

Behavioural ecology and conservation biology of ground pangolins *Smutsia temminckii* in the Kalahari Desert

By

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DECLARATION

I, Darren William Pietersen declare that the thesis, which I hereby submit for the degree Master of Science Zoology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

A handwritten signature in black ink, appearing to read 'D. Pietersen', written in a cursive style with a long horizontal stroke extending to the right.

Darren William Pietersen
February 2013

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SUMMARY

Ground pangolins *Smutsia temminckii* are inconspicuous, mainly nocturnal mammals that occur at low population densities. As a result, there is scant information available on the ecology and physiology of this species. To date the handful of studies focussing on this species were centred in the mesic eastern regions of its range, with no attention being given to ecological and biological traits in arid environments. To address these data shortfalls, a study was undertaken in the Kalahari Desert in north-western South Africa. Very High Frequency (VHF) transmitters or Global Positioning System (GPS) loggers were fitted to 16 ground pangolins and their ecology and physiology studied over a period of three years.

Throughout its range the ground pangolin is increasingly endangered, predominantly due to anthropogenic threats. Previous studies have identified threats facing this species, but very few of these studies included quantitative data as to the extent of these threats. The present study suggests that the main threats to ground pangolins in southern Africa are electrocution on electrified fences, the traditional medicine trade, habitat loss, road mortalities and capture in gin traps. Although accidental poisoning has previously been viewed as a threat, a review of the available literature suggests that this is not the case and that these views stemmed from two isolated incidents of captive animals. Electrocutions probably pose the greatest threat to ground pangolins, with mortality rates of one pangolin per 11 km of electrified fence per year recorded during this study.

Home range sizes of this arid-zone population are comparable to the home range sizes recorded in mesic populations. Study animals in the Kalahari had Minimum

Convex Polygon (MCP) home range values of $10.0 \pm 8.9 \text{ km}^2$ SD for adults and $7.1 \pm 1.1 \text{ km}^2$ SD for juveniles, in comparison to the $0.17 - 23.38 \text{ km}^2$ MCP in Zimbabwe and $1.3 - 7.9 \text{ km}^2$ MCP in mesic north-eastern South Africa. These results are surprising as arid-zone animals usually have larger home ranges than do their mesic counterparts. It is hypothesised that this discrepancy is due to the fact that ground pangolins in the Kalahari are on average 25 – 30 % smaller than their mesic counterparts. This smaller body size means that individuals require a smaller home range to meet their dietary requirements, which could be counteracting the trend of arid-zone individuals requiring larger home ranges.

This research also found ground pangolins to be more active during the day in winter and nearly entirely nocturnal during summer. These changes in photoperiodicity are likely driven by adaptations to the extreme climatic conditions present at the study site rather than predation pressure or changes in food resources, although the latter may be playing a role as well. By being diurnal in winter, individuals avoid the extremely cold night-time temperatures, thus saving energy that would otherwise be spent on maintaining their body temperature. By contrast, becoming nocturnal in summer allows them to avoid the extreme daytime temperatures, thus conserving water.

The results of this study reiterate previous findings that ground pangolins are entirely myrmecophagous and highly selective of the species that they eat. Study animals were recorded feeding on only four ant and two termite species, representing 7.5 % and 50 % of the total species richness of each of these families. This is similar to previous research in mesic savannahs where five ant one termite species constituted 97 % of the ground pangolin's diet. No seasonal differences in prey selection were

observed, although the species consumed did depend on the habitats that were available to individual ground pangolins.

This study is the first to investigate the core body temperature (T_b) of a free-ranging pangolin. These data indicated that T_b fluctuated cyclically between 32 – 35 °C and reflected the activity periods of the animal, peaking when the animal was active. When the individual was inactive, T_b steadily decreased, suggesting that it used daily heterothermy to cope with the low food availability in this unpredictable environment.

