seasons and ** indicates a $p<0.01$ statistically significant difference between seasons.

Analyses of ant and termite head counts in the scats revealed that, on average, 701.8 ± 223.5 individual prey items were recorded per gram of dry scat mass. On average, organic matter accounted for $31.2 \pm 15.1\%$ of the whole scat and was lowest during winter ($22.0 \pm 12.2\%$; ANOVA, $F_{(3,41)}=3.7$, $p<0.05$), which coincided with pangolins feeding on more subterranean prey items (*Anoplolepis* ants and *Trinervitermes* termites) and on fewer arboreal *Crematogaster* ants during winter compared to the rest of the year. In other words, when pangolins preyed on proportionally more *Crematogaster* ants, organic content of the scat was high ($r^2=0.331$, $p<0.0001$; Figure 3.10A), and when pangolins fed on proportionally more *Anoplolepis* ants and *Trinervitermes* termites, organic content of the scat was low ($r^2=0.372$, $p<0.0001$; Figure 3.10B).

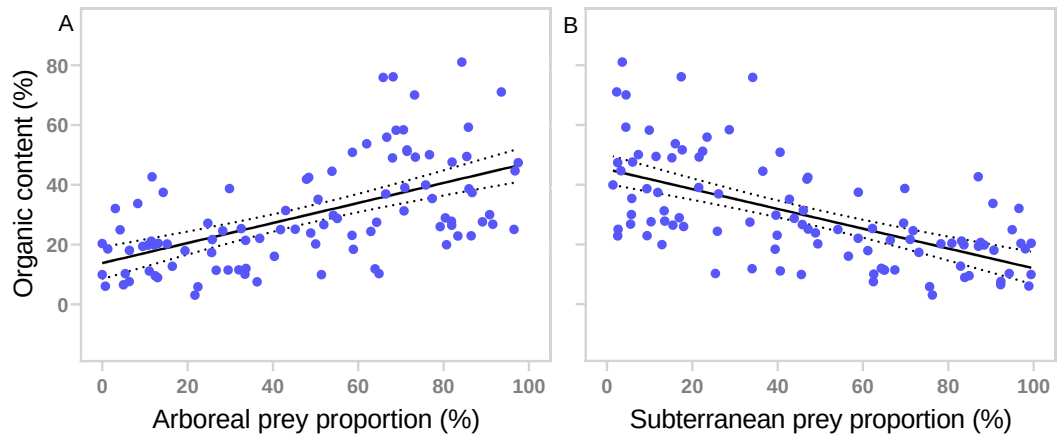


Figure 3.10: Relationship between the proportion of arboreal prey (*Crematogaster* ants) eaten and the organic content of the scat (A), and the relationship between the proportion of subterranean prey (*Anoplolepis* ants and *trinervitermes* termites combined) eaten and the organic content of the scat (B).

Extrapolation of prey items per gram per scat to the total number of ants and termites consumed per day resulted in a mean total of $15\,398.1 \pm 5814.4$ ants and termites consumed per 24h (absolute minimum: 1 366.8 prey items, absolute maximum: 59 736.1 prey items). There was seasonal and interannual variation in the number of prey items consumed per (ANOVA, $F_{(7,71)}=2.2$, $p<0.05$; Figure 3.11). During the first year, pangolins consumed more prey items per day during autumn ($24\,479 \pm 13\,490$ prey items) compared to spring ($7\,508 \pm 5225$ prey items), and during the second year, they consumed more prey items during summer ($19\,593 \pm 5290$ prey items) compared to winter (6785 ± 4744 prey items). Interannually, pangolins consumed more prey items per day during the autumn of the first year compared to the autumn of the second year, and more prey items during the spring of second year compared to spring of first year.

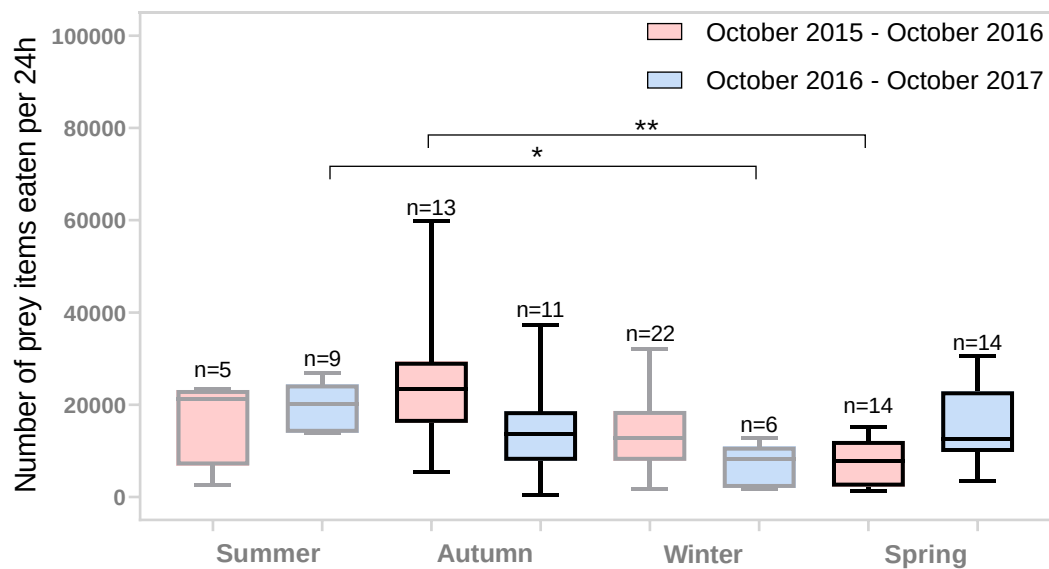


Figure 3.11: Seasonal and interannual number of prey items eaten per 24h. Black borders indicate significant differences between years. The centre line in the boxes represents the median, and the bars represent the minimums and maximum number of prey items eaten per 24h. n = the number of scats collected per season. * Indicates a $p < 0.05$ statistically significant difference between seasons and ** indicates a $p < 0.01$ statistically significant difference between seasons.

AIC model selection was used to identify the best suited model to test the effects of the explanatory variables on the number of prey items eaten daily by pangolins (Appendix; Table A6). The global model included the following explanatory variables: rainfall during the month in which transects were conducted, or rainfall that fell four, three, two, or one month prior to conducting transects, 24h mean black globe temperature, pangolin emergence and return to the burrow, the time spent active above ground, and prey abundance. The rainfall variable that yielded the best model to test the effects of explanatory variables on the number of prey items eaten by pangolins each day was rainfall that fell three months prior to conducting transects and was thus used in the model. Furthermore, the pangolin activity variable (duration of activity, time of emergence, time of return) that produced the best model was the duration of activity and was thus used in the model. AIC modelling also revealed that the 24h mean black globe temperature was highly correlated ($r > 0.82$) with the duration of activity and was thus removed from the model. The final model that tested the effects of rainfall, prey abundance, and pangolin activity on the number of prey items eaten daily by pangolins had a 98.37% probability of being correct. Multiple linear regression (Table 3.7) revealed that the number of prey items consumed per day was not associated with rainfall (Figure

3.12A) or prey abundance (Figure 3.12B) but was positively associated with the amount of time that pangolins spent active (Figure 3.12C). In other words, when pangolins were active above ground for longer durations, they consumed more ants and termites compared to when they were active for shorter durations.

Table 3.7: Multiple linear regression results of the effects of accumulated rainfall 3 months prior to conducting transects, prey abundance, and the amount of time pangolins spent active on the number of prey items eaten.

Variable	$\beta \pm SE$	t	95% CI	p
<i>Number of prey items eaten</i>				
Intercept	-9612.0 $\pm$ 7110.0	1.35	-24548.0 to 5325.0	0.19
Rainfall 3 month prior	6.47 $\pm$ 13.3	0.47	-22.59 to 35.54	0.65
Prey abundance	-216.30 $\pm$ 111.0	1.95	-449.60 to 16.98	0.07
Time active	4378.0 $\pm$ 1184.0	3.70	1890.0 to 6865.0	<0.01

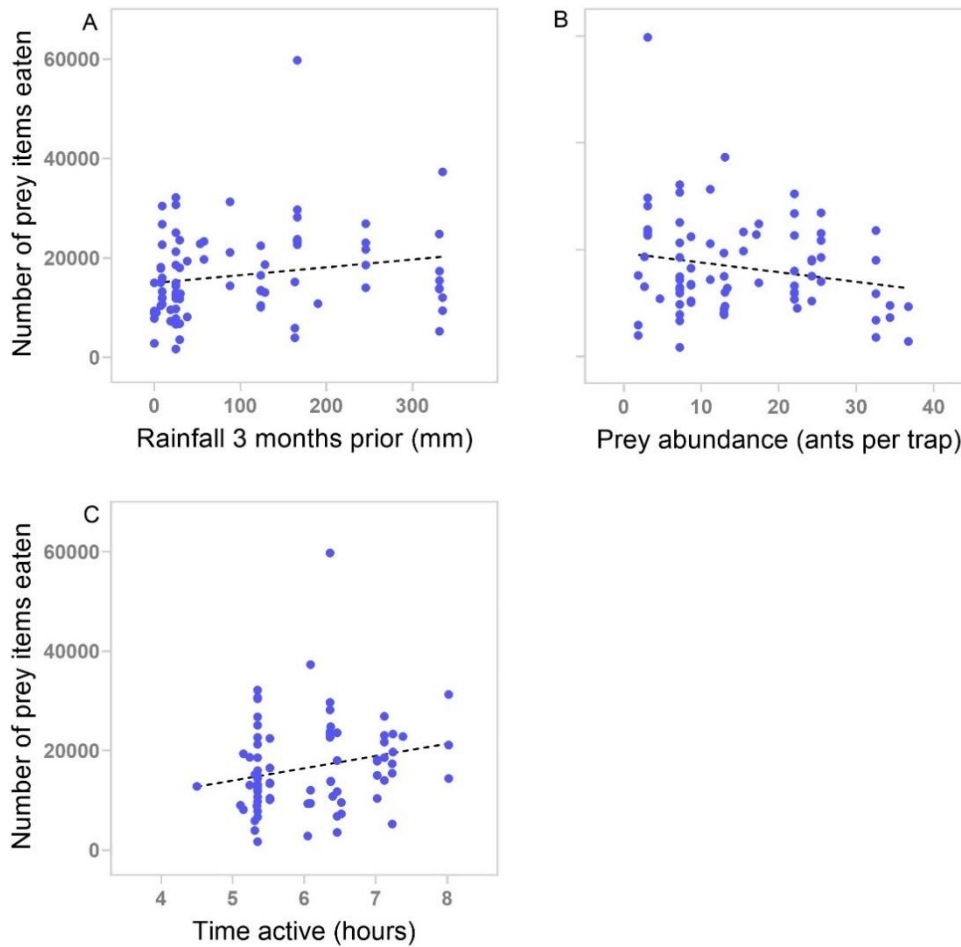


Figure 3.12: The relationship between the number of prey items eaten per day and rainfall three months prior to conducting transects (A), prey abundance (B), and the amount of time pangolins spent active (C). The black dashed lines represent the regression.

3.3.4.4 Estimated energy intake

Mean energy content per individual ant or termite varied between prey items (ANOVA, $F_{(4,31)}=7.4$, $p<0.0001$), with *Anoplolepis* soldiers containing the most energy (0.08 ± 0.05 kJ, $n=5$) compared to *Anoplolepis* workers (0.02 ± 0.003 kJ, $n=6$), *Crematogaster* (0.01 ± 0.001 kJ, $n=12$), *Trinervitermes* soldiers (0.01 ± 0.004 kJ, $n=4$), and *Trinervitermes* workers (0.02 ± 0.002 kJ, $n=9$). The overall mean daily energy intake by pangolins was 162.2 ± 73.2 kJ/day. The absolute minimum 24h energy intake was 26.2 kJ/day and the absolute maximum 24h energy intake was 597.3 kJ/day. Since the energy values of 'other' ants and termites were not measured, and thus not accounted for in the estimated energy equation, energy intake may have been 6.4% (% contribution of 'other' ants in the diet) higher than the calculated estimates. There was seasonal and interannual variation in energy intake by pangolins (ANOVA, $F_{(7,39)}=3.6$, $p<0.01$; Figure 3.13). During the first

year, pangolins took in more energy during autumn (226.8 ± 128.9 kJ/day) compared to winter (171.2 ± 91.5 kJ/day) and spring (78.1 ± 56.1 kJ/day), while during the second year, they took in more energy during summer (297.1 ± 132.8 kJ/day) compared to winter (104.1 ± 69.4 kJ/day). Interannually, pangolins took in more than twice the amount of energy during the summer of the second year compared to the summer of the first year. Energy intake also was higher during the spring of the second year compared to the spring of the first year.

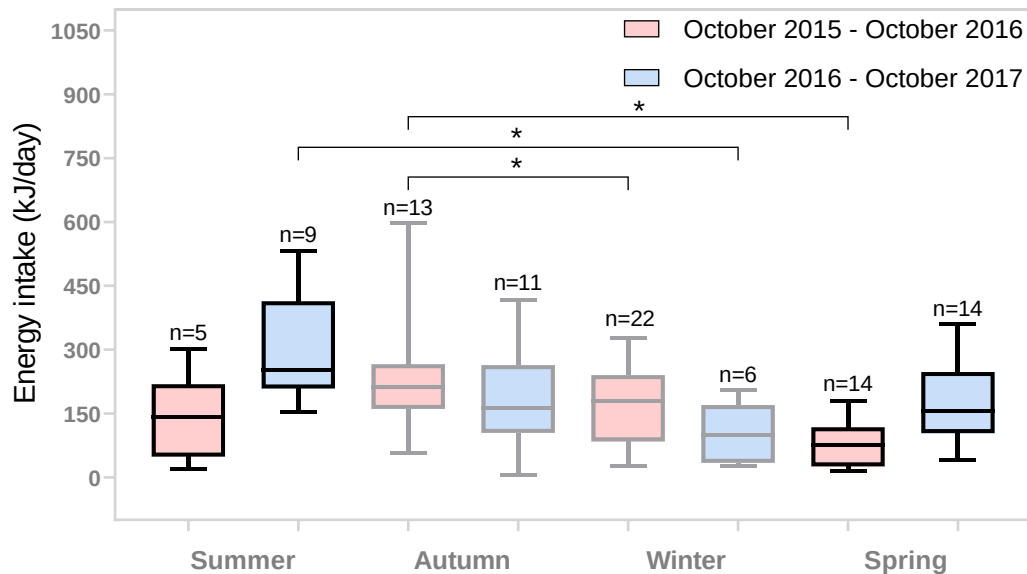


Figure 3.13: Seasonal and interannual 24h energy intake from the diet. * indicates statistical significance ($p < 0.05$). Black borders indicate significant differences between years. The centre line in the boxes represents the median, and the bars represent the minimums and maximum number of prey items eaten per 24h. n = the number of scats collected per season. * indicates statistical significance between seasons ($p < 0.05$).

AIC model selection was used to identify the best suited model to test the effects of the explanatory variables on the estimated 24h energy intake by pangolins (Appendix; Table A7). The global model included the following explanatory variables: rainfall during the month in which transects were conducted, or rainfall that fell four, three, two, or one month prior to conducting transects, 24h mean black globe temperature, pangolin emergence and return to the burrow, the time spent active above ground, and prey abundance. AIC modelling revealed that the rainfall variable that yielded the best model to test the effects of explanatory variables on the estimated 24h energy intake by pangolins was rainfall that fell during the month in which transects were conducted and was thus used in the model. Furthermore, the pangolin activity variable that produced the best model was the duration of activity and was thus used in the model. AIC modelling also revealed that the 24h mean black globe temperature was highly correlated ($r > 0.82$)

with the duration of activity and was thus removed from the model. The final model that tested the effects of rainfall, prey abundance, and pangolin activity on the estimated 24h energy intake by pangolins had an 84.72% probability of being correct. Multiple linear regression (Table 3.8) revealed that the amount of time that pangolins spent active positively affected energy intake (Figure 3.14A). In other words, energy intake was high when pangolins were active for longer periods. Energy intake, however, was not influenced by prey abundance (Figure 3.14B) or rainfall (Figure 3.14C).

Table 3.8: Multiple linear regression results of the effects of accumulated during the month in which transects were conducted, prey abundance, and the amount of time that pangolins spent active, on the 24h estimated energy intake by pangolins.

Variable	$\beta \pm SE$	t	95% CI	p
<i>Energy intake</i>				
Intercept	-254.90 $\pm$ 99.63	2.56	-467.20 to -42.51	<0.05
Rainfall during that month	0.12 $\pm$ 0.16	0.73	-0.23 to 0.47	0.47
Prey abundance	-2.19 $\pm$ 1.46	1.50	-5.30 to 0.92	0.15
Time active	63.54 $\pm$ 15.18	4.19	31.18 to 95.90	<0.01

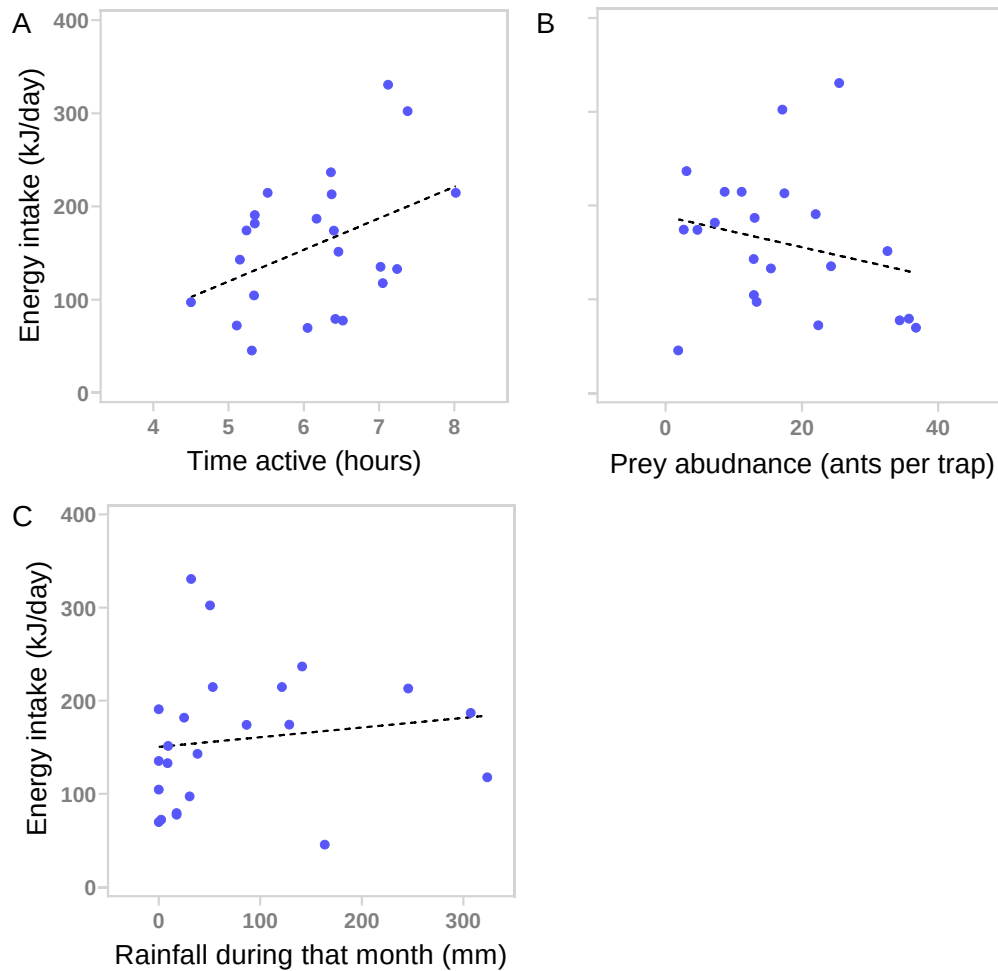


Figure 3.14: Relationship between energy intake and the amount of time that pangolins spent active (A), prey abundance (B), and rainfall that fell during the month in which transects were conducted (C). The black dashed lines represent the regression.

3.4 DISCUSSION

Pangolins were selective in their diet throughout the year, preying predominantly on three insect genera, namely *Crematogaster* ants, *Anoplolepis* ants, and *Trinervitermes* termites, regardless of how many of those insects were available. During the year of the study with less abundant prey resources, pangolins preyed predominantly on *Crematogaster* ants, except in winter. During winter, when prey abundance was at its lowest throughout the year, pangolins consumed more *Trinervitermes* termites and *Anoplolepis* ants compared to the rest of the year. During the year of the study with more abundant resources, pangolins also increased their termite consumption during winter when prey resources were more scarce compared to the rest of the year, but they did not decrease their *Crematogaster* consumption, nor did they increase their *Anoplolepis* consumption. However, during the summer and autumn following high rainfall in that

year, pangolins increased their consumption of *Anoplolepis* ants compared to the drier year. Contrary to my prediction that pangolins would increase the diversity of prey items in their diet when prey was scarce, pangolins only increased their prey diversity in the summer following high rainfall.

Pangolins experienced energy deficits during both winters when prey was scarce. The factor that predicted the daily estimated energy intake by pangolins was the amount of time that pangolins spent active above ground. I had hypothesized that prey abundance would influence the number of prey items consumed by pangolins, however only predictor of the number of prey items eaten was also the amount of time that pangolins spent active above ground. Although significant, the relationship between the number of prey items eaten and the amount of time spent active was noisy, the reasons for which are unclear. Nevertheless, when pangolins decreased their foraging duration during winter (Chapter 4), they consumed fewer prey items, and had low estimated energy intake during winter. By being active for longer periods, and by increasing their consumption of *Anoplolepis* ants during the winter of the study year in which prey abundance was the lowest, pangolins were able to obtain the same amount of energy during that winter compared to the year of study with more abundant resources.

Although this is the first study to estimate the daily energy intake by pangolins, the estimates may be underestimated. Whole pangolin scats could not always be collected because they were either scattered by the pangolin's tail or because parts of the scat had already been carried away by insects by the time the scat was found. Also, the estimated daily energy intake equation excluded any additional prey items consumed by pangolins (~6% of the diet). As a consequence, the estimated daily energy intake by pangolins was likely underestimated. The term 'energy deficit' in the context of my study refers to energy intake being lower during a particular season compared to another season, rather than energy imbalance as a consequence of energy expenditure being more than energy intake, especially because energy expenditure was not measured in this study. Future studies should consider including measurements of energy expenditure or glucocorticoid metabolites as a stress marker to further assess the seasonal and interannual fluctuations in pangolin energy balance, where repeated weighing could be used as a measure of body condition. The small sample size of six pangolins also did not allow me to elucidate any sex differences in the pangolin diet. I had aimed to determine how pangolins cope with resource scarcity by comparing data over two years, particularly because the study area had experienced drought conditions in recent years preceding the study. Even though the climate between the two study years differed and allowed me to assess interannual responses of pangolins to climatic conditions and prey resource variation, it was not extreme enough in either of the years to allow me to elucidate how pangolins respond to severe food shortage characteristic of a drought year.

Low and late rainfall during the first year coincided with low productivity as indicated by low grass cover and low prey abundance. It is known that rainfall from previous years can influence ecosystem productivity during the following years (Reichmann *et al.* 2013; Dudney *et al.* 2017). The low and late rainfall during the year preceding the study therefore likely also contributed to reduced grass growth during the first study year. Grass cover increased during the second year when above-average rainfall fell during the summer, mostly in January. On average, the majority of the annual rainfall fell in January for the preceding 16 years, therefore the rainfall during the second year fell on time. More specifically, it was the accumulated rainfall that fell three months prior that best predicted grass cover; accumulated rainfall from the preceding two months have been shown to influence food availability in Kalahari ecosystems (Ridley and Raihini 2007; van de Ven *et al.* 2020). When grass cover was high during the second study year, prey abundance was also high, particularly during the winter of that year.

Many ants and termites depend on grasses for survival (Witt and Giliomee 2005; Tschinkel 2010; Pol *et al.* 2011; Geerts *et al.* 2016; Weyer 2018). It was therefore surprising that rainfall, as a predictor of grass cover, did not affect prey abundance. One possible explanation is that, while high grass cover coincided with the peak rainy season (December to February), it also coincided with high environmental temperatures. Although insect activity and abundance increase with increasing environmental temperatures, the relationship is not linear (Evans and Gleeson 2001; Andrew *et al.* 2013). Many insects retreat to their nests or to cooler microclimates when environmental temperatures are high (Ma *et al.* 2020), making them less likely to fall into the pitfall traps and thereby reflecting as low prey abundance. Indeed, while prey abundance increased as a function of environmental temperatures in my study, when mean daily environmental temperatures exceeded 27 °C, prey abundance decreased. Therefore, even though grass cover was high following rainfall, the associated high summer environmental temperatures likely resulted in insects retreating to cooler microclimates, and they were not caught in the pitfall traps. Another possible explanation is that following summer rainfall, grass cover increased leading into the winter months, during which time some insects may have reduced or ceased their surface activity (Heatwole and Muir 1989; Adam *et al.* 2008; Davies *et al.* 2015), making them less likely to fall into the pitfall traps. Therefore, even though grass cover increased leading into winter, the low environmental temperatures associated with winter likely resulted in low prey abundance. However, higher prey abundance during the second winter compared to the first winter coincided with higher grass cover, which suggests that grass cover did positively influence prey abundance, at least during winter.

Behavioural observations of the pangolin diet alone did not account for all prey items occurring in the diet. Whereas only 3 ant genera and 1 termite genus were recorded from

the behavioural observations, ants from 10 genera and termites from 3 genera were found in the scat samples. The behavioural dietary records did, however, confirm a previous report of the dominant prey items in the pangolin diet in the Kalahari (Pietersen *et al.* 2016). Based on my findings, previous studies that used behavioural observations alone to quantify the pangolin's diet (Sweeney 1956; Jacobsen *et al.* 1991; Swart *et al.* 1999; Pietersen *et al.* 2016) are likely to have underrepresented the diet by omitting additional prey items consumed by pangolins that could not be recorded by an observer. Observations of pangolins in a more mesic area (Sabi Sands) found that pangolins there preyed on 11 ant and 5 termite genera (Swart *et al.* 1999), much more than I found for the Kalahari. It is possible that scat analysis may reveal an even wider diversity of prey genera in more mesic environments. Of the insects in the diet reported by Swart *et al.* 1999, 8 of the ant and 4 of the termite genera overlapped with the diet of the pangolins in my study. My study adds three new ant genera (*Tetraoponera*, *Tapinolepis*, and *Lepisiota*) and one new termite genus (*Psammotermes*) to the known prey items in the Temminck's ground pangolin diet in Africa and suggests that some geographical variation likely exists in the diet.

In agreement with other studies (Sweeney 1956; Coulson 1989; Jacobsen *et al.* 1991; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen *et al.* 2016), pangolins showed an overall preference towards ants over termites and did not necessarily target the most abundant genera. Despite a total of 17 ant and 6 termite genera being available at the study site, pangolins only consumed ants from 10 genera and termites from 3 genera. While *Monomorium* was the most abundant genus, these ants contributed less than 0.01% to the pangolin diet. Similarly, while *Pheidole* was the most widespread genus, these ants only contributed about 1% to the pangolin diet. Moreover, even though *Crematogaster* ants contributed the most (~50%) to the pangolin diet, the genus was not abundant across the transects, contributing only 0.5% to the pitfall traps. Apart from *Camponotus* ants, the remaining ~6% of prey items in the diet were likely consumed incidentally during foraging forays and not specifically targeted. Seven of the eight additional prey genera (including *Camponotus*) consumed formed part of the top eight most abundant (% contribution to the pitfalls) or most widespread (% occurrence in the pitfalls) across the transects, which likely increased their probability of being consumed incidentally by pangolins. The eighth ant genus, *Tetraoponera*, was not abundant nor widespread across the transects. However, *Tetraoponera* ants are arboreal (Shulz and Wagner 2002; Stoll *et al.* 2007) and were likely consumed incidentally while pangolins fed selectively on arboreal *Crematogaster* ants at the bases of trees and shrubs. On three occasions, pangolins were observed actively digging open *Camponotus fulvopilosus* nests to feed on these ants intentionally. The *Camponotus* genus contributed little to the pitfall trap contents but occurred across a large proportion of the transects, suggesting that these

ants may be widely distributed (Garcia *et al.* 2013) but likely do not occur in large colonies. That idea is supported by the low contribution, but high occurrence of *Camponotus* ants in the pangolin scats. *Camponotus* ants are large ants and, although their calorific value was not measured in this study, they likely are an energy-rich resource and may therefore be important in the pangolin diet when they are available.

It is important to distinguish between the abundance and the availability of prey (Swart *et al.* 1999); the most abundant species are not necessarily available to pangolins and *vice versa*. Despite their adaptations for digging, the forelimbs of pangolins are not as well-adapted as armadillos, for example, for digging deep into soils to access deep underground insect galleries (Endo *et al.* 2002). Some species may therefore be inaccessible and hence unavailable to pangolins. Even though *Crematogaster* and *Anoplolepis* ants, and *Trinervitermes* termites were not the most abundant prey items across the transects, they were likely available to pangolins because of the nesting or foraging habits of these genera, and their availability in concentrated 'pockets'.

Crematogaster ants excavate their nests inside tree trunks (Santini *et al.* 2011), where they are relatively slow-moving (Swart *et al.* 1999) and highly concentrated and are accessible to pangolins through the small nest entrance where they use their long, sticky tongue to gain access to the nest (W. Panaino, personal observations). Their concentrated and easily accessible nests and low mobility may increase the utilization of *Crematogaster* ants by pangolins relative to *Anoplolepis* ants and *Trinervitermes* termites. *Anoplolepis* ants, which predate on other invertebrates and forage for grass seeds (Henschel 1998; Witt and Giliomee 2005), occupy underground nests that are shallower than 30 cm in depth and occur in high densities (Picker *et al.* 2012; Hoffmann 2015), likely making them easily accessible and hence available to pangolins. The *Trinervitermes* termites inhabiting the dune habitats of Tswalu did not build epigeal mounds as they do in the mountainous habitats or elsewhere in South Africa (Field and Duncan 2013; Pietersen 2013). Instead, *Trinervitermes* termites nested in shallow underground termitaria, where they were highly concentrated, as they are in epigeal termitaria (W. Panaino, personal observations; Taylor *et al.* 2002).

Seasonal fluctuations in ant and termite activity are well documented (Haverty *et al.* 1974; Evans and Gleeson 2001; Adam *et al.* 2008; Davies *et al.* 2015; Asfiya *et al.* 2016). The activity of ants and termites is generally highest during summer and lowest during winter (Adam *et al.* 2008; Davies *et al.* 2015; Pietersen *et al.* 2016), making winter a period of resource scarcity for many insect-eating animals (Anderson 2004; Weyer 2018). Some insect-eating mammals, such as bat-eared foxes, increase termite intake during winter when their preferred prey items become less available (Klare *et al.* 2011). Contrary to a previous report (Pietersen *et al.* 2016), the pangolins in my study shifted their diet seasonally. Because *Crematogaster* abundance could not be accurately estimated

across the transects as a consequence of their arboreal nature (Tschinkel 2002), it is impossible to determine whether the increase in *Trinervitermes* termite intake during winter and the increased *Anoplolepis* intake during the first winter was because *Crematogaster*, their preferred prey, became less available during winter. One possible explanation for the increased termite intake during winter is that the foraging activity of *Trinervitermes* termites ceases during winter (Adam *et al.* 2008; Davies *et al.* 2015). By ceasing surface activity, the termites were likely more concentrated in their subterranean nests close to the surface and therefore less likely to fall into the pitfall traps. Unlike aardwolves, which do not dig for their termite prey that is less available to them during winter (Anderson 2004), the termites likely were available to pangolins during winter because pangolins are able to dig to expose termite colonies. Similarly, *Anoplolepis* ants were also less active above ground during winter, as indicated by their decreased abundance in the pitfall. *Anoplolepis* ants were likely more available to pangolins during winter by having remained underground in concentrated 'pockets', which explains the increased contribution of *Anoplolepis* to the diet during winter. However, the proportion of *Anoplolepis* ants consumed only increased during the first winter compared to the rest of the year and not during the second winter, but the proportion of these ants consumed did not differ between the two winters. Foraging on the same proportion of *Anoplolepis* ants during both winters suggests that these ants were still important during the second winter but were not more important compared to summer and autumn, resulting in less seasonal variation during the second year. Additionally, the calorific value of *Anoplolepis* ants was high compared to the other pangolin prey items, likely making them an important food source to pangolins during winter.

Ants in arid habitats have been shown to increase foraging activity in response to increased forage availability (Whitford and Ettershank 1975). However, delayed or winter rainfall may reduce forage growth. Indeed, in a North American arid grassland, ant abundance increased in response to summer rainfall but not to winter rainfall because grass seed production likely was limited by the cold environmental temperatures during the cooler months of the year (Kaspari and Valone 2002). *Anoplolepis* ant abundance in the pitfall traps increased after the summer rainfall during the second year, which may explain their increased consumption by pangolins during summer and autumn, but *Anoplolepis* ant abundance did not increase after the delayed rainfall during the first year. *Anoplolepis* ants, as seed harvesters, therefore likely ceased foraging activity and remained underground following the late rainfall during the first year because there was no grass seed production during the cooler months, making the ants less likely to fall into the pitfall traps. The hot and dry conditions during the summer of the first year resulted in low grass cover and thus low seed production was likely responsible for the reduced *Anoplolepis* abundance during the first summer, as shown by the positive relationship

between *Anoplolepis* abundance and monthly rainfall. The reduced abundance of *Anoplolepis* during the first summer and autumn likely reduced their consumption by pangolins. The increased *Anoplolepis* consumption during the summer and autumn of the second year suggests that pangolins increase their *Anoplolepis* utilization when these ants are abundant following summer rainfall.

It is unclear why *Trinervitermes* termite abundance was higher throughout the first year compared to the second year, but delayed rainfall during the first year may have had a positive effect on termite abundance during the first winter (Wolda 1978), since termites favour soil moisture (Woon *et al.* 2019). The increased *Trinervitermes* termite abundance during the first year also coincided with an increase in *Trinervitermes* consumption, suggesting that pangolins will also increase their *Trinervitermes* utilization when these termites are abundant.

To my knowledge, this is the first study to quantify the number of ants and termites consumed by Temminck's ground pangolins each day. Prey utilization by pangolins resulted in an average daily prey consumption of about 15 000 ants and termites (range: ~1000 to ~60 000). In another study, the daily prey consumption by a Chinese pangolin was >26 000 (Lee *et al.* 2017). Factors that influence the quantity of food eaten by mammals are foraging duration and food availability (Woodward 1997; Bergman *et al.* 2001). Indeed, when pangolins increased their foraging duration, they increased the number of prey items eaten. However, contrary to my hypothesis that pangolins would increase the number of prey items consumed when prey abundance increased, prey abundance did not influence food intake. One possible explanation is that during summer, when pangolins emerged from their burrows late during the night, their foraging time was shortened (Chapter 4), which would have reduced their food intake even when prey abundance was high. Furthermore, even though pangolins did not alter their duration of activity during spring of the two years (Chapter 4), they were able to consume more prey items and thus increase their energy intake during the second spring. A likely explanation is that during the second spring, pangolins preyed on more *Crematogaster* ants compared to the first spring. By feeding on more *Crematogaster* ants, pangolins ingested less inorganic sand material, and ingested more organic material because of the arboreal nature of *Crematogaster* ants. By ingesting less sand, pangolins likely were able to consume more ants before feeling satiated, which may have resulted in the increased number of ants consumed during the second spring. Another possible explanation for pangolins not increasing the number of prey items consumed when prey abundance increased is that pangolins may have only fed until they reached their energy demand. If pangolins had to continue foraging beyond their energy requirements, additional foraging would increase energy expenditure and might not be efficient. Therefore, when food was

abundant, pangolins were not likely to increase food intake in proportion to prey abundance.

The amount of food that mammals eat influences their daily energy balance. My study is the first to estimate the daily energy intake by pangolins from their food. Prey utilization by pangolins resulted in an average daily energy intake of ~160 kJ/day, which may have been up to ~6% higher if the calorific value of the additional prey items was included. The average daily energy intake was lower than the range of field metabolic rates estimated for pangolins (324 – 5475 kJ/day; Boyles *et al.* 2019). Some energy values (7% of the scat samples) in my study did, however, fall within the range of the estimated field metabolic rates, across all seasons except for winter. The low energy intake by pangolins relative to the estimated field metabolic rates would suggest that the pangolins in this study were in negative energy balance throughout most of the year. However, the pangolins in my study were smaller (male: 7.8 ± 1.5 kg, female: 7.8 ± 0.9 kg) than the pangolins studied by Boyles *et al.* (2019) (male: 12.8 ± 1.4 kg, female: 11.6 ± 0.6 kg) and likely had lower energy requirements compared to larger pangolins, since it is known that smaller animals generally have lower absolute energy requirements than do larger ones (Dodds *et al.* 2001).

Energy deficits are common for many mammals during winter when prey resources decline (Garvey *et al.* 2004; Williams *et al.* 2015; Weyer *et al.* 2020). In agreement with Pietersen (2013), winter was a stressful period for pangolins, as indicated by the low energy intake by pangolins during winter in parallel with low prey abundance. The low energy intake during winter reflected an inability for pangolins to consume enough ants as a consequence of reduced foraging time during winter (Chapter 4). Energy intake was low during winter despite pangolins increasing their intake of the energy rich *Anoplolepis* ants. When prey resources were scarce, pangolins were expected to increase their foraging time to increase their foraging efforts, but instead foraging time was decreased during winter (Chapter 4), thereby reducing the amount of prey that could be consumed, resulting in pangolins experiencing energy deficits during winter.

Some mammals shift their diet to different species during winter to compensate for reductions in prey resources (Williams *et al.* 1997; Klare *et al.* 2011), which may allow them to maintain energy intake through the winter. Even though pangolins shifted their diet during winter, they were not able to compensate for reduced prey abundance, as is evidenced by the low energy intake during winter. Perhaps the dietary shift to increase termite intake during winter was an attempt to increase water intake, since termites have high water content (Weyer 2018), but this idea requires further investigation. Nevertheless, by foraging for longer and increasing their *Anoplolepis* ant intake during the winter of the first year, the pangolins were able to maintain their energy intake during the

first year when resources were the scarcest, such that energy intake was not lower compared to the second year. Contrary to my prediction that pangolins would increase the diversity of prey in their diet when prey was scarce, the diversity of prey items in their diet was constant throughout the study, except during the summer in which rainfall was high. Aardvarks in the Kalahari died, presumably of starvation, when their preferred prey resources declined during a drought because they did not shift their diet in response to food scarcity (Rey *et al.* 2017; Weyer 2018; Weyer *et al.* 2020). The environmental conditions during my study were not characteristic of a drought, which may have reduced the need for pangolins to exploit additional prey items outside of their preferred niche. The increased prey diversity in the pangolin diet during the summer in which rainfall was high likely occurred as a consequence of the high rainfall increasing the abundance of 'other' ants at the study site, where the chances of pangolins incidentally consuming additional prey items were likely high.

Although the analyses of scats were a more accurate method for assessing the diet of pangolins compared to behavioural observations, alternative methods may be less labour-intensive and less reliant on human ability to visually identify species. One example may be the application of molecular approaches, such as the use of DNA sequencing of arthropods to analyse the prey items in the diets of African great apes (Hamad *et al.* 2014). DNA analysis has the potential to greatly improve the work in my study and should be considered for future studies investigating the diet of pangolins. Analyses that could further improve my study might include measuring the water, lipid, protein, and carbohydrate content of the diet during the different seasons to help explain the diet selection of pangolins, since it is known that the demand for these nutrients may shift in relation to the varying water demands of animals throughout the year (Becker and McCluney 2021).