In summary, ecological parameters between arid and mesic ground pangolin populations are similar in some respects, but divergent in others. Arid-zone populations are smaller overall and show a higher degree of diurnal activity. Despite this smaller body size, home range values appear to be similar between arid and mesic populations. Although the prey species eaten by ground pangolins in the Kalahari differ from prey species in eastern South Africa and Zimbabwe, they belonged to the same genera and were of similar morphology and ecology. The core body temperature results confirm findings from previous captive studies that pangolin body temperatures are lower than those of other eutherian mammals of a similar size. Furthermore, these data indicate that core body temperature is a lot more variable than previously believed, and thus warrants further study. Overall ground pangolin densities in the Kalahari appear to be double those in eastern South Africa and Zimbabwe, although it is unclear whether this is genuine or whether it is an artefact of individuals being easier to locate in the Kalahari. This study also confirmed that electrocutions are probably the greatest threat to this species, and new threats such as accidental capture in gin traps and road mortalities have also come to light.

TABLE OF CONTENTS

CONTENTS	PAGE
DECLARATION.....	ii
FUNDING.....	iii
ACKNOWLEDGEMENTS.....	iv
SUMMARY.....	vi
TABLE OF CONTENTS.....	ix
LIST OF TABLES.....	xiii
LIST OF FIGURES.....	xiv
CHAPTER ONE: GENERAL INTRODUCTION.....	1
CHAPTER TWO: STUDY AREA.....	5
2.1 LOCATION.....	5
2.2 CLIMATE.....	7
2.3 GEOLOGY.....	8
2.4 VEGETATION.....	9
2.4.1 <i>Acacia erioloba</i> veld.....	11
2.4.2 <i>Acacia haematoxylon</i> Savannah.....	12
2.4.3 <i>Acacia mellifera</i> Thickets.....	13
2.4.4 <i>Acacia mellifera</i> - <i>Rhigozum trichotomum</i> Veld.....	14
2.4.5 Duneveld Grassland.....	14
2.4.6 Dwarf Karroid Shrubland.....	15

2.4.7	Grassy Dwarf Shrubland.....	16
2.4.8	Mixed Savannah.....	16
2.4.9	Mountain Veld.....	17

CHAPTER THREE: REVIEW OF THE ANTHROPOGENIC THREATS FACED BY GROUND PANGOLINS *SMUTSIA TEMMINCKII* IN SOUTHERN AFRICA.....

19

3.1	INTRODUCTION.....	19
3.2	MATERIALS AND METHODS.....	20
3.3	THREATS.....	22
3.3.1	Electrified Fences.....	22
3.3.2	Traditional Medicine and the Bushmeat Trade.....	26
3.3.3	Gin Traps.....	27
3.3.4	Habitat Loss.....	28
3.3.5	Road Mortalities.....	28
3.3.6	Poisoning.....	29
3.3.7	Pet Trade.....	30
3.4	POSSIBLE MITIGATION MEASURES.....	30
3.5	CONCLUSIONS.....	34

CHAPTER FOUR: HOME RANGE SIZE, ACTIVITY PERIODS AND REFUGE SITE SELECTION OF AN ARID-ZONE POPULATION OF GROUND PANGOLINS *SMUTSIA TEMMINCKII*.....

35

4.1	INTRODUCTION.....	35
-----	-------------------	----

4.2	MATERIALS AND METHODS.....	37
4.3	RESULTS.....	42
4.3.1	Home Range Extent.....	42
4.3.2	Habitat Use.....	46
4.3.3	Dispersal.....	47
4.3.4	Activity Periods.....	49
4.3.5	Refuge Site Selection.....	51
4.3.6	Densities.....	52
4.4	DISCUSSION.....	55
4.4.1	Home Range Extent.....	55
4.4.2	Habitat Use.....	57
4.4.3	Dispersal.....	58
4.4.4	Activity Periods.....	59
4.4.5	Refuge Site Selection.....	60
4.4.6	Densities.....	62

CHAPTER FIVE: DIET AND PREY SELECTIVITY OF GROUND		
PANGOLINS <i>SMUTSIA TEMMINCKII</i> (SMUTS, 1832) IN THE SOUTHERN		
KALAHARI DESERT.....		63
5.1	INTRODUCTION.....	63
5.2	MATERIALS AND METHODS.....	64
5.2.1	Study Site.....	64
5.2.2	Ant and Termite Sampling.....	66
5.2.3	Feeding Observations.....	68
5.2.4	Statistical Analyses.....	69

5.3	RESULTS.....	69
5.3.1	Ant and Termite Richness and Abundance.....	69
5.3.2	Feeding Observations.....	76
5.4	DISCUSSION.....	79

CHAPTER SIX: CORE BODY TEMPERATURE OF A FREE-ROAMING GROUND PANGOLIN <i>SMUTSIA TEMMINCKII</i>.....		84
6.1	INTRODUCTION.....	84
6.2	MATERIALS AND METHODS.....	86
6.3	RESULTS.....	88
6.4	DISCUSSION.....	90
REFERENCES.....		93

LIST OF TABLES

TABLE	PAGE
<p>TABLE 4.1: Three measures of home range size for seven adult (≥ 6 kg) and six juvenile (< 6 kg) ground pangolins. Field numbers marked with an asterisk indicate individuals for which a 95 % Incremental Area Analysis indicated that home range stationarity had been reached and that the entire home range had thus likely been mapped.....</p>	43
<p>TABLE 4.2: Habitat selectivity values for 12 ground pangolins. A value of zero represents no habitat selectivity, whereas a value of one represents maximum habitat selectivity.....</p>	47
<p>TABLE 4.3: The type and proportion of refuges utilised by 16 ground pangolins between September 2009 and October 2012. N is the total number of times ground pangolins were seen utilising each refuge type and % is the proportional use of each refuge type.....</p>	52
<p>TABLE 5.1: Epigaeic ant and termite species collected in each of the eight vegetation types at the study site between March 2011 and February 2012. The photoperiod in which most activity occurred is also indicated for each species. Numbers in non-boldface indicate species that form part of a morphospecies complex and although its presence at the study site was confirmed, it may not occur in all vegetation types indicated. Totals for these species are for the entire morphospecies complex. Vegetation type codes are: DKS = Dwarf Karroid Shrubland; AMRT = <i>Acacia mellifera</i> - <i>Rhigozum trichotomum</i> Veld; AE = <i>Acacia erioloba</i> Veld; AM = <i>Acacia mellifera</i> Thicket; MV = Mountain Veld; MS = Mixed Savannah; DG = Duneveld Grassland; AH = <i>Acacia haematoxylon</i> Savannah. AFRC-za = AfriBugs collection morphospecies code.....</p>	71
<p>TABLE 5.2: Number of foraging bouts, proportion of foraging bouts and standardised forage ratio for each of the ant and termite species preyed on by ground pangolins at Kalahari Oryx Private Game Farm.....</p>	77

LIST OF FIGURES

FIGURE	PAGE
FIGURE 2.1: Layout of the study site and its location within South Africa. Names refer to the different sub-farms.....	6
FIGURE 2.2: Average climatic conditions recorded at the study site between July 2000 and June 2012. Average temperatures are presented as mean \pm SD while rainfall is presented as the monthly average only.....	7
FIGURE 2.3: Geological formations present at the study site (Adapted from the base map available on the SANBI website < http://bgis.sanbi.org/mapsearch.asp >).....	8
FIGURE 2.4: Vegetation communities identified at the study site (Adapted from Mucina & Rutherford 2006).....	9
FIGURE 2.5: Vegetation types present at the study site (Adapted from the base map of Birch & Birch 2007).....	11
FIGURE 3.1: Morphometric data for 25 ground pangolins found electrocuted at Kalahari Oryx Private Game Farm between September 2009 and August 2012, compared to the morphometric data for all ground pangolins recorded at this site.....	25
FIGURE 3.2: Total numbers of ground pangolin electrocutions recorded between December 2007 and July 2012 on Kalahari Oryx Private Game Farm, shown per month.....	26
FIGURE 4.1: Location of the present study in relation to previous ground pangolin research. (A) Hans Hoheison Wildlife Research Station and (B) Thabazimbi: van Aarde <i>et al.</i> 1990, Jacobsen <i>et al.</i> 1991; (C) Sengwa Wildlife Research Station: Heath & Coulson 1997a,b, 1998, Richer <i>et al.</i> 1997; and (D) Sabi Sand Game Reserve: Swart 1996, Swart <i>et al</i> 1999.....	38