In conclusion, climate impacted the abundance of pangolin prey resources through the effects of rainfall of grass cover and though environmental temperatures, which in turn impacted the energy balance of pangolins. Although pangolins shifted their diet in response to the resource scarcity associated with winter, they still experienced energy deficits during that period. However, by increasing their foraging time and by eating prey of high caloric value, pangolins were able to compensate for reduced prey abundance during the winter in which prey resources were the scarcest across the study period compared to the winter in which prey was more abundant. As insect populations continue to decline with climate change, pangolins will likely have to work harder to find their food, thereby increasing energy expenditure, potentially putting them in negative energy balance more often. Their apparent inability to exploit resources outside of their preferred dietary niche increases their risks of starvation in the future.

Chapter 4

**Seasonal patterns of pangolin activity
are influenced by food availability
and 24h minimum body temperature**

4.1 INTRODUCTION

Mammals with slow life histories and those that cannot move to more suitable habitats must rely on shifts in their behaviours if they are to buffer the effects of rapid climate change (Fuller *et al.* 2016). Understanding the behavioural flexibility of mammals is key to predicting their responses to changing environments (Kearney *et al.* 2009). In hot environments, the use of favourable microclimate conditions, such as shade or burrows (Ostrowski *et al.* 2003; Fick *et al.* 2009), reduces exposure to solar radiation, which reduces the need for evaporative cooling (Mitchell *et al.* 2018). When favourable microclimates are not available, diurnal mammals may need to shift their 24h activity and become crepuscular or nocturnal to reduce the costs of thermoregulation (Levy *et al.* 2019).

While diurnal mammals must contend with high environmental heat loads and high rates of water loss to keep cool, nocturnal mammals must contend with cold temperatures and high radiative heat loss at night and must increase their metabolic rate to maintain a high body temperature (Jessen 2001a; Silva 2005), which requires food energy. Some nocturnal mammals can shift their 24h activity to become more diurnal to offset the metabolic costs of keeping warm at night (van der Vinne *et al.* 2019; Weyer *et al.* 2020). Under cold conditions, energy-conserving behaviours are particularly important for mammals when food is scarce (Giroud *et al.* 2008; Signer *et al.* 2011). When food is scarce, some mammals may reduce foraging time to conserve energy (Christian and Geiser 2007; Weyer *et al.* 2020) while others may increase foraging time to compensate for energy deficits (Genin and Perret 2003; Giroud *et al.* 2008). Behavioural shifts in response to food shortages may be particularly pronounced during the winter of years of below-average rainfall in arid areas where food availability is closely linked to rainfall (Dean and Milton 2001).

The predominantly nocturnal pangolin has been shown to shift its 24h activity seasonally by increasing diurnal activity during winter (Swart 1996; Pietersen *et al.* 2014b; Challender *et al.* 2020), although the reasons for doing so are not clear. It has been suggested that environmental temperature plays a role in driving the emergence of pangolins from their burrows (Pietersen *et al.* 2014b; Challender *et al.* 2020). By being nocturnal during summer, pangolins avoid high daytime temperatures, and by being diurnal during winter, pangolins avoid cold night-time temperatures. Another study suggested that prey activity may play a role in driving pangolin activity (Swart 1996), while another concluded that the activity of ants likely does not drive pangolin 24h activity during winter, since ant activity is consistently low at that time, regardless of the diel cycle (Pietersen 2013; Pietersen *et al.* 2014b). The factors driving changes in pangolin activity therefore require clarity.

Understanding the role of climate and food resources in driving the 24h activity pattern of pangolins is crucial for predicting the future responses of pangolins to climate change. I therefore aimed to identify the key drivers of pangolin 24h activity in the Kalahari. I predicted that pangolins would be predominantly nocturnal throughout the year, and that they would increase diurnal activity during winter. I also predicted that the main drivers for the onset of pangolin activity (emergence from the burrow) would be environmental temperatures, and food availability, particularly when it was cold. Since food energy is required to maintain constant high body temperatures and some animals can shift their 24h activity to offset metabolic costs of keeping warm, I predicted that the 24h body temperature patterns of pangolins would also influence pangolin 24h activity. Based on previous reports (Swart 1996; Heath and Coulson 1997; Pietersen *et al.* 2014b), I predicted that pangolins would be active above ground for about four to eight hours each day to forage, and that the duration of activity would increase during winter in response to food shortages. Because I expected the duration of activity to vary seasonally, I predicted that the relationship between the time of emergence and return would not be linearly related. I also predicted that the increase in diurnal activity during winter would be particularly pronounced in the study year in which there was below-average rainfall in summer, provided that environmental temperatures were similar during winter.

4.2 MATERIAL AND METHODS

4.2.1 Climatic variables

A weather station measuring black globe temperature at 30-minute intervals was placed approximately 10 km from the area where study pangolins ranged. Our research team had previously shown that weather was similar across the range of pangolins, however a weather station could not be placed in the pangolin range because of the risk of damage by wildlife. Black globe temperature was measured by inserting a temperature-sensitive probe into a 150 mm black globe (see Chapter 2 for details). The time of sunrise and sunset for each day within the study period (October 2015 to October 2017) was obtained from the South African Weather Services (SAWS), and photoperiod was determined by calculating the time difference between sunrise and sunset. Seasons were defined as: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November), based on previous studies in the Kalahari (Weyer 2018; van de Ven *et al.* 2020).

4.2.2 Prey abundance

A total of 30 permanent transects were selected randomly across the reserve where pangolins had been previously detected (in grass- and shrub-dominated areas in the dune fields). Prey abundance was recorded once a month using pitfall traps across the

transects. Each transect consisted of 10 pitfall traps placed five metres apart for a total of 300 traps per month. Traps were placed in the ground with the opening of the trap level with the ground surface. All traps remained in the ground for four days. Ants that fell into the traps were counted and used as a proxy for pangolin prey abundance at Tswalu. See Chapter 3 for more details.

4.2.3 Pangolin body temperature

Six pangolins (three males and three females, 6.5 – 9.4 kg), tagged with VHF tracking transmitters, were located and captured so that a veterinarian could anaesthetize them to implant each animal with a wax-coated miniature temperature-sensitive data logger, using the methods described in Chapter 2. The body temperature data loggers, which were implanted into the retroperitoneum, recorded core body temperature at 5-minute intervals.

4.2.4 Pangolin activity

Pangolins were tracked in the mornings during their inactive phase using telemetry (see Chapter 2 for details) to locate their burrows, and camera traps were placed outside the burrows to assess time of emergence and return for the six pangolins. Camera traps did not always trigger for emergence or return events, and pangolins did not always return to the same burrow, thus the camera traps could not always detect time of emergence and return. However, inspection of body temperature records, for which I had observations of emergence or return to burrows, showed a conspicuous change (notch) in body temperature around the onset of activity and the return to the burrow (Figure 4.1). I visually analysed each 24h body temperature pattern for each pangolin to estimate time of emergence or return, indicated by an increase or decrease in body temperature by at least 0.6 °C in less than one hour. I validated this method to estimate additional times of emergence and return to burrows and then supplemented the actual observations of emergence and return with estimated times of emergence and return derived from the 24h body temperature patterns. Where there was no conspicuous body temperature notch, time of emergence or return was not estimated.

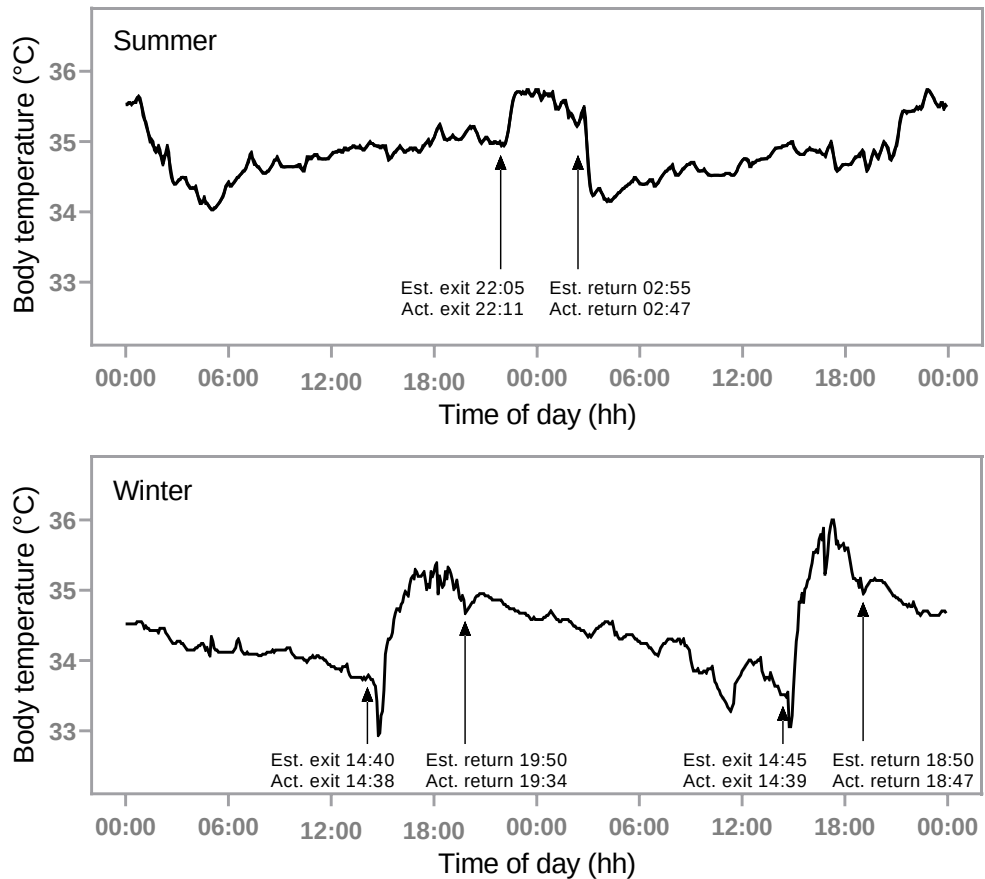


Figure 4.1: The 24h body temperature patterns of a pangolin, showing the estimated and actual (camera trap data) burrow emergence and return times for two consecutive summer days (top) and two consecutive winter days (bottom).

This indirect method for estimating pangolin activity was validated by matching 201 camera trap times of emergence and 65 camera trap times of return with 24h body temperature records. The use of a conspicuous body temperature notch to detect emergence or return was calculated by counting the number of times the notch was obvious and detectable to within one hour of the actual emergence and return. For the time of emergence during autumn, winter, and spring, use of the conspicuous body temperature notch to detect emergence was between 89 and 100% successful. During summer, however, the conspicuous body temperature notch detection of emergence success was only 64% because the notches were not as distinct during summer compared to the rest of the year. The low detection success during summer resulted in fewer estimated times of emergence during summer compared to the rest of the year. For time of return to the burrow, the conspicuous body temperature notch detection success was 92 to 100% across all seasons. The time of emergence and return estimation error was determined by calculating the difference between the estimated time of activity using 24h body temperature patterns and the actual time of activity using camera traps. On

average, the time of emergence estimation error was 32 ± 28 (mean $\pm$ SD) minutes for summer, 20 ± 22 minutes for autumn, 12 ± 11 minutes for winter, and 18 ± 15 minutes for spring. The time of return estimation error was 17 ± 18 minutes for summer, 13 ± 7 minutes for autumn, 11 ± 15 minutes for winter, and 21 ± 24 minutes for summer.

Frequency histograms created using activity obtained from camera traps only ($n=266$) and activity derived from 24h body temperature only ($n=3955$) revealed that the overall distribution of the data was similar for the two methods (Figure 4.2). I was therefore confident that conspicuous 24h body temperature notches could be used to accurately estimate time of emergence and return from the burrow to within one hour of actual activity. Further evidence supporting the use of body temperature patterns to estimate pangolin emergence and return is included in the Appendix (Figure A1). By combining camera trap data with activity data extracted from 24h body temperature patterns, a total of 1966 observations for time of emergence from the burrow and 1633 observations for time of return to the burrow were obtained for the study period.

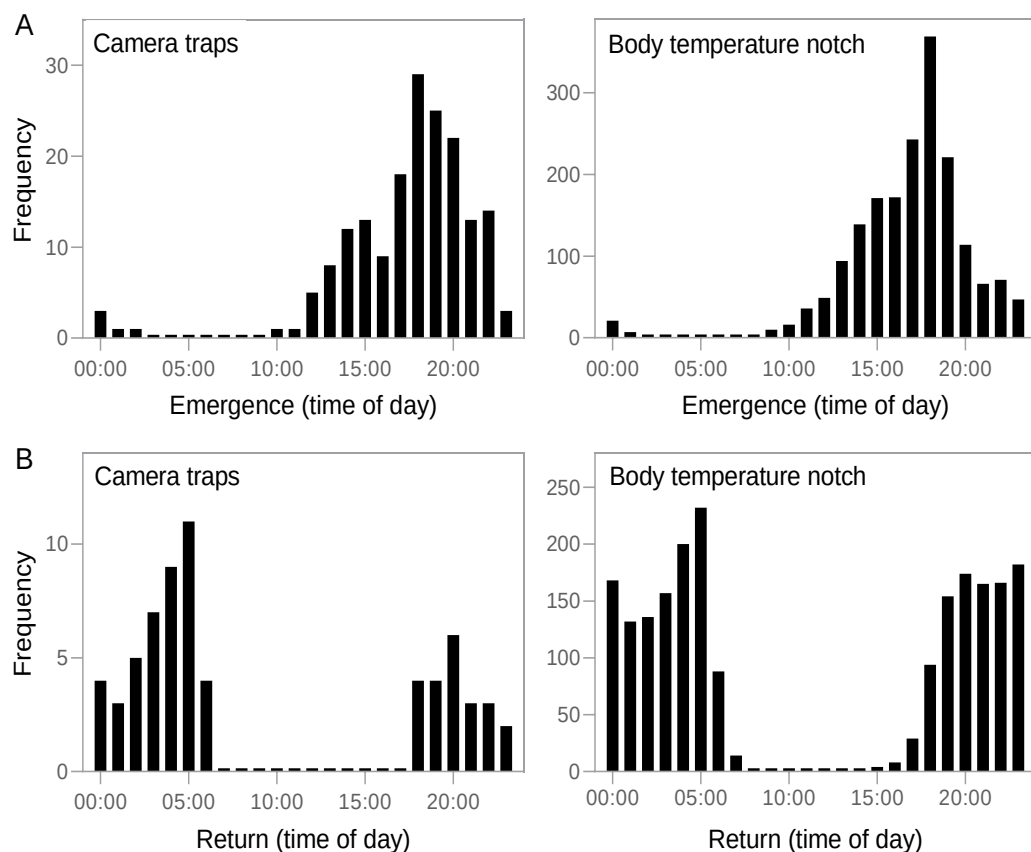


Figure 4.2: Frequency distribution of time of emergence (A) and return (B) data obtained directly from camera traps only (*left*) and indirectly from 24h body temperature patterns only (*right*).

4.2.5 Data analyses

Data analyses were conducted using GraphPad (version 8.00; GraphPad Prism, 2021) and R software (R Core Team, 2021) for this chapter. For all models, residuals were examined to assess the accuracy of the models. For time-series models including pangolin time of emergence and return to the burrow, the data were autocorrelated in R software, and 24 units were added to each time data point to account for time data that rolled over midnight and to allow time data to be used in mixed models in R. Interactive effects could not be included into the models because the small sample size of individual pangolins did not have the power necessary to test interactions among variables.

The 24h mean, 24h minimum and 24h maximum black globe temperatures were determined for each day across the study period. Seasonal means were calculated by averaging the 24h mean, 24h minimum and 24h maximum for summer (December to February), autumn (March to May), winter (June to August), and spring (September to November).

The number of ants per trap was calculated by totalling the number of ants captured in the traps at each transect and dividing the total by the number of traps retrieved per transect. Prey abundance was then calculated by averaging the number of ants per trap across all transects. An ANOVA was used to assess seasonal and interannual differences.

Circular statistics were used to determine whether time series data differed from random using the 'lubridate' package (Grolemund and Wickham 2011). To assess whether the onset of pangolin activity was predominantly nocturnal throughout the year, the percentage of observations occurring between 18:00 and 06:00 was calculated. To assess whether pangolins increased diurnal activity during winter, the percentage of winter (June to August) time of emergence observations occurring between 06:00 and 18:00 was calculated. To assess how often pangolins were truly nocturnal or truly diurnal, the percentage of time that both emergence and return observations that occurred strictly between 18:00 and 06:00 (nocturnal) and between 06:00 and 18:00 (diurnal) was calculated.

The overall seasonal proportion of emergence was calculated by totalling the number of observations occurring per time category per season across 2h intervals and dividing them by the total number of observations per season to account for different sample sizes in activity data. The seasonal and interannual proportion of emergence and return was calculated by totalling the number of observations occurring per time category per season per year across 1h intervals and dividing them by the total number of observations per season per year to account for different sample sizes in activity data. Watson two-sample

tests were conducted to test for seasonal and interannual differences in the time of emergence and return to the burrow for the pangolins with the longest datasets. Thereafter, data from all pangolins were pooled together, and an ANOVA was used to test for seasonal and interannual differences in the time of emergence and return to the burrow. Dunnett's multiple comparisons tests were used to identify where the differences occurred. The duration of above-ground activity was calculated by subtracting time of emergence from time of return for a total of 1616 observations of the duration of activity. An ANOVA and Dunnett's multiple comparison's test were used to test for seasonal interannual differences in the amount of time that pangolins spent active above ground.

Linear mixed model analyses were used to test the effects of photoperiod (time between sunrise and sunset), prey abundance, 24h mean black globe temperature, and 24h minimum body temperature (explanatory variables) on the time of emergence and return to the burrow, and the duration of above-ground activity (response variables), using individual pangolin identity as a random factor. For the models involving time series data, the effects of pangolin activity from the previous day on present day activity were not included since the data were autocorrelated and hence the effects of previous day activity were already factored in. R packages that were used include 'lmerTest' (Kuznetsova *et al.* 2017), 'performance' (Ludecke *et al.* 2020), 'robustlmm' (Koller 2016), 'patchwork' (Pederson 2020), 'knitr' (Xie 2015, 2015), 'ggplot2' (Wickham 2016), 'dplyr' (Wickham *et al.* 2021), and 'tidyr' (Wickham 2021). The only black globe temperature variable used in the models was 24h mean black globe temperature because there was a weak relationship between the time of emergence and the black globe temperature at the time of emergence ($r^2=0.020$, slope=0.051, $p<0.001$), and the 24h mean, 24h minimum, and 24h maximum black globe temperatures were all linearly associated with time of emergence (Figure 4.3; time of emergence vs 1) 24h mean globe: $r^2=0.473$, slope=0.040, $p<0.0001$; 2) 24h minimum globe: $r^2=0.301$, slope=0.047, $p<0.0001$; 3) 24h maximum globe: $r^2=0.496$, slope=0.043, $p<0.0001$). The relationship between time of emergence and return and prey abundance was not linear, therefore a piecewise regression was used to assess the relationship before a breakpoint and after a breakpoint. A search was conducted to determine the breakpoint by running the models using various breakpoints between 0 and 17 ants/trap, and then comparing the models for the best fit using (AIC, where the model with the lowest AIC value was selected as the best model (Symonds and Moussalli 2011).

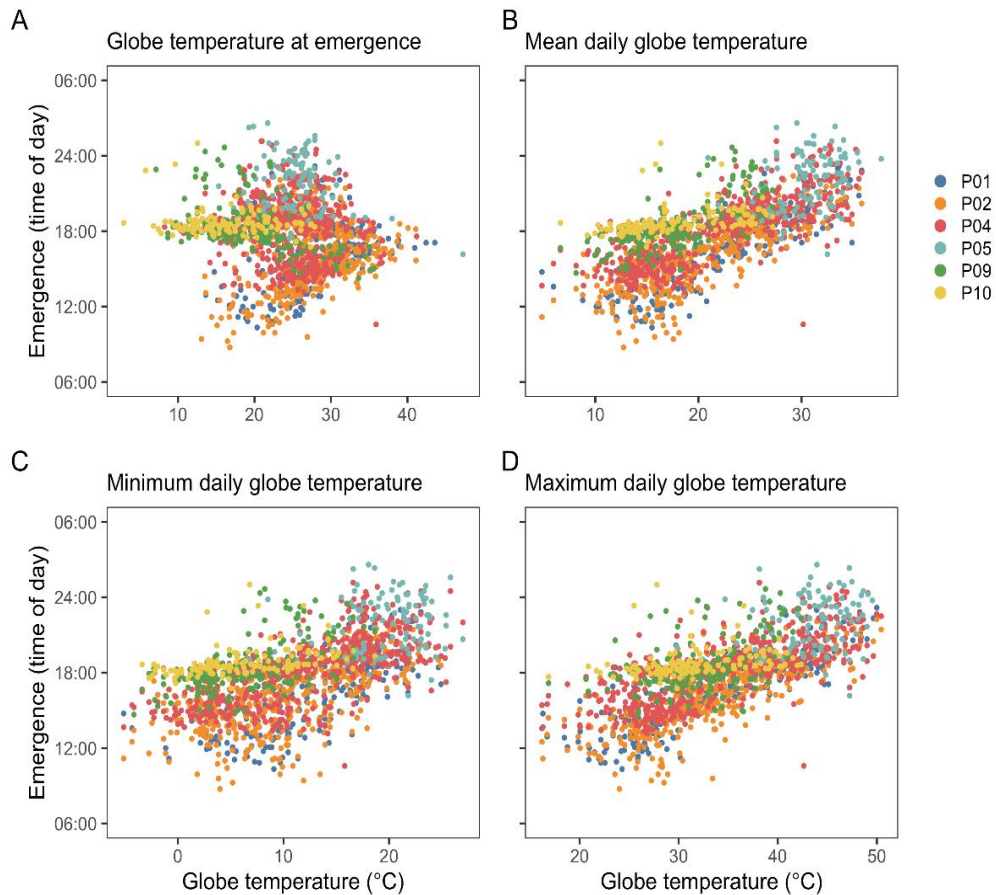


Figure 4.3: The relationship between pangolin time of emergence from the burrow and black globe temperature at the time of emergence (A), 24h mean (B), 24h minimum (C), and 24h maximum (D) black globe temperatures. P01 to P10 represent the different study animals.

4.3 RESULTS

4.3.1 Climatic variables

Black globe temperatures at Tswalu ranged between -5.1°C and 50.4°C across the study period (October 2015 to October 2017; Figure 4.4). The 24h mean black globe temperature varied seasonally and interannually and was higher during the summer of the first study year (October 2015 to October 2016) compared to during the summer of the second year (October 2016 to October 2017) (Table 4.1). Due to a failed weather station, weather data for the first autumn were not collected, therefore only the second autumn is shown in the results. The mean 24h minimum black globe temperature varied seasonally and interannually and was higher during the summer, winter, and spring of the first year compared to second year (Table 4.1). The mean 24h maximum black globe temperature also varied seasonally and interannually and was higher during the summer of the first year compared to the summer of the second year but was lower during the winter of the first year compared to the winter of the second year. Rainfall was below

average (~278 mm) during the first study year and above average during the second study year (~370 mm; see Chapter 3).

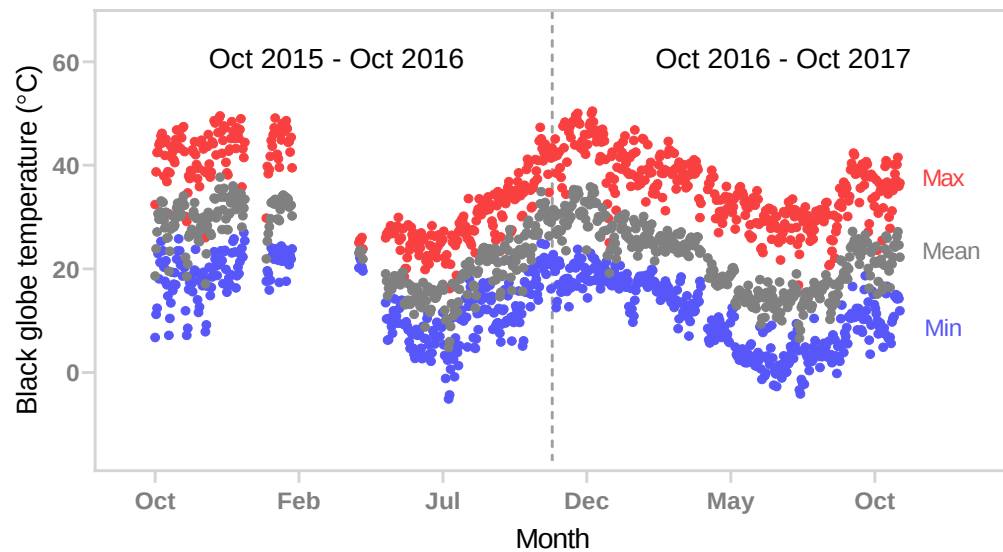


Figure 4.4: The 24h mean, 24 minimum, and 24h maximum black globe temperatures at Tswalu for the period October 2015 to October 2017. The gaps in the data occurred due to a failed weather station.

Table 4.1: Seasonal and interannual summary statistics of the 24h mean, 24h minimum, and 24h maximum black globe temperature for two years (mean $\pm$ SD). Red shaded columns show 2015-2016, the warmer year, as indicated by higher 24h mean black globe temperature in all seasons, except autumn, compared to 2016-2017, shaded blue. Grey blocks indicate significant differences between the two years.

	Summer			Autumn			Winter			Spring		
	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean
Globe temperature (°C)												
24h mean	31.8 $\pm$ 2.8	27.9 $\pm$ 3.7	29.4 $\pm$ 3.9	-	20.5 $\pm$ 4.4	-	15.7 $\pm$ 3.7	14.5 $\pm$ 2.7	15.1 $\pm$ 3.3	23.6 $\pm$ 4.3	22.4 $\pm$ 3.1	24.3 $\pm$ 4.5
24h minimum	21.2 $\pm$ 2.7	17.9 $\pm$ 2.5	19.2 $\pm$ 3.0	-	9.7 $\pm$ 4.7	-	7.9 $\pm$ 4.6	3.1 $\pm$ 3.3	5.5 $\pm$ 4.7	15.5 $\pm$ 4.6	10.6 $\pm$ 3.4	13.6 $\pm$ 4.8
24h maximum	44.3 $\pm$ 3.8	41.2 $\pm$ 5.1	42.4 $\pm$ 4.9	-	35.3 $\pm$ 4.3	-	25.6 $\pm$ 3.7	28.9 $\pm$ 3.5	27.3 $\pm$ 3.9	37.2 $\pm$ 6.1	35.9 $\pm$ 4.2	36.7 $\pm$ 5.5

4.3.2 Prey abundance

The overall monthly ant abundance varied seasonally across the study period and was highest during summer (20.2 ± 13.0 ants/trap) and spring (25.9 ± 20.9 ants/trap), and lowest during autumn (7.4 ± 6.0 ants/trap) and winter (9.2 ± 10.5 ants/trap). Ant abundance did not differ between years for summer and spring but was significantly higher during the autumn (11.1 ± 6.8 ants/trap) and winter (15.7 ± 12.3 ants/trap) of the second study year compared to in the autumn (4.7 ± 3.3 ants/trap) and winter (4.0 ± 4.2 ants/trap) of the first study year.

4.3.3 Pangolin body temperature

Pangolin 24h minimum body temperature varied seasonally, whereby the 24h minimum body temperatures were lowest during winter and highest during summer. Pangolin 24h minimum body temperature also varied interannually, whereby 24h minimum body temperatures were lower during the autumn, winter, and spring of the first year compared to the autumn, winter and spring of the second year, but 24h minimum body temperature did not vary between the two years for summer. See Chapter 5 for more details.

4.3.4 Pangolin activity

For each pangolin, time of emergence and return to the burrow differed from random as indicated by the strong Rayleigh statistics (using “rayleigh.test” in R, in library ‘circular’; Table 4.2) and were not distributed uniformly around the clock (Appendix, Figure A2; Figure A3). The onset of activity and return to the burrow, as well as the amount of time that pangolins spent active varied seasonally (Figure 4.5), with emergence and return times across the day occurring earliest during winter and latest during summer, and with the duration of activity being the lowest during winter and the highest during summer for both study years. The earliest recorded emergence time occurred at 08:30, the earliest time of return occurred at 15:20, the latest time of emergence occurred at 02:48, and the latest time of return occurred at 08:15. The overall mean amount of time that pangolins spent out of their burrows and active above ground was $6\text{h}16\text{m} \pm 0\text{h}46\text{m}$ (shortest duration = $1\text{h}07\text{m}$, longest duration = $15\text{h}45\text{m}$).

Table 4.2: Rayleigh test output using the strength of the Rayleigh statistic to determine whether each pangolin's burrow emergence and return data differed from random.

Pangolin ID	Emergence		Return	
	Rayleigh statistic	p	Rayleigh statistic	p
P01	0.77	<0.001	0.68	<0.001
P02	0.76	<0.001	0.74	<0.001
P04	0.79	<0.001	0.62	<0.001
P05	0.87	<0.001	0.91	<0.001
P09	0.88	<0.001	0.80	<0.001
P10	0.96	<0.001	0.89	<0.001

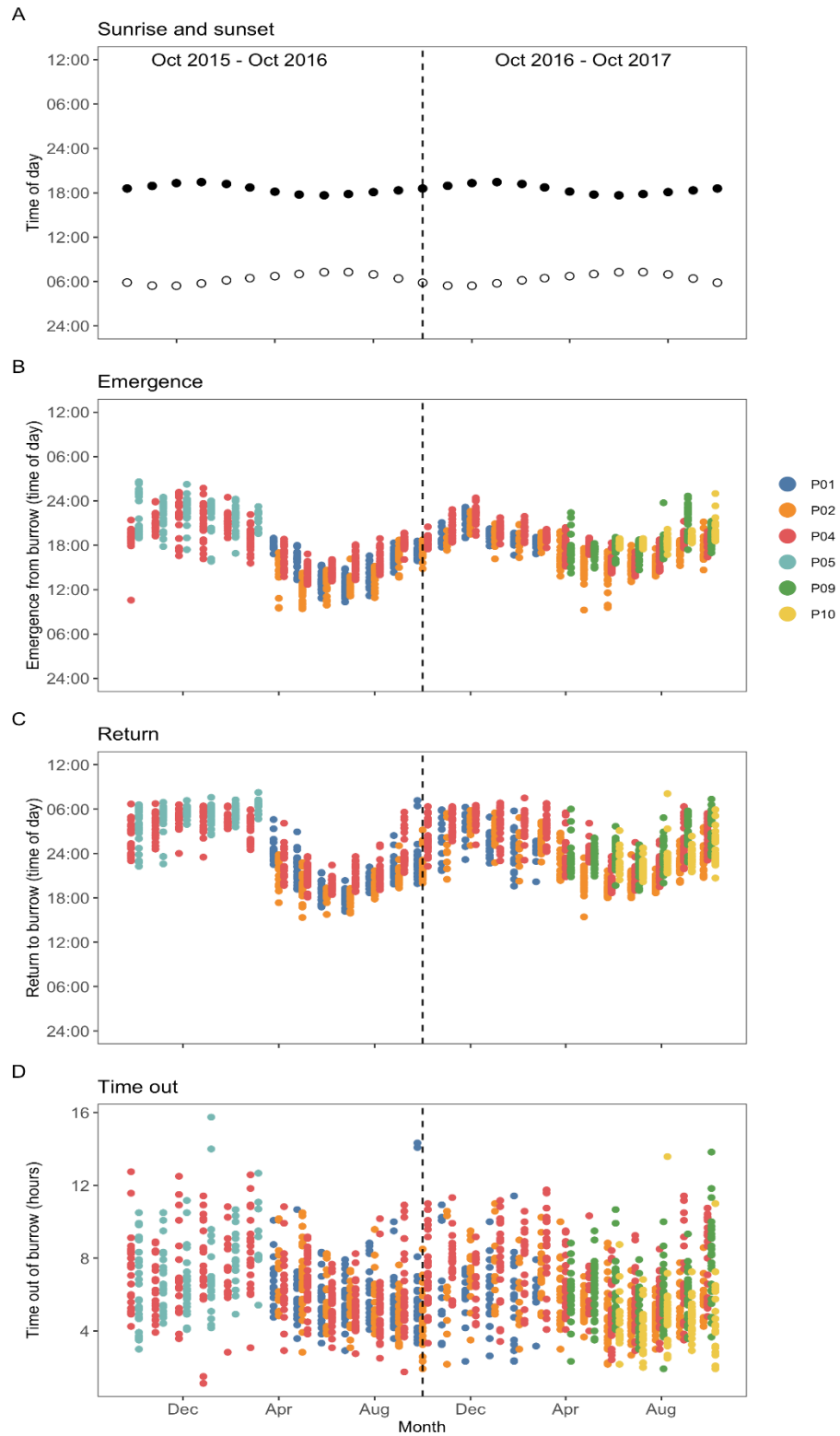


Figure 4.5: Time of sunrise and sunset; closed circles represent time of sunset, open circles represent time of sunrise (A), time of emergence from the burrow (B), time of return to the burrow (C), and the time spent out of the burrow (D) of six pangolins from October 2015 to October 2017. P01 to P10 represent the different study animals.

Over the whole year, pangolins emerged from their burrows predominantly at night (after 18:00), with 56% of all burrow emergence data (n=1966) occurring between 18:00 and 06:00. However, they were only truly nocturnal (both time of emergence and time of return occurring between 18:00 and 06:00) for 48% of the time (n=1616). During winter, pangolins emerged from their burrows predominantly during the day, with 82% of all winter burrow emergence data (n=632) occurring between 06:00 and 18:00. Overall, pangolins were only truly diurnal (both time of emergence and time of return occurred between 06:00 and 18:00) for 2% of the time (n=1616). True diurnal activity occurred predominantly (60 events) during winter, with the remaining six observations occurring during autumn. Of the 60 true diurnal events, 59 occurred during the first study year (October 2015 to October 2016). Across both winters, true diurnal activity occurred on 123 occasions, with 4 of those occasions occurring during the first winter and 119 of the occasions occurring during the winter of the second year. Emergence from the burrow across the study period occurred predominantly between 20:00 and 22:00 during summer (30% of all summer emergences, n=378), between 18:00 and 20:00 during autumn (32% of all autumn emergences, n=494), between 14:00 and 16:00 during winter (35% of all winter emergences, n=632), and between 18:00 and 20:00 during spring (50% of all spring emergences, n=462) (Figure 4.6).

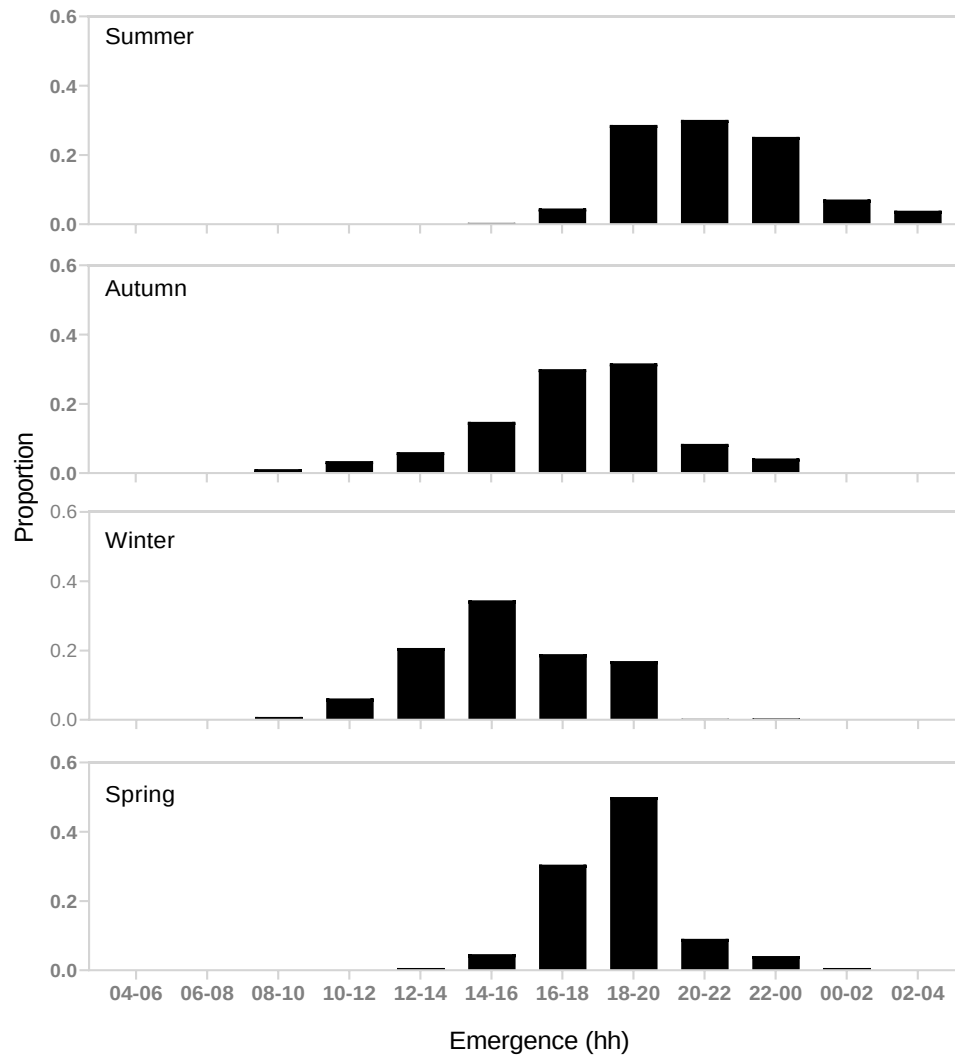


Figure 4.6: Seasonal time of emergence of six pangolins across the full study period, expressed as the proportion of observations that occurred per 2h time category.

The Watson two-sample tests (using “watson.two.test” in R, in library ‘circular’) revealed that, for the three pangolins with the longest datasets, there was seasonal and interannual variation in the time of emergence and return to the burrow (Table 4.3). Therefore, data for all pangolins were pooled together for further analyses of the seasonal and interannual differences in time of emergence and return to the burrow.

Table 4.3: Watson two-sample test output for the pangolins with the longest datasets to assess the seasonal and interannual differences in time of emergence and return to the burrow.

Pangolin ID	Season		Year	
	U ²	p	U ²	p
<i>Emergence</i>				
P01	3.22	<0.05	2.75	<0.05
P02	4.10	<0.05	2.19	<0.05
P04	5.83	<0.05	1.29	<0.05
<i>Return</i>				
P01	2.29	<0.05	1.22	<0.05
P02	2.66	<0.05	0.71	<0.05
P04	5.74	<0.05	0.33	<0.05

There was seasonal and interannual variation in the time of emergence (ANOVA, $F_{(7,1203)}=236.8$, $p<0.0001$) and return (ANOVA; $F_{(7,989)}=107.0$, $p<0.0001$) to the burrow (Table 4.4). Seasonally, during the first year, on average, pangolins emerged from their burrow 07h43m earlier in winter compared to summer, whereas during the second year, pangolins emerged from their burrows only 03h09m earlier in winter compared to in summer. During the first year, pangolins returned to their burrows 08h29m earlier during winter compared to summer, while during the second year, pangolins only returned to their burrows 05h11m earlier during winter compared to summer. Interannually, pangolins emerged from their burrows earlier during the day during the autumn, winter, and spring of the first study year compared to the autumn, winter, and spring of the second study year (Figure 4.7), but they emerged earlier during the summer of the second year compared to the summer of the first year. Pangolins returned to their burrows later during the day during the summer of the first year compared to the summer of the second year, but earlier during the day during the autumn, winter, and spring of the first year compared to the autumn, winter, and spring of the second year (Figure 4.7). There was seasonal and interannual variation in the amount of time that pangolins spent active above ground (Table 4.4; ANOVA; $F_{(7,1201)}=32.0$; $P<0.0001$). During the first year, pangolins were active for shorter periods during the winter compared to summer. During the second year, pangolins were also active for shorter periods during winter compared to summer. There was interannual variation in the amount of time that pangolins spent out of their burrows and active above ground, with the amount of time spent out of their burrows being longer during the autumn and winter of the first year compared to the autumn and winter of the second year (Figure 4.7).