- FIGURE 4.2:** Summer (Nov – Feb) and winter (May – Aug) home ranges for an adult female (STEM 5) and adult male (STEM 38) ground pangolin. (A) STEM 5 summer home range (n = 61); (B) STEM 5 winter home range (n = 24); (C) STEM 38 summer home range (n = 154); (D) STEM 38 winter home range (n = 210). The 50th, 75th & 95th percentile Kernel home ranges are displayed for each season. Solid dark lines show electrified game-proof fences; the dashed dark line indicates an electrified fence that was removed during this study..... 45
- FIGURE 4.3:** Emergence times of two adult male (STEM 38 & STEM 47) and a young adult female (STEM 39) ground pangolin. Emergence times are based on 1-hour intervals according to the 24-hour clock..... 50
- FIGURE 4.4:** Distribution of ground pangolin sightings at the study site between September 2009 and October 2012. Solid boundary lines indicate electrified game-proof fences, the dashed line indicates a new electrified fence that was erected during the course of this study and the dotted line indicates an electrified fence that was removed during the course of this study. Dark triangles indicate ground pangolin sightings and solid lines indicate the MCP home ranges of study animals..... 54
- FIGURE 5.1:** Location of the present study in relation to previous ground pangolin research. (A) Hans Hoheison Wildlife Research Station and (B) Thabazimbi: van Aarde *et al.* 1990, Jacobsen *et al.* 1991; (C) Sengwa Wildlife Research Station: Heath & Coulson 1997a,b, 1998, Richer *et al.* 1997; and (D) Sabi Sand Game Reserve: Swart 1996, Swart *et al.* 1999..... 65
- FIGURE 5.2:** Absolute numbers of epigaeic ants and termites captured in day and night samples between March 2011 and February 2012. The average minimum and maximum temperatures as well as rainfall during this period are also shown..... 76
- FIGURE 5.3:** (A) Winter (May – Aug) and (B) Summer (Nov – Feb) variation in the relative abundance of the five most common ant species, and ant and termite species that were preyed on by ground pangolins, pooled for all eight sites. Species marked with a ‘*’ were preyed on by ground pangolins..... 78

FIGURE 6.1: Core body temperature trace of a free-ranging adult female ground pangolin *Smutsia temminckii* measured between 31 May and 3 July 2011. The exploded section shows daily core body temperature variation between 11 and 19 June.....

89

CHAPTER ONE

GENERAL INTRODUCTION

Pangolins (Pholidota: Manidae) are unique amongst mammals in that they are covered in scales rather than fur (Smithers 1983; Swart 1997). These scales consist of a keratin layer overlying a harder plate of calcareous origin (*pers. obs.*) and afford them effective protection against predators (Swart 1997). When threatened, pangolins roll into a ball, thus protecting the vulnerable head and soft underbelly from attack and presenting a formidable barrier of sharp scales to any would-be predator (Kingdon 1971; Smithers 1971; Robinson 1983; Heath 1992; Richer *et al.* 1997; Swart 1997; Heath & Coulson 1998; *pers. obs.*). There are eight species of pangolin in three genera, all of which are restricted to Africa and the Oriental regions. Of these eight species, two arboreal (*Phataginus tricuspis* and *P. tetradactyla*) and two terrestrial (*Smutsia temminckii* and *S. gigantea*) species occur in Africa, of which only the ground pangolin *S. temminckii* reaches the southern African subregion (Gaudin *et al.* 2009).

Ground pangolins are scarce, mostly nocturnal mammals that occur from the northern portions of South Africa in the south to Chad and southern Sudan in the north (Heath 1992). They are variable in size, averaging between 12 – 18 kg and in excess of 1.2 m in length in the moister eastern portions of southern and East Africa (Kingdon 1971; Smithers & Wilson 1979; Coulson 1989; van Aarde *et al.* 1990; Jacobsen *et al.* 1991; Heath & Coulson 1998; Richer *et al.* 1997; Swart 1997; Swart *et al.* 1999), while averaging 5 – 10 kg and rarely exceeding 1.2 m in the more arid

western portions of South Africa (*pers. obs.*). Despite their fairly wide distribution, ground pangolins remain poorly studied.

Sweeney (1956) was the first person to report on the ecology of this species when he studied the dietary preferences of two captive individuals in Sudan. Later van Ee (1966, 1978) published some notes on the captive husbandry of ground pangolins at the Bloemfontein Zoo in the Free State. Many years later, van Aarde *et al.* (1990) studied eleven ground pangolins in the former Transvaal (present-day Mpumalanga, Limpopo, Gauteng and North-West Provinces) in a pilot study for the research to be undertaken by Swart (1996). Jacobsen *et al.* (1991) were the first to publish results on home range size and translocation success, also in the former Transvaal. Heath & Coulson (1997a,b) reported on the home range size and relocation success of ground pangolins, Richer *et al.* (1997) studied the diet and activity patterns of this species and Coulson (1989) reported on aspects of ground pangolin ecology, all in Zimbabwe. Most recently Swart (1996; see also Swart *et al.* 1999) studied the diet and activity patterns of this species in the Sabi Sand Game Reserve in north-eastern South Africa. All of these studies focussed on the ecology and physiology of this species in moist environments, and at present there is no data available on these aspects in arid environments. This lack of data precludes any comparisons being drawn on how these important attributes vary between the two environments and also hampers the formation of comprehensive conservation guidelines for this species as a whole.

Ground pangolins are described as being predominantly nocturnal (Wilson 1994; Gaubert 2011) or crepuscular (van Aarde *et al.* 1990; Jacobsen *et al.* 1991) although certain authors make mention of some diurnal activity (Smithers 1971; Smithers &

Wilson 1979; Coulson 1989; Jacobsen *et al.* 1991; Swart 1996; Heath & Coulson 1997a; Richer *et al.* 1997). Swart (1996) suggested that the apparent crepuscular activity recorded by some authors may be due to an increase in observer activity at this time of day rather than a true reflection of ground pangolin activity, and also recorded individuals emerging from their burrows significantly earlier in winter.

Ground pangolins are edentate and wholly myrmecophagous, showing a preference for formicid ants (Sweeney 1956; Smithers 1971; Robinson 1983; Jacobsen *et al.* 1991; Heath 1992; Swart 1996, 1997; Swart *et al.* 1999) and litter-feeding termites (Jacobsen *et al.* 1991; Swart 1996). These are typically located by smell and the subterranean nests broken open with the powerful front claws before feeding commences (Sweeney 1956; Jacobsen *et al.* 1991; Heath 1992; Swart 1996, 1997). Ants and termites of all castes are 'captured' with the long sticky tongue and transferred to the muscular stomach (Jacobsen *et al.* 1991; Heath 1992; Swart 1996, 1997) where they are ground up with the aid of grit that is inadvertently ingested while foraging (Kingdon 1971; Swart 1997).

This species is currently listed as *Least Concern* by the IUCN, although many assessment criteria are data deficient and the population is believed to be declining throughout its distribution (Hoffmann 2008). This species' vulnerability is currently attributed to three main causes, *viz.* the *muthi* (traditional medicine) trade, indiscriminate application of pesticides and the degradation of natural habitats (Swart 1996). The *muthi* trade affects ground pangolins directly by individuals being killed for their perceived medicinal properties and value in superstitious rituals, for their scales which are used in traditional ornaments, for food, and out of fear or ignorance (Ansell 1960; Kingdon 1971; van Aarde *et al.* 1990; Heath 1992, and references therein;

Swart 1996; Heath & Coulson 1997b; Kyle 2000; Friedmann & Daly 2004). The indiscriminate application of pesticides affects ground pangolins directly through secondary or inadvertent poisoning, while also reducing the amount of available food by killing the ants and termites in the area (van Ee 1966; Swart 1996). Habitat degradation affects ground pangolins by removing suitable foraging habitat and refuges, while also reducing food availability by making areas unsuitable for habitation by this species' preferred prey species (Swart 1996).

This study represents the first ecological and biological study of ground pangolins in an arid environment. These data provide insights into how this species copes with the challenges that are peculiar to arid environments, while also allowing comparisons to be drawn between the ecology of this species in arid and mesic environments. These data will greatly assist with determining conservation priorities for this species and will provide additional data to consider when compiling conservation action plans. As is often the case with any research, this study also highlights gaps in our present knowledge relating to this species, and it is hoped that this study will provide a baseline for further studies of all four African pangolin species to build on and will reignite interest in this oft-forgotten mammalian family.

CHAPTER TWO

STUDY AREA

2.1 Location

Kalahari Oryx Private Game Farm is situated midway between Upington and Olifantshoek in the Northern Cape Province of South Africa. The farm lies between latitudes 28°21'S – 28°42'S and longitudes 21°55'E – 22°15'E and falls wholly within the Kalahari biome of South Africa. The farm is characterised by flat plains in the extreme west, grading through fossil duneveld throughout most of the interior and northern portions, and with pronounced rocky mountains which form part of the greater Skurweberg range in the east and extreme south. The altitude gradually increases from west to east, with the lowest point on the farm situated at 936 metres above sea level (asl) in the extreme west, through to 1 297 m asl on a mountain top in the north-east.