Table 4.4: Seasonal and interannual summary statistics of the pangolin burrow emergence and return times, as well as the duration of activity for two years (mean $\pm$ SD). Red shaded columns show 2015-2016, the warmer year, compared to 2016-2017, shaded blue. Grey blocks indicate significant differences between the two years.

	Summer			Autumn			Winter			Spring		
	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean
Activity												
Emergence	21:51 $\pm$ 02:06	20:01 $\pm$ 01:32	20:46 $\pm$ 02:00	16:50 $\pm$ 03:56	17:38 $\pm$ 01:53	17:13 $\pm$ 03:06	14:08 $\pm$ 02:23	16:52 $\pm$ 02:10	15:41 $\pm$ 02:38	17:53 $\pm$ 01:45	19:29 $\pm$ 01:53	18:50 $\pm$ 01:59
Return	03:59 $\pm$ 05:14	02:51 $\pm$ 02:31	03:25 $\pm$ 04:08	22:35 $\pm$ 04:35	23:44 $\pm$ 03:47	23:12 $\pm$ 04:13	19:30 $\pm$ 01:33	21:39 $\pm$ 02:44	20:46 $\pm$ 02:33	00:08 $\pm$ 04:06	01:04 $\pm$ 03:08	00:34 $\pm$ 03:42
Duration	07:10 $\pm$ 02:01	06:52 $\pm$ 01:59	07:00 $\pm$ 02:00	06:58 $\pm$ 01:52	06:22 $\pm$ 01:39	06:40 $\pm$ 01:47	05:29 $\pm$ 01:17	05:03 $\pm$ 01:28	05:14 $\pm$ 01:25	05:58 $\pm$ 02:06	06:06 $\pm$ 02:07	06:02 $\pm$ 02:06

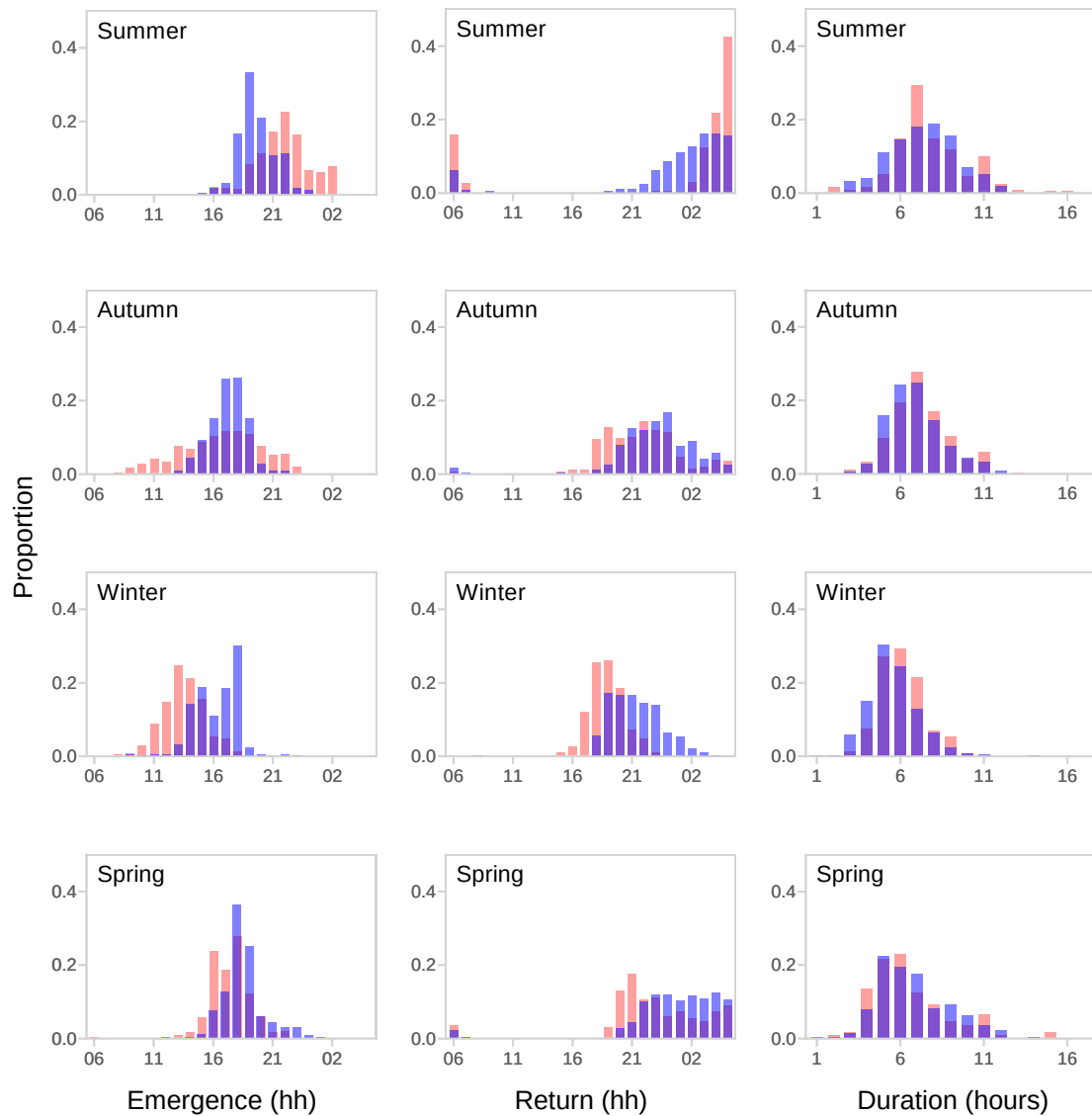


Figure 4.7: Seasonal and interannual emergence and return times, and the duration of activity of six pangolins for October 2015 to October 2016 (pink) and for October 2016 to October 2017 (blue), expressed as the proportion of observations that occurred per 1h time category.

The range of black globe temperatures at which pangolins emerged from their burrows was 0.9 to 47.3 °C, which was only a slightly narrower range than the range of black globe temperatures recorded at Tswalu throughout the study period (-5.1 °C and 50.4 °C). A linear mixed model (using “lme” in R, library ‘nlme’) was used to test the effects of photoperiod, prey abundance, 24h mean black globe temperature, and 24h minimum pangolin body temperature on pangolin time of emergence from the burrow. The model

(Table 4.5) revealed that pangolin time of emergence was positively associated with photoperiod (Figure 4.8A), prey abundance (Figure 4.8B), 24h mean black globe temperature (Figure 4.8C), and 24h minimum body temperature (Figure 4.8D). In other words, the onset of activity was early during the day when days were short (winter), when prey was scarce, when the environmental temperatures were low, and when pangolin 24h minimum body temperature was low. Piecewise regression and a search for the best-fit model (using AIC; Appendix; Table A8) revealed that the breakpoint in the relationship between time of emergence and prey abundance was at ~16 ants/trap. In other words, time of emergence was only positively associated with prey abundance until ~16 ants/trap, but when prey abundance was greater than ~16 ants/trap there was no relationship (Figure 4.8B).

Table 4.5: Linear mixed model results of the effects of photoperiod, prey abundance, mean black globe temperature, and 24h minimum body temperature on pangolin time of emergence from the burrow.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	-23.42 ± 2.18	-10.72	-27.70 to -19.13	<0.01
Photoperiod	1.12 ± 0.09	14.44	1.08 to 1.42	<0.01
Prey abundance (<~16 ants/trap)	0.07 ± 0.02	4.43	0.04 to 0.11	<0.01
Prey abundance (>~16 ants/trap)	-0.05 ± 0.01	-5.58	-0.07 to -0.03	<0.01
24h mean black globe temperature	0.06 ± 0.01	4.70	0.03 to 0.08	<0.01
24h minimum body temperature	0.74 ± 0.06	11.93	0.62 to 0.87	<0.01

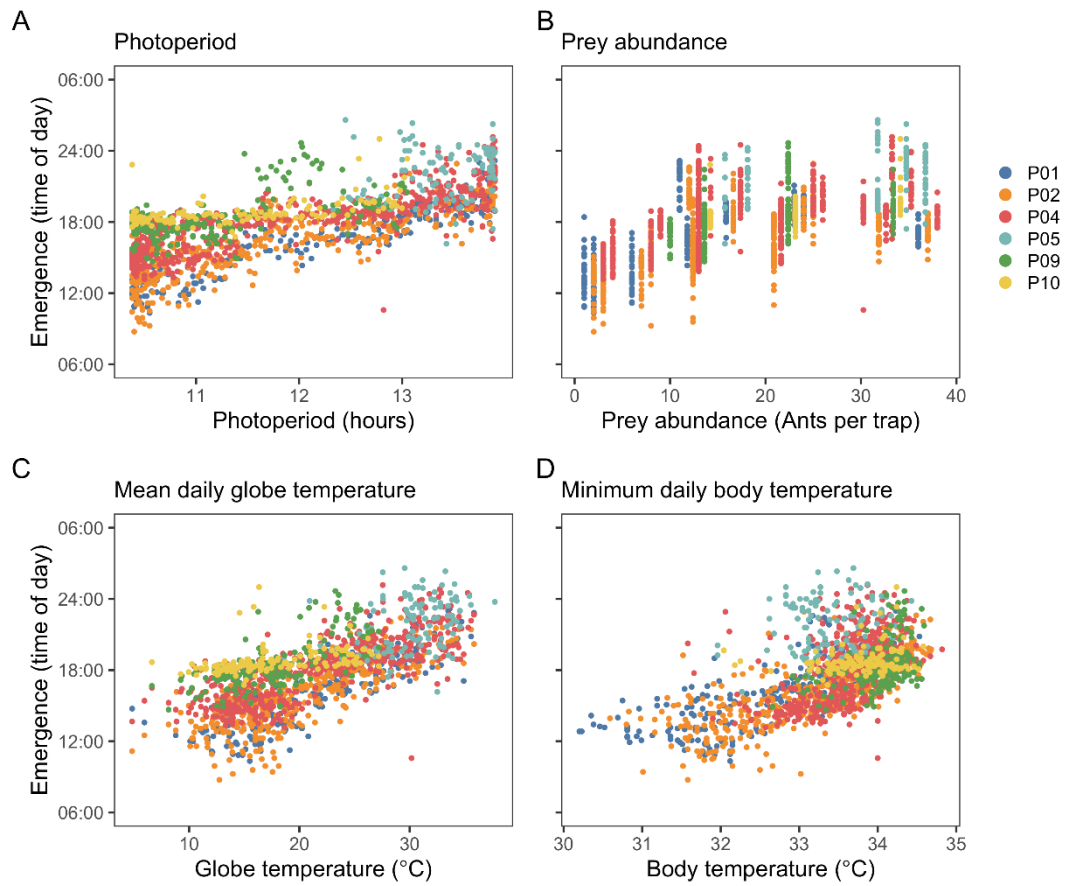


Figure 4.8: The relationship between pangolin emergence from the burrow and photoperiod (A), prey abundance (B), 24h mean black globe temperature (C), and pangolin 24h minimum body temperature (D). P01 to P10 represent the different study animals.

A linear mixed model (using “lme” in R, library ‘nlme’) was used to test the effects of photoperiod, prey abundance, 24h mean black globe temperature, and 24h minimum pangolin body temperature on pangolin time of return to the burrow. The model (Table 4.6) revealed that pangolin time of return to the burrow was positively associated with photoperiod (Figure 4.9A), prey abundance (Figure 4.9B), 24h mean black globe temperature (Figure 4.9C), and 24h minimum body temperature (Figure 4.9D). In other words, pangolins ceased activity early during the day when days were short (winter), when prey was scarce, when the environment was cold, and when pangolin 24h body temperature was low. Piecewise regression and a search for the best-fit model (using AIC; Appendix; Table A9) revealed that the breakpoint in the relationship between time of return and prey abundance was at ~17 ants/trap. In other words, time of return was only positively associated with prey abundance until ~17 ants/trap, but when prey abundance was greater than ~17 ants/trap there was no relationship (Figure 4.9B).

Table 4.6: Linear mixed model results of the effects of photoperiod, prey abundance, 24h mean black globe temperature, and 24h minimum body temperature on pangolin time of return to the burrow.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	-7.55 ± 3.07	-2.46	-13.57 to -1.53	<0.05
Photoperiod	1.38 ± 0.11	12.46	1.17 to 1.60	<0.01
Prey abundance (<~17 ants/trap)	0.07 ± 0.02	3.82	0.04 to 0.11	<0.01
Prey abundance (>~17 ants/trap)	-0.05 ± 0.01	-4.95	-0.08 to -0.03	<0.01
Mean black globe temperature	0.16 ± 0.02	9.88	0.13 to 0.20	<0.01
24h minimum body temperature	0.33 ± 0.09	3.69	0.15 to 0.50	<0.01

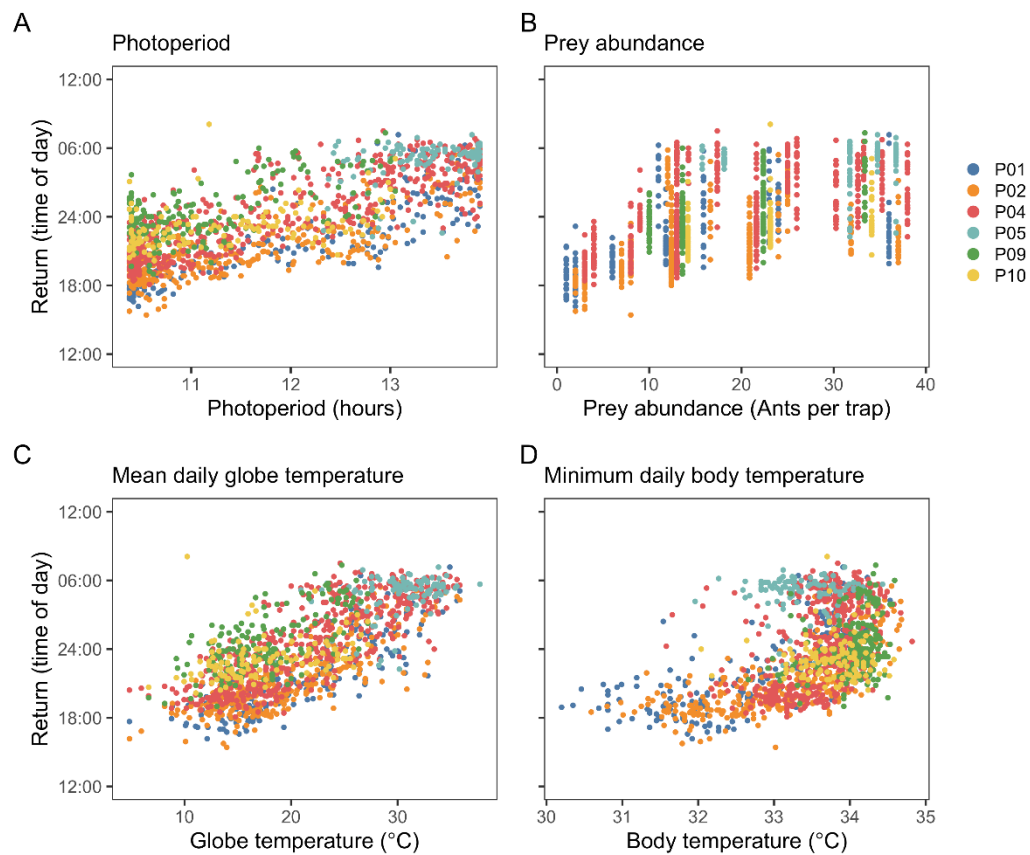


Figure 4.9: The relationship between pangolin return to the burrow and photoperiod (A), prey abundance (B), 24h mean black globe temperature (C), and pangolin 24h minimum body temperature (D). P01 to P10 represent the different study animals.

A linear mixed model (using “lme” in R, library ‘nlme’) was used to test the effects of photoperiod, prey abundance, 24h mean black globe temperature, and 24h minimum pangolin body temperature on the amount of time that pangolins spent active. The model (Table 4.7) revealed that the amount of time that pangolins spent out of their burrows was positively associated with photoperiod (Figure 4.10A) and 24h mean black globe temperature (Figure 4.10C), and negatively associated with 24h minimum body temperature (Figure 4.10D) but was not associated with prey abundance (Figure 4.10B). In other words, when days were short (winter) and when it was cold, pangolins were active on the surface for short periods.

Table 4.7: Linear mixed model results of the effects of photoperiod, prey abundance, mean black globe temperature, 24h minimum body temperature, and the duration of activity the previous day on the amount of time pangolins spent out of their burrows.

Explanatory variable	$\beta \pm SE$	t	95 % CI	P
Intercept	15.29 $\pm$ 2.75	5.55	9.89 to 20.70	<0.01
Photoperiod	0.18 $\pm$ 0.09	1.97	<0.01 to 0.37	<0.05
Prey abundance (<~16 ants/trap)	<-0.01 $\pm$ 0.02	-0.13	-0.03 to 0.03	0.79
Prey abundance (>~16 ants/trap)	<-0.01 $\pm$ 0.01	-0.44	-0.02 to 0.01	0.58
24h mean black globe temperature	0.08 $\pm$ 0.01	5.70	0.06 to 0.11	<0.01
24h minimum body temperature	-0.42 $\pm$ 0.08	-5.10	-0.59 to -0.26	<0.01

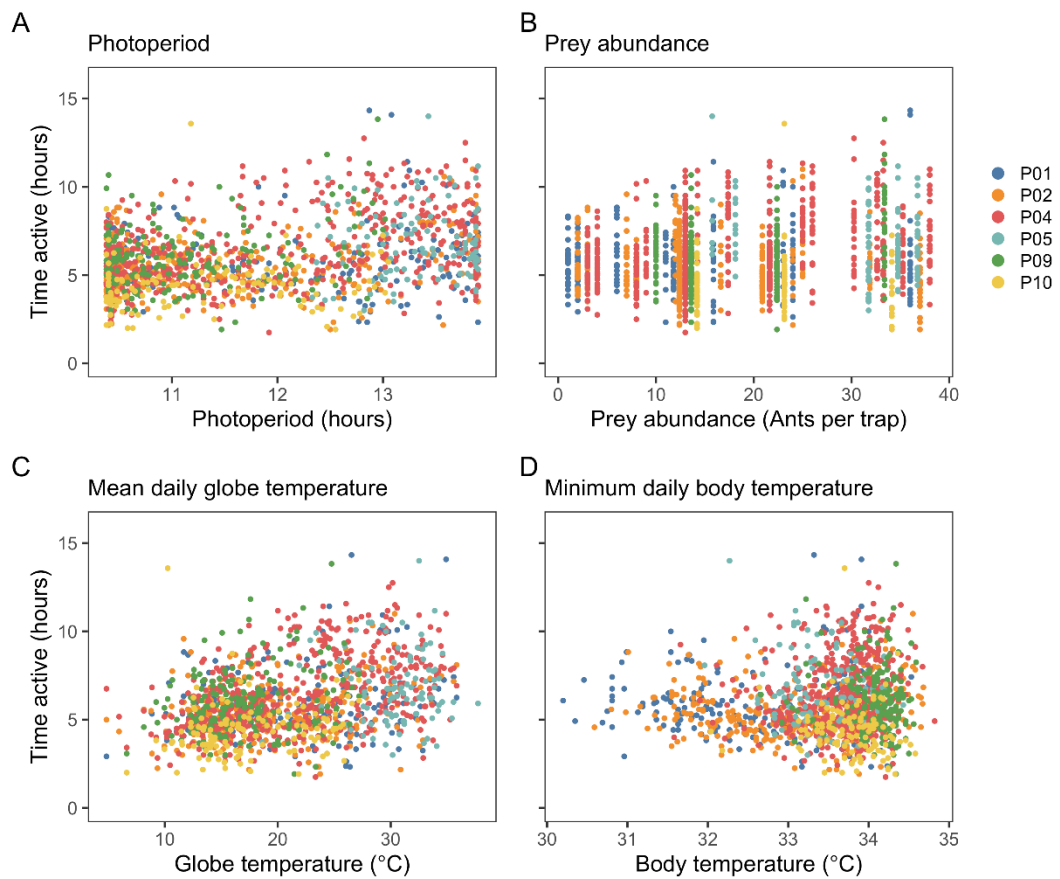


Figure 4.10: The relationship between the duration of activity and photoperiod (A), prey abundance (B), mean black globe temperature (C), and 24h minimum body temperature (D). P01 to P10 represent the different study animals.

The relationship between time of emergence and return was positive, although not linear (Figure 4.11). Piecewise regression and a search for the best-fit model (using AIC; Appendix; Table A10) revealed that the breakpoint in the relationship between time of emergence and return was at an emergence time of ~21:50. In other words, time of emergence was only significantly and positively associated with time of return when pangolins emerged from their burrows before 21:50, but after 21:50 there was no relationship. The non-linear relationship indicated that the duration of above ground activity was not constant when pangolins emerged before and after the breakpoint. Since emergence that occurred after 21:50 predominantly occurred during summer (70%), the duration of activity of pangolins that emerged before and after 21:50 was compared for summer only, so as to avoid seasonal influences on the duration of activity. Indeed, during summer, when pangolins emerged from their burrows after 21:50 ($n=116$), they always returned to their burrows before 07:30 and were active for significantly shorter

periods ($6\text{h}12\text{m} \pm 1\text{h}20\text{m}$) compared to when they emerged after before 21:50 ($n=206$; $7\text{h}17\text{m} \pm 2\text{h}19\text{m}$; $t=5.4$, $\text{d.f.}=320$, $p<0.0001$).

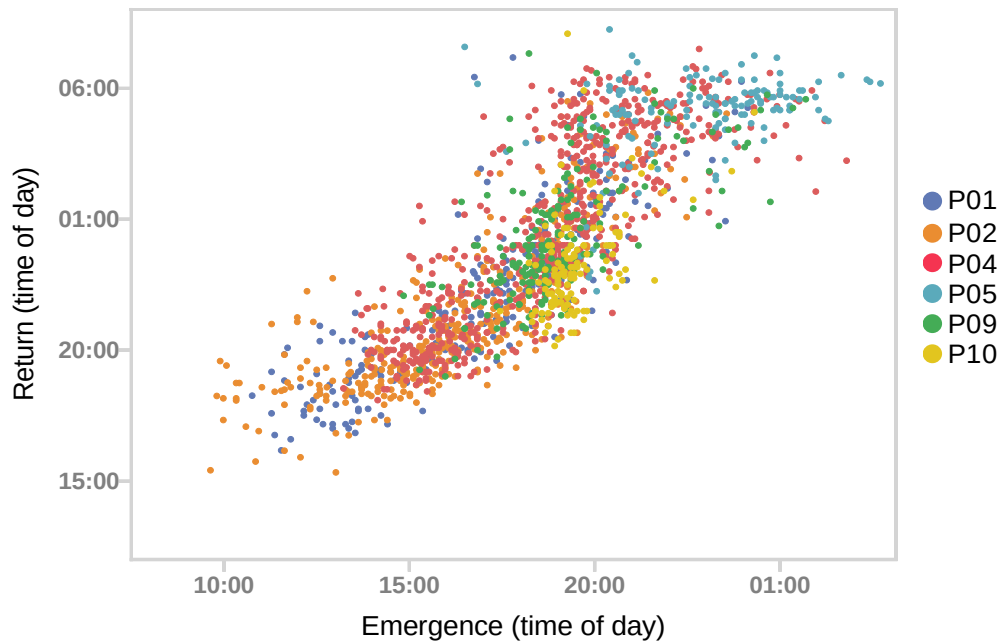


Figure 4.11: The relationship between pangolin time of emergence and return to the burrow. P01 to P10 represent the different study animals.

Further analyses revealed that during summer, pangolins emerged from their burrows after 21:50 when 24h mean, 24h minimum, and 24h maximum black globe temperatures were higher compared to when they emerged before 21:50 (Table 4.8; ANOVA, $F_{(7,1070)}=1004$, $p<0.0001$). The black globe at the time of emergence did not differ significantly when pangolins emerged before or after 21:50 ($t=0.60$, $\text{d.f.}=243$, $p>0.05$).

Table 4.8: The 24h mean, 24h minimum, 24h maximum black globe temperatures, and the globe temperature at the time of emergence from the burrow when pangolins emerged either before or after 21:50 (mean $\pm$ SD). Grey blocks indicate significant differences between when pangolins emerged from their burrows before 21:50 and when they emerged after 21:50.

Black globe temperature ($^{\circ}\text{C}$)	Before 21:50	After 21:50
24h mean	27.9 ± 3.6	32.0 ± 2.7
24h minimum	18.2 ± 3.0	20.3 ± 2.7
24h maximum	40.8 ± 4.9	45.1 ± 3.5
At emergence	26.3 ± 4.7	26.0 ± 2.9

4.4 DISCUSSION

By studying the long-term activity patterns of wild pangolins in the Kalahari, I was able to detect both seasonal and interannual variation in pangolin 24h activity in response to climatic conditions, prey abundance, and pangolin body temperature patterns. To my knowledge, this is the most comprehensive study of the 24 activity patterns of wild pangolins. I show that the factors affecting the time that pangolins emerged and returned to their burrows, as well as the duration of their above ground activity, were photoperiod (as an indication of seasonality), environmental temperatures, prey abundance, and pangolin 24h minimum body temperature.

I obtained data over two years, with one year having lower prey availability than the other (Chapter 3). During the year of the study with more abundant prey resources, pangolins emerged from their burrows predominantly nocturnally (after 18:00) throughout the year, except during the winter, when they switched to diurnal (before 18:00) emergence. During the winter, when prey abundance was lowest in that year, pangolins emerged from their burrows around 17:00, which was about three hours earlier than in summer. Despite emerging from their burrows earlier during the day in the winter, pangolins continued their foraging activity into the night and were only truly diurnal (with no night-time activity) on one occasion. The pangolins returned to their burrows before 03:00 during the winter, except on two occasions. In contrast to my prediction that feeding duration would increase in winter when less prey items were available, pangolins shortened their foraging duration in the winter compared to that in summer, by two hours.

During the study year in which prey resources were more scarce, pangolins still emerged from their burrows predominantly nocturnally throughout summer and spring, although they emerged later in the evening during that summer compared to the year with more abundant resources. However, during autumn and winter they switched to diurnal emergence. During the winter, when prey abundance was at its lowest throughout my study, pangolins emerged from their burrows around 14:00, and were truly diurnal on 59 occasions. Compared to the summer of that year, pangolins emerged about eight hours earlier, and compared to the winter of the year with more abundant food, pangolins emerged about five hours earlier. Except for four occasions, pangolins always returned to their burrows before 22:30 during the winter, thereby avoiding the coldest parts of the night. The pangolins shortened their foraging activity in the winter compared to that in summer, as they did in the year with more food availability, but because they emerged earlier during the day compared to the winter of the year with more food availability, they foraged for about 30 minutes longer during the year with less food availability.

The earlier emergence of pangolins in the year with less food availability indicates that time of year was not the only driver of pangolin emergence. Other factors that affected

pangolin 24h activity were environmental temperatures, prey abundance, and pangolin 24h minimum body temperature. Environmental temperatures differed between the two years, whereby the environmental temperatures during the summer and winter of the year with more abundant food resources were lower compared to the year with less abundant food resources, and so that difference may explain some of the variation in the 24h activity patterns of pangolins over the two years. Prey abundance was higher during the winter of the second year compared to the winter of the first year, but prey abundance did not differ between the two years for summer. Similarly, pangolin 24h minimum body temperature was higher during the winter of the year with more abundant prey resources compared to the winter of the year with less abundant food resources but 24h minimum body temperature did not differ between the two years for summer. The fact that prey abundance and pangolin 24h minimum body temperature differed between years in winter but not in summer, yet the time at which pangolins emerged and returned to their burrows differed between years across all seasons indicated that prey abundance and pangolin 24h minimum body temperature affected pangolin 24h activity when prey was scarce, but not when prey was abundant.

While this is the first study to assess the drivers of pangolin activity patterns in detail, there were some limitations. Locating and following pangolins in the field was difficult, and camera traps often could not be used to detect return times to burrows as pangolins often moved to new burrows following their period of activity. I was able to supplement my dataset of observed pangolin burrow emergence and return times with estimated times using an indirect method based on changes in the pangolin 24h body temperature patterns. While my validation of this method revealed a high success rate, and a pattern of activity similar to that yielded by direct observations, there may have been some errors introduced through the use of the estimation. Future studies should consider the use of biologging technology such as 'daily diary' tags, that record animal activity remotely and accurately, and that can store or transmit large quantities of data (Wilson *et al.* 2008). I was not able to elucidate any sex differences as a consequence of the small sample size in 24h activity patterns, and I was unable to collect continuous data over the full two-year study period for study individuals. Also, the methods used to collect data on prey abundance are measures that represent overall prey availability, and may thus be arbitrary units, rather than definite numbers.

The study years were not characterised by drought, as such, but they were still hot and dry, particularly compared to other regions where Temminck's pangolin is found. Previous reports have suggested that environmental temperatures play a role in driving pangolin activity (Swart 1996; Pietersen *et al.* 2014b). I found that when environmental temperatures were higher, pangolins emerged and returned to their burrows later during the day and remained active on the surface for longer periods compared to when

environmental temperatures were lower. In response to high environmental heat loads during the day, mammals often seek cooler microclimates, such as those provided by burrows, as thermal refugia (Pike and Mitchell 2013; Fuller *et al.* 2016). Burrows in my study environment typically are cooler than the prevailing globe temperature by up to 20 °C during the heat of the day (M. Phakoago, unpublished observations). Another way for pangolins to avoid high air temperatures and high solar radiation is through being active at night. When pangolins are active in the day, they may be exposed to operative temperatures that exceed their surface temperature, making evaporative cooling obligatory for dissipating heat (Mitchell *et al.*, 2018). Whether pangolins use evaporative cooling is not known. As a result of their relatively small body size and poor insulation the body temperature of pangolins is likely to rise rapidly when they are exposed to high environmental heat loads. By avoiding above-ground activity during the day, particularly in summer, pangolins reduce the risk of becoming hyperthermic, or dehydrating if they do employ evaporative cooling to maintain homeothermy.

Being active at night, however, is not without costs. While the heat generated through activity and metabolism can be dissipated by dry heat loss routes, the pangolins in their arid habitat face a substantial heat sink at night. In addition to low air temperatures, typically clear night skies with effective temperatures between -10 and -30 °C facilitate substantial radiant heat loss (Mitchell *et al.* 2018). Exposed pangolins therefore face high energetic costs in maintaining a high body temperature. The stable and warmer temperatures of burrows help to buffer mammals from the cold nights. Burrows in my study environment at night typically are up to 18 °C warmer inside compared to the outside (M. Phakoago, unpublished observations). By emerging from their burrows diurnally, in the late afternoon, during winter, pangolins returned to their burrows well before the coldest part of the night. In the year in which prey was more scarce they often confined all their activity to the day. By remaining inside warmer burrows when it was cold outside at night when prey was scarce, pangolins likely conserved energy by reducing the metabolic costs of maintaining a constant and high body temperature outside the burrow. However, when pangolins had sufficient food energy available to counter the costs of being active over the cold night, they extended their foraging activity into the colder parts of the night.

The onset of activity, however, was not driven by environmental temperatures at the time that the pangolins emerged from their burrows, suggesting that they used other cues to initiate foraging activity. Pangolins commenced activity at a wide range of environmental temperatures (0.9 to 47.3 °C), suggesting also that the onset of activity was not limited by environmental temperatures. However, when pangolins were active above ground, they were exposed to the prevailing above-ground climate, which may have limited their activity. Indeed, during summer, when they emerged after 21:50, pangolins shortened

their foraging duration by 15% compared to when they emerged before 21:50. By shortening their foraging duration during summer when pangolins emerged after 21:50, pangolins returned to their burrows before the approaching sunrise and thus before the rapidly rising environmental temperatures. While time of emergence was not related to environmental temperature at the time that pangolins came out of their burrows, emergence was related to mean 24h globe temperature, with pangolins emerging earlier from their burrows when 24h mean environmental temperature was low. Although burrows buffer the external climate, the temperatures inside the burrows in my study environment still increase to some degree as a function of outside temperature (M. Phakoago, unpublished observations). The finding that pangolins emerged later during the night in the first summer, when 24h mean environmental temperatures were higher compared to in the first summer, suggests that pangolins likely used environmental temperatures as a cue for emergence, at least during summer. Indeed, emergence after 21:50 during summer coincided with higher daily environmental temperatures, further suggesting that environmental temperatures act as a cue for emergence.

Previous reports have also suggested that prey availability plays a role in driving pangolin activity (Swart 1996; Pietersen *et al.* 2014b). The onset of pangolin activity in this study was positively associated with prey abundance only when prey abundance was low (<~16 ants per trap). Conversely, when prey was abundant (>~16 ants per trap), pangolins commenced activity independently of prey abundance. The mechanism through which prey abundance influenced the onset of activity was likely through resulting changes in body temperature. When animals do not have sufficient food, they experience a lower than normal 24h body temperature (Yoda *et al.* 2000; Wang *et al.* 2006; Hetem *et al.* 2016; Weyer *et al.* 2020). When pangolin 24h minimum body temperature was low, which coincided low prey abundance in winter, pangolins were more likely to emerge from their burrows diurnally. Furthermore, lower 24h minimum body temperatures during the winter with less abundant prey resources were associated with even earlier diurnal emergence compared to the winter with more abundant prey resources. By becoming active early during the day in winter, and by being exposed to environmental temperatures that were ~10 °C higher (22 vs 11 °C, data not shown) compared to if they had emerged nocturnally, pangolins were likely able to offset the metabolic costs of maintaining constant high body temperatures and thereby likely reduced energy expenditure, especially during a time when prey was scarce. Also, by shifting to earlier emergence, pangolins were able to spend less time active during the cold night, thereby conserving energy that would otherwise be used to maintain a constant high body temperature.

In addition to changing the times of day at which they are active, some mammals reduce foraging time to conserve energy when prey resources are scarce (Christian and Geiser

2007; Weyer *et al.* 2020) while others increase foraging time to compensate for reduced energy intake per unit time (Genin and Perret 2003; Giroud *et al.* 2008). During the summer of the year with abundant resources, pangolins were active above ground for ~7 hours per day as expected based on previous studies (Swart 1996; Heath and Coulson 1997; Pietersen *et al.* 2014b), but instead of increasing their foraging duration when prey abundance was low during winter, their foraging duration decreased from summer to winter. Pangolins likely reduced their foraging time because of the high costs incurred by foraging activity, since digging for food is a costly exercise (Luna and Antinuchi 2006; Romanach *et al.* 2007) and because the patchiness of their prey requires pangolins to walk around in search of their prey. Another possible reason that pangolins reduced their foraging time is that, despite commencing activity early, it may still have been too energetically costly to continue activity into the cold night to allow the same duration of feeding as in summer. By reducing foraging duration during winter, pangolins were likely able to reduce their daily energy expenditure and conserve energy during a time when food resources were less available. However, during the year in which prey resources were scarce, pangolins increased their foraging duration in winter compared to the year with more abundant resources. By emerging from their burrows earlier during the day in the winter of the year with lower prey abundance compared to the year with higher prey abundance, pangolins were able to be active for longer periods before sunset and before the cold temperatures approaching with night-time. Pangolins were therefore likely able to reduce the costs of maintaining high body temperatures in the cold, particularly when resources were scarce. However, by emerging earlier during the day, pangolins were exposed to higher environmental heat loads, which would have increased the need for evaporative cooling.

The negative relationship between pangolin 24h minimum body temperature and the amount of time spent foraging was surprising. Seasonal variation in the duration of activity indicated that foraging activity was short in winter when prey resources were scarce and pangolin 24h minimum temperature was low, and that foraging duration was longer in summer when prey resources were more abundant and pangolin 24h minimum body temperature was higher. The seasonal variation in the duration of activity therefore suggests that there should be a positive relationship between the foraging time and pangolin 24h minimum body temperature. The discrepancy can be best explained when assessing each opposing season (winter and summer) separately. During winter, when pangolin 24h minimum body temperature was high, pangolins emerged from their burrows later during the day, but the duration of their activity was likely constrained by the approaching cold night-time temperatures, and they likely needed to return to their burrows sooner compared to when they emerged earlier during the day. As such, when pangolins emerged later during the day as a consequence of higher 24h minimum body

temperatures, the duration of activity was shortened, resulting in the negative relationship between foraging time and 24h minimum body temperatures. Similarly, during summer, when pangolins emerged from their burrows later during the night when 24h minimum body temperature was high, their duration of activity was likely constrained by the approaching increasing daytime temperatures, at which point pangolins had to return to their burrows sooner. The resulting shortened foraging period at high 24h minimum body temperatures therefore resulted in the negative relationship between foraging time and 24h minimum body temperatures.

Similar findings of a link between prey abundance, 24h minimum body temperature, and 24h activity have been reported for another myrmecophagous mammal, the armadillo (*Oryzomys ather*). Armadillos are ecologically similar to pangolins in that they are nocturnal, burrowing mammals feeding exclusively on a diet of ants and termites (Taylor *et al.* 2002; Rey *et al.* 2017; Weyer *et al.* 2020). In the Kalahari, decreased grass cover reduced the abundance of the northern harvester termite, which armadillos depend on heavily to meet their daily energy requirements (Weyer *et al.* 2018). When armadillos experienced energy deficits as a consequence of their preferred prey becoming less available, and hence experienced lower than normal 24h minimum body temperatures, they shifted their 24h activity to become diurnal (Weyer *et al.* 2020). Conversely, when their prey was abundant and when armadillos were in positive energy balance, resulting in normal 24h minimum body temperatures, they remained nocturnal throughout most of the year.

My finding that pangolins exhibited seasonal variation in the amount of time they spent active above ground differs from that of previous studies (Swart 1996; Pietersen *et al.* 2014b). Swart (1996) reported that pangolins inhabiting a more mesic area in eastern South Africa were nocturnal throughout most of the year and remained predominantly nocturnal even during winter, with only ~20% of all winter emergence events occurring before 18:00. The almost exclusively nocturnal activity throughout the year likely suggests that the pangolins in the more mesic area did not experience energy deficits during winter and were able to maintain constant high body temperature at night. The pangolins studied by Swart (1996) therefore likely did not need to emerge from their burrows diurnally in an attempt to conserve energy. Less diurnal activity in those pangolins in winter as compared to the pangolins in my study likely explains the lack of seasonal variation in the duration of activity of mesic area pangolins. The cost of foraging activity likely could be met when pangolins did not experience energy deficits. However, Pietersen *et al.* (2014c) also reported no seasonal variation in the duration of above-ground activity, yet the pangolins in their study did become diurnally active during winter. Although Pietersen *et al.* (2014c) did not report the seasonal distribution of their data, two of their study pangolins, for which emergence data were reported, emerged from their

burrows before 18:00 for ~86% of all observations, suggesting that the data may have been collected predominantly during the cooler months of the year. Most (~36%) of their pangolin emergences occurred between 16:00 and 18:00. In my study, pangolins were most likely to emerge from their burrows between 14:00 and 16:00 during winter, suggesting that the pangolins in my study were more diurnally active compared to the pangolins observed by Pietersen *et al.* (2014c). Greater diurnal activity for my pangolins suggests that they likely experienced greater energy deficits during winter compared to the pangolins observed by Pietersen *et al.* (2014c).