The farm is 52 000 ha in extent, which for managerial purposes has been divided into four units (Figure 2.1). The farm is fenced as per the Northern Cape Nature Conservation Act 9/2009 (NCNCA 9/2009) specifications for large predators, *viz.* a 2.4 m high, 21-strand game fence with wire mesh extending 950 mm up the fence and buried to a depth of 250 mm. There are six electrified live strands and five earth strands offset from the fence with insulated brackets, and a double-strand live : earth (inside) or single-strand live (outside) tripwire offset 500 mm from the fence and set at a height of 200 mm. It should be noted that the farm is fenced as per the specifications of the draft Northern Cape Nature Conservation Act, which requires a single live strand on the outside tripwire. The updated NCNCA 9/2009 requires that

both internal and external tripwires consist of an upper live and a lower earth strand. Glen Ruby and Langkloof do not have electrified fence strands, except where they share a common boundary with Bergvlakte and Tweepoort.

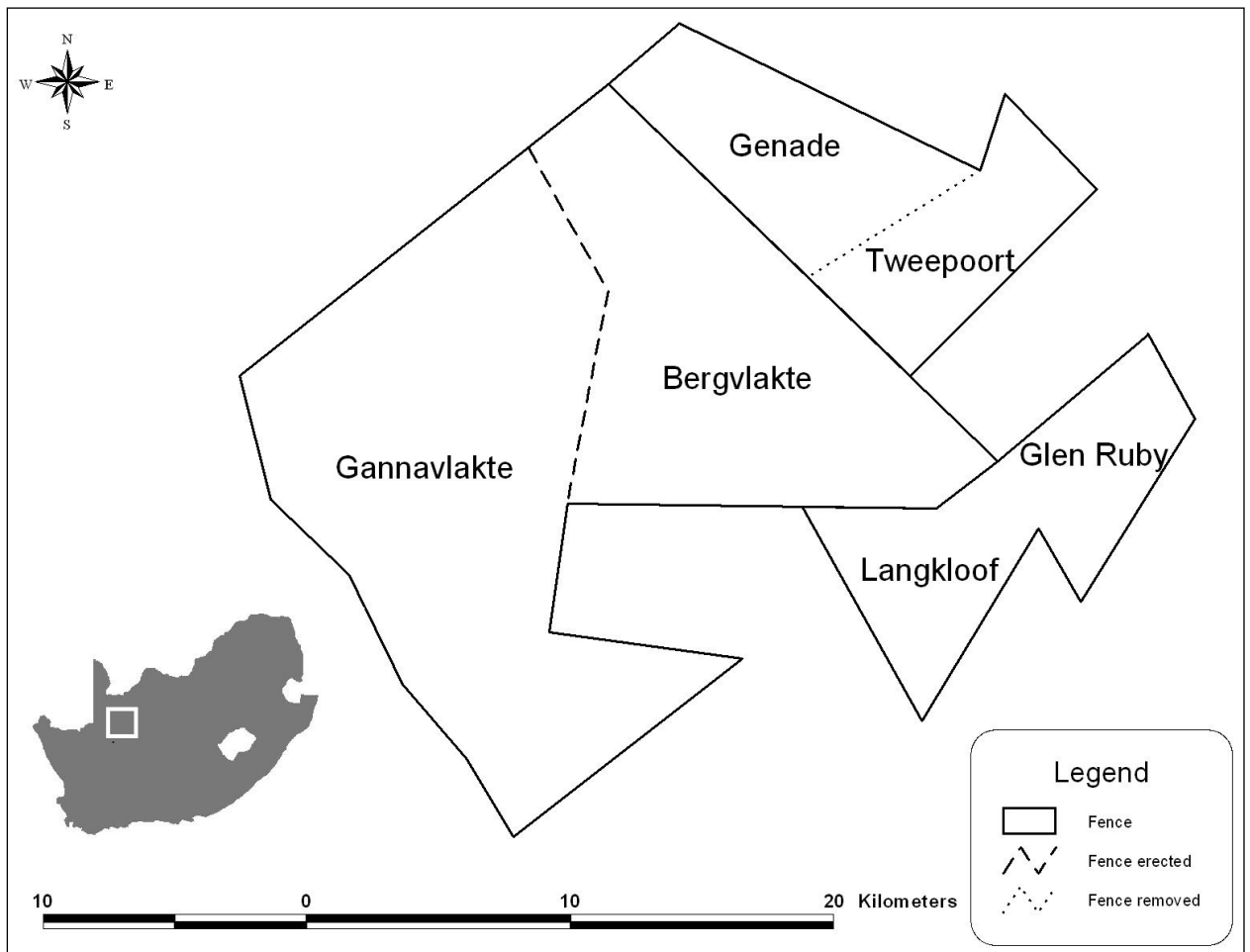


Figure 2.1. Layout of the study site and its location within South Africa. Names refer to the different sub-farms.

2.2 Climate