The results of my study provide a clearer understanding of the link between climatic conditions, food availability and pangolin 24h activity than previously reported (Swart 1996; Pietersen *et al.* 2014b). The main factors that influenced the activity patterns of my study pangolins were photoperiod and 24h minimum body temperature. When pangolin 24h minimum body temperature was low as a consequence of energy deficits accrued from low prey abundance, pangolins emerged from their burrows earlier during the day compared to when prey was abundant. Diurnal emergence likely facilitated energy conservation in pangolins when food resources were scarce. The amount of time that pangolins could spend foraging, however, appeared to be constrained by environmental temperatures, suggesting that pangolins prioritize energy homeostasis over foraging activity in the Kalahari, regardless of the availability of food resources. Even though diurnal activity presumably allowed pangolins to conserve energy, if pangolins emerge from their burrows even earlier during the day as food resources become more scarce, they will face increasing winter daytime temperatures associated with climate change, and will likely increase their risk of dehydration, hyperthermia and heat illness. The physiological adaptations that allowed pangolins to cope with variation in climate and food resources in my study may not sufficiently buffer them against future warming and reductions in food availability associated with climate change.

Chapter 5

Ground pangolins relax the precision of body temperature regulation when resources are scarce in the Kalahari

5.1 INTRODUCTION

Maintaining the relatively high and constant body temperatures characteristic of mammals requires sufficient access to food energy and water (Fuller *et al.* 2014; Fuller *et al.* 2016). When food energy is limited, mammals exhibit decreased 24h minimum body temperatures (Yoda *et al.* 2000; Wang *et al.* 2006; Hetem *et al.* 2016). For example, when Comisana sheep (*Ovis aries*) and Maltese goats (*Capra aegagrus hircus*) were food deprived, their 24h minimum body temperatures decreased (Piccione *et al.* 2002). Although lower 24h minimum body temperatures may allow mammals to conserve energy by reducing their metabolism via the Q_{10} effect, which is a measure of the rate of change of enzymatic reaction rates per 10 °C change in body temperature (Heldmaier and Ruf 1992), negative energy balance can still lead to deterioration in body condition, which can be fatal (Jagoe *et al.* 2002; Weyer 2018; Weyer *et al.* 2020). Conversely, water-deprived mammals exhibit increased 24h maximum body temperatures, particularly when heat-exposed (Mitchell *et al.* 2002; Angilletta *et al.* 2010; Samara *et al.* 2012; McKinley *et al.* 2017). For example, during hot months, Arabian oryx (*Oryx leucoryx*) exhibited increased maximum daily body temperatures in response to reduced water availability compared to cooler months when water was readily available (Hetem *et al.* 2010). Although increased 24h maximum body temperatures can reduce the need for evaporative cooling, dehydration-induced hyperthermia may place animals closer to heat illness or death (Terrien *et al.* 2011).

The decreased 24h body temperature minima and increased 24h body temperature maxima result in increased amplitudes of the 24h rhythm of body temperature, also known as heterothermy. Increased heterothermy associated with energy and water deficits in mammals may be used as a proxy for the physiological welfare of mammals (Hetem *et al.* 2016). Because energy and water balance also affect the growth and reproduction of mammals, increased heterothermy may also provide an indication of the performance of mammals. Indeed, increased amplitudes of the 24h rhythm of body temperature reflected poorer breeding performance in wild rabbits (*Oryctolagus cuniculus*); rabbits had fewer pregnancies when they exhibited greater amplitudes of the 24h rhythm of body temperature prior to breeding (Maloney *et al.* 2017). Therefore, although heterothermy may allow mammals to conserve energy and water when resources are limited, increased body temperature variability may ultimately be associated with a reduction in their performance.

In mammals, the patterns of body temperature may vary throughout the year, depending on resource availability (Weyer *et al.* 2020). Nocturnal mammals in dry environments must contend with cold night-time temperatures when the night sky also acts as a large heat sink, whereby heat is lost passively to the sky (Mitchell *et al.* 2018). However, the

heat generated by nocturnal activity may counter that heat loss. Nocturnal mammals may switch to diurnal activity during periods of resource scarcity, when their energy intake is insufficient to maintain homeothermy on cold nights (van der Vinne *et al.* 2019; Guiden and Orrock 2020; Weyer *et al.* 2020). When they do so, even during the cooler winter in dry environments, they may be exposed to heat loads that also may challenge their ability to maintain homeothermy. Some mammals may also increase the duration of their activity to compensate for food scarcity (Shaffer *et al.* 2001), and in the case of some mammals switching to diurnal activity and thus being exposed to high heat loads, the prolonged duration of exposure to high solar radiation may further challenge their ability to maintain homeothermy. Mammals in such circumstances may have to trade off increased 24h maximum body temperatures with decreased 24h minimum body temperatures or may experience both. Indeed, in the Kalahari, drought conditions affected aardvark prey availability, which likely affected both aardvark nutritional and hydration status, since aardvarks obtain water from their prey, and led to both unusually high 24h maximum and low 24h minimum body temperatures (Weyer 2018).

Little is known about how pangolins regulate body temperature under natural conditions because long-term body temperature recordings have never been measured for any pangolin species in the wild. While records of body temperature (usually rectal temperature measurements) of captive pangolins may yield important insights for understanding pangolin physiology, measurements from wild pangolins will provide more realistic insights into pangolin physiology under natural conditions. In one study, which measured core body temperature of one wild female Temminck's ground pangolin for 34 days during winter, the core body temperature was low compared to other placental mammals and varied predominantly between 32 – 35 °C (Pietersen 2013). Given the finding that 24h body temperature variability may be used to assess the welfare of free-living mammals (Hetem *et al.* 2016; Maloney *et al.*, 2017), long-term pangolin body temperature may provide insights for us to predict how these predominantly nocturnal myrmecophagous mammals respond to seasonal and interannual fluctuations in climate and food resources.

With access to miniature temperature data loggers and a team with expertise in implanting such devices in mammals in the field, I therefore investigated the long-term body temperature patterns of free-living pangolins. I predicted that pangolin body temperature would be lower than for most other placental mammals but that they would regulate body temperature within a narrow 24h range when food resources were abundant. When food resources were scarcer, I predicted that pangolins would exhibit increased heterothermy as indicated by decreased 24h minimum temperatures, and possibly also increased 24h maximum body temperatures given that they, like aardvarks, obtain water primarily from their diet. Because diurnally emerging pangolins could be

exposed to high heat loads, particularly as a result of high solar radiation, I predicted that the 24h maximum body temperature would increase as a function of the time of emergence. In other words, when pangolins emerged from their burrows earlier during the day, I predicted that their 24h maximum body temperature would be higher compared to when they emerged later during the day since they would subsequently be exposed to higher environmental heat loads.

5.2 MATERIAL AND METHODS

5.2.1 Climatic and seasonal variables

A weather station, placed approximately 10 km from the area where study pangolins ranged, measured black globe temperature. Previously, our research team had shown that black globe temperatures at this site were similar to those in the area in which our pangolins ranged. We could not place the weather station closer to the pangolin range area because of likely damage by wildlife, such as baboons and buffalos. Black globe temperature was measured at 30-minute intervals by a temperature-sensitive probe inserted into a 150 mm matt black, hollow copper globe (see Chapter 2 for details). The time of sunrise and sunset for each day within the study period (October 2015 to October 2017) was obtained from the South African Weather Services (SAWS), and photoperiod (day length) was determined by calculating the time difference between sunrise and sunset. The seasons were defined as summer (December to February), autumn (March to May), winter (June to August), and spring (September to November) based on previous studies in the Kalahari (Weyer 2018; van de Ven *et al.* 2020).

5.2.2 Prey abundance

A total of 30 permanent transects were selected randomly across the reserve where pangolins had been previously detected (in grass- and shrub-dominated areas in the dune fields). Using pitfall traps at each transect, prey abundance was recorded once a month. Each transect consisted of 10 pitfall traps placed five metres apart for a total of 300 traps per month. The traps were placed in the ground with the opening of the trap level with the ground surface. All the traps remained in the ground for four days. Ants that fell into the traps were counted and used as a proxy for pangolin prey abundance at the study site. See Chapter 3 for more details.

5.2.3 Pangolin activity

Pangolins were tracked in the mornings during their inactive phase using telemetry (see Chapter 2 for details) to locate their burrows, and camera traps were placed outside the burrows to assess time of emergence and return for the six pangolins. Camera traps did not always trigger for emergence or return events, and pangolins did not always return to the same burrow, thus the camera traps could not always detect time of emergence and

return. Therefore, time of emergence and return data obtained from camera traps were supplemented with data extracted from the 24h body temperature patterns of pangolins (see Chapter 4 for details). The duration of above ground activity could then be estimated from the time of emergence and return data obtained from the camera traps and body temperature records.

5.2.4 Pangolin body temperature

Six pangolins (three males and three females, 6.5 – 9.4 kg), tagged with VHF tracking transmitters, were located and captured so that a veterinarian could anaesthetize them to implant each animal with a wax-coated miniature temperature-sensitive data logger, using the methods described in Chapter 2. The body temperature data loggers, which were implanted into the retroperitoneum, recorded core body temperature at 5-minute intervals. As a result of their scarcity and difficulty in locating suitable individuals, pangolins were implanted at different times of the year (Chapter 2, Table 2.2), resulting in varying durations of data collection of body temperature across the study period (October 2015 to October 2017). For the first five months of the study (October 2015 to February 2016), body temperature was collected from two pangolins, and for the following 20 months of the study (March 2016 to October 2017), body temperature data was collected from at least three pangolins simultaneously.

5.2.5 Data analyses

Data analyses were conducted using GraphPad (version 8.00; GraphPad Prism, 2021) and R software (R Core Team, 2021) for this chapter. For all models, residuals were examined to assess the accuracy of the models. Interactive effects could not be included into the models because the small sample size of individual pangolins did not have the power necessary to test interactions among variables.

The 24h mean, 24h minimum and 24h maximum black globe temperatures were determined for each day across the study period. Seasonal means were calculated by averaging the 24h mean, 24h minimum and 24h maximum for summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). The globe temperature at the time of pangolin emergence from the burrow was also determined for each pangolin for each day.

The number of ants per trap was calculated by totalling the number of ants captured in the traps at each transect and dividing the total by the number of traps retrieved per transect. Prey abundance was then calculated by averaging the number of ants per trap across all transects. An ANOVA was used to analyse seasonal and interannual differences. See Chapter 3 for more details.

The seasonal and interannual proportion of pangolin emergence and return was calculated by totalling the number of observations occurring per time category per season per year across 1h intervals and dividing them by the total number of observations per season per year to account for different sample sizes in activity data. The duration of above-ground activity was calculated by subtracting time of emergence from time of return. See Chapter 4 for more details.

The pangolin 24h mean, 24h minimum, and 24h maximum body temperature was averaged across all pangolins and then averaged for each season. The amplitude of the 24h rhythm of body temperature was calculated by subtracting the 24h minimum from the 24h maximum body temperature. The amplitude of the 24h rhythm of body temperature was then averaged across all pangolins and then averaged for each season. One-way ANOVAs were used to assess seasonal and interannual differences in 24h mean, 24h minimum, 24h maximum and amplitude of the 24h rhythm of body temperature and a Dunnett's multiple comparisons tests was used to identify where the differences occurred.

Linear mixed models were used to test the effects of photoperiod (daylength), prey abundance, and environmental temperatures on the 24h minimum and 24h maximum body temperatures, and on the amplitude of the 24h rhythm of body temperature. Photoperiod, prey abundance, and environmental temperature were the explanatory variables, and the body temperature variables were the response variables. Individual pangolins were included as a random factor in the models. R packages that were used include 'lmerTest' (Kuznetsova *et al.* 2017), 'performance' (Ludecke *et al.* 2020), 'robustlmm' (Koller 2016), 'patchwork' (Pederson 2020), 'knitr' (Xie 2015, 2015), 'ggplot2' (Wickham 2016), 'dplyr' (Wickham *et al.* 2021), and 'tidyr' (Wickham 2021). The relationship between prey abundance and the body temperature variables was not linear therefore a piecewise regression was used to assess the relationship before a breakpoint and after a breakpoint. A search was conducted to determine the breakpoint by running the models using various breakpoints between 0 and 18 ants per trap, and then comparing the models for the best fit using AIC, where the model with the lowest AIC value was selected as the best model (Symonds and Moussalli 2011).

To assess whether the time that pangolins emerged from their burrows influenced pangolin 24h maximum body temperature, a linear mixed model was used where time of emergence was the explanatory variable and 24h maximum body temperature was the response variable.

5.3 RESULTS

5.3.1 Climatic variables

Black globe temperatures at Tswalu ranged between -5.1 °C and 50.4 °C across the study period (October 2015 to October 2017). The 24h mean black globe temperature varied seasonally and was higher during the first study year (October 2015 to October 2016) compared to during the second year (October 2016 to October 2017) for summer and winter (see also Chapter 3 and 4). Due to a failed weather station, weather data for the first autumn were not collected. The mean 24h minimum black globe temperature varied seasonally and was higher during the summer, winter, and spring of the first year compared to second year (Chapter 4). The mean 24h maximum black globe temperature also varied seasonally and was higher during the summer of the first year compared to the summer of the second year but was lower during the autumn and winter of the first year compared to the autumn and winter of the second year.

5.3.2 Prey abundance

As analysed and reported in Chapter 3, the overall monthly ant abundance varied seasonally across the study period and was highest during summer (20.2 ± 13.0 ants per trap) and spring (25.9 ± 20.9 ants per trap), and lowest during autumn (7.4 ± 6.0 ants per trap) and winter (9.2 ± 10.5 ants per trap). Ant abundance did not differ between years for summer and spring but was significantly higher during the autumn (11.1 ± 6.8 ants per trap) and winter (15.7 ± 12.3 ants per trap) of the second study year compared to in the autumn (4.7 ± 3.3 ants per trap) and winter (4.0 ± 4.2 ants per trap) of first study year.

5.3.3 Pangolin activity

As analysed and reported in Chapter 4, pangolins were predominantly nocturnal throughout the year, but they emerged from their burrows earlier during the day in winter compared to in summer. Pangolins were active above ground for shorter periods during winter compared to in summer. During the winter following a summer of below-average rainfall, pangolins emerged from their burrows earlier during the day and were active above ground for longer periods compared to during the winter following a summer of above-average rainfall.

5.3.4 Pangolin body temperature

Core body temperature measured at 5-minute intervals was recorded for six pangolins for a total of 2207 days across the study period (October 2015 to October 2017; Figure 5.1). Over these days, the pangolin body temperature data showed a unimodal distribution whereby pangolins predominantly (~95% of the time) regulated body temperature between 34 and 36 °C (Figure 5.2). The absolute minimum 24h body temperature

recorded throughout the study period was 29.5 °C (December 2016) and the absolute maximum 24h body temperature recorded was 38.2 °C (September 2017). The maximum amplitude of the 24h rhythm of body temperature across all pangolins was 6.8 °C, with 24h body temperature increasing from a minimum of 30.2 to a maximum of 37.0 °C (within 2 hours and 39 minutes) during July 2016.

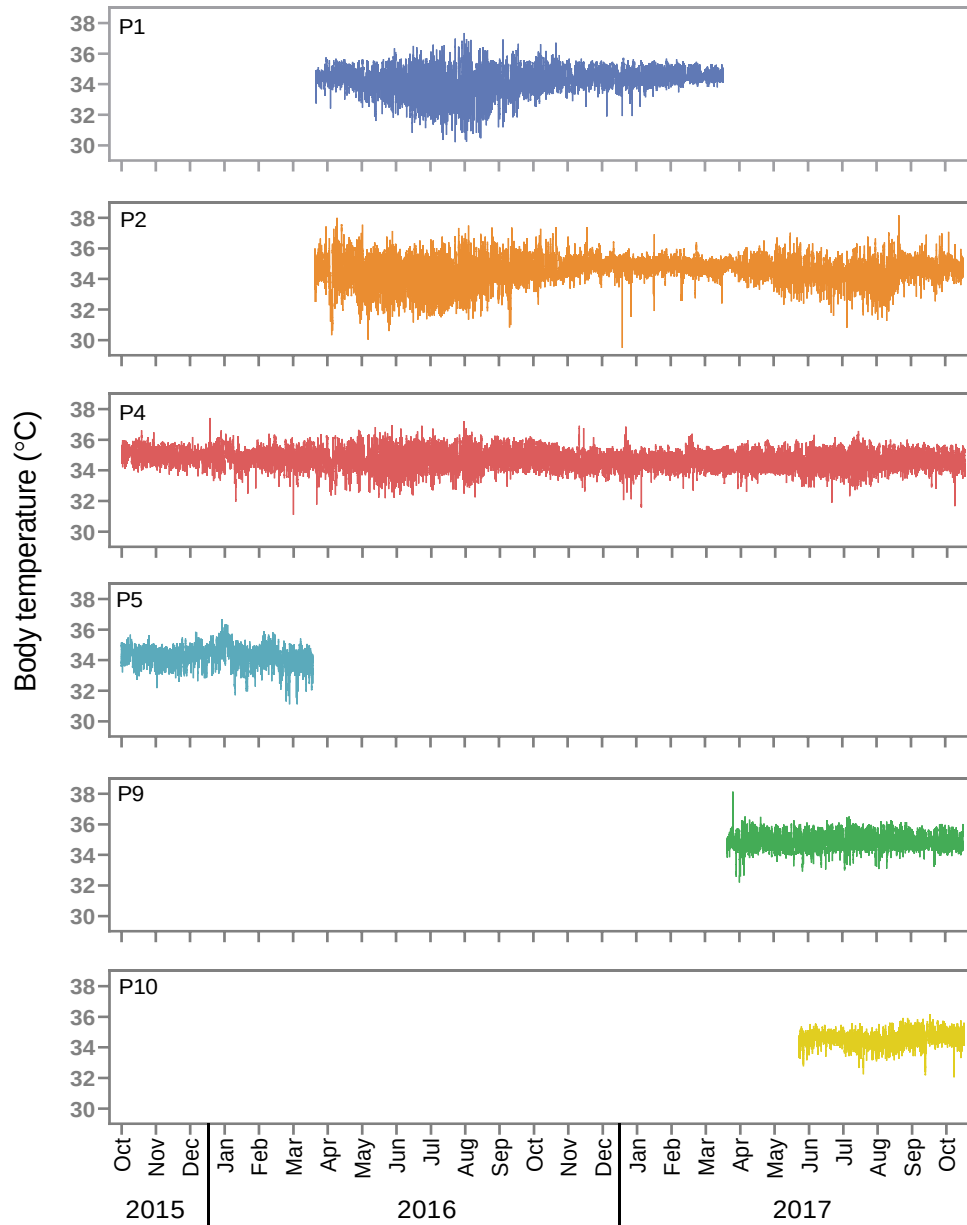


Figure 5.1: Body temperature patterns recorded at 5-minute intervals for six individual pangolins at Tswalu across the study period.

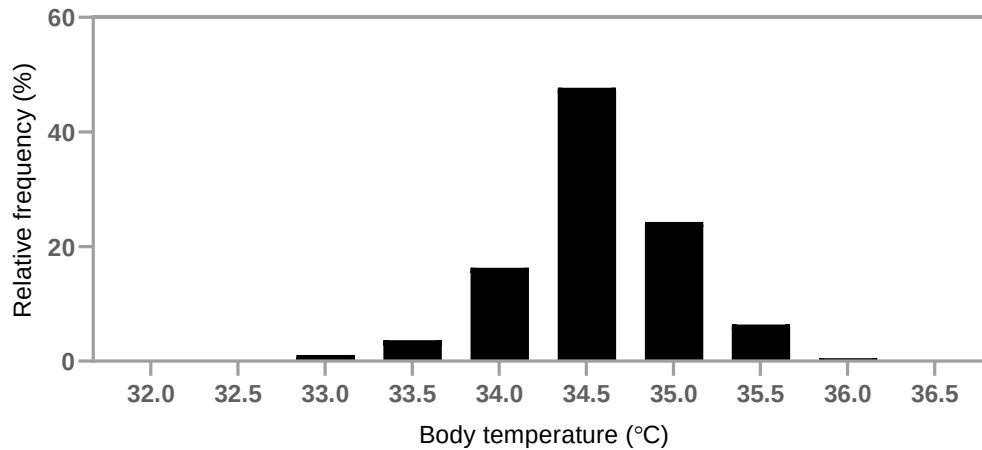


Figure 5.2: Frequency distribution (%) of body temperature averaged across six pangolins for the study period (October 2015 to October 2017).

There was seasonal or interannual (or both) variation in all of the 24h body temperature variables (24h mean, 24h minimum, 24h maximum, and 24h amplitude; Figure 5.3, Table 5.1). The seasonal and interannual differences for the pangolins with the longest datasets yielded the same results in terms of statistical significance between seasons and years as when the data for all pangolins were pooled together, therefore the mean body temperatures parameters of all pangolins were pooled together for seasonal and interannual comparisons. The mean 24h body temperature did not vary seasonally for either study year, but there was some, although slight (0.3°C), interannual variation (ANOVA, $F_{(7,307)}=116.2$, $p<0.0001$). The 24h mean body temperature of pangolins was lower during the autumn, winter, and spring of the first study year compared to the autumn, winter, and spring of the second study year. There was both seasonal and interannual variation in the 24h minimum body temperature of pangolins (ANOVA, $F_{(7,487)}=148.6$, $p<0.0001$). The 24h minimum body temperature during both years was highest during summer and lowest during winter. Interannually, the 24h minimum body temperature was lower during the autumn, winter, and spring of the first study year compared to the autumn, winter and spring of the second study year. There was also seasonal and interannual variation in the 24h maximum body temperature of pangolins (ANOVA, $F_{(7,555)}=25.1$, $p<0.0001$). During the first year, the 24h maximum body temperature was highest during winter and lowest during summer. During the second study year, the 24h maximum body temperatures varied to a lesser degree seasonally compared to the first year, and the 24h maximum body temperature was highest during autumn, winter, and spring, and lowest during summer. Interannually, the 24h maximum body temperatures did not differ between years for summer ($t=0.34$, d.f.=129, $p>0.05$), autumn ($t=1.37$, d.f.=154, $p>0.05$), or spring ($t=1.00$, d.f.=96, $p>0.05$), but were higher during the winter of the first year compared to the winter of the second year. The

seasonal and interannual variation in the 24h body temperature minima and maxima resulted in seasonal and interannual variation in the amplitude of the 24h rhythm of body temperature (ANOVA, $F_{(7,593)}=160.2$, $p<0.0001$). During both years, the amplitude of the 24h rhythm of body temperature was the greatest during winter and lowest during summer. Interannually, the amplitude of the 24h rhythm of body temperature was greater during the autumn, winter, and spring of the first year compared to the autumn, winter, and spring of the second year.

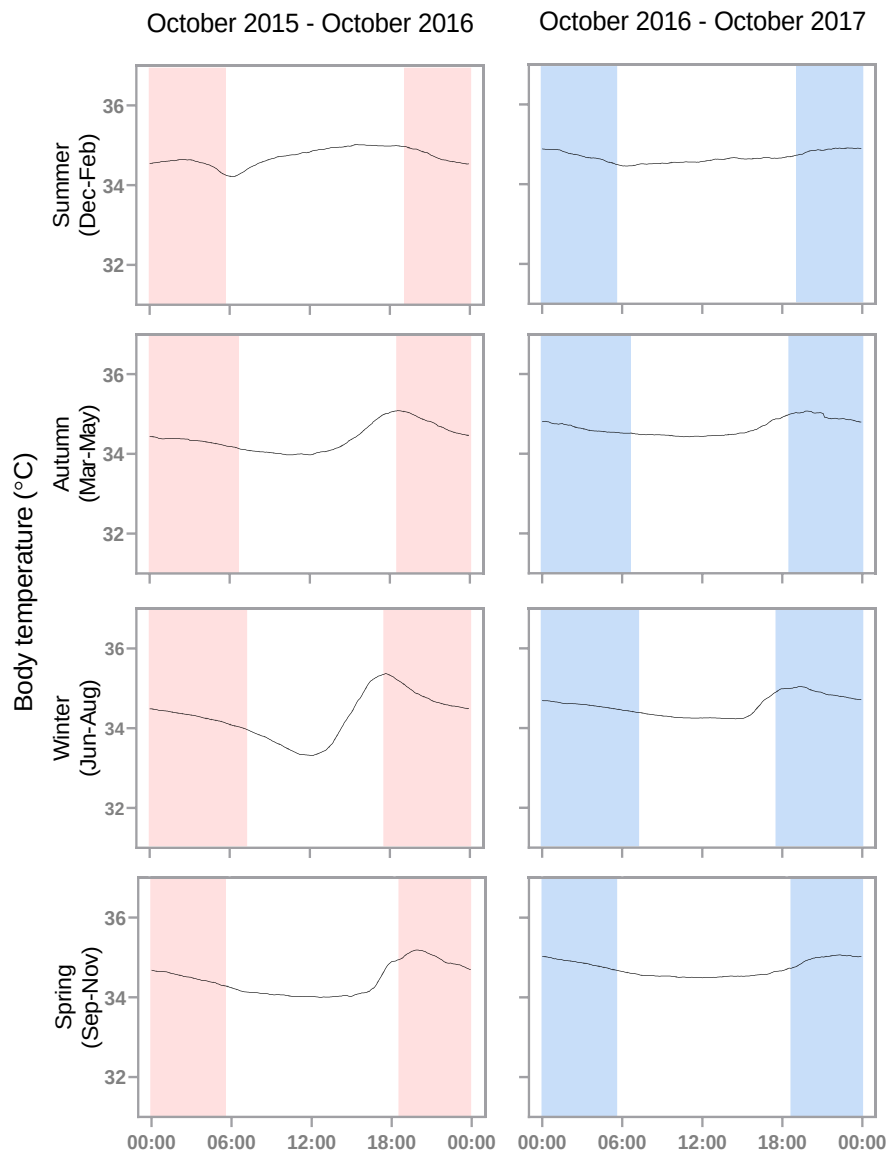


Figure 5.3: The seasonal and interannual 24h body temperature patterns for two years. The black lines represent the average 24h body temperature across all pangolins across each month in that season. The pink (first study year) and blue (second study year) shaded areas represent the dark phase for each study year.

Table 5.1: Seasonal and interannual summary statistics of the 24h mean, 24h minimum, 24h maximum, and 24h amplitude of body temperature for two years (mean $\pm$ SD). Pink shaded columns show 2015-2016, the year in which rainfall, grass cover, and prey abundance was low, and the blue shaded columns show 2016-2017, the year in which rainfall, grass cover, and prey abundance was high. Grey blocks indicate significant differences between the two years.

	Summer			Autumn			Winter			Spring		
	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean	2015-2016	2016-2017	Mean
Body temperature (°C)												
24h mean	34.7 $\pm$ 0.3	34.7 $\pm$ 0.1	34.7 $\pm$ 0.2	34.4 $\pm$ 0.2	34.7 $\pm$ 0.1	34.5 $\pm$ 0.2	34.3 $\pm$ 0.1	34.6 $\pm$ 0.1	34.4 $\pm$ 0.2	34.4 $\pm$ 0.1	34.7 $\pm$ 0.1	34.6 $\pm$ 0.2
24h minimum	33.8 $\pm$ 0.4	33.9 $\pm$ 0.5	33.9 $\pm$ 0.5	33.2 $\pm$ 0.6	33.8 $\pm$ 0.3	33.5 $\pm$ 0.6	32.4 $\pm$ 0.3	33.5 $\pm$ 0.2	32.9 $\pm$ 0.6	33.5 $\pm$ 0.3	33.9 $\pm$ 0.3	33.7 $\pm$ 0.4
24h maximum	35.5 $\pm$ 0.3	35.4 $\pm$ 0.2	35.4 $\pm$ 0.3	35.5 $\pm$ 0.4	35.6 $\pm$ 0.3	35.6 $\pm$ 0.3	35.9 $\pm$ 0.4	35.6 $\pm$ 0.4	35.8 $\pm$ 0.4	35.7 $\pm$ 0.3	35.6 $\pm$ 0.6	35.7 $\pm$ 0.3
24h amplitude	1.8 $\pm$ 0.4	1.6 $\pm$ 0.4	1.7 $\pm$ 0.5	2.6 $\pm$ 0.7	1.9 $\pm$ 0.4	2.1 $\pm$ 0.7	3.5 $\pm$ 0.6	2.4 $\pm$ 0.9	2.8 $\pm$ 0.9	2.4 $\pm$ 0.5	1.9 $\pm$ 0.8	1.9 $\pm$ 0.5

A linear mixed model (using “lmer” in R, library ‘lme4’) was used to test the effects of photoperiod, prey abundance, and 24h mean black globe temperature on pangolin 24h minimum body temperature. The model (Table 5.2) revealed that pangolin 24h minimum body temperature was positively associated with photoperiod (Figure 5.4A), prey abundance (Figure 5.4B), and 24h minimum black globe temperature (Figure 5.4C). In other words, when days were short (in winter), when prey abundance was low, and when environmental temperatures were low, pangolin 24h minimum body temperature was low. Furthermore, pangolin 24h minimum body temperature was only associated with prey abundance when prey abundance was lower than ~12 ants per trap (AIC modelling; Appendix; Table A11). When prey abundance was higher than ~12 ants per trap, there was no relationship between pangolin 24h minimum body temperature and prey abundance.

Table 5.2: Linear mixed model results of the effects of photoperiod, prey abundance, and 24h minimum black globe temperature on pangolin 24h minimum body temperature.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	31.14 $\pm$ 0.31	99.48	30.52 to 31.78	<0.0001
Photoperiod	0.10 $\pm$ 0.02	4.00	0.05 to 0.14	<0.001
Prey abundance (<~12 ants/trap)	0.08 $\pm$ 0.01	14.67	0.07 to 0.10	<0.0001
Prey abundance (>~12 ants/trap)	0.001 $\pm$ 0.002	0.50	-0.003 to 0.01	0.62
24h minimum black globe temperature	0.02 $\pm$ 0.003	6.55	0.02 to 0.03	<0.0001

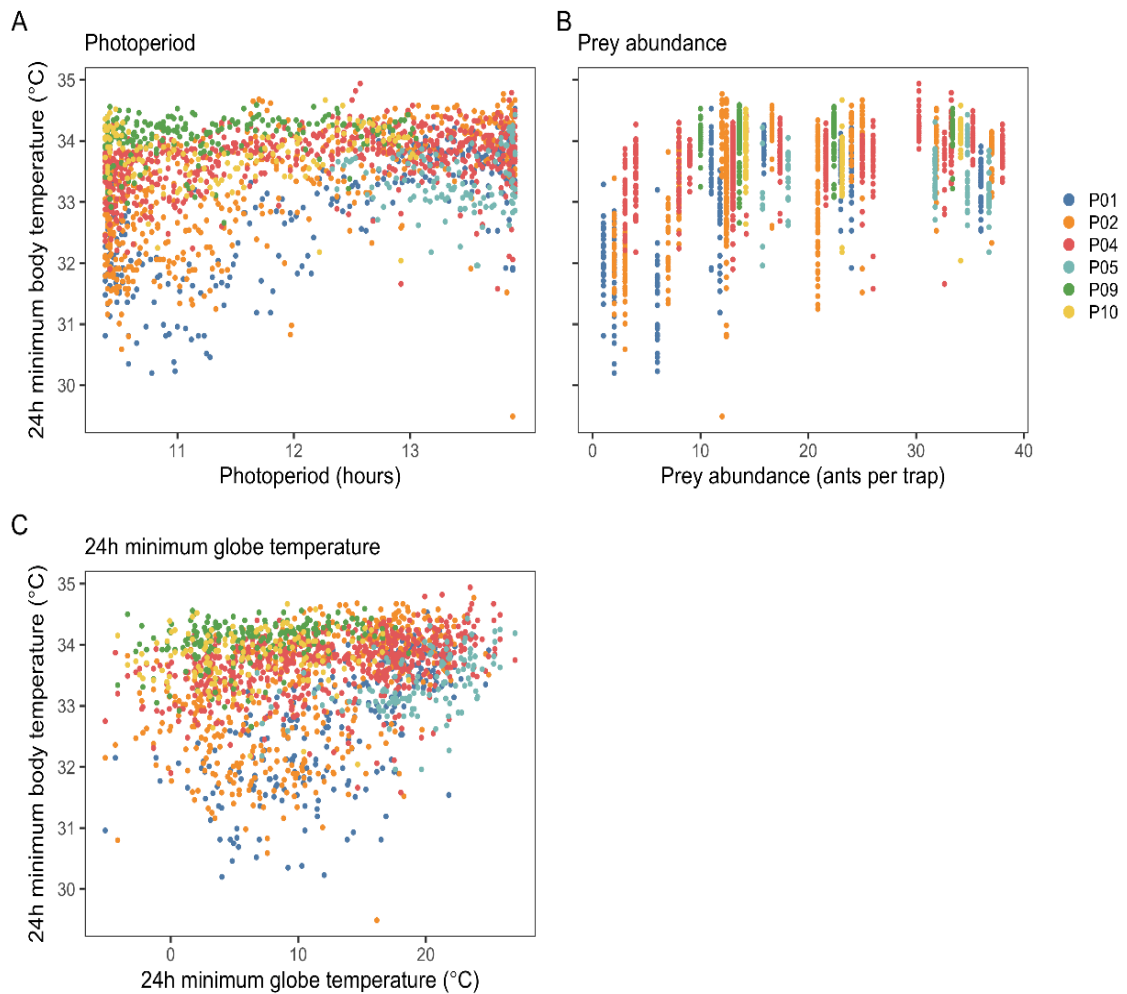


Figure 5.4: The relationship between pangolin 24h minimum body temperature and photoperiod (A), prey abundance (B) and 24h minimum black globe temperature (C). P01 to P10 represent the different study animals.

A linear mixed model (using “lmer” in R, library ‘lme4’) was used to test the effects of photoperiod, prey abundance, and 24h maximum black globe temperature on pangolin 24h maximum body temperature. The model (Table 5.3) revealed that pangolin 24h maximum body temperature was negatively associated with photoperiod (Figure 5.5A) and prey abundance (Figure 5.5B) but was not associated with the 24h maximum black globe temperature (Figure 5.5C). In other words, when days were short (in winter), and prey abundance was low, pangolin 24h maximum body temperature was high, but 24h maximum black globe temperature did not significantly influence pangolin 24h maximum body temperature. Furthermore, pangolin 24h maximum body temperature was only associated with prey abundance when prey abundance was lower than ~17 ants per trap (AIC modelling; Appendix; Table A12). When prey abundance was higher than ~17 ants

per trap, there was no relationship between pangolin 24h maximum body temperature and prey abundance.

Table 5.3: Linear mixed model results of the effects of photoperiod, prey abundance, and 24h maximum black globe temperature on pangolin 24h maximum body temperature.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	36.55 ± 0.17	213.72	36.21 to 36.88	<0.0001
Photoperiod	-0.11 ± 0.01	-7.97	-0.14 to -0.09	<0.0001
Prey abundance (<~17 ants/trap)	-0.03 ± 0.002	-9.53	-0.03 to -0.02	<0.0001
Prey abundance (>~17 ants/trap)	0.01 ± 0.002	7.85	0.01 to 0.02	<0.0001
24h maximum black globe temperature	0.02 ± 0.002	8.73	0.01 to 0.02	<0.0001

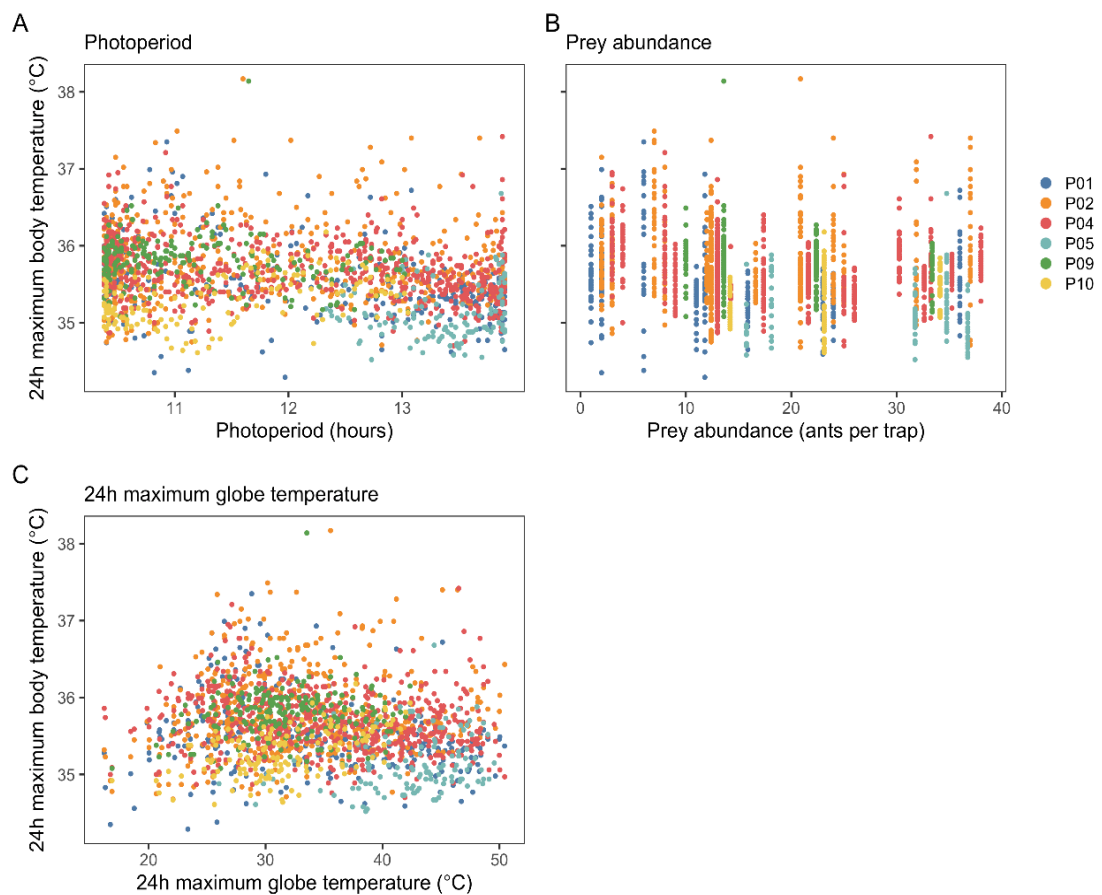


Figure 5.5: The relationship between 24h maximum body temperature and photoperiod (A), prey abundance (B) and 24h maximum black globe temperature (C). P01 to P10 represent the different study animals.

A linear mixed model (using “lmer” in R, library ‘lme4’) was used to test the effects of photoperiod, prey abundance, and the amplitude of the 24h rhythm of black globe temperature on the amplitude of the 24h rhythm of pangolin body temperature. The model (Table 5.4) revealed that the amplitude of the 24h rhythm of pangolin body temperature was negatively associated with photoperiod (Figure 5.6A) and prey abundance (Figure 5.6B) but was not associated with the amplitude of the 24h rhythm of black globe temperature (Figure 5.6C). In other words, when days were short (in winter), and prey abundance was low, the amplitude of the 24h rhythm of pangolin body temperature was high, but amplitude of the 24h rhythm of black globe temperature did not significantly influence the amplitude of the 24h rhythm of pangolin body temperature. Furthermore, the amplitude of the 24h rhythm of pangolin body temperature was only associated with prey abundance when prey abundance was lower than ~12 ants per trap (AIC modelling; Appendix; Table A13). When prey abundance was higher than ~12 ants per trap, there was no relationship between the amplitude of the 24h rhythm of pangolin body temperature and prey abundance.

Table 5.4: Linear mixed model results of the effects of photoperiod, prey abundance, and the amplitude of the 24h rhythm of black globe temperature on the amplitude of the 24h rhythm of pangolin body temperature.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	5.84 $\pm$ 0.29	20.45	5.28 to 6.40	<0.0001
Photoperiod	-0.24 $\pm$ 0.02	-12.19	-0.28 to -0.20	<0.0001
Prey abundance (<~12 ants/trap)	-0.07 $\pm$ 0.01	-14.23	-0.08 to -0.06	<0.0001
Prey abundance (>~12 ants/trap)	0.02 $\pm$ 0.003	7.12	0.02 to 0.03	<0.05
Amplitude of 24h black globe temperature	-0.003 $\pm$ 0.003	-1.07	-0.01 to 0.002	0.85

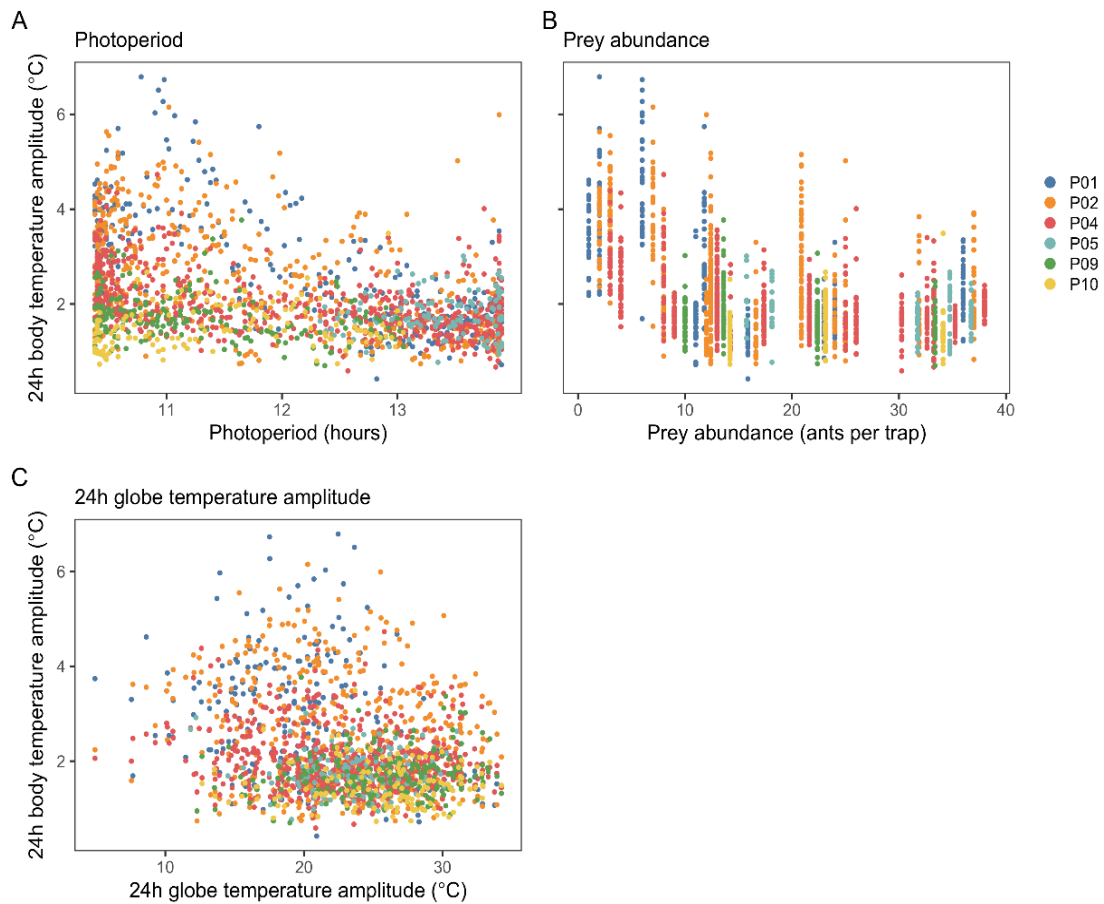


Figure 5.6: The relationship between amplitude of the 24h rhythm of body temperature and photoperiod (A), prey abundance (B) and the amplitude of 24h black globe temperature (C). P01 to P10 represent the different study animals.

A linear mixed model (using “lmer” in R, library ‘lme4’) was used to test the relationship between pangolin time of emergence and pangolin 24h maximum body temperature. The model revealed a significant, negative relationship between pangolin time of emergence from the burrow and pangolin 24h maximum body temperature (Table 5.5), such that when pangolins emerged from their burrows earlier during the day, their 24h maximum body temperatures were higher compared to when they emerged later during the day (Figure 5.7).

Table 5.5: Linear mixed model results of the effect of pangolin time of emergence from the burrow on their 24h maximum body temperature.

Explanatory variable	$\beta \pm SE$	t	95% CI	p
Intercept	82.78 ± 4.3	19.16	74.31 to 91.26	<0.01
24h maximum body temperature	-1.81 ± 0.12	-15.13	-2.05 to -1.58	<0.01

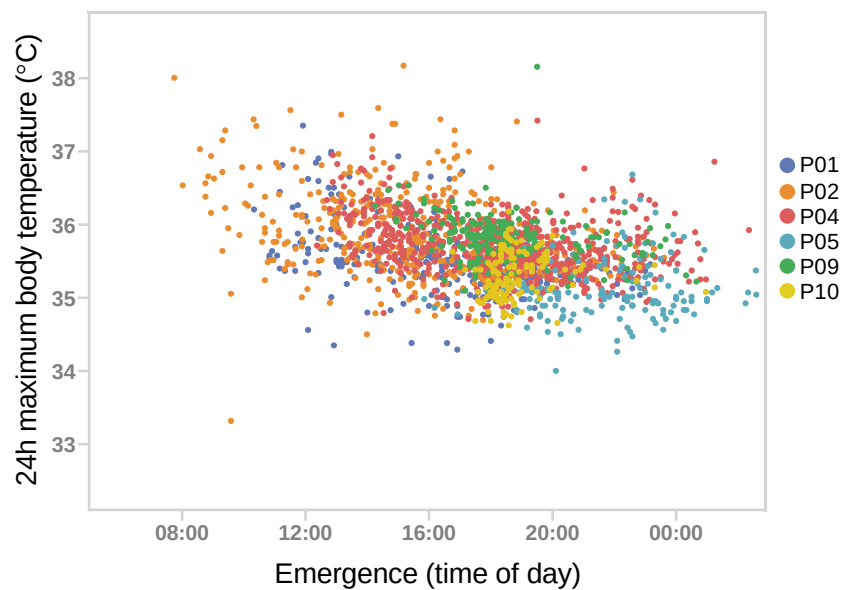


Figure 5.7: The relationship between pangolin time of emergence from the burrow and 24h maximum body temperature. P01 to P10 represent the different study animals.

5.4 DISCUSSION

Pangolins regulated body temperature within a narrow 24h range during summer, but during winter when prey resources were scarce, they become more heterothermic, as indicated by decreased 24h body temperature minima and increased 24h body temperature maxima. The body temperatures of the pangolins fluctuated more over 24h during the year in which prey resources were scarce compared to the year in which prey resources were abundant. The main predictors of pangolin body temperature parameters, including the 24h minimum body temperature, 24h maximum body temperature and the amplitude of the 24h rhythm of body temperature, were photoperiod and prey abundance. A shorter photoperiod, as an indication of seasonality, and lower prey abundance was associated with a lower 24h minimum body temperature, and a higher 24h maximum body temperature and amplitude of the 24h rhythm of body temperature. The only environmental temperature variable that was associated with pangolin body temperature was 24h minimum globe temperature, with lower 24h minimum body temperature associated with lower 24h minimum globe temperature.

Although this study is the first to investigate the long-term body temperature patterns of wild pangolins, I was able to collect data continuously from only one animal for the full two years. However, at any given time (except from October 2015 to February 2016), body temperature data were collected from at least three pangolins. Future studies should consider combining VHF tracking transmitters with satellite tags to reduce the chances of losing contact with animals that move large distances, thereby ensuring a

more continuous sampling of individuals. The small sample size did not allow me to elucidate any possible differences based on sex or body size. Nevertheless, I present the most comprehensive data on body temperature collected to date for this rare and elusive mammal. Also, although data collected on prey abundance allowed me to assess the role of food availability in the body temperature regulation of pangolins, the values provided in the results are merely a proxy for prey abundance, rather than an absolute number.

The main reason I measured body temperature in pangolins was to investigate whether patterns of body temperature were related to changing food availability. Food energy is required for mammals to generate the metabolic heat needed to maintain relatively high and constant body temperatures (Hetem *et al.* 2016). Pangolins maintained homeothermy throughout most of the year by regulating their core body temperature between 34 and 36 °C, but they exhibited increased heterothermy during winter. Pangolin 24h minimum body temperature was closely linked to prey abundance, such that when prey abundance was low (<~12 ants per trap) during winter, they exhibited decreased 24h minimum body temperatures. Low 24h minimum body temperatures presumably allowed pangolins to conserve energy by reducing metabolism, as could be explained by the Q_{10} effect in mammals (Heldmaier and Ruf 1992). Another advantage of the resulting lower 24h minimum body temperatures is that the thermal gradient between the body surface and the cold winter environment was likely decreased, thereby reducing dry heat loss to the environment, and reducing the energy demand for heat production. By relaxing the precision of body temperature regulation during winter, pangolins, like many other mammals (Pereira *et al.* 2002; Hetem *et al.* 2016; Theimer *et al.* 2017; Weyer *et al.* 2020), appeared to prioritize energy conservation over thermoregulation during a period when food energy was less available. A lower 24h minimum body temperature, however, may put mammals at risk of hypothermia and death, as seen in starving aardvarks (Rey *et al.* 2017, Weyer *et al.* 2020). Pangolins in this study experienced 24h minimum body temperatures of about 32 °C in the year with food scarcity, but these were only about 2 °C lower than in the year with available food. Whether lowering of body temperature will be sufficient to buffer pangolins against food scarcity in drought years, or in future as climate change reduces resource availability, is unknown.

While food energy is important for the maintenance of high body temperatures, water availability is also important for preventing excessive increases in body temperature in mammals in hot environments (Ostrowski *et al.* 2003; Fuller *et al.* 2016; Hetem *et al.* 2016). It is unknown whether pangolins lose water through panting, but an increased breathing rate was observed in Chinese pangolins (*Manis pentadactyla*) when air temperatures rose above 32 °C (Heath and Hammel 1986). Pangolins lack sweat glands (Hyman and Wake 1992; Feldhamer *et al.* 2007) so they cannot sweat but it is not known if cutaneous evaporation can occur across the skin, as in elephants (Dunkin *et al.* 2013).

Pangolins rarely actively seek free-standing water and obtain almost all of their body water through their diet (Pietersen *et al.* 2020). In my study site, free-standing water from water holes was available within the pangolin range, but I never observed a pangolin drinking from these sources. On one occasion I observed a pangolin drinking from a cup-like woody structure at the base of a shrub that had filled with water after a rain event during summer, suggesting that they will opportunistically drink water when it is available. Because pangolins get most of their body water from their food, when they experienced energy deficits as a consequence of reduced prey abundance, they likely also experienced water deficits. Indeed, pangolins exhibited increased 24h maximum body temperatures during winter when prey abundance was low (<17 ants per trap) and they usually emerged before nightfall, suggesting that they may have had insufficient body water to prevent a rise in body temperature. Perhaps pangolins increased their termite intake during winter (Chapter 3) in attempt to increase their water intake since termites have high water content (Weyer 2018), but this dietary shift did not prevent a rise in body temperature. By switching to diurnal activity during winter, pangolins were exposed to higher thermal heat loads that they would otherwise avoid by being nocturnal. In the Kalahari, globe temperatures can still be as high as 37 °C in the late afternoon in winter. Pangolins are poorly insulated by their scale covering (Heath and Hammel 1986; Weber *et al.* 1986; Challender *et al.* 2020). The poor insulation together with their relatively small body size means that they would likely gain heat rapidly when exposed to heat loads, particularly if they did not actively cool themselves by evaporative water loss. Indeed, when pangolins emerged from their burrows in the afternoon, they exhibited increased 24h maximum body temperatures following the emergence. When pangolins emerged from their burrows earlier during the day, sometimes even as early as 08:30 (Chapter 4), such that they were exposed to heat loads for longer periods, they developed even higher 24h maximum body temperatures compared to when they emerged later during the day. Although an advantage of emerging from their burrows earlier during the day was that pangolins increased their energy intake (Chapter 3), the change in behaviour resulted in higher 24h maximum body temperatures. Nevertheless, the highest body temperature recorded in a pangolin was only just greater than 38 °C, well below the level typically associated with heat illness and death in mammals (41 to 43.5 °C) (Fuller *et al.* 2016). One advantage of higher body temperatures during the day is an increased thermal gradient for dry heat loss. However, if those higher body temperatures are carried over into the cold night, the pangolin then faces a large thermal gradient for heat loss to the cooler night-time environment and may have to seek refuge in a burrow sooner. The higher body temperatures evident at times in the pangolins during my study, however, did not appear to compromise the welfare of the animals to the extent of fatality, and may well have assisted in water conservation if they resulted from inhibition of evaporative water loss to conserve body water.

Changes to the 24h minimum or 24h maximum body temperatures also will alter the 24h amplitude of the body temperature rhythm. An increased amplitude of the 24h rhythm of body temperature has previously been proposed as a proxy for the physiological welfare of mammals (Hetem *et al.* 2016), with mammals exhibiting homeothermy only when they have sufficient food and water and are not energetically challenged. The pangolins in this study exhibited amplitudes of the 24h rhythm of body temperature that were inversely related to prey abundance, such that when prey abundance, and hence water, was low, pangolins exhibited greater amplitudes of the 24h rhythm of body temperature compared to when prey was abundant. Similar findings were reported for aardvarks, in the Kalahari, where vegetation greenness was used as a proxy for the availability of the primary food item, the northern harvester termite (Weyer *et al.* 2020). When drought conditions reduced the availability of grass, the availability termites decreased (Weyer *et al.* 2018), and aardvarks, animals that also get their source of body water predominantly from their prey, exhibited greater amplitudes of the 24h rhythm of body temperature. Greater amplitudes of the 24h rhythm of body temperatures associated with reductions in food availability coincided with aardvarks losing body condition, and some aardvarks succumbed. Although pangolin body condition was not measured in this study and could not be visually observed with the scale covering on the animals, Pietersen (2013) reported that pangolins lost body condition during winter and that some pangolins died of starvation. The finding that pangolins increased heterothermy in response to food shortages in this study provides further evidence that the amplitude of the 24h rhythm of body temperature can be used as an index of the physiological welfare of mammals.

The body temperatures of pangolins in my study (on average, 34 – 36 °C) were similar, if not somewhat higher, compared to the body temperatures of pangolins measured previously both in captivity (32 – 35 °C; Boyles *et al.* 2019; Wicker *et al.* 2020) and in the wild (32 – 35 °C; Pietersen 2013). Nevertheless, pangolin body temperature was lower than other mammals of similar size and may be attributed to their low metabolic rates (McNab 1984; Griebeler and Werner 2016; Boyles *et al.* 2019). The absolute maximum body temperature recorded in this study was higher than has ever been recorded for all pangolin species in captivity for which rectal temperature records are available (Jones 1973; McNab 1984; Challender *et al.* 2020). Although data on the body temperature of pangolins in captivity is useful for understanding pangolin physiology, they data likely do not accurately reflect the body temperature patterns of wild pangolins exposed to natural conditions. Pangolins housed under captive conditions are not as active as wild pangolins and likely are not exposed to high radiant heat loads like the pangolins in the present study were when they emerged from their burrows diurnally, which may explain the higher maximum body temperature recorded in this study. The highest 24h maximum body temperature recorded by Pietersen (2013) was 35.4 °C, which was 2.8 °C lower

than the 38.2 °C recorded in my study. Pietersen (2013) recorded body temperature for one pangolin for a short period (34 days) during June (winter), whereas the highest 24h maximum body temperature recorded in my study occurred during September, when environmental heat loads were higher compared to in June.

The absolute minimum 24h body temperature of pangolins in my study, recorded for one pangolin, was the same (29.5 °C) as that recorded by Pietersen (2013). In my study, the body temperature of the pangolin fell from 35.0 °C at 01:00 to 29.5 °C at 03:15 (duration 2h15m) while the pangolin was active outside the burrow. The rapid decline in body temperature coincided with a rainfall event. The black globe temperature at 03:15, when pangolin body temperature reached the absolute minimum was 16.7 °C, which was 3-4 °C lower than the globe temperature at that time for three days before and three days after that day at the same time (data not shown). In conjunction with the lower globe temperature, the water on the surface of and between the pangolin's scales likely facilitated heat loss, especially if it was windy.

In conclusion, pangolins regulated core body temperature within a narrow 24h range when food resources and hence, water, were abundant, but relaxed the precision of body temperature regulation when food resources became scarcer. In doing so, pangolins appeared to prioritize energy and water conservation over thermoregulation. Although this physiological plasticity allowed pangolins to cope with environmental temperatures and food resource fluctuations in this study, whether these adaptations may sufficiently buffer them against the increasing environmental temperatures and reduced food availability associated with climate change remains to be determined.

Chapter 6

Conclusion

I investigated the dietary, behavioural, and physiological responses of pangolins to seasonal and interannual fluctuations in climate and food availability for two years. To my knowledge, this is the first study to assess in detail how pangolins respond to changes in the environment, and therefore the first to allow for predicting the potential responses of pangolins to climate change based on how they cope in their current environment. For parts of Africa, including much of the range of Temminck's ground pangolin, climate change models predict increasing air and surface temperatures, unpredictable rainfall, as well as an increased frequency of extreme weather events, such as droughts and heatwaves (Solomon *et al.* 2007; James and Washington 2013; Stocker *et al.* 2013; Engelbrecht *et al.* 2015; Nangombe *et al.* 2018). By studying pangolins in the already hot and dry Kalahari, it will be possible to make better predictions about how pangolins and, indeed, other myrmecophagous animals, are likely to respond to increasing heat and aridity elsewhere.

During the two years of my study, environmental conditions differed, resulting in varying food availability for the pangolins. Late and low rainfall resulted in low grass cover during the first study year, and in conjunction with high summer environmental temperatures, coincided with low prey abundance during that subsequent winter. Pangolins responded to resource scarcity by shifting their diet, which was normally dominated by *Crematogaster* ants, to include more *Anoplolepis* ants and *Trinervitermes* termites. Despite shifting their diet during winter, pangolins still experienced energy deficits, compared to the year in which there was greater grass and insect availability. The energy deficits were reflected in the 24h body temperature patterns of pangolins. They exhibited lower than normal 24h minimum body temperatures when prey resources were scarce. When 24h minimum body temperatures were low, which was most likely to occur when days were short in winter, pangolins emerged from their burrows earlier during the day, presumably to offset the metabolic costs of maintaining constant high body temperatures at night, especially during a time when resources were scarce. However, by emerging from their burrows earlier during the day, pangolins were exposed to higher environmental heat loads and they consequently exhibited higher than normal 24h maximum body temperatures compared to when they emerged later during the day. Although the increased heterothermy displayed by pangolins during winter, and particularly during the resource-poor winter, likely allowed them to conserve water and energy, increased heterothermy has been associated with reduced performance in other mammals (for example, Maloney *et al.* 2017). Mammals may be at greater risk of morbidity or mortality when they experience body temperatures outside their normal range (Hetem *et al.* 2016). Whether shifts in behaviour, diet and the precision with which body temperature is regulated will buffer pangolins and other myrmecophagous mammals in the future is likely to depend on the extent of the environmental change.

6.1 CLIMATE CHANGE

Global average air temperatures have increased by 0.2 °C per decade since the 1970's (Solomon *et al.* 2007), and global surface temperatures are expected to increase by up to 4.5 °C in the 21st century (Stocker *et al.* 2013). In parts of Africa, surface temperatures have been rising at more than double the global rate (Engelbrecht *et al.* 2015). Data obtained from the van Zylsrus weather station (South African Weather Services), situated about 60 km from my study site, show an overall trend of increasing daily mean and daily maximum air temperatures in the southern Kalahari over the last 26 years (Figure 6.1). The changes in daily mean air temperature between 1993 and 2019 resulted in an increase of 0.7 °C per decade, which is more than three times the global rate. The air temperatures that prevailed throughout 2015 and 2016 were some of the highest recorded air temperatures compared to the 22 years preceding the study, making the first year of my study (October 2015 to October 2016) a good model for predicting the responses of pangolins to the air temperatures that are likely to become more prevalent in the future. Other national parks in South Africa in which pangolins and other myrmecophagous mammals are found are also experiencing increasing air temperatures, although the increase is most rapid in the more arid regions (van Wilgen *et al.* 2016; Dube and Nhamo 2020).

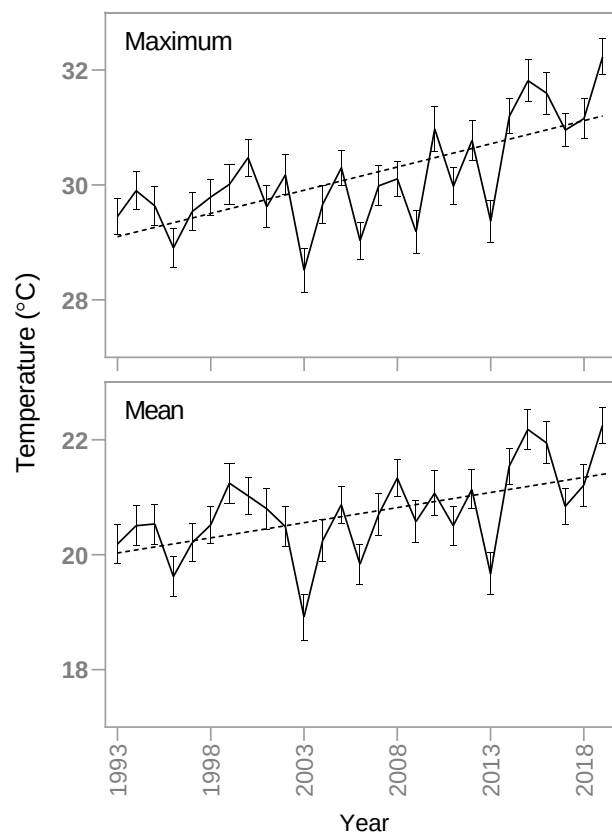


Figure 6.1: Daily mean and maximum air temperatures (mean $\pm$ SD) for the period 1993 to 2019 for van Zylsrus (data obtained from the South African Weather Services).

In addition to increased air and surface temperatures, the El Niño-Southern Oscillation (ENSO) strongly affects southern Africa through reductions in rainfall, which impacts the hydrological cycle (Hulme *et al.* 2001). The IPCC has predicted precipitation reductions of between 20 – 30% in the future, particularly for dry habitats (Stocker *et al.* 2013), but increases in rainfall are predicted elsewhere across the ground pangolin distribution, particularly in more eastern regions of Africa (Engelbrecht *et al.* 2015). As a consequence of rainfall reductions and temporal shifts in rainfall, the south-western regions of southern Africa are predicted to experience more extreme droughts and reductions in primary productivity (Hulme *et al.* 2001; Shongwe *et al.* 2009). Annual rainfall data from my study site since 2001 show that the amount of rainfall has not decreased over the last 19 years (Figure 6.2). However, even if the amount of rainfall remains constant in the future across South Africa, increasing air and surface temperatures will increase evaporation and transpiration, which will reduce ground and surface water necessary for organism survival, particularly in the more arid regions (Pereira 2017). Indeed, a previous study conducted at my study site showed that soil moisture content during the hottest month of the year declined between 1980 and 2015 even though rainfall remained relatively constant (Rey *et al.* 2017).

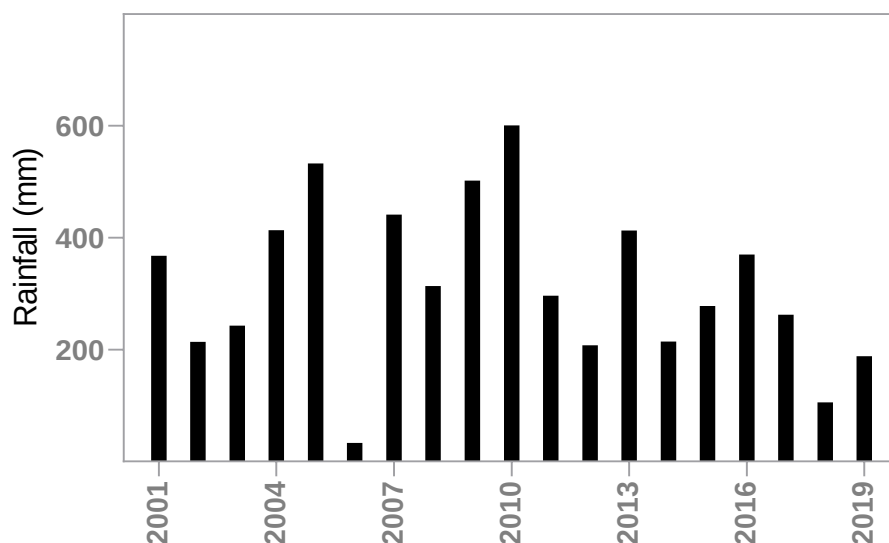


Figure 6.2: Annual rainfall for the period 2001 to 2019. Each year (E.g., 2001) represents rainfall that fell between June of the previous year (E.g., June 2000) and May of the next year (E.g., May 2001).

The rainfall data at my study site did, however, reveal that the timing of major rainfall events may be shifting (Figure 6.3). Rainfall in the Kalahari historically has fallen from about October each year, with the highest rainfall in January. Over the last seven years (with the exception of 2017), including the three years preceding my study, major rainfall

events have been delayed by two to three months each year. The timing of rainfall affects primary productivity (Kaspari and Valone 2002; Zhang *et al.* 2018). While delayed rainfall may still stimulate some grass growth, if rainfall is delayed into late summer or the cooler months of the year, seed production may be limited (Kaspari and Valone 2002), with cascading effects throughout various trophic levels. Although the impacts of shifts in rainfall regimes are likely to be more pronounced in the arid regions within the pangolin distribution range, other national parks in which pangolins and other myrmecophagous mammals are found in the more mesic regions are experiencing similar shifts, whereby major rainfall events are occurring outside of the typical rainfall season (MacFadyen *et al.* 2018).

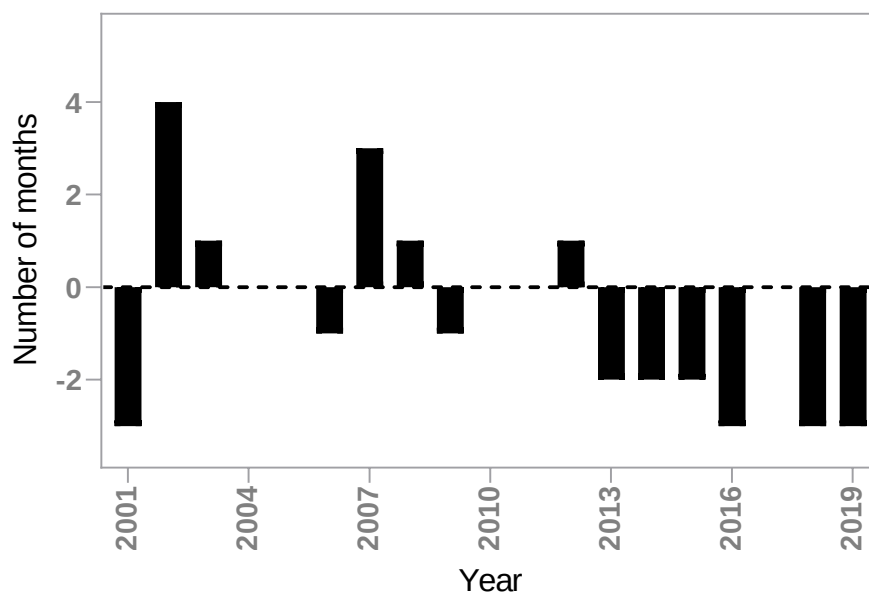


Figure 6.3: The number of months in which the major rainfall events occurred before (positive numbers) or after (negative numbers) January each year from 2001 to 2019 at Tswalu. The dotted line at zero represents January, the month in which major rainfall events occurred, on average, for the 14 years preceding the study.

6.2 IMPLICATIONS OF CLIMATE CHANGE FOR MYRMECOPHAGOUS ANIMALS

Many ants and termites depend on soil moisture and vegetation for survival (Witt and Giliomee 2005; Tschinkel 2010; Poll *et al.* 2011; Geerts *et al.* 2016; Weyer 2018; Woon *et al.* 2018). In conjunction with shifts in rainfall regimes, increasing environmental temperatures will result in reductions in soil moisture and surface water as a consequence of increased evaporation and evapotranspiration (Norby and Luo 2004; Engelbrecht *et al.* 2015), particularly in arid environments. Changes in water availability will ultimately impact primary productivity and the insects that depend on soil moisture and vegetation for survival (Hawkins and Holyoak 1998; Kaspari and Valone 2002; Zhang

et al. 2018). Because only a few insects can survive dehydration (Benoit 2009), many insects will not be able to tolerate increased environmental temperatures and the resulting reductions in soil moisture, particularly in hot and dry environments (Cornelius and Osbrink 2010). Social insects such as ants and termites may need to either limit or cease surface activity when conditions become unfavourable (Barrow and Parr 2008; Davies *et al.* 2015). Some ants and termites may even need to move deeper underground to escape hot and dry conditions (Williams and Middleton 2008), making them less accessible to their predators. Under drought conditions, many insects cannot withstand the extreme weather conditions and often succumb and may even become locally extinct (Hawkins and Holyoak 1998; Harrison 2005).

There are very few long-term records of insect abundance, particularly in Africa. However, data collected at my study site for the last six years reveal an overall decreasing trend in the abundance of ants and termites, although the termites appear to have recovered from a low in 2019 (Figure 6.4). Whether the reduction in ants and termites is a general trend across arid regions or whether it is a localized phenomenon is unknown and warrants further investigation. In the European Alps, budmoth (*Zeiraphera diniana*) population numbers have fluctuated over the last 1173 years and have peaked approximately every nine years (Esper *et al.* 2006). Since 1981, the multi-annual cycle of these budmoths has collapsed and has been attributed to increased environmental warming in the last few decades. Whether the declining ant and termite numbers at my study site are part of a natural multi-annual cycle or whether declining population numbers can be attributed to other factors such as habitat or climate shifts at the study site is unknown and requires long-term monitoring.

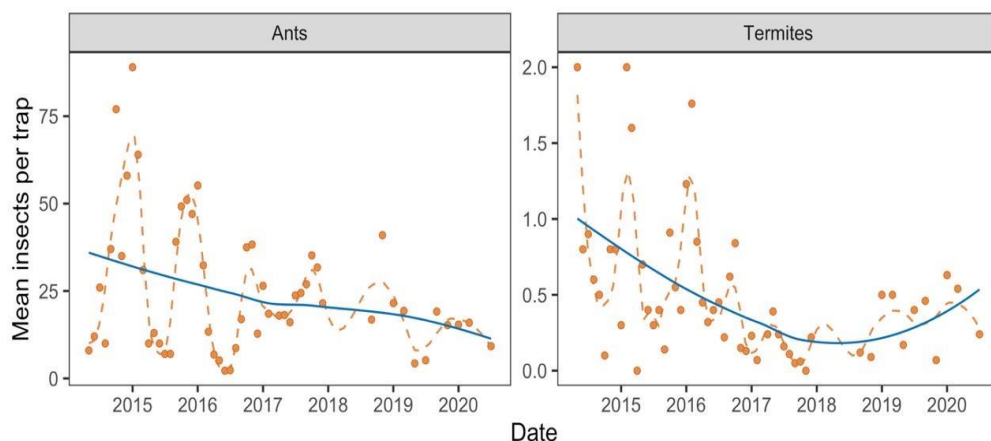


Figure 6.4: Mean monthly insects per trap for the period 2014 to 2020, showing seasonal fluctuations (orange dotted line) and the overall decreasing trend (blue solid line) in ant and termite abundance at Tswalu. Data collected during my study (2015 to 2017) were supplemented with data collected by N. Weyer (2014 to 2015) and M. Phakoago (2018 to 2020).

The mesic areas within the Temminck's ground pangolin range are predicted to experience increased temperatures as well as increased precipitation with climate change (Engelbrecht *et al.* 2015). Hotter and wetter conditions may increase insect abundance through increased outbreaks, but outbreaks may result in a negative feedback loop through destruction of available forage (Pureswaran *et al.* 2018), which may directly compromise the insects themselves by reducing food availability and increasing competition. Alternatively, it may impact the predators and herbivores that depend on insects and vegetation as food resources. Hotter and wetter conditions may also alter insect phenology by advancing their development rates (Gordo and Sanz 2005; Carey 2009; Forrest 2016). Phenological shifts may result in trophic mismatches between insects and their plant hosts, or between insects and their predators (Damien and Toueron 2019). In one study, insects and plants shifted their phenology under increased environmental temperatures, but the advancement of insects occurred at a faster rate, resulting in a mismatch between flowers and their insect pollinators and between herbivorous insects and the plants they depend on as food resources (Gordo and Sanz 2005). Animals often match the timing of reproduction with the timing of peak resource availability (Visser *et al.* 2006). If myrmecophagous mammals match the timing of reproduction with peak resource availability, and if the phenology of ants and termites changes with climate change, a trophic mismatch could occur that could ultimately impact the performance of myrmecophagous mammals by impacting their offspring survival.

Hotter and wetter conditions are also expected outside of the Temminck's ground pangolin range, like in mesic Central and Western Africa (Engelbrecht *et al.* 2015), where the other three African pangolin species (*Phataginus tetradactyla*, *Phataginus tricuspis*, and *Smutsia gigantea*) occur. All African pangolin species specialize on a diet of ants and termites, many of which overlap with the prey genera consumed by Temminck's ground pangolins (Challender *et al.* 2020). Therefore, the responses to fluctuations in prey resources exhibited by the pangolins in my study likely provide insights for how other pangolin species in Africa may respond to fluctuations in their food resources.

Ants and termites are key prey resources not only for pangolins, but for many other insect-eating mammals, such as armadillos (*Orycteropus afer*; Taylor *et al.* 2002; Weyer *et al.* 2020), aardwolves (*Proteles cristata*; Anderson 2004), bat-eared foxes (*Otocyon megalotis*; Klare *et al.* 2011), and rodents (Murray *et al.* 1999; Lathiya *et al.* 2008), and also for non-mammalian animals such as geckos (Hibbitts *et al.* 2005) and multiple bird species (Kopij 2003; Dean and Milton 2018). While pangolins were able to shift their diet in response to reductions in prey resources, another myrmecophage, the armadillo, did not do so when the availability of its preferred prey item, the northern harvester termite (*Hodotermes mossambicus*), declined (Weyer 2018). As a consequence of the reduction in available termites, armadillos lost body condition and some animals succumbed (Rey *et*

al. 2017; Weyer *et al.* 2020). Aardvarks are large animals relative to pangolins and thus likely have higher absolute energy requirements. The northern harvester termite is a highly calorific insect (Weyer 2018). If aardvarks had to switch to alternative prey resources, they likely would not have been able to obtain sufficient energy to meet their daily requirements and would likely have needed to consume more prey items each day, which would have increased their foraging effort and subsequent energy expenditure. Although shifting their diet allowed pangolins to cope with fluctuations in prey resources in my study, it did not prevent them from experiencing energy deficits when prey was scarce. Whether pangolins or other myrmecophages will be able to cope with further reductions in prey resources in the future is uncertain. If other myrmecophages cannot shift their diet or if they need to switch to prey of lower caloric value in response to resource scarcity, then starvation and mortality are likely to become more prevalent in myrmecophages in the future.

Declines in prey resources also result in increased local inter- and intraspecific competition (Ayala 1970; Moore and Yong 1991; Williams *et al.* 2006). Increased competition in response to reductions in food availability have been shown to result in reduced performance (Gustafsson 1987; Bolnick 2004). Many myrmecophagous mammals overlap in their ranges and likely compete for resources, but competition may be limited by each myrmecophage specializing on a different prey item. For example, in the Kalahari, pangolins fed preferentially on *Crematogaster* ants, aardvarks fed preferentially on *Hodotermes* termites (Weyer *et al.* 2020), and aardwolves fed preferentially on *Trinervitermes* termites (Anderson 2004). Although these three myrmecophages coinhabit the ecosystem, because each species specializes on a different prey item, the interspecific competition is likely limited. Aardvarks will also prey on *Anoplolepis* ants and *Trinervitermes* termites (Weyer 2018) and aardwolves will also prey on *Hodotermes* termites (Richardson 1987) in addition to or as an alternative to their preferred prey items.

To cope with declining insects as food resources, and increased local competition, some myrmecophages may need to expand their dietary niche breadth. Many myrmecophages, such as giant anteaters (*Myrmecophaga tridactyla*; de Freitas *et al.* 2014), silky anteaters (*Cyclopes didactylus*; Miranda *et al.* 2009), pangolins (Mahmood *et al.* 2013; Pietersen *et al.* 2016), numbats (Cooper 2011), aardvarks (Taylor *et al.* 2002), and aardwolves (Anderson 2004) are obligate myrmecophages and cannot expand their dietary niche beyond ants and termites. As insects decline with climate change, some myrmecophagous mammals may need to switch to the alternative prey resources, which may overlap with other species, and will increase local competition. Their specialization does thus not bode well for their survival in the face of reductions in ant and termite populations. Other mammals that have diets normally dominated by ants and termites

have been recorded expanding their dietary niche breadth, such as some species of tamanduas and Armadillos in South America, which have been recorded eating wild fruits, leaves, and seeds (Abba and Cassini 2010; Brown 2011). Short-beaked echidnas (*Tachyglossus aculeatus*) in Australia have been recorded eating scarab larvae and moth larvae (Sprent and Nicol 2016). Although these myrmecophages may be able to expand their dietary niche breadth and may be better equipped to cope with reductions in insects as food resources, whether shifting their diet will allow them to meet their daily energy demands is unclear.

Declines in insect populations will affect not only the energy balance but also the water balance of many myrmecophages. Like pangolins, other insect-eating animals such as echidnas (Green *et al.* 1992), bat-eared foxes (Clark 2005) and armadillos (Weyer *et al.* 2020) rarely drink free-standing water and instead get their source of body water from their prey. Hotter and drier conditions also may lead to dehydration in insects (Cornelius and Osbrink 2010), which will impact myrmecophages through reduced water gain from their prey. In the face of increasing environmental temperatures, myrmecophagous mammals will be exposed to higher environmental temperatures, which will increase the need for evaporative cooling (Mitchell *et al.* 2018). However, if they cannot meet their water demands through their prey, myrmecophages face increased risks of becoming dehydrated. Myrmecophagous mammals may therefore need to rely on free-standing water sources to achieve their water requirements. Increased environmental temperatures will, however, also increase evaporation and evapotranspiration and will likely limit the surface water available to animals. Artificial water sources provided by landowners will thus likely become more important in the face of climate change. In areas where artificial water sources cannot be provided, or where increased provision of artificial sources results in other ecological imbalances (Thrash 1998; Shannon *et al.* 2009; Shrader *et al.* 2010), myrmecophages may be at greater risk of local extinctions.