The study site is characterised by extremes in climate with very hot summers and very cold winters which combined with a low, unpredictable rainfall and strong winds result in a very harsh environment. Summer air temperatures may exceed 40 °C, with an average maximum summer temperature of 34 °C and an average minimum temperature of 17 °C. Winter temperatures may drop as low as -14 °C and minimum

winter temperatures average 3 °C while winter maximum temperatures average 19 °C (Figure 2.2). Severe frost is a common occurrence and can occur from the beginning of May to the middle of October. The majority of rain falls between October and April with a peak from December to March, predominantly in the form of thunderstorms. There is, however, some rainfall recorded throughout all months of the year (Figure 2.2). Rainfall tends to decrease on a northeast – southwest axis, with the highest rainfall being recorded in the northeast and east, and the lowest rainfall recorded in the southern portions of the study site. Sleet has been recorded on three occasions in winter, but these are exceptional occurrences. The temperature variations recorded during the course of this study mirror the long-term averages at the study site, while the average annual rainfall during the study (341 mm) was higher than the long-term average (284 mm).

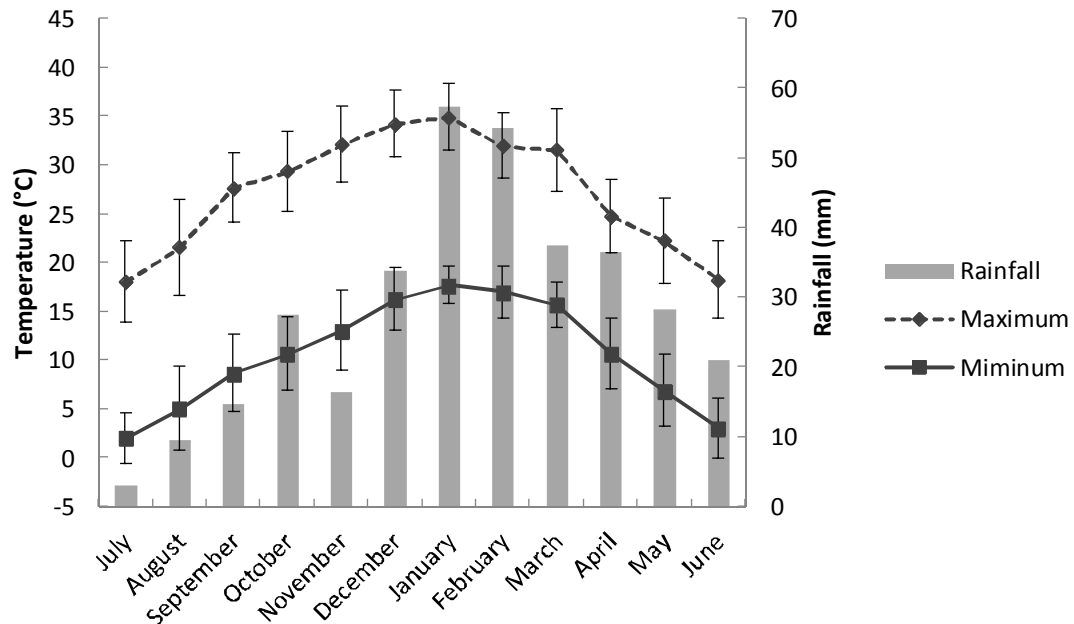


Figure 2.2. Average climatic conditions recorded at the study site between July 2000 and June 2012. Average temperatures are presented as mean \pm SD while rainfall is presented as the monthly average only.