Myrmecophagous mammals in other parts of the world that are predicted to become hotter and drier are also likely to be impacted by climate change. Parts of Australia (Hughes 2003), Asia (Shi *et al.* 2014) and South America (Nunez *et al.* 2008) are already experiencing hotter and drier conditions that are predicted to increase over time. These continents are home to a diversity of insect-eating mammals, including numbats, echidnas, and mulgaras in Australia, pangolins in Asia, and anteaters and tamanduas in South America. Therefore, increasing environmental temperatures, shifts in rainfall regimes, and declines or phenological shifts in insect populations will likely also affect the insect-eating animals in other parts of the world beyond just in Africa.

6.3 IMPLICATIONS FOR ECOSYSTEM FUNCTION

As predators to ants and termites, pangolins play a role in controlling social insect populations (Akande *et al.* 2018; Chao *et al.* 2020). Controlling social insect populations may refer to pangolins preventing an overabundance of insect populations through predation, or it may refer to an increased reproductive output by insects to compensate for predation by pangolins, or it may refer to predation risk playing a role in shifts in the social structure of insects as is seen in cichlid fish (*Neolamprologus pulcher*) (Groenewoud *et al.* 2016). In my study, the average number of ants and termites eaten per 24h by pangolins was ~15 400, which can be extrapolated to ~5.6 million ants and termites per pangolin per year. Pangolins coexist with aardvarks and aardwolves in the Kalahari and elsewhere in sub-Saharan Africa. Aardvarks require ~37 000 *Hodotermes* termites to meet their ideal daily energetic needs (Weyer 2018), which can be extrapolated to ~13.5 million termites per aardvark per year, while it is estimated that aardwolves consume ~222 000 *Trinervitermes* termites per night in summer (Williams *et al.* 1997), or ~81 million termites per year. Cumulatively, these myrmecophages likely play an enormous role in controlling insect populations in ecosystems each year. Insect populations will be further controlled by the additional insect-eating species such as reptiles, rodents, and birds in ecosystems.

In the absence of myrmecophagous animals, an overabundance of insects may cause trophic cascades in ecosystems. Many myrmecophages have slow histories, whereby they have long lifespans, reproduce slowly, and produce few offspring (Symonds 2005; Nicol and Andersen 2007; Naverette and Ortega 2011; Boyles *et al.* 2019). Even if insect populations crash and then recover, which they could do relatively quickly given the insects' fast life histories (Gardmark *et al.* 2003; Karley *et al.* 2004), populations of the myrmecophages that prey on them may not be able to recover quickly enough because of their slow life histories. Without the presence of myrmecophages in the system, an overabundance of insects may lead to habitat deterioration by overharvesting of vegetation (Branson *et al.* 2006; Jaworski and Hilszczanski 2013), which can lead to soil erosion (Kairis *et al.* 2015). Trophic cascades may extend to other animals, such as herbivores, as a result of the effect on the vegetation. An impact on herbivores would have further cascadic effects for predators.

The absence of myrmecophagous mammals that dig and burrow may also influence the landscape by reducing soil turnover and by reducing the availability of burrows used by many other species. Pangolins and aardvarks, which are considered ecosystem engineers (Haussman *et al.* 2018), create, or modify burrows. Burrowing and soil turnover can shift the nutrient composition in the soil, making more nutrients available to plants (Kurek *et al.* 2014). By creating and modifying burrows, burrowing myrmecophagous

animals also provide thermal refugia for other species (Pike and Mitchell 2013), which will become particularly important in the face of increasing environmental temperatures with climate change. The loss of burrowing animals in ecosystems may therefore limit the number of microclimate options available for other species, which will further result in cascading effects throughout the landscape at multiple trophic levels.

Another advantage of having myrmecophagous mammals present in ecosystems is that their foraging behaviour may benefit other insect-eating animals. On their foraging excursions, myrmecophagous mammals dig up ants and termites, and rarely deplete a colony, leaving behind exposed ants and termites when they move on to the next source. The leftover insects can be fed on by other insect-eating animals such as birds. Associative feeding between myrmecophagous mammals and birds has been documented for aardvarks (Taylor and Skinner 2001), northern tamanduas (*Tamandua Mexicana*; Pollock 2017), aardwolves (Anderson 1992), and bat-eared foxes (Stenkewitz and Kamler 2008). During my study, birds such as ant-eating chats (*Myrmecocichla formicivora*) and chat flycatchers (*Bradornis infuscatus*), were frequently seen following pangolins during afternoon foraging excursions and flying down to the exposed ants and termite colonies to feed. Although it is not known how dependent birds are on such associative feeding events, particularly during winter when resources are scarce, myrmecophagous mammals likely reduce the foraging costs for birds and other animals by providing an easily accessible resource.

6.4 RESEARCH GAPS ON TEMMINCK'S GROUND PANGOLIN AND OTHER MYRMECOPHAGES

6.4.1 Thermoregulation

While my study provided valuable insights into the 24h body temperature patterns of pangolins in the wild, thermoregulation in this mammal remains poorly understood. The 24h minimum body temperature of the pangolins declined while pangolins were inside their burrows throughout the day during winter when prey resources were scarce. Pangolins lack a functional mitochondrial uncoupling protein 1 (UCP1), a protein found in brown adipose tissue that is essential for non-shivering thermogenesis (Gaudry *et al.* 2017), however there are other mechanisms that underly non-shivering thermogenesis, but these mechanisms have not been explored in pangolins. Although pangolins (including another pangolin species, *Manis pentadactyla*; Heath and Hammel 1986) have been occasionally observed shivering on very cold days (W. Panaino unpublished observations), which produces body heat (Hohtola 2004), the extent to which shivering can be used to regulate body temperature is unknown. Furthermore, because burrow temperatures were not measured during my study, the body temperature regulation of

pangolins while in their burrows remains poorly understood. Although burrows buffer the external climate (Pike and Mitchell 2013), there are still some fluctuations that occur as a function of fluctuations in the external climate (M. Phakoago unpublished data), which likely influence pangolin body temperature regulation.

When pangolins emerged from their burrows diurnally and were subsequently exposed to high environmental heat loads, their 24h maximum body temperature rapidly increased. Since pangolins lack sweat glands (Hyman and Wake 1992; Feldhamer *et al.* 2007), they cannot sweat to facilitate evaporative cooling. Whether water can diffuse through the skin of pangolins via insensible water loss to facilitate evaporative cooling is unclear. Chinese pangolins (*Manis pentadactyla*) increased their breathing rate when air temperatures exceeded 32°C in laboratory conditions (Heath and Hammel 1986), suggesting that pangolins may use panting to regulate body temperature when it is hot, but this idea warrants further investigation. While foraging during the day, pangolins occasionally rested under trees and shrubs, but these events were not detailed during my study. It is unclear whether pangolins used shade to thermoregulate behaviourally when they were active during the day, a behaviour they may become more important in the face of increasing environmental temperatures. Future studies should include microclimate measures to further the understanding of pangolin thermoregulation.

I was also not able to elucidate any sex differences with my small sample size of individual pangolins. Male and female animals may experience different energetic demands throughout the year. Competition among males for females, and pregnancy and lactation in females are energetically costly and may have implications for body temperature regulation (Speakman 2008; Lane *et al.* 2010). Climate-induced reductions in insect prey resources will reduce the energy available to mammals to sustain them during energetically costly periods, such as during the breeding season. Future research should investigate body temperature regulation of males and females separately to further understanding of how males and females may respond differently to climate change, given that they have differing energetic demands.

Another issue requiring further study is thermoregulation and energy balance in juvenile pangolins. Juvenile mammals have higher mass-specific energetic demands compared to adults, since they require additional energy for growth and development (Munn and Dawson 2003; Batavia *et al.* 2010). Climate-induced declines in insect prey resources will therefore likely have implications for the body temperature regulation of juvenile pangolins. Juvenile animals are also smaller than adult animals and have a lower thermal inertia, which means that they gain and lose heat more rapidly than adults (Gardner *et al.* 2011; Mitchell *et al.* 2018). Their smaller body mass means that they also dehydrate more rapidly in the heat (Fuller *et al.* 2016). In the face of insufficient energy and water

intake as a consequence of climate change juvenile pangolins will likely be more prone to dehydration and hypothermia than are adults. Juvenile pangolins also face high energetic costs in leaving their natal home range and dispersing (Benoit *et al.* 2019) to establish their own home ranges. When establishing a home range in a new area, a juvenile animal also must gather information about the resources in its new environment. Climate change will not only reduce the abundance of resources, but these resources will also become patchier (Nori *et al.* 2008; Adams-Hosking *et al.* 2012). Dispersing juveniles will need to therefore work harder to find food, which may have implications for their energy balance and thus their thermoregulation. Measuring the body temperature patterns of juvenile pangolins will be important if we wish to further our understanding of how pangolin populations might respond to climate change.

Although not explored in my thesis, an apparent surprising finding was that pangolins did not exhibit a robust circadian rhythm of body temperature. On many days, especially in summer, no 24-h rhythm of body temperature was evident. A circadian rhythm of body temperatures was observed in the smaller Chinese pangolin (*Manis pentadactyla*), but these animals were housed in captivity, exposed to constant light-dark cycles and were fed an unnatural diet (Heath 1987). A lack of circadian rhythm of locomotor activity or body temperature has been reported for other animals, such as reindeer (*Rangifer tarandus* and *Rangifer tarandus platyrhynchus*) and mole rats (*Heterocephalus glaber*), either inhabiting polar regions and habitats with constant physical environments or not exposed to light-dark cycles (Riccio and Goldman 2000; van Oort *et al.* 2007; Lu *et al.* 2010). There are therefore several aspects related to thermoregulation in pangolins that require further study.

6.4.2 Ecosystem dynamics

Although the diets of myrmecophagous mammals have been studied separately in various ecosystems in the past (Richardson 1987; Kuntzsch and Nel 1992; Swart 1999; Taylor *et al.* 2002; Anderson 2004; Klare *et al.* 2011; Pietersen *et al.* 2016; Weyer 2018), studying multiple myrmecophages simultaneously will improve our understanding of the responses of co-existing myrmecophages to climate-induced changes in food resources. The diets of myrmecophages may shift across space and time, and by studying the diets of multiple myrmecophages simultaneously and in the same environment, we can improve our understanding of how these animals compete for resources and how they might cope with future reductions in insects as food resources. Food webs are complex, making ecosystem conservation extremely challenging. Using a multispecies approach to understand animal responses to climate change will improve our understanding of how species across multiple trophic levels interact across these complex food webs.

Additional dynamics in ecosystems may also influence the ecology of myrmecophages. The presence or absence of predators can significantly alter the behaviour of prey (Tambling *et al.* 2015), which may result in varying responses of myrmecophages to climatic shifts across regions where apex predators are present or absent. Many small reserves or reserves with inadequate fencing do not house apex predators, particularly lions (*Panthera leo*). The responses of myrmecophages inhabiting such areas may differ from those in areas where apex predators are present. Although other predators, such as leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), may be present in many reserves, these predators likely rarely predate on myrmecophagous mammals and thus probably will not significantly alter their behaviour. Future studies should consider the effects of the presence or absence of apex predators on myrmecophagous mammal behaviour and whether the predation pressure will affect their ability to cope with climate change.

6.5 CONSIDERATIONS FOR CONSERVATION MANAGEMENT

6.5.1 Habitat degradation

Climate change is not the only threat to ecosystems across the globe. Habitat loss from deforestation and agriculture has resulted in mass biodiversity losses worldwide (Brooks *et al.* 2002; Pardini *et al.* 2017). Healthy and balanced ecosystems are more likely to be resilient to climate change than overgrazed and degraded ones (Neely *et al.* 2009; O'Mara 2012; Gaitan *et al.* 2017). Vegetation improves soil structure, reduces soil erosion and reduces surface temperatures (Kairis *et al.* 2015). While more unpredictable weather and increased frequencies of droughts will reduce the potential for new vegetation growth, overgrazing will directly reduce palatable vegetation species and cover, which can lead to desertification (Ibanez *et al.* 2007). Climate effects on insect populations may be exacerbated in degraded ecosystems, resulting in trophic cascades throughout the ecosystem. Management practices should aim to prioritize the sustainability of habitats that favour insect survival to create a more resilient system in the face of climate change (Gaitan *et al.* 2015). However, a bottom-up approach to ecosystem management often neglects the importance of predators in the system. Predators not only influence prey densities, but they regulate prey spatial movement in ecosystems (Frank 2008), reducing the potential for overgrazing. A top-down approach, where predators are considered as ecologically important, also will enhance palatable vegetation cover through the trophic cascades generated by the presence of predation pressure (del Rio *et al.* 2001; van Klink *et al.* 2015) and will ultimately promote the insect conservation required to sustain myrmecophagous populations.

6.5.2 Ecotourism

Ecotourism is an important contributor to the sustainability of wildlife conservation practices when it is done right (Stronza *et al.* 2019). Experienced tourists show preference towards more rare and elusive species (Di Minin *et al.* 2013), such as the pangolin. Some pangolins habituate to human presence fairly quickly (Swart 1996). However, the first defence for a shy, unhabituated pangolin when there is a disturbance is to either stop moving or to move to the nearest shrub and hide (Swart 1996; W. Panaino personal observation). In my study pangolins were only active above the surface and foraging for 5 to 7 hours each day, and the duration of activity appeared to be constrained by environmental temperatures, particularly during winter. A previous study found that pangolins only fed for 16% of their active time (Swart *et al.* 1999). If disturbed by a human observer, a pangolin that stops foraging to display hiding behaviour will likely need to prolong its activity period to achieve its daily food requirements, depending on the duration of the disturbance or the duration of time it takes for a pangolin to commence foraging. A prolonged activity period may not always be possible as a consequence of the constraints on activity by environmental temperatures, resulting in shortened activity phases. Disturbances will be particularly harmful to pangolins when insect availability is low, since pangolin activity is already shortened, and pangolins experience energy deficits. Furthermore, the pangolins in my study exhibited higher than normal 24h maximum body temperatures when they were active during the day in winter. If a pangolin is disturbed and remains motionless while not under a bush and while exposed to solar radiation, pangolin body temperature may continue to rise, increasing the risk of heat illness. As temperatures continue to increase with climate change, disturbances to unhabituated pangolins may result in even more exaggerated increases in 24h maximum body temperatures.

In reserves or protected areas with ecotourism, management should employ protocols for pangolin viewing that minimize the disturbance around pangolins, especially since insect reductions will likely result in pangolins experiencing energy deficits more often. When pangolins are active, the initial tracking and approach towards the pangolin should be done cautiously; if the initial approach towards a pangolin is not done with caution, pangolins appear visibly disturbed for prolonged periods during their active phase (Swart 1996; W. Panaino unpublished observations). Once the pangolin is located, it should be observed quietly from a distance of at least 10 m since pangolins are sensitive to sound (Swart 1996; W. Panaino unpublished observations). Pangolins have a highly developed olfactory system (Imam *et al.* 2017), and caution should be taken to remain downwind while viewing the animal. If a pangolin is tracked and is still inside its burrow, caution should be taken to minimize the disturbance around the burrow since a disturbance can delay emergence of the pangolin by up to several hours (W. Panaino unpublished

observations). A delayed emergence can either reduce a pangolin's foraging duration or it may force the pangolin to be active at times it would otherwise avoid, likely because of environmental temperature constraints. Furthermore, the pangolins in my study exhibited lower than normal 24h minimum body temperature declines throughout the day during winter, which then rapidly increased when they emerged from their burrows during the day. By delaying emergence, pangolin 24h minimum body temperature may continue to decline, perhaps to dangerously low temperatures. Caution should thus be taken to prevent delays in pangolin emergence as a result of nearby human activity.

6.5.3 Methods for assessing pangolin welfare

The body condition and welfare of wild pangolins is difficult to assess without handling and weighing them, procedures that are likely to induce stress and disturb normal activity. Pangolins also are difficult to locate. My study revealed that there were altered behavioural and physiological responses of pangolins, which were indicative of compromised welfare, when prey abundance was lower than about 17 ants per trap (as indicated by using pitfall trapping). When prey abundance was lower than this value, pangolin emergence from their burrows and their 24h minimum body temperature were a function of prey abundance. Above this value, the onset of activity occurred independently of increasing prey abundance and pangolin 24h minimum and maximum body temperatures were not affected by prey abundance. The welfare of pangolins was therefore not compromised when at least 17 ants per trap, on average, were measured across their range. I therefore propose that pitfall trapping as a proxy for prey abundance can be used as an indirect measure of the welfare of pangolins, at least in the Kalahari. Faecal glucocorticoid metabolites, measurements of parasite load in the faeces, and developing a normalized body size index for body condition may be alternative and non-invasive methods for measuring pangolin welfare, but these require further investigation.

6.6 THREATS BEYOND THE ILLEGAL WILDLIFE TRADE

Pangolins face numerous threats that do not bode well for their future survival. The major threat is their overexploitation for the illegal wildlife trade (Ingram *et al.* 2018; Challender *et al.* 2020). Much of the research in the last decade has focused on mitigation measures for combating the illegal trade of pangolins, a trade which is largely unsustainable (Pires and Moreto 2016; Wallen and Daut 2018; Halbwax 2020). The problem is exacerbated by the fact that pangolins have slow life histories and low survival in captivity (Boyles *et al.* 2019; Challender *et al.* 2020), making any recovery of populations extremely challenging. Further threats include road mortalities and electrocution by electrified fences (Beck 2008; Pietersen *et al.* 2014a). Although habitat destruction through agriculture and human land use change has been identified as a potential threat to pangolins (Pietersen *et al.* 2014a), this destruction has not necessarily been attributed to the impacts of

climate change. Furthermore, the direct impacts of climate change have not been explored as a potential threat to pangolins, until now. My study shows the consequences of climate-induced shifts in primary productivity and insect availability on pangolin physiological welfare. My study also provides an analogue for the conditions likely to become more prevalent elsewhere across the African pangolin distribution, where the responses of pangolins and other myrmecophagous mammals may be similar to the responses exhibited by the pangolins in my study. I propose that climate change is a fast-approaching threat to pangolins across their distribution and should be an important consideration for assessing their conservation status. If local insect population numbers decline, then local pangolin extinctions are imminent.

References

- Abba, A.M. and Cassini, M.H., 2010. Ecological differences between two sympatric species of armadillos (Xenarthra, Mammalia) in a temperate region of Argentina. *Acta Theriologica*, 55(1), 35-44.
- Abraham, J.O., Hempson, G.P., and Staver, A.C., 2019. Drought-response strategies of savanna herbivores. *Ecology and Evolution*, 9(12), 7047-7056.
- Adam, R.A., Mitchell, J.D., and Van Der Westhuizen, M.C., 2008. Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae). *African Entomology*, 16(2), 153-161.
- Adams-Hosking, C., McAlpine, C., Rhodes, J.R., Grantham, H.S. and Moss, P.T., 2012. Modelling changes in the distribution of the critical food resources of a specialist folivore in response to climate change. *Diversity and Distributions*, 18(9), 847-860.
- Ahmed, M.M., and El Kheir, I.M., 2004. Thermoregulation and water balance as affected by water and food restrictions in Sudanese desert goats fed good-quality and poor-quality diets. *Tropical Animal Health and Production*, 36(2), 191-204.
- Aisher, A., 2016. Scarcity, alterity and value: decline of the pangolin, the world's most trafficked mammal. *Conservation and Society*, 14(4), 317-329.
- Alagaili, A.N., Bennett, N.C., Amor, N.M., and Hart, D.W., 2020. The locomotory activity patterns of the arid-dwelling desert hedgehog, *Paraechinus aethiopicus*, from Saudi Arabia. *Journal of Arid Environments*, 177, 104141.
- Alamer, M. and Al-hozab, A., 2004. Effect of water deprivation and season on feed intake, body weight and thermoregulation in Awassi and Najdi sheep breeds in Saudi Arabia. *Journal of Arid Environments*, 59(1), 71-84.
- Albright, T.P., Mutibwa, D., Gerson, A.R., Smith, E.K., Talbot, W.A., O'Neill, J.J., McKechnie, A.E., and Wolf, B.O., 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, 114(9), 2283-2288.
- Alcalá-Galván, C.H., and Krausman, P., 2013. Home range and habitat use by desert mule deer in altered habitats. *California Fish and Game*, 99(2), 65-79.
- Altizer, S., Bartel, R., and Han, B.A., 2011. Animal migration and infectious disease risk. *Science*, 331(6015), 296-302.
- Anderson, M.D., 1992. Anteating chats feeding in association with aardwolves. *Ostrich*, 63(4), 186.

- Anderson, M.D., 2004. Aardwolf adaptations: a review. *Transactions of the Royal Society of South Africa*, 59(2), 99-104.
- Andrew, N.R., Hart, R.A., Jung, M.P., Hemmings, Z., and Terblanche, J.S., 2013. Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *Journal of Insect Physiology*, 59(9), 870-880.
- Angilletta, M.J., Cooper, B.S., Schuler, M.S., and Boyles, J.G., 2010. The evolution of thermal physiology in endotherms. *Frontiers in Bioscience E*, 2, 861-881.
- Arnold, W., Beiglböck, C., Burmester, M., Guschlbauer, M., Lengauer, A., Schröder, B., Wilkens, M., and Breves, G., 2015. Contrary seasonal changes of rates of nutrient uptake, organ mass, and voluntary food intake in red deer (*Cervus elaphus*). *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 309(3), R277-R285.
- Asfiya, W., Yeeles, P., Lach, L., Majer, J.D., Heterick, B., and Didham, R.K., 2016. Abiotic factors affecting the foraging activity and potential displacement of native ants by the invasive African big-headed ant *Pheidole megacephala* (FABRICIUS, 1793) (Hymenoptera: Formicidae). *Myrmecological News*, 22, 43-54.
- Ayala, F.J., 1970. Competition, coexistence, and evolution. In *Essays in evolution and genetics in honor of Theodosius Dobzhansky*, 121-158. Springer, Boston, Massachusetts.
- Baldo, M.B., Antenucci, C.D. and Luna, F., 2015. Effect of ambient temperature on evaporative water loss in the subterranean rodent *Ctenomys talarum*. *Journal of Thermal Biology*, 53, 113-118.
- Barrow, L. and Parr, C.L., 2008. A preliminary investigation of temporal patterns in semiarid ant communities: variation with habitat type. *Austral Ecology*, 33(5), 653-662.
- Batavia, M., Matsushima, A., Eboigboden, O. and Zucker, I., 2010. Influence of pelage insulation and ambient temperature on energy intake and growth of juvenile Siberian hamsters. *Physiology and Behavior*, 101(3), 376-380.
- Bathiany, S., Dakos, V., Scheffer, M. and Lenton, T.M., 2018. Climate models predict increasing temperature variability in poor countries. *Science Advances*, 4(5), 5809.
- Baumont, R., Prache, S., Meuret, M. and Morand-Fehr, P., 2000. How forage characteristics influence behaviour and intake in small ruminants: a review. *Livestock Production Science*, 64(1), 15-28.

Beauchamp, G., 2009. How does food density influence vigilance in birds and mammals? *Animal Behaviour*, 78(2), 223-231.

Beauchamp, G., 2015. *Animal vigilance: monitoring predators and competitors*, 74. Academic Press.

Beck, A., 2008. *Electric fence induced mortality in South Africa*, MSc dissertation, University of the Witwatersrand, South Africa.

Becker, J.E. and McCluney, K.E., 2021. Urbanization-driven climate change increases invertebrate lipid demand, relative to protein—A response to dehydration. *Functional Ecology*, 35(2), 411-419.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365-377.

Benoit, J.B., 2010. Water management by dormant insects: comparisons between dehydration resistance during summer aestivation and winter diapause. In *Aestivation*, 209-229. Springer, Berlin, Heidelberg.

Benoit, L., Hewison, A.M., Coulon, A., Debeffe, L., Gremillet, D., Ducros, D., Cargnelutti, B., Chaval, Y. and Morellet, N., 2019. Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology*, 89(1), 173-185.

Bergman, C.M., Fryxell, J.M., Gates, C.C. and Fortin, D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing?. *Journal of Animal Ecology*, 70(2), 289-300.

Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, 3, 595–708.

Bernabucci, U., Lacetera, N., Baumgard, L.H., Rhoads, R.P., Ronchi, B. and Nardone, A., 2010. Metabolic and hormonal acclimation to heat stress in domesticated ruminants. *Animal*, 4(7), 1167-1183.

Berteaux, D., Réale, D., McAdam, A.G. and Boutin, S., 2004. Keeping pace with fast climate change: can arctic life count on evolution?. *Integrative and Comparative Biology*, 44(2), 140-151.

Bicca-Marques, J.C. and Calegario-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: The Official Publication of the American Association of Physical Anthropologists*, 106(4), 533-546.

- Bignell, D.E. and Eggleton, P., 2000. Termites in ecosystems. In *Termites: evolution, sociality, symbioses, ecology*, 363-387. Springer, Dordrecht.
- Bloor, J.M., Pichon, P., Falcimagne, R., Leadley, P. and Soussana, J.F., 2010. Effects of warming, summer drought, and CO₂ enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems*, 13(6), 888-900.
- Boakye, M. K., Pietersen, D. W., Kotzé, A., Dalton, D. L. and Jansen, R., 2015. Knowledge and uses of African pangolins as a source of traditional medicine in Ghana. *PLoS One*, 10(1): e0117199.
- Boakye, M.K., Kotzé, A., Dalton, D.L. and Jansen, R., 2016. Unravelling the pangolin bushmeat commodity chain and the extent of trade in Ghana. *Human Ecology*, 44(2), 257-264.
- Bolnick, D.I., 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, 58(3), 608-618.
- Bulova, S.J., 2002. How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. *Journal of Thermal Biology*, 27(3), 175-189.
- Botes, A., McGeoch, M.A., Robertson, H.G., Van Niekerk, A., Davids, H.P. and Chown, S.L., 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography*, 33(1), 71-90.
- 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), 676-690.
- Boyles, J. G., Swart, J. M., Bennett, N. C., Ferguson, W., Speakman, J. R. and Scantlebury, D. M. 2019. Energetics suggest cause for even further conservation concern for Temminck's ground pangolin. *Animal Conservation*, 1-5.
- Bragg, C.J., Donaldson, J.D. and Ryan, P.G., 2005. Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *Journal of Arid Environments*, 61(2), 261-275.
- Branson, D.H., Joern, A. and Sword, G.A., 2006. Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. *Bioscience*, 56(9), 743-755.
- Brierley, A.S. and Kingsford, M.J., 2009. Impacts of climate change on marine organisms and ecosystems. *Current Biology*, 19(14), R602-R614.

- Bronson, F. H., 2009. Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3331-3334.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. and Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, 16(4), 909-923.
- Brown, K.J. and Downs, C.T., 2007. Basking behaviour in the rock hyrax (*Procavia capensis*) during winter. *African Zoology*, 42(1), 70-79.
- Brown, D.D., 2011. Fruit-eating by an obligate insectivore: palm fruit consumption in wild northern tamanduas (*Tamandua mexicana*) in Panamá. *Edentata*, 12(1), 63-65.
- Buffington, D.E., Collazo-Arocho, A., Canton, G.H., Pitt, D., Thatcher, W.W. and Collier, R.J., 1981. Black globe-humidity index (BGHI) as comfort equation for dairy cows. *Transactions of the ASAE*, 24(3), 711-0714.
- Bulova, S.J., 2002. How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. *Journal of Thermal Biology*, 27(3), 175-189.
- Burda, H., Šumbera, R. and Begall, S., 2007. Microclimate in burrows of subterranean rodents revisited. In *Subterranean Rodents*, 21-33. Springer, Berlin, Heidelberg.
- Burthe, S., Butler, A., Searle, K.R., Hall, S.J., Thackeray, S.J. and Wanless, S., 2011. Demographic consequences of increased winter births in a large aseasonally breeding mammal (*Bos taurus*) in response to climate change. *Journal of Animal Ecology*, 80(6), 1134-1144.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. and Wiens, J.J., 2013. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), 20121890.
- Cain III, 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), 570-581.
- Caputa, M., 2004. Selective brain cooling: a multiple regulatory mechanism. *Journal of Thermal Biology*, 29(7-8), 691-702.
- Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J. and Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, 3(3), 109-122.

- Carey, C., 2009. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3321-3330.
- Chakravorty, J., Ghosh, S., Megu, K., Jung, C. and Meyer-Rochow, V.B., 2016. Nutritional and anti-nutritional composition of *Oecophylla smaragdina* (Hymenoptera: Formicidae) and *Odontotermes* sp.(Isoptera: Termitidae): Two preferred edible insects of Arunachal Pradesh, India. *Journal of Asia-Pacific Entomology*, 19(3), 711-720.
- Challender, D., Wu, S., Kaspal, P., Khatiwada, A., Ghose, A., Ching-Min Sun, N., Mohapatra, R.K. & Laxmi Suwal, T. 2019a. *Manis pentadactyla*. *The IUCN Red List of Threatened Species* 2019a: e.T12764A168392151. <https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12764A168392151.en>. Accessed on 18 May 2020.
- Challender, D., Willcox, D.H.A., Panjang, E., Lim, N., Nash, H., Heinrich, S. & Chong, J. 2019b. *Manis javanica*. *The IUCN Red List of Threatened Species* 2019b: e.T12763A123584856. <https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12763A123584856.en>. Accessed on 18 May 2020.
- Challender, D.W., Nash, H.C. and Waterman, C., 2020. *Pangolins: Science, Society and Conservation*. Academic Press.
- Chao, J.T., Li, H.F. and Lin, C.C., 2020. The role of pangolins in ecosystems. In *Pangolins*, 43-48. Academic Press.
- Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E. and Sheldon, B.C., 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320(5877), 800-803.
- Chedid, M., Jaber, L. S., Giger-Reverdin, S., Duvaux-Ponter, C., and Hamadeh, S. K., 2014. Review: Water stress in sheep raised under arid conditions. *Canadian Journal of Animal Science*, 94(2), 243–257.
- Choo, S.W., Rayko, M., Tan, T.K., Hari, R., Komissarov, A., Wee, W.Y., Yurchenko, A.A., Kliver, S., Tamazian, G., Antunes, A. and Wilson, R.K., 2016. Pangolin genomes and the evolution of mammalian scales and immunity. *Genome Research*, 26(10), 1312-1322.
- Christian, N. and Geiser, F., 2007. To use or not to use torpor? Activity and body temperature as predictors. *Naturwissenschaften*, 94(6), 483-487.
- Cloudsley-Thompson, J., 2001. Thermal and water relations of desert beetles, *Naturwissenschaften*, 88(11), 447-460.

- Collier, R.J., Kobayashi, Y. and Gentry, P., 2002, October. The use of genomics in genetic selection programs for environmental stress tolerance in domestic animals. In *Proceedings of the 15th Conference on Biometeorology and Aerobiology*, 2003b. American Meteorological Society Press.
- Cooper, C. E., and Withers, P. C., 2004. Termite digestibility and water and energy contents determine the water economy index of numbats (*Myrmecobius fasciatus*) and other myrmecophages. *Physiological and Biochemical Zoology*, 77, 641–650.
- Cooper, C.E., 2011. *Myrmecobius fasciatus* (Dasyuromorphia: Myrmecobiidae). *Mammalian Species*, 43(881), 129-140.
- Cornelissen, T., 2011. Climate change and its effects on terrestrial insects and herbivory patterns. *Neotropical Entomology*, 40(2), 155-163.
- Cornelius, M.L. and Osbrink, W.L., 2010. Effect of soil type and moisture availability on the foraging behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology*, 103(3), 799-807.
- Cornelius, M.L. and Osbrink, W.L., 2011. Effect of seasonal changes in soil temperature and moisture on wood consumption and foraging activity of Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology*, 104(3), 1024-1030.
- Coulson, I. 1989. The pangolin (*Manis temminckii* Smuts, 1835) in Zimbabwe. *African Journal of Ecology*, 27(2), 149-155.
- Crocker, D.E., Kofahl, N., Fellers, G.D., Gates, N.B. and Houser, D.S., 2007. High rates of energy expenditure and water flux in free-ranging Point Reyes mountain beavers *Aplodontia rufa phaea*. *Physiological and Biochemical Zoology*, 80(6), 635-642.
- Cros, S., Cerdá, X. and Retana, J., 1997. Spatial and temporal variations in the activity patterns of Mediterranean ant communities. *Ecoscience*, 4(3), 269-278.
- Cunningham, S.J., Martin, R.O. and Hockey, P.A., 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird?. *Ostrich*, 86(1-2), 119-126.
- Damien, M. and Tougeron, K., 2019. Prey–predator phenological mismatch under climate change. *Current Opinion in Insect Science*, 35, 60-68.
- Daunt, F., Afanasyev, V., Silk, J.R.D. and Wanless, S., 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird, *Behavioral Ecology and Sociobiology*, 59(3), 381-388.

- Davies, A.B., Eggleton, P., van Rensburg, B.J. and Parr, C.L., 2015. Seasonal activity patterns of African savanna termites vary across a rainfall gradient. *Insectes Sociaux*, 62(2), 157-165.
- Davis, A. L., Scholtz, C. H., Kryger, U., Deschodt, C. M. and Strümpher, W. P., 2010. Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. *Environmental Entomology*, 39(3), 811-820.
- Dawson, T.J. and Brown, G.D., 1970. A comparison of the insulative and reflective properties of the fur of desert kangaroos. *Comparative Biochemistry and Physiology*, 37(1), 23-38.
- Dawson, T.J., Blaney, C.E., Munn, A.J., Krockenberger, A. and Maloney, S.K., 2000. Thermoregulation by kangaroos from mesic and arid habitats: influence of temperature on routes of heat loss in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*). *Physiological and Biochemical Zoology*, 73(3), 374-381.
- de Freitas, C.H., Justino, C.S. and Setz, E.Z., 2015. Road-kills of the giant anteater in south-eastern Brazil: 10 years monitoring spatial and temporal determinants. *Wildlife Research*, 41(8), 673-680.
- de Sherbinin, A. 2014. Climate change hotspots mapping: what have we learned?. *Climatic Change*, 123(1), 23-37.
- De Vries, J.L., Pirk, C.W.W., Bateman, P.W., Cameron, E.Z. and Dalerum, F., 2011. Extension of the diet of an extreme foraging specialist, the aardwolf (*Proteles cristata*). *African Zoology*, 46(1), 194-196.
- Dean, W.R.J. and Milton, S.J., 2001. Responses of birds to rainfall and seed abundance in the southern Karoo, South Africa. *Journal of Arid Environments*, 47(1), 101-121.
- Dean, W.R.J. and Milton, S.J., 2018. Ants (Formicidae) as food for birds in southern Africa: opportunism or survival?. *Ostrich*, 89(1), 1-4.
- Degen, A.A., 2012. Deserts. In: *Ecophysiology of small desert mammals*, 102. Springer Science & Business Media.
- Del Toro, I., Ribbons, R.R. and Pelini, S.L., 2012. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*, 17, 133-146.
- DeWitt, T.J. and Scheiner, S.M. (eds.), 2004. Phenotypic Variation from Single Genotypes - A Primer. In: *Phenotypic plasticity: functional and conceptual approaches*, 1-9. Oxford University Press.

- Diffenbaugh, N.S. and Giorgi, F. 2012. Climate change hotspots in the CMIP5 global climate model ensemble. *Climatic Change*, 114(3-4), 813-822.
- Dmitrieva, N.I. and Burg, M.B., 2011. Increased insensible water loss contributes to aging related dehydration. *PloS one*, 6(5), 1-3.
- Dodds, P.S., Rothman, D.H. and Weitz, J.S. 2001. Re-examination of the “3/4-law” of metabolism. *Journal of Theoretical Biology*, 209(1), 9-27.
- Donald, J. and Pannabecker, T.L., 2015. Osmoregulation in desert-adapted mammals. In *Sodium and Water Homeostasis*, 191-211. Springer, New York, New York.
- Donázar, J.A., Cortés-Avizanda, A. and Carrete, M., 2010. Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *European Journal of Wildlife Research*, 56(4), 613-621.
- Donovan, S.E., Eggleton, P. and Bignell, D.E., 2001. Gut content analysis and a new feeding group classification of termites. *Ecological Entomology*, 26(4), 356-366.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitaó, P.J. and Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27-46.
- Dube, K. and Nhamo, G., 2020. Evidence and impact of climate change on South African national parks. Potential implications for tourism in the Kruger National Park. *Environmental Development*, 33, 100485.
- Dudney, J., Hallett, L.M., Larios, L., Farrer, E.C., Spotswood, E.N., Stein, C. and Suding, K.N., 2017. Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands?. *Journal of Ecology*, 105(2), 484-495.
- Dunkin, R.C., Wilson, D., Way, N., Johnson, K. and Williams, T.M., 2013. Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution. *Journal of Experimental Biology*, 216(15), 2939-2952.
- Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M. and Heurich, M., 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography*, 40(8), 1014-1027.
- Ehleringer, J.R., Schwinning, S. and Gebauer, R., 1998. Water use in arid land ecosystems. *Physiological Plant Ecology*, 347-366.

- Engelbrecht, F., Adegoke, J., Bopape, M.J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C. and Gatebe, C., 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, 10(8), 085004.
- Engelbrecht, C.J. and Engelbrecht, F.A., 2016. Shifts in Köppen-Geiger climate zones over southern Africa in relation to key global temperature goals. *Theoretical and Applied Climatology*, 123(1-2), 247-261.
- Esper, J., Büntgen, U., Frank, D.C., Nievergelt, D. and Liebhold, A., 2007. 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society B: Biological Sciences*, 274(1610), 671-679.
- Evans, T.A. and Gleeson, P.V., 2001. Seasonal and daily activity patterns of subterranean, wood-eating termite foragers. *Australian Journal of Zoology*, 49(3), 311-321.
- Feldhamer, G.A., Drickamer, L.C., Vessey, S.H., Merritt, J.F. and Krajewski, C., 2007. Integument, Support, and Movement. In: *Mammalogy: adaptation, diversity, ecology*, 101. JHU press.
- Fey, S.B., Vasseur, D.A., Alujević, K., Kroeker, K.J., Logan, M.L., O'Connor, M.I., Rudolf, V.H., DeLong, J.P., Peacor, S., Selden, R.L. and Sih, A., 2019. Opportunities for behavioral rescue under rapid environmental change. *Global Change Biology*, 25(9), 3110-3120.
- Fick, L.G., Kucio, T.A., Fuller, A., Matthee, A. and Mitchell, D., 2009. The relative roles of the parasol-like tail and burrow shuttling in thermoregulation of free-ranging Cape ground squirrels, *Xerus inauris*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152(3), 334-340.
- Field, M.A. and Duncan, F.D., 2013. Does thermoregulation occur in the mounds of the harvester termite, *Trinervitermes trinervoides* (Sjöstedt)(Isoptera: Termitidae)?. *African Entomology*, 21(1), 45-57.
- Finch, V.A. and Robertshaw, D., 1979. Effect of dehydration on thermoregulation in eland and hartebeest. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 237(3), R192-R196.
- Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E. and Hardy, G.E.S., 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?. *Mammal Review*, 44(2), 94-108.

- Folks, D.J., Gann, K., Fulbright, T.E., Hewitt, D.G., DeYoung, C.A., Wester, D.B., Echols, K.N. and Draeger, D.A., 2014. Drought but not population density influences dietary niche breadth in white-tailed deer in a semiarid environment. *Ecosphere*, 5(12), 1-15.
- Forcada, J., Trathan, P.N. and Murphy, E.J., 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, 14(11), 2473-2488.
- Forister, M.L. and Shapiro, A.M., 2003. Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, 9(7), 1130-1135.
- Forrest, J.R., 2016. Complex responses of insect phenology to climate change. *Current Opinion in Insect Science*, 17, 49-54.
- 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*, 83(5), 713-720.
- Fuller, A., Hetem, R.S., Maloney, S.K. and Mitchell, D., 2014. Adaptation to heat and water shortage in large, arid-zone mammals. *Physiology*, 29(3), 159-167.
- 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(1), 10.
- Ganguly, S., 2013. Pangolin-zoological characteristics and its uniqueness in mammalian group. *Journal of Entomology and Zoology Studies*, 1(1), 1-2.
- Garant, D.A.N.Y., Forde, S.E. and Hendry, A.P., 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, 21(3), 434-443.
- Garcia, F.H., Wiesel, E. and Fischer, G., 2013. The ants of Kenya (Hymenoptera: Formicidae)—faunal overview, first species checklist, bibliography, accounts for all genera, and discussion on taxonomy and zoogeography. *Journal of East African Natural History*, 101(2), 127-222.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. and Heinsohn, R., 2011. Declining body size: a third universal response to warming?. *Trends in Ecology and Evolution*, 26(6), 285-291.
- Gårdmark, A., Enberg, K., Ripa, J., Laakso, J. and Kaitala, V., 2003, January. The ecology of recovery. In *Annales Zoologici Fennici*, 131-144. Finnish Zoological and Botanical Publishing Board.

- Garvey, J.E., Ostrand, K.G. and Wahl, D.H., 2004. Energetics, predation, and ration affect size-dependent growth and mortality of fish during winter. *Ecology*, 85(10), 2860-2871.
- Gaubert, P., Antunes, A., Meng, H., Miao, L., Peigné, S., Justy, F., Njiokou, F., Dufour, S., Danquah, E., Alahakoon, J. and Verheyen, E. 2017. The complete phylogeny of pangolins: scaling up resources for the molecular tracing of the most trafficked mammals on earth. *Journal of Heredity*, 109(4): 347-359.
- Gaudry, M.J., Jastroch, M., Treberg, J.R., Hofreiter, M., Paijmans, J.L., Starrett, J., Wales, N., Signore, A.V., Springer, M.S. and Campbell, K.L., 2017. Inactivation of thermogenic UCP1 as a historical contingency in multiple placental mammal clades. *Science Advances*, 3(7), e1602878.
- Geerts, S., Van der Linden, J. and Van der Linden, E., 2016. The ecology and foraging behaviour of the harvester termite, *Baicaliotes hainesi* in semi-arid grasslands in the northwestern interior of South Africa. *Insectes sociaux*, 63(3), 457-465.
- Genin, F. and Perret, M., 2003. Daily hypothermia in captive grey mouse lemurs (*Microcebus murinus*): effects of photoperiod and food restriction. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 136(1), 71-81.
- George, K., Masters, A. and Dawnay, N., 2019. Development of HyBeacon® probes for the forensic detection of Panthera, rhinoceros, and pangolin species. *Molecular and Cellular Probes*, 48, 101450.
- Giorgi, F. 2006. Climate change hot-spots. *Geophysical Research Letters*, 33 (8), 1-4.
- Giroud, S., Blanc, S., Aujard, F., Bertrand, F., Gilbert, C. and Perret, M., 2008. Chronic food shortage and seasonal modulations of daily torpor and locomotor activity in the grey mouse lemur (*Microcebus murinus*). *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 294(6), R1958-R1967.
- Gitay, H., Suarez, A., Watson, R.T. and Dokken, D.J., 2002. Climate Change and Biodiversity. IPCC Technical Paper V, Intergovernmental Panel on Climate Change. *Trends in Ecology and Evolution*, 16, 437-54.
- Gomulkiewicz, R. and Holt, R.D., 1995. When does evolution by natural selection prevent extinction?. *Evolution*, 49(1), 201-207.
- Gordo, O. and Sanz, J.J., 2005. Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia*, 146(3), 484-495.

GraphPad Prism, 2021. GraphPad version 8.0.0 for Windows, GraphPad Software, San Diego, California USA. www.graphpad.com.

Green, B., Griffiths, M. and Newgrain, K., 1992. Seasonal patterns in water, sodium and energy turnover in free-living echidnas, *Tachyglossus aculeatus* (Mammalia: Monotremata). *Journal of Zoology*, 227(3), 351-365.

Griebeler, E.M. and Werner, J., 2016. Mass, phylogeny, and temperature are sufficient to explain differences in metabolic scaling across mammalian orders?. *Ecology and Evolution*, 6(23), 8352-8365.

Groenewoud, F., Frommen, J.G., Josi, D., Tanaka, H., Jungwirth, A. and Taborsky, M., 2016. Predation risk drives social complexity in cooperative breeders. *Proceedings of the National Academy of Sciences*, 113(15), 4104-4109.

Grolemund, G., and Wickham, H., 2011. Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, 40(3), 1-25.

Gudehus, M., Pietersen, D.W., Hoffmann, M., Cassidy, R., Cassidy, T., Sodeinde, O., Lapuente, J., Assovi, B.G.M. and Shirley, M.H., 2020. Black-bellied pangolin *Phataginus tetradactyla* (Linnaeus, 1766). In *Pangolins*, 123-138. Academic Press.

Guiden, P.W. and Orrock, J.L., 2020. Seasonal shifts in activity timing reduce heat loss of small mammals during winter. *Animal Behaviour*, 164, 181-192.

Gustafsson, L., 1987. Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, 68(2), 291-296.

Hamad, I., Delaporte, E., Raoult, D. and Bittar, F., 2014. Detection of termites and other insects consumed by African great apes using molecular fecal analysis. *Scientific reports*, 4(1), 1-9.

Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M.L.J.C., Lovett, J.C., Scott, D. and Woodward, F.I., 2002. Conservation of biodiversity in a changing climate. *Conservation Biology*, 16(1), 264-268.

Harley, C.D., 2011. Climate change, keystone predation, and biodiversity loss. *Science*, 334(6059), 1124-1127.

Harrison, R.D., 2005. A severe drought in Lambir Hills National Park. In *Pollination Ecology and the Rain Forest*, 51-64. Springer, New York, New York.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. and Samuel, M.D., 2002. Climate warming and disease risks for terrestrial and marine biota. *Science*, 296(5576), 2158-2162.

- Harvell, D., Altizer, S., Cattadori, I.M., Harrington, L. and Weil, E., 2009. Climate change and wildlife diseases: when does the host matter the most?. *Ecology*, 90(4), 912-920.
- Harvey, J.A., Poelman, E.H. and Tanaka, T., 2013. Intrinsic inter-and intraspecific competition in parasitoid wasps. *Annual Review of Entomology*, 58, 333-351.
- Haugen, M.J., Tieleman, B.I. and Williams, J.B., 2003. Phenotypic flexibility in cutaneous water loss and lipids of the stratum corneum. *Journal of Experimental Biology*, 206(20), 3581-3588.
- Hausmann, N.S., Louw, M.A., Lewis, S., Nicol, K.J., Van der Merwe, S. and le Roux, P.C., 2018. Ecosystem engineering through armadillo (*Oryzomys afer*) burrowing: Mechanisms and effects. *Ecological Engineering*, 118, 66-72.
- Haverty, M.I., LaFage, J.P. and Nutting, W.L., 1974. Seasonal activity and environmental control of foraging of the subterranean termite, *Heterotermes aureus* (Snyder), in a desert grassland. *Life Sciences*, 15(6), 1091-1101.
- Hawkins, B.A. and Holyoak, M., 1998. Transcontinental crashes of insect populations? *The American Naturalist*, 152(3), 480-484.
- Heath, M.E., 1987. Twenty-four hour variations in activity, core temperature, metabolic rate, and respiratory quotient in captive Chinese pangolins. *Zoo Biology*, 6, 1-10.
- Heath, M. E., 1992. *Manis temminckii*. *Mammalian species*, 415: 1-5.
- Heath, M. E., and Coulson, I. A. N., 1997. Home range size and distribution in a wild population of Cape pangolins, *Manis temminckii*, in north-west Zimbabwe. *African Journal of Ecology*, 35(2): 94-109.
- Heath, M. E., and Hammel, H. T., 1986. Body temperature and rate of O₂ consumption in Chinese pangolins. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 250(3), R377-R382.
- Heatwole, H. and Muir, R., 1989. Seasonal and daily activity of ants in the pre-Saharan steppe of Tunisia. *Journal of Arid Environments*, 16(1), 49-67.
- Heldmaier, G. and Ruf, T., 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. *Journal of Comparative Physiology B*, 162(8), 696-706.
- Henschel, J.R., 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *Journal of Arachnology*, 61-69.
- Hentley, W.T., Vanbergen, A.J., Hails, R.S., Jones, T.H. and Johnson, S.N., 2014. Elevated atmospheric CO₂ impairs aphid escape responses to predators and conspecific alarm signals. *Journal of Chemical Ecology*, 40(10), 1110-1114.

Hetem, R.S., Maloney, S.K., Fuller, A., Meyer, L.C. and Mitchell, D., 2007. Validation of a biotelemetric technique, using ambulatory miniature black globe thermometers, to quantify thermoregulatory behaviour in ungulates. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 307(6), 342-356.

Hetem, R.S., de Witt, B.A., Fick, L.G., Fuller, A., Kerley, G.I., Meyer, L.C., Mitchell, D. and Maloney, S.K., 2009. Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152(3), 379-388.

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*, 180(7), 1111-1119.

Hetem, R.S., Strauss, W.M., Fick, L.G., Maloney, S.K., Meyer, L.C., Shobrak, M., Fuller, A. and Mitchell, D., 2012. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis?. *Zoology*, 115(6), 411-416.

Hetem, R.S., Fuller, A., Maloney, S.K. and Mitchell, D., 2014. Responses of large mammals to climate change. *Temperature*, 1(2), 115-127.

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

Hibbitts, T.J., Pianka, E.R., Huey, R.B. and Whiting, M.J., 2005. Ecology of the common barking gecko (*Ptenopus garrulus*) in southern Africa. *Journal of Herpetology*, 39(3), 509-515.

Higgins, S.I. and Scheiter, S., 2012. Atmospheric CO₂ forces abrupt vegetation shifts locally, but not globally. *Nature*, 488(7410), 209-212.

Hoffmann, B.D., 2015. Integrating biology into invasive species management is a key principle for eradication success: the case of yellow crazy ant *Anoplolepis gracilipes* in northern Australia. *Bulletin of Entomological Research*, 105(2), 141.

Hoffmann, M., Nixon, S., Alempijevic, D., Ayebare, S., Bruce, T., Davenport, T.R., Hart, J., Hart, T., Hega, M., Maisels, F. and Mills, D., 2020. Giant pangolin *Smutsia gigantea* (Illiger, 1815). In *Pangolins*, 157-173. Academic Press.

- Hohtola, E., 2004. Shivering thermogenesis in birds and mammals. In *Life in the cold: evolution, mechanisms, adaptation, and application. 12th International Hibernation Symposium*, 241-252. Institute of Arctic Biology.
- Huey, R.B. and Tewksbury, J.J., 2009. Can behavior douse the fire of climate warming?. *Proceedings of the National Academy of Sciences*, 106(10), 3647-3648.
- Hughes, L., 2003. Climate change and Australia: trends, projections and impacts. *Austral Ecology*, 28(4), 423-443.
- Hulme, M., Doherty, R., Ngara, T., New, M. and Lister, D., 2001. African climate change: 1900-2100. *Climate Research*, 17(2), 145-168.
- Humphries, M.M., Thomas, D.W. and Kramer, D.L., 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiological and Biochemical Zoology*, 76(2), 165-179.
- Huynh, T.T.T., Aarnink, A.J.A., Gerrits, W.J.J., Heetkamp, M.J.H., Canh, T.T., Spoolder, H.A.M., Kemp, B. and Verstegen, M.W.A., 2005. Thermal behaviour of growing pigs in response to high temperature and humidity. *Applied Animal Behaviour Science*, 91(1-2), 1-16.
- Hyman, L.H. and Wake, M.H., 1992. *Hyman's comparative vertebrate anatomy*, 140. University of Chicago Press.
- Ibáñez, J., Martínez, J. and Schnabel, S., 2007. Desertification due to overgrazing in a dynamic commercial livestock–grass–soil system. *Ecological Modelling*, 205(3-4), 277-288.
- Imam, A., Ajao, M.S., Bhagwandin, A., Ihunwo, A.O. and Manger, P.R., 2017. The brain of the tree pangolin (*Manis tricuspis*). I. General appearance of the central nervous system. *Journal of Comparative Neurology*, 525(11), 2571-2582.
- Ingram, D. J., Coad, L., Abernethy, K. A., Maisels, F., Stokes, E. J., Bobo, K. S., Breuer, T., Gandiwa, E., Ghiurghi, A., Greengrass, E. and Holmern, T., 2018. Assessing Africa-wide pangolin exploitation by scaling local data. *Conservation Letters*, 11(2): e12389.
- Ingram, D.J., Shirley, M.H., Pietersen, D., Godwill Ichu, I., Sodeinde, O., Moumbolou, C., Hoffmann, M., Gudehus, M. & Challender, D., 2019a. *Phataginus tetradactyla*. *The IUCN Red List of Threatened Species* 2019: e.T12766A123586126.
<https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12766A123586126.en>. Accessed on 18 May 2020.

- Irons, K.S., Sass, G.G., McClelland, M.A. and Stafford, J.D., 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, USA Is this evidence for competition and reduced fitness?. *Journal of Fish Biology*, 71, 258-273.
- Irshad, N., Mahmood, T., Hussain, R. and Nadeem, M.S., 2015. Distribution, abundance and diet of the Indian Pangolin (*Manis crassicaudata*). *Animal Biology*, 65(1), 57-71.
- Islam, M.Z.U. and Rahmani, A.R., 2011. Thar Desert, Rajasthan, India: anthropogenic influence on biodiversity and grasslands. *Biodiversity*, 12(2), 75-89.
- IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-3. Available from <https://www.iucnredlist.org/>. Accessed on 28 February 2020.
- Jaber, L., Chedid, M. and Hamadeh, S., 2013. Water stress in small ruminants. *Responses of Organisms to Water Stress*, 115-149.
- Jacobs, R. L., McClure, P. J., Baker, B. W. and Espinoza, E. O., 2019. Myth debunked: Keratinous pangolin scales do not contain the analgesic tramadol. *Conservation Science and Practice*, 1(9), 1-6.
- Jacobsen, N. H. G., Newbery, R. E., De Wet, M. J., Viljoen, P. C. and Pietersen, E., 1991. A contribution of the ecology of the Steppe pangolin *Manis temminckii* in the Transvaal. *Zeitschrift für Säugetierkunde*, 56(2), 94-100.
- Jagoe, R.T., Lecker, S.H., Gomes, M. and Goldberg, A.L., 2002. Patterns of gene expression in atrophying skeletal muscles: response to food deprivation. *The FASEB Journal*, 16(13), 1697-1712.
- James, R. and Washington, R., 2013. Changes in African temperature and precipitation associated with degrees of global warming. *Climatic Change*, 117(4), 859-872.
- Jaworski, T. and Hilszczański, J., 2013. The effect of temperature and humidity changes on insects development their impact on forest ecosystems in the expected climate change. *Forest Research Papers*, 74(4), 345-355.
- 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. *Pflügers Archiv*, 436(5), 659-666.
- Jessen, C., 2001a. *Temperature regulation in humans and other mammals*. Springer Science & Business Media.
- Jessen, C., 2001b. Selective brain cooling in mammals and birds. *The Japanese Journal of Physiology*, 51(3), 291-301.

- Jones, C., 1973. Body Temperatures of *Manis gigantea* and *Manis tricuspis*. *Journal of Mammalogy*, 54(1), 263-266.
- Kadzere, C.T., Murphy, M.R., Silanikove, N. and Maltz, E., 2002. Heat stress in lactating dairy cows: a review. *Livestock Production Science*, 77(1), 59-91.
- Kairis, O., Karavitis, C., Salvati, L., Kounalaki, A. and Kosmas, K., 2015. Exploring the impact of overgrazing on soil erosion and land degradation in a dry Mediterranean agro-forest landscape (Crete, Greece). *Arid Land Research and Management*, 29(3), 360-374.
- Kamili, A., Bengoumi, M., Oukessou, M., Faye, B. and Lefebvre, H.P., 2013. Assessment of glomerular filtration rate in normally hydrated and dehydrated dromedary camel by plasma exogenous creatinine clearance test. *Emirates Journal of Food and Agriculture*, 314-319.
- Karley, A.J., Parker, W.E., Pitchford, J.W. and Douglas, A.E., 2004. The mid-season crash in aphid populations: why and how does it occur?. *Ecological Entomology*, 29(4), 383-388.
- Kaspari, M. and Valone, T.J., 2002. On ectotherm abundance in a seasonal environment-studies of a desert ant assemblage. *Ecology*, 83(11), 2991-2996.
- Kearney, M., Shine, R. and Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences*, 106(10), 3835-3840.
- Keeping, D. 2014. Rapid assessment of wildlife abundance: estimating animal density with track counts using body mass–day range scaling rules. *Animal Conservation*, 17(5): 486-497.
- Kelly, M.J., Betsch, J., Wultsch, C., Mesa, B. and Mills, L.S., 2012. Non-invasive sampling for carnivores. In Boitani, L., and Powell, R. (Eds.): *Carnivore ecology and conservation: a handbook of techniques*, 47-69. Oxford University Press.
- Kiesecker, J.M., Blaustein, A.R. and Belden, L.K., 2001. Complex causes of amphibian population declines. *Nature*, 410(6829), 681-684.
- Klare, U., Kamler, J.F. and Macdonald, D.W., 2011. The bat-eared fox: A dietary specialist?. *Mammalian Biology*, 76(5), 646-650.
- Kolbe, J.A. and Squires, J.R., 2006. A longevity record for Canada lynx, *Lynx canadensis*, in western Montana. *Western North American Naturalist*, 66(4), 535-536.
- Koller, M., 2016. An R Package for Robust Estimation of Linear Mixed-Effects Models. *Journal of Statistical Software*, 75(6), 1-24.

- Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299(5611), 1388-1391.
- Kurek, P., Kapusta, P. and Holeksa, J., 2014. Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecological Research*, 29(1), 1-11.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1-26.
- Lambert, T.D., Kays, R.W., Jansen, P.A., Aliaga-Rossel, E. and Wikelski, M., 2009. Nocturnal activity by the primarily diurnal Central American agouti (*Dasyprocta punctata*) in relation to environmental conditions, resource abundance and predation risk. *Journal of Tropical Ecology*, 25(2), 211-215.
- Lane, J.E., Boutin, S., Speakman, J.R. and Humphries, M.M., 2010. Energetic costs of male reproduction in a scramble competition mating system. *Journal of Animal Ecology*, 79(1), 27-34.
- Laws, A.N., 2017. Climate change effects on predator–prey interactions. *Current Opinion in Insect Science*, 23, 28-34.
- Lee, R.H., Cheung, K., Fellowes, J.R. and Guenard, B., 2017. Insights Into the Chinese Pangolin's (*Manis pentadactyla*) Diet in a Peri-Urban Habitat: A Case Study From Hong Kong. *Tropical Conservation Science*, 10: 1940082917709648.
- Le Roux, A., Engelbrecht, F., Paige-Green, P., Verhaeghe, B., Khuluse-Makhanya, S., McKelly, D., Dedekind, Z., Muthige, M., Van Der Merwe, J. and Maditse, K., 2016. Climate adaptation: Risk management and resilience optimisation for vulnerable road access in Africa. *Climate Threats Report: Council of Scientific and Industrial Research (CSIR), Paige-Green Consulting (Pty) Ltd and St Helens Consulting Ltd*, 1-65.
- Legendre, L.J. and Botha-Brink, J., 2018. Digging the compromise: investigating the link between limb bone histology and fossoriality in the armadillo (*Oryzomys azer*). *PeerJ*, 6, p.e5216.
- Levy, O., Dayan, T., Porter, W.P. and Kronfeld-Schor, N., 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity?. *Ecological Monographs*, 89(1), e01334.
- Lovegrove, B.G., 2012. The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biological Reviews*, 87(1), 128-162.
- Lu, W., Meng, Q.J., Tyler, N.J., Stokkan, K.A. and Loudon, A.S., 2010. A circadian clock is not required in an arctic mammal. *Current Biology*, 20(6), 533-537.

- Lüdecke, D., Makowski, D., Waggoner, P., and Patil, I., 2020. Assessment of Regression Models Performance. CRAN. Available from <https://easystats.github.io/performance/>.
- Luna, F. and Antinuchi, C.D., 2006. Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. *Canadian Journal of Zoology*, 84(5), 661-667.
- Ma, C.S., Ma, G. and Pincebourde, S., 2020. Survive a warming climate: Insect responses to extreme high temperatures. *Annual Review of Entomology*, 66, 8.1-8.21.
- MacFadyen, S., Zambatis, N., Van Teeffelen, A.J. and Hui, C., 2018. Long-term rainfall regression surfaces for the Kruger National Park, South Africa: a spatio-temporal review of patterns from 1981 to 2015. *International Journal of Climatology*, 38(5), 2506-2519.
- Mader, T.L., Davis, M.S. and Brown-Brandl, T., 2006. Environmental factors influencing heat stress in feedlot cattle. *Journal of Animal Science*, 84(3), 712-719.
- Mahmood, T., Jabeen, K., Hussain, I. and Kayani, A.R., 2013. Plant species association, burrow characteristics and the diet of the Indian pangolin, *Manis crassicaudata*, in the Potohar plateau, Pakistan. *Pakistan Journal of Zoology*, 45(6), 1533-1539.
- Mahmood, T., Challender, D., Khatiwada, A., Andleeb, S., Perera, P., Trageser, S., Ghose, A. & Mohapatra, R., 2019. *Manis crassicaudata*. *The IUCN Red List of Threatened Species* 2019: e.T12761A123583998. <https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12761A123583998.en>. Accessed on 18 May 2020.
- Maloney, S.K., Moss, G. and Mitchell, D., 2005. Orientation to solar radiation in black wildebeest (*Connochaetes gnou*). *Journal of Comparative Physiology A*, 191(11), pp.1065-1077.
- Maloney, S.K., Mitchell, D. and Blache, D., 2007. The contribution of carotid rete variability to brain temperature variability in sheep in a thermoneutral environment. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 292(3), R1298-R1305.
- Maloney, S.K., Fuller, A. and Mitchell, D., 2009. Climate change: is the dark Soay sheep endangered?. *Biology Letters*, 5(6), 826-829.
- 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), 20170521.
- Maron, M., McAlpine, C.A., Watson, J.E., Maxwell, S. and Barnard, P., 2015. Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions*, 21(7), 731-743.

- Martínez, B. and Gilabert, M.A., 2009. Vegetation dynamics from NDVI time series analysis using the wavelet transform. *Remote Sensing of Environment*, 113(9), 1823-1842.
- Mason, T.H., Apollonio, M., Chirichella, R., Willis, S.G. and Stephens, P.A., 2014. Environmental change and long-term body mass declines in an alpine mammal. *Frontiers in Zoology*, 11(1), 69.
- McFarland, R., Barrett, L., Boner, R., Freeman, N.J. and Henzi, S.P., 2014. Behavioral flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology*, 154(3), 357-364.
- McKechnie, A.E. and Wolf, B.O., 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6(2), 253-256.
- McKinley, M., Trevaks, D., Weissenborn, F. and McAllen, R., 2017. Interaction between thermoregulation and osmoregulation in domestic animals. *Revista Brasileira de Zootecnia*, 46(9), 783-790.
- McNab, B.K., 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology*, 203(4), 485-510.
- Metcalf, N.B. and Steele, G.I., 2001. Changing nutritional status causes a shift in the balance of nocturnal to diurnal activity in European Minnows. *Functional Ecology*, 15(3), 304-309.
- Mikhaylov, A., Moiseev, N., Aleshin, K. and Burkhardt, T., 2020. Global climate change and greenhouse effect. *Entrepreneurship and Sustainability Issues*, 7(4), 2897-2913.
- Mills, L.S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T. and Lukacs, P.M., 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences*, 110(18), 7360-7365.
- Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. and Relyea, R.A., 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution*, 20(12), 685-692.
- Miranda, F., Veloso, R., Superina, M. and Zara, F.J., 2009. Food habits of wild silky anteaters (*Cyclopes didactylus*) of São Luis do Maranhão, Brazil. *Edentata*, 2009(10), 1-5.
- Mirzabaev, A., J. Wu, J. Evans, F. García-Oliva, I.A.G. Hussein, M.H. Iqbal, J. Kimutai, T. Knowles, F. Meza, D. Nedjraoui, F. Tena, M. Türkeş, R.J. Vázquez, M. Weltz, 2019: Desertification. In: *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and*

greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D.C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)].

Mitchell, D., Maloney, S.K., Jessen, C., Laburn, H.P., Kamerman, P.R., Mitchell, G. and Fuller, A., 2002. Adaptive heterothermy and selective brain cooling in arid-zone mammals. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 131(4), 571-585.

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), 956-973.

Mole, M.A., Rodrigues DÁraujo, S., Van Aarde, R.J., Mitchell, D. and Fuller, A., 2016. Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology*, 4(1), 1-11.

Moll, K., Federle, W. and Roces, F., 2012. The energetics of running stability: costs of transport in grass-cutting ants depend on fragment shape. *Journal of Experimental Biology*, 215(1), 161-168.

Moore, F.R. and Yong, W., 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology*, 28(2), 85-90.

Mphale, K.M., Dash, S.K., Adedoyin, A. and Panda, S.K., 2014. Rainfall regime changes and trends in Botswana Kalahari Transect's late summer precipitation. *Theoretical and Applied Climatology*, 116(1-2), 75-91.

Munguia, P., Backwell, P.R. and Darnell, M.Z., 2017. Thermal constraints on microhabitat selection and mating opportunities. *Animal Behaviour*, 123, 259-265.

Munn, A.J. and Dawson, T.J., 2003. Energy requirements of the red kangaroo (*Macropus rufus*): impacts of age, growth and body size in a large desert-dwelling herbivore. *Journal of Comparative Physiology B*, 173(7), 575-582.

Murphy, S.R. and Lodge, G.M., 2002. Ground cover in temperate native perennial grass pastures. I. A comparison of four estimation methods. *The Rangeland Journal*, 24(2), 288-300.

Murray, B.R., Dickman, C.R., Watts, C.H.S. and Morton, S.R., 1999. The dietary ecology of Australian desert rodents. *Wildlife Research*, 26(4), 421-437.

Nagashima, K., 2006. Central mechanisms for thermoregulation in a hot environment. *Industrial Health*, 44(3), 359-367.

- Nagendra, H. and Gopal, D., 2010. Tree diversity, distribution, history and change in urban parks: studies in Bangalore, India. *Urban Ecosystems*, 14(2), 211-223.
- Nagy, K.A. and Knight, M.H., 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *Journal of Mammalogy*, 75(4), 860-872.
- Nangombe, S., Zhou, T., Zhang, W., Wu, B., Hu, S., Zou, L. and Li, D., 2018. Record-breaking climate extremes in Africa under stabilized 1.5 C and 2 C global warming scenarios. *Nature Climate Change*, 8(5), 375.
- Nash, H., Lee, P.B. and Low, M.R., 2018. Rescue, rehabilitation and release of Sunda pangolins in Singapore. *Global Reintroduction Perspectives: 2018. Case studies from around the globe*, 221.
- Niang I, Ruppel OC, Abdrabo MA, Essel A, Lennard C, Padgham J, Urquhart P, 2014. Africa. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. 1199–1265. Cambridge University Press, Cambridge, United Kingdom and New York, New York.
- Nic Lughadha, E., Bachman, S.P., Leão, T.C., Forest, F., Halley, J.M., Moat, J., Acedo, C., Bacon, K.L., Brewer, R.F., Gâteblé, G. and Gonçalves, S.C., 2020. Extinction risk and threats to plants and fungi. *Plants, People, Planet*, 2(5), 389-408.
- Nicol, S. and Andersen, N.A., 2007. The life history of an egg-laying mammal, the echidna (*Tachyglossus aculeatus*). *Ecoscience*, 14(3), 275-285.
- Nicolaus, M.L., Bergdall, V.K., Davis, I.C. and Hickman-Davis, J.M., 2016. Effect of ventilated caging on water intake and loss in 4 strains of laboratory mice. *Journal of the American Association for Laboratory Animal Science*, 55(5), 525-533.
- Nixon, S., Pietersen, D., Challender, D., Hoffmann, M., Godwill Ichu, I., Bruce, T., Ingram, D.J., Matthews, N., and Shirley, M.H., 2019. *Smutsia gigantea*. *The IUCN Red List of Threatened Species* 2019: .T12762A123584478.
<https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12762A123584478.en>. Accessed on 18 May 2020.
- Norby, R.J. and Luo, Y., 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist*, 162(2), 281-293.

- Nori, M., Taylor, M. and Sensi, A., 2008. *Browsing on fences: pastoral land rights, livelihoods and adaptation to climate change*. 148, 1-22. IIED.
- Norris, A.L. and Kunz, T.H., 2012. Effects of solar radiation on animal thermoregulation. *Solar Radiation*, 195-220.
- Nunez, M.N., Solman, S.A. and Cabré, M.F., 2009. Regional climate change experiments over southern South America. II: Climate change scenarios in the late twenty-first century. *Climate Dynamics*, 32(7-8), 1081-1095.
- Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H. and Doswald, N., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology*, 20(7), 2221-2229.
- Ostrowski, S., Williams, J.B. and Ismael, K., 2003. Heterothermy and the water economy of free-living Arabian oryx (*Oryx leucoryx*). *Journal of Experimental Biology*, 206(9), 1471-1478.
- Ostrowski, S., Williams, J.B., Mesochina, P. and Sauerwein, H., 2006. Physiological acclimation of a desert antelope, Arabian oryx (*Oryx leucoryx*), to long-term food and water restriction. *Journal of Comparative Physiology B*, 176(3), 191-201.
- Owen-Smith, N., and Ogutu, J.O., 2013. Changing rainfall and obstructed movements: impact on African ungulates. In: Brodie, J.F., Post, E.S., and Doak, D.F., (eds). *Wildlife conservation in a changing climate*. University of Chicago Press, Chicago.
- Pacifici, M., Visconti, P., Butchart, S.H., Watson, J.E., Cassola, F.M. and Rondinini, C., 2017. Species' traits influenced their response to recent climate change. *Nature Climate Change*, 7(3), 205.
- Pagano, A.M., Durner, G.M., Rode, K.D., Atwood, T.C., Atkinson, S.N., Peacock, E., Costa, D.P., Owen, M.A. and Williams, T.M., 2018. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science*, 359(6375), 568-572.
- Pagon, N., Grignolio, S., Pipia, A., Bongi, P., Bertolucci, C. and Apollonio, M., 2013. Seasonal variation of activity patterns in roe deer in a temperate forested area. *Chronobiology International*, 30(6), 772-785.
- Pamperin, N.J., Follmann, E.H. and Petersen, B., 2006. Interspecific killing of an arctic fox by a red fox at Prudhoe Bay, Alaska. *Arctic*, 361-364.

- Pardini, R., Nichols, E. and Püttker, T., 2017. Biodiversity response to habitat loss and fragmentation. *Reference Module In Earth Systems And Environmental Sciences. Encyclopedia of the Anthropocene*, 3, 229-239.
- Pavey, C.R. and Geiser, F., 2008. Basking and diurnal foraging in the dasyurid marsupial *Pseudantechinus macdonnellensis*. *Australian Journal of Zoology*, 56(2), 129-135.
- Pedersen, T.L., 2020. patchwork: The Composer of Plots. R package version 1.1.1. Available at <https://CRAN.R-project.org/package=patchwork>.
- Pereira, M.E., Aines, J. and Scheckter, J.L., 2002. Tactics of heterothermy in eastern gray squirrels (*Sciurus carolinensis*). *Journal of Mammalogy*, 83(2), 467-477.
- Pereira, J.A., 2010. Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. *Journal of Arid Environments*, 74(9), 1106-1109.
- Pereira, L., 2017. Climate change impacts on agriculture across Africa. In *Oxford Research Encyclopedia of Environmental Science*. Oxford University Press, Oxford, United Kingdom.
- Piccione, G., Caola, G. and Refinetti, R., 2002. Circadian modulation of starvation-induced hypothermia in sheep and goats. *Chronobiology International*, 19(3), 531-541.
- Picker, M.D., Ross-Gillespie, V.E.R.E., Vlieghe, K. and Moll, E., 2012. Ants and the enigmatic Namibian fairy circles—cause and effect?. *Ecological Entomology*, 37(1), 33-42.
- Pietersen, D. W., 2013. *Behavioural ecology and conservation biology of ground pangolins Smutsia temminckii in the Kalahari Desert*. Doctoral dissertation, University of Pretoria, South Africa.
- Pietersen, D. W., McKechnie, A. E. and Jansen, R., 2014a. A review of the anthropogenic threats faced by Temminck's ground pangolin, *Smutsia temminckii*, in southern Africa. *African Journal of Wildlife Research*, 44(2), 167-179.
- Pietersen, D. W., McKechnie, A. E. and Jansen, R., 2014b. Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolins, *Smutsia temminckii*. *African Zoology*, 49(2), 265-276.
- Pietersen, D. W., Symes, C. T., Woodborne, S., McKechnie, A. E. and Jansen, R., 2016. Diet and prey selectivity of the specialist myrmecophage, Temminck's ground pangolin. *Journal of Zoology*, 298(3), 198-208.
- Pietersen, D., Moumbolou, C., Ingram, D.J., Soewu, D., Jansen, R., Sodeinde, O., Keboy Mov Linkey Iflankoy, C., Challender, D. & Shirley, M.H., 2019a. *Phataginus tricuspis*. *The IUCN Red List of Threatened Species* 2019a: e.T12767A123586469.

<https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T12767A123586469.en>. Accessed on 18 May 2020.

Pietersen, D. W., Jansen, R., and Connelly, E., 2019b. *Smutsia temminckii*. *The IUCN Red List of Threatened Species* 2019b: e.T12765A123585768. Available at <https://www.iucnredlist.org/species/12765/123585768>. Accessed 29 February 2020.

Pietersen, D. W., Jansen, R., Swart, J., Panaino, W., Kotze, A., Rankin, P., and Nebe, B., 2020. Temminck's pangolin *Smutsia temminckii* (Smuts, 1832). In Challender, D. W., Nash, H., and Waterman, C. (eds.), *Pangolins*, 175-193. Academic Press.

Pike, D.A. and Mitchell, J.C., 2013. Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation*, 16(6), 694-703.

Pires, S.F. and Moreto, W., 2016. The illegal wildlife trade, 1-41. Oxford University Press, Oxford, United Kingdom.

Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.M., Delorme, D., Warnant, C. and Bonenfant, C., 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS biology*, 12(4).

Podolski, I., Belotti, E., Bufka, L., Reulen, H. and Heurich, M., 2013. Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills. *Wildlife Biology*, 19(1), 69-77.

Pol, R.G., Lopez de Casenave, J. and Pirk, G.I., 2011. Influence of temporal fluctuations in seed abundance on the foraging behaviour of harvester ants (*Pogonomyrmex* spp.) in the central Monte desert, Argentina. *Austral Ecology*, 36(3), 320-328.

Pollock, H.S., 2017. First observation of a disturbance foraging association between obligate ant-following birds and a tamandua anteater in central Panama. *The Wilson Journal of Ornithology*, 129(4), 871-874.

Post, E. and Forchhammer, M.C., 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1501), 2367-2373.

Pureswaran, D.S., Roques, A. and Battisti, A., 2018. Forest insects and climate change. *Current Forestry Reports*, 4(2), 35-50.

Purse, B.V., Mellor, P.S., Rogers, D.J., Samuel, A.R., Mertens, P.P. and Baylis, M., 2006. Climate change and the recent emergence of bluetongue in Europe. *Nature Reviews Microbiology*, 3(2), 171-181.

- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rabaiotti, D. and Woodroffe, R., 2019. Coping with climate change: limited behavioral responses to hot weather in a tropical carnivore. *Oecologia*, 189(3), 587-599.
- Raven, P.H., 2020. Biological Extinction and Climate Change. In *Health of People, Health of Planet and Our Responsibility*, 11-20. Springer, Cham.
- Réale, D., McAdam, A.G., Boutin, S. and Berteaux, D., 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1515), 91-596.
- Reed, T.E., Jenouvrier, S. and Visser, M.E., 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, 82(1), 131-144.
- Reichmann, L.G., Sala, O.E. and Peters, D.P., 2013. Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology*, 94(2), 435-443.
- Rey, B., Fuller, A., Mitchell, D., Meyer, L.C. and Hetem, R.S., 2017. Drought-induced starvation of aardvarks in the Kalahari: an indirect effect of climate change. *Biology Letters*, 13(7), 20170301.
- Rezende, E.L. and Bozinovic, F., 2001. Patterns of daily activity in the leaf-eared mouse (*Phyllotis darwini*): effects of food availability. *Journal of Arid Environments*, 47(1), 95-100.
- Reznick, D.N. and Ghalambor, C.K., 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. In *Microevolution rate, pattern, process*, 183-198.. Springer, Dordrecht.
- Riccio, A.P. and Goldman, B.D., 2000. Circadian rhythms of locomotor activity in naked mole-rats (*Heterocephalus glaber*). *Physiology and Behavior*, 71(1-2), 1-13.
- Richardson, P.R.K., 1987. Aardwolf: the most specialized myrmecophagous mammal. *South African Journal of Science*, 83(10), 643-646.
- Richer, R., Coulson, I. A. N. and Heath, M., 1997. Foraging behaviour and ecology of the Cape pangolin (*Manis temminckii*) in north-western Zimbabwe. *African Journal of Ecology*, 35(4), 361-369.
- Ridley, A.R. and Raihani, N.J., 2007. Variable postfledging care in a cooperative bird: causes and consequences. *Behavioral Ecology*, 18(6), 994-1000.

- Robertshaw, D., 2006. Mechanisms for the control of respiratory evaporative heat loss in panting animals. *Journal of Applied Physiology*, 101(2), 664-668.
- Rohr, J.R. and Raffel, T.R., 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences*, 107(18), 8269-8274.
- Romanach, S.S., Seabloom, E.W. and Reichman, O.J., 2007. Costs and benefits of pocket gopher foraging: Linking behavior and physiology. *Ecology*, 88(8), 2047-2057.
- Rondinini, C. and Visconti, P., 2015. Scenarios of large mammal loss in Europe for the 21st century. *Conservation Biology*, 29(4), 1028-1036.
- Ross, S., Munkhtsog, B. and Harris, S., 2010. Dietary composition, plasticity, and prey selection of Pallas's cats. *Journal of Mammalogy*, 91(4), pp.811-817.
- Row, J.R., Wilson, P.J., Gomez, C., Koen, E.L., Bowman, J., Thornton, D. and Murray, D.L., 2014. The subtle role of climate change on population genetic structure in Canada lynx. *Global Change Biology*, 20(7), 2076-2086.
- Saalfeld, S.T., McEwen, D.C., Kesler, D.C., Butler, M.G., Cunningham, J.A., Doll, A.C., English, W.B., Gerik, D.E., Grond, K., Herzog, P. and Hill, B.L., 2019. Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecology and Evolution*, 9(11), 6693-6707.
- Samara, E.M., Abdoun, K.A., Okab, A.B. and Al-Haidary, A.A., 2012. A comparative thermophysiological study on water-deprived goats and camels. *Journal of Applied Animal Research*, 40(4), 316-322.
- Santini, G., Ramsay, P.M., Tucci, L., Ottonetti, L. and Frizzi, F., 2011. Spatial patterns of the ant *Crematogaster scutellaris* in a model ecosystem. *Ecological Entomology*, 36(5), 625-634.
- Schleuning, M., Fruend, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., Beil, M., Benadi, G., Bluethgen, N., Bruelheide, H. and Boehning-Gaese, K., 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications*, 7(1), 1-9.
- Schoppe, S., Katsis, L. and Lagrada, L. 2019. *Manis culionensis*. *The IUCN Red List of Threatened Species* 2019: e.T136497A123586862.
<https://dx.doi.org/10.2305/IUCN.UK.20193.RLTS.T136497A123586862.en>. Accessed on 18 May 2020.

- Schwimmer, H. and Haim, A., 2009. Physiological adaptations of small mammals to desert ecosystems. *Integrative Zoology*, 4(4), 357-366.
- Selebatso, M., Fynn, R. and Maude, G., 2017. Adaptive activity patterns of a blue wildebeest population to environmental variability in fragmented, semi-arid Kalahari, Botswana. *Journal of Arid Environments*, 136, 15-18.
- Shaffer, S.A., Costa, D.P. and Weimerskirch, H., 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology*, 864-874.
- Shah, R.D.T., Narayan Shah, D. and Domisch, S., 2012. Range shifts of a relict Himalayan dragonfly in the Hindu Kush Himalayan region under climate change scenarios. *International Journal of Odonatology*, 15(3), 209-222.
- Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. and Smith, R.J., 2009. The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15(5), 776-783.
- Sheriff, M.J., Buck, C.L. and Barnes, B.M., 2015. Autumn conditions as a driver of spring phenology in a free-living arctic mammal. *Climate Change Responses*, 2(1), 4.
- Shi, P., Sun, S., Wang, M., Li, N., Jin, Y., Gu, X. and Yin, W., 2014. Climate change regionalization in China (1961–2010). *Science China Earth Sciences*, 57(11), 2676-2689.
- Shi, N.N., Tsai, C.C., Camino, F., Bernard, G.D., Yu, N. and Wehner, R., 2015. Keeping cool: Enhanced optical reflection and radiative heat dissipation in Saharan silver ants. *Science*, 349(6245), 298-301.
- Shongwe, M.E., Van Oldenborgh, G.J., Van Den Hurk, B.J.J.M., De Boer, B., Coelho, C.A.S. and Van Aalst, M.K., 2009. Projected changes in mean and extreme precipitation in Africa under global warming. Part I: Southern Africa. *Journal of Climate*, 22(13), 3819-3837.
- Shrader, A.M., Pimm, S.L. and van Aarde, R.J., 2010. Elephant survival, rainfall and the confounding effects of water provision and fences. *Biodiversity and Conservation*, 19(8), 2235-2245.
- 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(3), 537-547.
- Silva, J.E., 2005. Thyroid hormone and the energetic cost of keeping body temperature. *Bioscience Reports*, 25(3-4), 129-148.

- Silva, D.P., Dew, R.M., Vilela, B., Stevens, M.I., Schwarz, M.P., 2018. No deaths in the desert: predicted responses of an arid-adapted bee and its two nesting trees suggest resilience in the face of warming climates. *Insect Conservation and Diversity*, 11(5), 449-63.
- Slingsby, P., 2017. *Ants of southern Africa: The ant book for all*. Slingsby Maps.
- Solomon, S., Manning, M., Marquis, M. and Qin, D., 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*, 4. Cambridge university press, Cambridge, United Kingdom.
- Speakman, J.R., 2000. The cost of living: field metabolic rates of small mammals. In *Advances in ecological research*, 30, 177-297. Academic Press.
- Speakman, J.R., 2008. The physiological costs of reproduction in small mammals *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1490), 375-398.
- Sprent, J.A. and Nicol, S.C., 2016. Diet of the short-beaked echidna (*Tachyglossus aculeatus*) in the Tasmanian Southern Midlands. *Australian Mammalogy*, 38(2), 188-194.
- Stenkewitz, U. and Kamler, J.F., 2008. Birds feeding in association with bat-eared foxes on Benfontein Game Farm, South Africa. *Ostrich-Journal of African Ornithology*, 79(2), 235-237.
- Stephens, D. W. & Krebs, J. R., 1986. Foraging theory. Princeton University Press, Princeton, NJ.
- Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P.M., 2013. Climate change 2013: *The physical science basis. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report AR5*. Cambridge University Press. New York.
- Stoll, S., Gadau, J., Gross, R.O.Y. and Feldhaar, H., 2007. Bacterial microbiota associated with ants of the genus *Tetraponera*. *Biological Journal of the Linnean Society*, 90(3), 399-412.
- Storms, D., Aubry, P., Hamann, J.L., Saïd, S., Fritz, H., Saint-Andrieux, C. and Klein, F., 2008. Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology*, 14(2), .237-250.
- Strauss, W.M., Hetem, R.S., Mitchell, D., Maloney, S.K., Meyer, L.C. and Fuller, A., 2015. Selective brain cooling reduces water turnover in dehydrated sheep. *PLoS One*, 10(2).

Svanbäck, R. and Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), 839-844.

Swart, J.M., 1996. *Foraging behaviour of the Cape pangolin Manis temminckii in the Sabi Sand Wildtuin*. Doctoral dissertation, University of Pretoria, South Africa.

Swart, J. M., Richardson, P. R. K. and Ferguson, J. W. H., 1999. Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology* 247(3), 281-292.

Swart, J., 2013. *Smutsia temminckii* Ground Pangolin. In: Kingdon, J., Hoffmann, M. (eds.), *Mammals of Africa*, vol. V, Carnivores, Pangolins, Equids, Rhinoceroses, 400-405. Bloomsbury Publishing, London.

Sweeney, R. C. H. 1956. Some notes on the feeding habits of the Ground Pangolin, *Smutsia Temminckii* (Smuts). *Annals and Magazine of Natural History*, 9(108), 893-896.

Symonds, M.R., 2005. Phylogeny and life histories of the 'Insectivora': controversies and consequences. *Biological Reviews*, 80(1), 93-128.

Symonds, M.R. and Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13-21.

't Sas-Rolfes, M., Challender, D.W., Hinsley, A., Veríssimo, D. and Milner-Gulland, E.J., 2019. Illegal wildlife trade: scale, processes, and governance. *Annual Review of Environment and Resources*, 44, 201-228.

Taylor, W.A., Lindsey, P.A. and Skinner, J.D., 2002. The feeding ecology of the aardvark *Orycteropus afer*. *Journal of Arid Environments*, 50(1): 135-152.

Taylor, W.A. and Skinner, J.D., 2001. Associative feeding between Ant-eating Chats, *Myrmecocichla formicivora*, and Aardvarks, *Orycteropus afer*. *Ostrich-Journal of African Ornithology*, 72(3-4), 199-200.

Terrien, J., Perret, M. and Aujard, F., 2011. Behavioral thermoregulation in mammals: a review. *Frontiers in Bioscience*, 16(4), 1428-1444.

Theimer, T.C., Williams, C.T., Johnson, S.R., Gilbert, A.T., Bergman, D.L. and Buck, C.L., 2017. Den use and heterothermy during winter in free-living, suburban striped skunks. *Journal of Mammalogy*, 98(3), 867-873.

Thrash, I., 1998. Impact of water provision on herbaceous vegetation in Kruger National Park, South Africa. *Journal of Arid Environments*, 38(3), 437-450.

- Tokura, W., Jack, S. L., Anderson, T. and Hoffman, M. T., 2018. Long-term variability in vegetation productivity in relation to rainfall, herbivory and fire in Tswalu Kalahari Reserve. *Koedoe*, 60(1), 1-18.
- Traill, L.W., Bradshaw, C.J., Field, H.E. and Brook, B.W., 2009. Climate change enhances the potential impact of infectious disease and harvest on tropical waterfowl *Biotropica*, 41(4), 414-423.
- Trebatická, L., Ketola, T., Klemme, I., Eccard, J.A. and Ylönen, H., 2007. Is reproduction really costly? Energy metabolism of bank vole (*Clethrionomys glareolus*) females through the reproductive cycle. *Ecoscience*, 14(3), 306-313.
- Tschinkel, W.R., 2002. The natural history of the arboreal ant, *Crematogaster ashmeadi* *Journal of Insect Science*, 2(1), 1-15.
- Tschinkel, W.R., 2010. The foraging tunnel system of the Namibian desert termite, *Baicaliotermes hainesi*. *Journal of Insect Science*, 10(1), 1-16.
- Turesson, H., Persson, A. and Brönmark, C., 2002. Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. *Ecology of Freshwater Fish*, 11(4), 223-233.
- Ullmann, T., Veríssimo, D. and Challender, D. W., 2019. Evaluating the application of scale frequency to estimate the size of pangolin scale seizures. *Global Ecology and Conservation*, 20, e00776.
- Vafidis, J., Smith, J. and Thomas, R., 2019. Climate change and insectivore ecology, *eLS*, 1-8.
- Van de Ven, T.M., Fuller, A. and Clutton-Brock, T.H., 2020. Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. *Functional Ecology*, 34(1), 194-202.
- Van der Vinne, V., Gorter, J.A., Riede, S.J. and Hut, R.A., 2015. Diurnality as an energy-saving strategy: energetic consequences of temporal niche switching in small mammals. *Journal of Experimental Biology*, 218(16), 2585-2593.
- Van der Vinne, V., Tachinardi, P., Riede, S.J., Akkerman, J., Scheepe, J., Daan, S. and Hut, R.A., 2019. Maximising survival by shifting the daily timing of activity. *Ecology Letters*, 22(12), 2097-2102.
- Van Ee, C. A. 1966. A note on breeding the Cape pangolin *Manis temminckii* at Bloemfontein zoo. *International Zoo Yearbook*, 6(1): 163-164.

- Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. and Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science*, 323(5913), 521-524.
- Van Oort, B.E., Tyler, N.J., Gerkema, M.P., Folkow, L. and Stokkan, K.A., 2007. Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions. *Naturwissenschaften*, 94(3), 183-194.
- Van Rooyen, N. and van Rooyen, G., 2017. Ecological Evaluation of Tswalu Kalahari Reserve. In *Ekotrust.*, 7-8.
- Van Wilgen, N.J., Goodall, V., Holness, S., Chown, S.L. and McGeoch, M.A., 2016. Rising temperatures and changing rainfall patterns in South Africa's national parks. *International Journal of Climatology*, 36(2), 706-721.
- Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 275(1635), 649-659.
- Visser, M.E., Holleman, L.J. and Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, 147(1), 164-172.
- Visser, M.E., Caro, S.P., Van Oers, K., Schaper, S.V. and Helm, B., 2010. Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3113-3127.
- Wallen, K.E. and Daut, E., 2018. The challenge and opportunity of behaviour change methods and frameworks to reduce demand for illegal wildlife. *Nature Conservation*, 26, 55.
- Walsberg, G.E. and Wolf, B.O., 1995. Effects of solar radiation and wind speed on metabolic heat production by two mammals with contrasting coat colours. *Journal of Experimental Biology*, 198(7), 1499-1507.
- Walsberg, G.E., 2000. Small mammals in hot deserts: some generalizations revisited. *BioScience*, 50(2), 109-120.
- Wang, T., Hung, C.C. and Randall, D.J., 2006. The comparative physiology of food deprivation: from feast to famine. *Annual Review of Physiology.*, 68, 223-251.
- Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas?. *African Journal of Range and Forage Science*, 22(2), 101-105.

- Warnecke, L., Turner, J.M. and Geiser, F., 2008. Torpor and basking in a small arid zone marsupial. *Naturwissenschaften*, 95(1), 73-78.
- Weber, R.E., Heath, M.E. and White, F.N., 1986. Oxygen binding functions of blood and hemoglobin from the Chinese pangolin, *Manis pentadactyla*: possible implications of burrowing and low body temperature. *Respiration Physiology*, 64(1), 103-112.
- Wehner, R., Marsh, A.C. and Wehner, S., 1992. Desert ants on a thermal tightrope *Nature*, 357(6379), 586-587.
- Welbergen, J.A., Klose, S.M., Markus, N. and Eby, P., 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B: Biological Sciences*, 275(1633), 419-425.
- Weyer, N. M. 2018. *Physiological flexibility of free-living aardvarks (Orycteropus afer) in response to environmental fluctuations*. Doctoral dissertation, University of the Witwatersrand, South Africa.
- Weyer, N.M., Fuller, A., Haw, A.J., Meyer, L.C.R., Mitchell, D., Picker, M., Rey, B. and Hetem, R.S., 2020. Increased diurnal activity is indicative of energy deficit in a nocturnal mammal, the aardvark. *Frontiers in Physiology*, 11, 637.
- Whitford, W.G. and Ettershank, G., 1975. Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environmental Entomology*, 4(5), 689-696.
- Wicker, L.V., Lourens, K. and Hai, L.K., 2020. Veterinary health of pangolins. In *Pangolins*, 461-493. Academic Press.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
- Wickham, H., François, R., Henry, L., and Müller, K., 2021. dplyr: A Grammar of Data Manipulation. R package version 1.0.5. Available at <https://CRAN.R-project.org/package=dplyr>.
- Wickham, H., 2021. tidyr: Tidy Messy Data. R package version 1.1.3. Available at <https://CRAN.R-project.org/package=tidyr>.
- Williams, J.B., Anderson, M.D. and Richardson, P.R.K., 1997. Seasonal differences in field metabolism, water requirements, and foraging behavior of free-living aardwolves. *Ecology*, 78(8), 2588-2602.
- Williams, P.J., Floyd, T.A. and Rossong, M.A., 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters,

Homarus americanus (Milne Edwards). *Journal of Experimental Marine Biology and Ecology*, 329(1), 66-74.

Williams, S.E. and Middleton, J., 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*, 14(1), 69-77.

Williams, C.M., Henry, H.A. and Sinclair, B.J., 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90(1), 214-235.

Wilson, R.P., Shepard, E.L.C. and Liebsch, N., 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered species research*, 4(1-2), 123-137.

Withers, P.C., Cooper, C.E., Maloney, S.K., Bozinovic, F. and Cruz-Neto, A.P., 2016. *Ecological and environmental physiology of mammals*, 5. Oxford University Press, New York.

Witt, A.B.R. and Giliomee, J.H., 2005. Dispersal of elaiosome-bearing seeds of six plant species native species of ants and the introduced invasive ant, *Linepithema humile* (Mayr)(Hymenoptera: Formicidae) in the Western Cape Province, South Africa. *African Plant Protection*, 11(1), 1-7.

Wolda, H., 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *The Journal of Animal Ecology*, 369-381.

Woodward, S.J., 1997. Formulae for predicting animals' daily intake of pasture and grazing time from bite weight and composition. *Livestock Production Science*, 52(1), 1-10.

Woon, J.S., Boyle, M.J.W., Ewers, R.M., Chung, A. and Eggleton, P., 2019. Termite environmental tolerances are more linked to desiccation than temperature in modified tropical forests. *Insectes Sociaux*, 66(1), 57-64.

Xie, Y., 2014. knitr: A Comprehensive Tool for Reproducible Research in R. In Stodden, V., Leisch, F., and Peng, R.D. (Eds)., *Implementing Reproducible Computational Research*. Chapman and Hall/CRC.

Xie, Y., 2015. *Dynamic Documents with R and knitr*. 2nd edition. Chapman and Hall/CRC.

Yoda, T., Crawshaw, L.I., Yoshida, K., Su, L., Hosono, T., Shido, O., Sakurada, S., Fukuda, Y. and Kanosue, K., 2000. Effects of food deprivation on daily changes in body temperature and behavioral thermoregulation in rats. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 278(1), R134-R139.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. and Hairston, N.G., 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424(6946), 303-306.

Ytrehus, B., Bretten, T., Bergsjø, B. and Isaksen, K., 2008. Fatal pneumonia epizootic in musk ox (*Ovibos moschatus*) in a period of extraordinary weather conditions. *EcoHealth*, 5(2), 213-223.

Zachariassen, K.E. and Pedersen, S.A., 2002. Volume regulation during dehydration of desert beetles. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 133(3), 805-811.

Zhang, W., Brandt, M., Tong, X., Tian, Q. and Fensholt, R., 2018. Impacts of the seasonal distribution of rainfall on vegetation productivity across the Sahel. *Biogeosciences*, 15(1), 319.

Appendix

Table A1: Summary of available literature on Temminck's pangolins found through online libraries and reference lists.

Year	Author(s)	Journal/book	Region	Wild/captive/museum	Theme
1939	Lawrence	Parasitology	SA	Captive	Disease
1956	Sweeny	Annals and Magazine of Natural History	Sudan	Wild and captive	Diet
1958	Zumt	Bulletin of Entomological Research	Botswana	Wild	Disease
1966	Van Ee	International Zoo Yearbook	SA	Captive	Husbandry and farming
1981	Deligne <i>et al.</i>	Social Insects	Africa and Asia	Wild	Diet
1986	Larson	Botswana Notes and Records	Botswana	Wild	Culture
1989	Coulson	African Journal of Ecology	Zimbabwe	Museum	Population
1991	Jacobsen <i>et al.</i>	Zeitschrift für Säugetierkunde	SA	Wild	Ecology
1992	Heath	American Society of Mammalogists	SA	Museum	Broad
1994	Brautigam <i>et al.</i>	TRAFFIC Bulletin	Africa	Wild	Trade
1994	Wilson	International Zoo Yearbook.	Africa and Asia	Captive	Husbandry and farming
1995	Walsh	International Committee on Urgent Anthropological and Ethnological Research	Tanzania	Wild	Culture
1996	Schloeder and Jacobs	African Journal of Ecology	Ethiopia	Wild	Population
1997	Heath and Coulson	African Journal of Ecology	Zimbabwe	Wild	Ecology
1997	Heath and Coulson	South African Journal of Wildlife Research	Zimbabwe	Wild	Ecology
1997	Richer <i>et al.</i>	African Journal of Ecology	Zimbabwe	Wild	Ecology
1998	Heath and Coulson	African Journal of Ecology	Zimbabwe	Wild	Biology
1999	Eltringham <i>et al.</i>	Royal Geographic Society	Tanzania	Wild	Population
1999	Gaudin and Wible	Journal of Mammalian Evolution	N/A	Museum	Phylogeny
1999	Swart <i>et al.</i>	Zoology	SA	Wild	Ecology

2000	Kyle	Koedoe	SA	Wild	Population
2007	Botha and Gaudin	Journal of Vertebrate Paleontology	SA	N/A	Paleontology
2007	Walsh	Animal symbolism	Tanzania	Wild	Culture
2007	Yang <i>et al.</i>	Zoo Biology	N/A	Captive	Husbandry and farming
2009	Gaudin <i>et al.</i>	Journal of Mammalian Evolution	Africa	Museum	Phylogeny
2011	Whiting <i>et al.</i>	Zoology	SA	N/A	Trade
2012	Challender and Hywood	TRAFFIC Bulletin	Africa	Wild	Trade
2013	Swart	Mammals of Africa	Africa	All	Broad
2014	Du Toit <i>et al.</i>	Gene	SA	Wild	Phylogeny
2014	Keeping	Animal Conservation	Botswana	Wild	Population
2011	Pietersen <i>et al.</i>	African Journal of Wildlife Research	Southern Africa	Wild	Broad
2014	Pietersen <i>et al.</i>	African Zoology	SA	Wild	Ecology
2014	Pietersen <i>et al.</i>	The IUCN Red List	Africa	N/A	Broad
2015	Boakye <i>et al.</i>	PLoS One	Ghana	N/A	Culture
2015	Gaubert and Antunes	Gene	N/A	N/A	Phylogeny
2015	Hassanin <i>et al.</i>	Comptes Rendus Biologies	Africa and Asia	Wild	Phylogeny
2015	Kingdon	Field guide	Africa	N/A	Broad
2015	Soewu and Sodeinde	Biodiversity Conservation	Africa	Wild	Trade
2016	Gaudin	Smithsonian Contribution to Paleobiology	N/A	N/A	Anatomy
2016	Heinrich <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Wild	Trade
2016	Ingram <i>et al.</i>	Zenodo	Africa	Wild	Trade
2016	Mohapatra <i>et al.</i>	Journal of Parasitic Diseases.	Africa and Asia	Wild and captive	Disease
2016	Mwale <i>et al.</i>	Genome	Africa	Wild	Population
2016	Pietersen <i>et al.</i>	Zoology	SA	Wild	Diet

2017	Chon <i>et al.</i>	Journal of Mechanical Behaviour of Biomedical Materials	Africa	Wild	Anatomy
2017	Du Toit <i>et al.</i>	BMC Genomics	Africa	Wild	Phylogeny
2017	Du Toit <i>et al.</i>	Conservation Genetics Resources	SA	Wild	Population
2017	Gaubert <i>et al.</i>	Journal of Heredity	Africa and Asia	N/A	Phylogeny
2017	Heinrich <i>et al.</i>	TRAFFIC Report	N/A	Wild	Trade
2017	Shepherd <i>et al.</i>	Oryx	Zimbabwe	Wild	Trade
2018	Baiyewu <i>et al.</i>	Society and Animals	SA	N/A	Culture
2018	Ingram <i>et al.</i>	Conservation Letters	Africa	Wild	Trade
2018	Keeping <i>et al.</i>	Biological Conservation	Botswana	Wild	Population
2018	Kumar <i>et al.</i>	Mitochondrial DNA A	Africa and Asia	Wild	Phylogeny
2018	Kumar <i>et al.</i>	Mitochondrial DNA B	Africa and Asia	Wild	Phylogeny
2018	Steyn <i>et al.</i>	Anatomical Record	SA	Wild	Anatomy
2018	Okonkwo and Okaka	International Journal of Health Safety and Environment	Nigeria	Wild	Disease
2019	Boyles <i>et al.</i>	Animal Conservation	SA	Wild	Physiology
2019	Cavada <i>et al.</i>	PLoS One	Tanzania	Wild	Population
2019	Challender <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Wild and captive	Husbandry and Farming
2019	Chapelle	Journal of Paleontology	N/A	N/A	Anatomy
2019	Ferreira-Cardoso	Zoological Journal of the Linnean Society	Africa and Asia	Museum	Anatomy
2019	George <i>et al.</i>	Molecular and Cellular Probes	N/A	Wild	Trade
2019	Ingram <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Wild	Population
2019	Jacobs <i>et al.</i>	Conservation Science and Practice.	Africa and Asia	Museum	Trade
2019	Khwaja <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Wild	Population

2019	Musila <i>et al.</i>	Zoological Research	Kenya	Wild	Population
2019	Piel <i>et al.</i>	African Journal of Ecology	Tanzania	Wild	Population
2019	Power <i>et al.</i>	Annals of the Ditsong Museum of Natural History	SA	Wild	Population
2019	Ullmann <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Museum	Trade
2019	Wilcox <i>et al.</i>	Global Ecology and Conservation	Africa and Asia	Wild	Population
2020	Challender <i>et al.</i>	Elsevier	Africa and Asia	All	Broad
2020	Connelly <i>et al.</i>	African Zoology	Zimbabwe	Wild and captive	Physiology
2020	Du Toit <i>et al.</i>	Journal of Genetics	Africa	Wild	Phylogeny

Table A2: Model selection of best fit based on AIC values for the effects of accumulated rainfall four, three, two, and one month prior to conducting transects, as well as during the same month of conducting transects.

Explanatory variable	AIC	Δ AIC
Rainfall three months prior	87.67	0.00
Rainfall four months prior	88.92	-1.25
Rainfall two months prior	90.43	-2.76
Rainfall one month prior	91.52	-3.85
Rainfall during the same month	92.30	-4.62

Table A3: Model selection of best fit based on AIC values for the effects of rainfall and black globe temperature on grass cover, comparing the model with and without interactive effects between rainfall and globe temperature.

Model	AIC	Δ AIC
Interactive effects	73.21	0.00
No interactive effects	82.32	-9.11

Table A4: Model selection of best fit based on AIC values for the effects of rainfall, grass cover, and black globe temperature on prey abundance, comparing the model with and without interactive effects between rainfall, grass cover, and globe temperature.

Model	AIC	Δ AIC
No interactive effects	103.80	0.00
Interactive effects	114.20	-10.36

Table A5: Model search for a breakpoint in the relationship between environmental temperature and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
27	2999.00	0.00
28	3000.00	-1.00
26	3003.00	-4.00
29	3008.00	-9.00
24	3014.00	-15.00
22	3026.00	-27.00
30	3026.00	-27.00
20	3037.00	-38.00
18	3043.00	-44.00
16	3044.00	-45.00
0	3044.00	-45.00

Table A6: Model selection of best fit based on AIC values for the effects of explanatory variables on the daily number of prey items consumed by pangolins. The 24h black globe temperature was removed from the global model because it was highly correlated ($r>0.82$) with the duration of pangolin activity. Interactive effects were not tested since the small sample size of pangolins did not provide the statistical power necessary for testing interactive effects.

Explanatory variable	AIC	Δ AIC
<i>Rainfall</i>		
Rainfall one month prior	379.60	0.00
Rainfall two months prior	380.10	-0.50
Rainfall four months prior	380.40	-0.80
Rainfall during the same month	381.20	-1.60
Rainfall three months prior	381.30	-1.70
<i>24h black globe temperature</i>		
Excluded from model	346.5	0.00
Included in model	349.9	-3.40
<i>Pangolin activity</i>		
Duration of activity	379.60	0.00
Time of return	384.40	-4.80
Time of emergence	386.90	-7.30

Table A7: Model selection of best fit based on AIC values for the effects of explanatory variables on the estimated 24h energy intake by pangolins. The 24h black globe temperature was removed from the global model because it was highly correlated ($r>0.82$) with the duration of pangolin activity. Interactive effects were not tested since the small sample size of pangolins did not provide the statistical power necessary for testing interactive effects.

Explanatory variable	AIC	Δ AIC
<i>Rainfall</i>		
Rainfall during the same month	187.80	0.00
Rainfall one month prior	191.60	-3.80
Rainfall four months prior	191.90	-4.10
Rainfall three months prior	193.10	-5.30
Rainfall two months prior	193.20	-5.40
<i>24h black globe temperature</i>		
Excluded from model	95.66	0.00
Included in model	96.18	-0.52
<i>Pangolin activity</i>		
Duration of activity	187.80	0.00
Time of return	187.90	0.10
Time of emergence	189.90	-2.10

Table A8: Model search for a breakpoint in the relationship between pangolin time of emergence from the burrow and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
16	8259.00	0.00
17	8262.00	-3.00
15	8264.00	-5.00
12	8264.00	-5.00
11	8265.00	-6.00
10	8277.00	-18.00
14	8283.00	-24.00
9	8301.00	-42.00
13	8308.00	-49.00
8	8324.00	-65.00
0	8588.00	-329.00

Table A9: Model search for a breakpoint in the relationship between pangolin time of return to the burrow and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
17	7804.00	0.00
16	7808.00	-4.00
15	7815.00	-11.00
11	7817.00	-13.00
10	7822.00	-18.00
12	7824.00	-20.00
9	7831.00	-27.00
14	7832.00	-28.00
8	7840.00	-36.00
13	7851.00	-47.00
0	7965.00	-161.00

Table A10: Model search for a breakpoint in the relationship between pangolin time of emergence from the burrow and time of return to the burrow using AIC values.

Breakpoint (time of emergence)	AIC	Δ AIC
21:50	-8432.00	0.00
22:00	-8431.00	1.00
21:30	-8430.00	2.00
21:40	-8430.00	2.00
21:20	-8428.00	4.00
21:00	-8425.00	7.00
17:00	-8420.00	12.00
20:00	-8406.00	26.00
18:00	-8400.00	32.00
19:00	-8394.00	38.00
00:00	-8393.00	39.00

Table A11: Model search for a breakpoint in the relationship between pangolin 24h minimum body temperature and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
12	4176.00	0.00
11	4177.00	-1.00
10	4177.00	-1.00
15	4182.00	-6.00
9	4183.00	-7.00
14	4183.00	-7.00
16	4185.00	-9.00
13	4189.00	-13.00
17	4192.00	-16.00
8	4204.00	-28.00
0	4376.00	-200.00

Table A12: Model search for a breakpoint in the relationship between pangolin 24h maximum body temperature and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
17	2530.00	0.00
16	2531.00	-1.00
15	2534.00	-4.00
14	2536.00	-6.00
12	2538.00	-8.00
13	2540.00	-10.00
11	2543.00	-13.00
10	2549.00	-19.00
9	2558.00	-28.00
8	2571.00	-41.00
0	2616.00	-86.00

Table A13: Model search for a breakpoint in the relationship between the amplitude of the 24h rhythm of pangolin body temperature and prey abundance using AIC values.

Breakpoint (ants per trap)	AIC	Δ AIC
12	5053.00	0.00
16	5054.00	-1.00
15	5054.00	-1.00
14	5057.00	-4.00
11	5058.00	-5.00
17	5059.00	-6.00
10	5064.00	-11.00
13	5067.00	-14.00
9	5080.00	-27.00
8	5115.00	-62.00
0	5319.00	-266.00

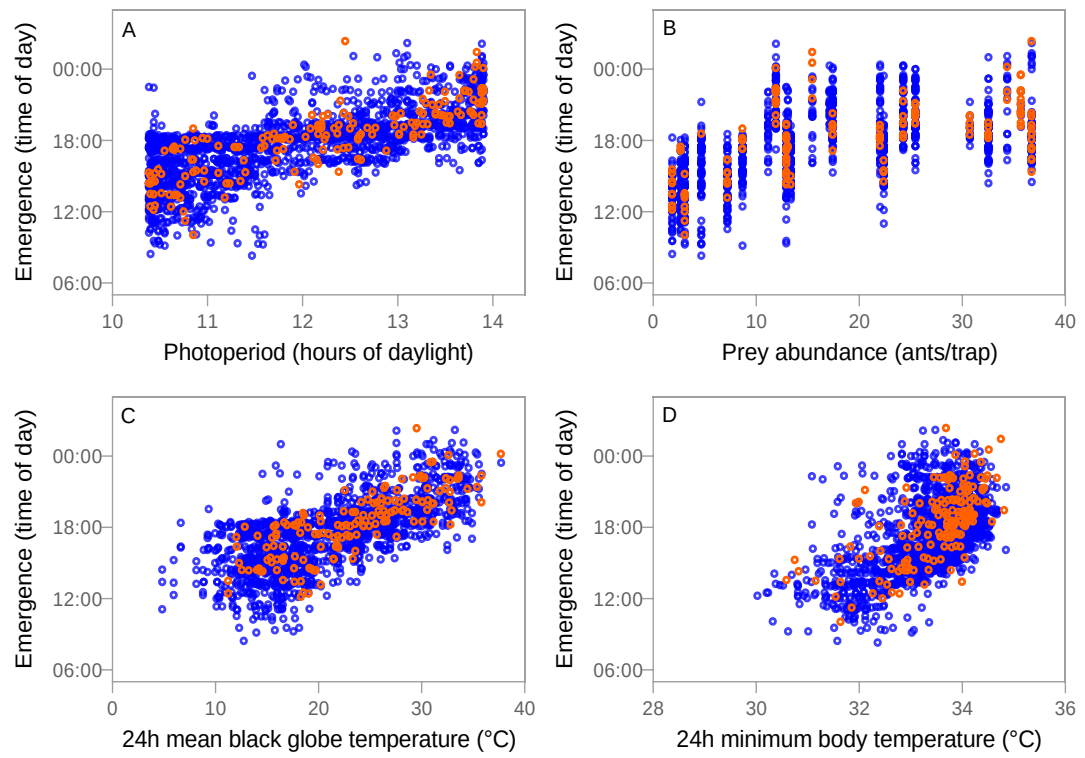


Figure A1: Relationship between photoperiod (A), prey abundance (B), 24h mean black globe temperature (C), and 24h minimum body temperature (D) and pangolin time of emergence from the burrow, comparing data obtained from camera traps only (orange circles) and data obtained from 24h body temperature patterns only (blue circles).

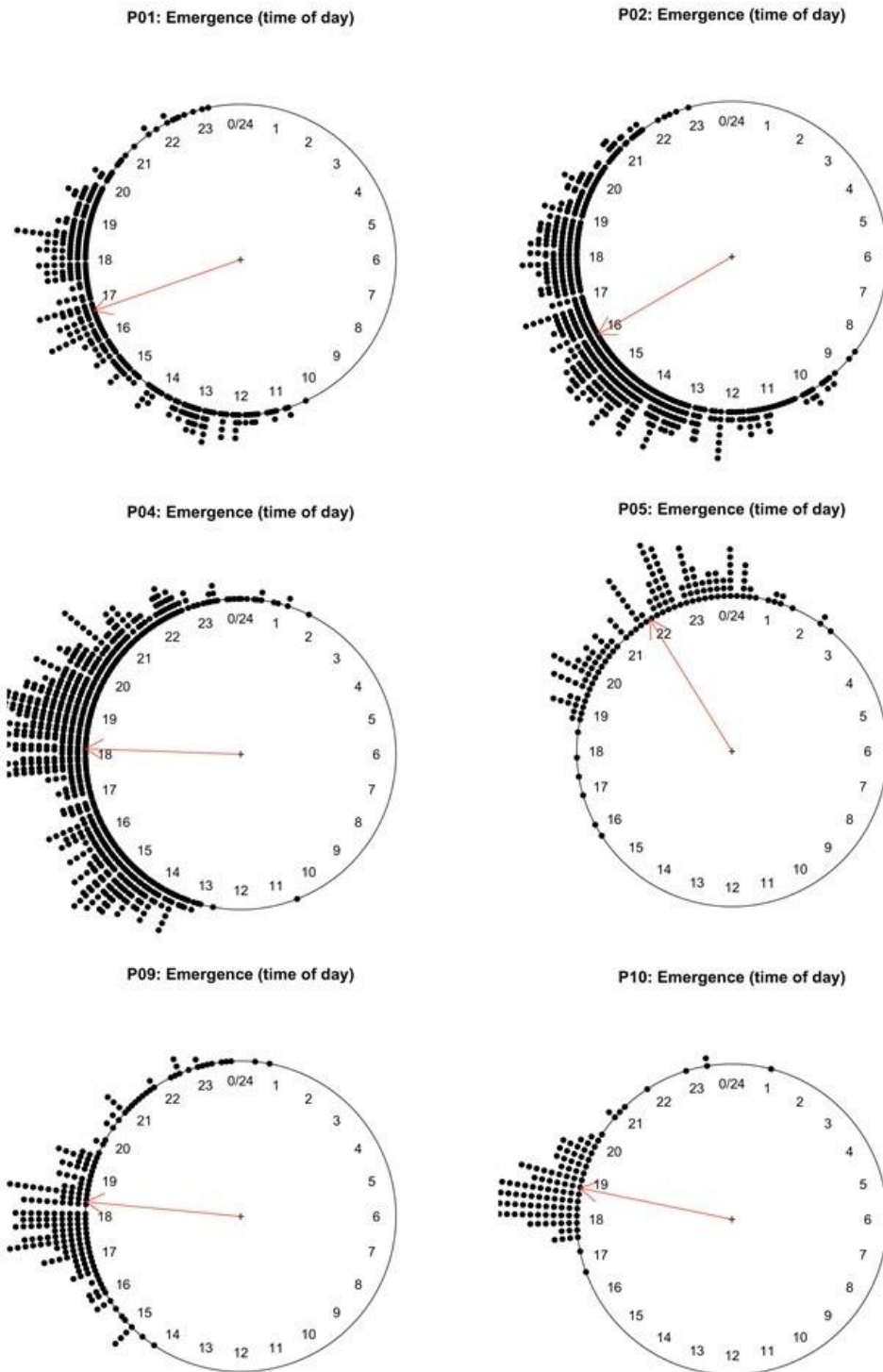


Figure A2: The circular distribution of each pangolin's burrow emergence data throughout the study period. The red arrow indicates the mean time of emergence.

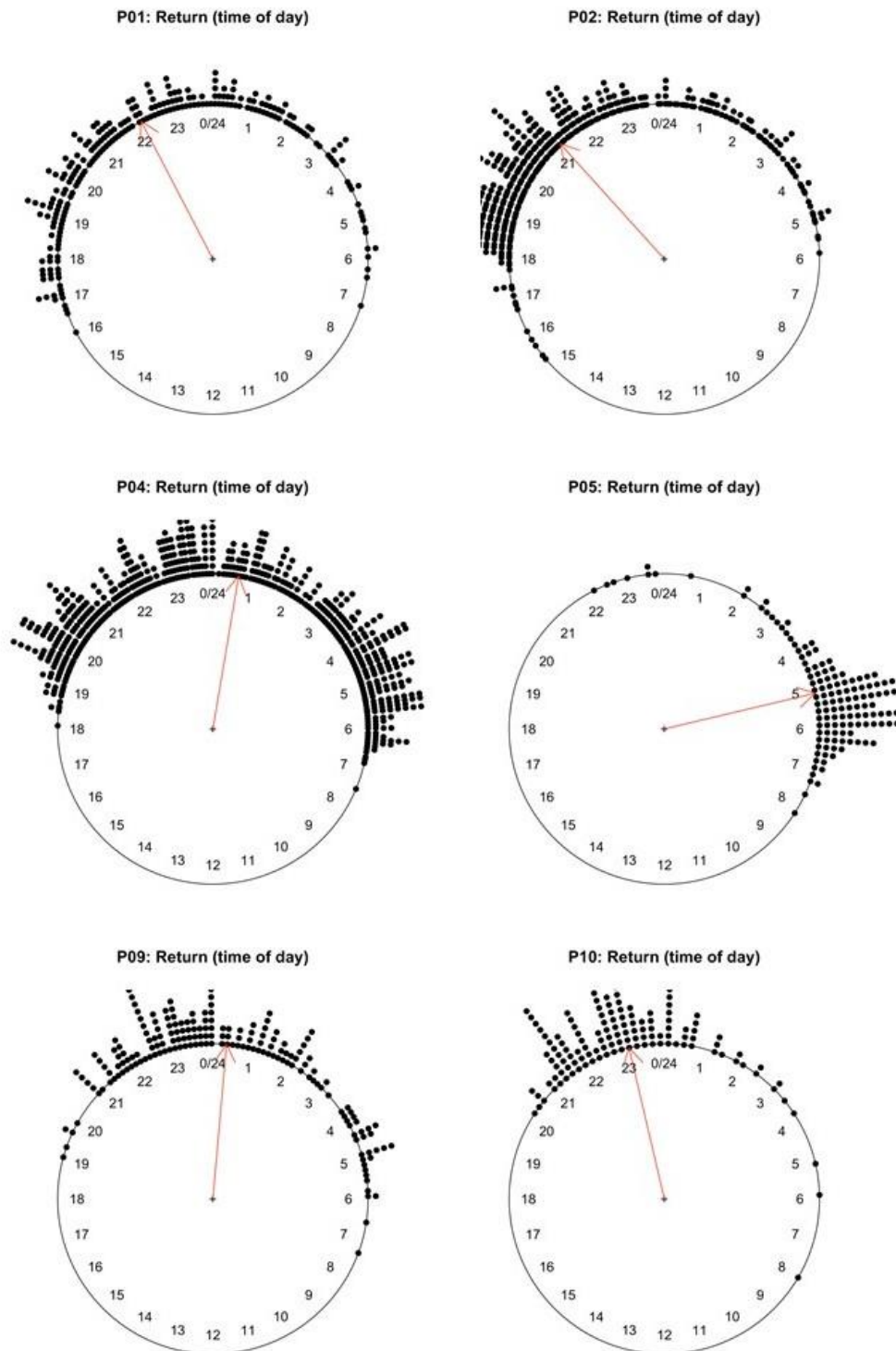


Figure A3: The circular distribution of each pangolin's burrow return data throughout the study period. The red arrow indicates the mean time of return.