2.3 Geology

The soils at the study site largely consist of undifferentiated, structureless soils. In the extreme west undifferentiated, structureless soils of calcareous origin are present in a narrow band orientated on a north – south axis (Figure 2.3). These soils also penetrate marginally into the eastern portions of the study site, notably on the extreme north-eastern portions of Glen Ruby. These soils are hard and poorly drained. Mountainous regions are restricted to the eastern portions of the study site and are characterised by rocky landscapes that are 30 – 195 m above the surrounding plains. Soils in these mountainous regions are shallow sandy-clay-loam and moderately to well-drained. The majority of the study site is characterised by unstructured, well-drained red Aeolian sands that occur in the form of parallel fossil dunes orientated in a NNW – SSE direction and raised 3 – 8 m above the surrounding plains, with dune streets of varying diameter between successive dunes.

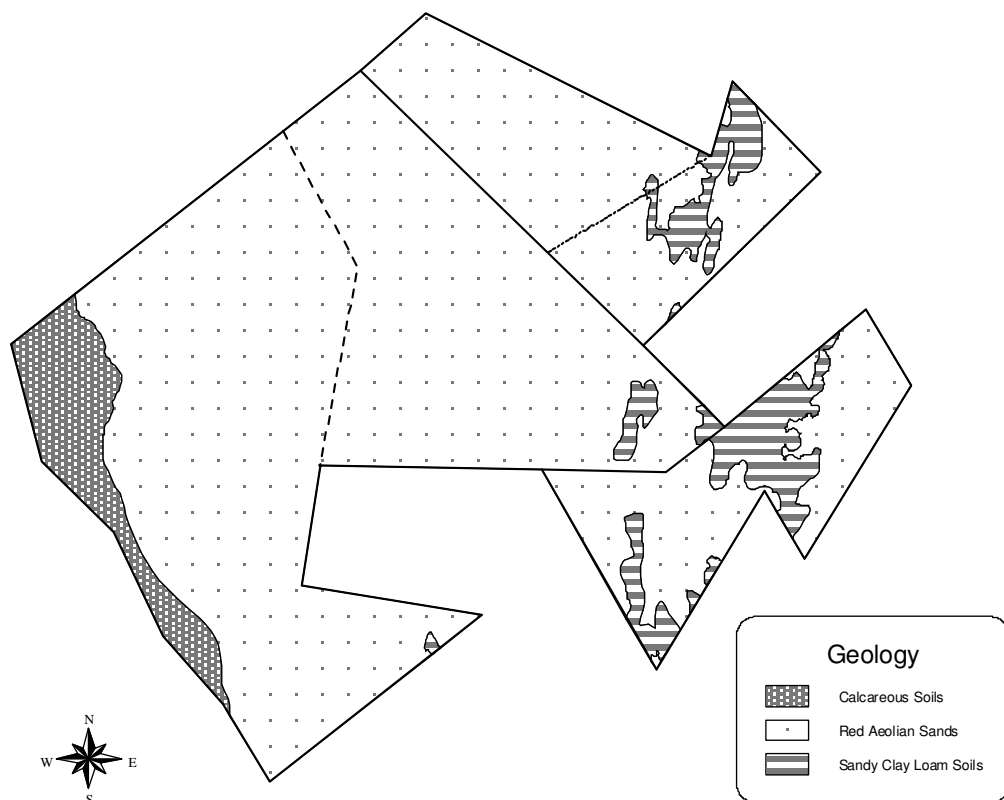


Figure 2.3. Geological formations present at the study site (Adapted from the base map available on the SANBI website <<http://bgis.sanbi.org/mapsearch.asp>>).

2.4 Vegetation

The vegetation communities on the study site represent a convergence between five major vegetation types as described by Mucina & Rutherford (2006), *viz.* Gordonia Duneveld (SVkd 1), Olifantshoek Plains Thornveld (SVk 13), Koranna-Langeberg Mountain Bushveld (SVk 15), Gordonia Plains Shrubland (SVk 16) and Kalahari Karroid Shrubland (NKb 5) (Figure 2.4).

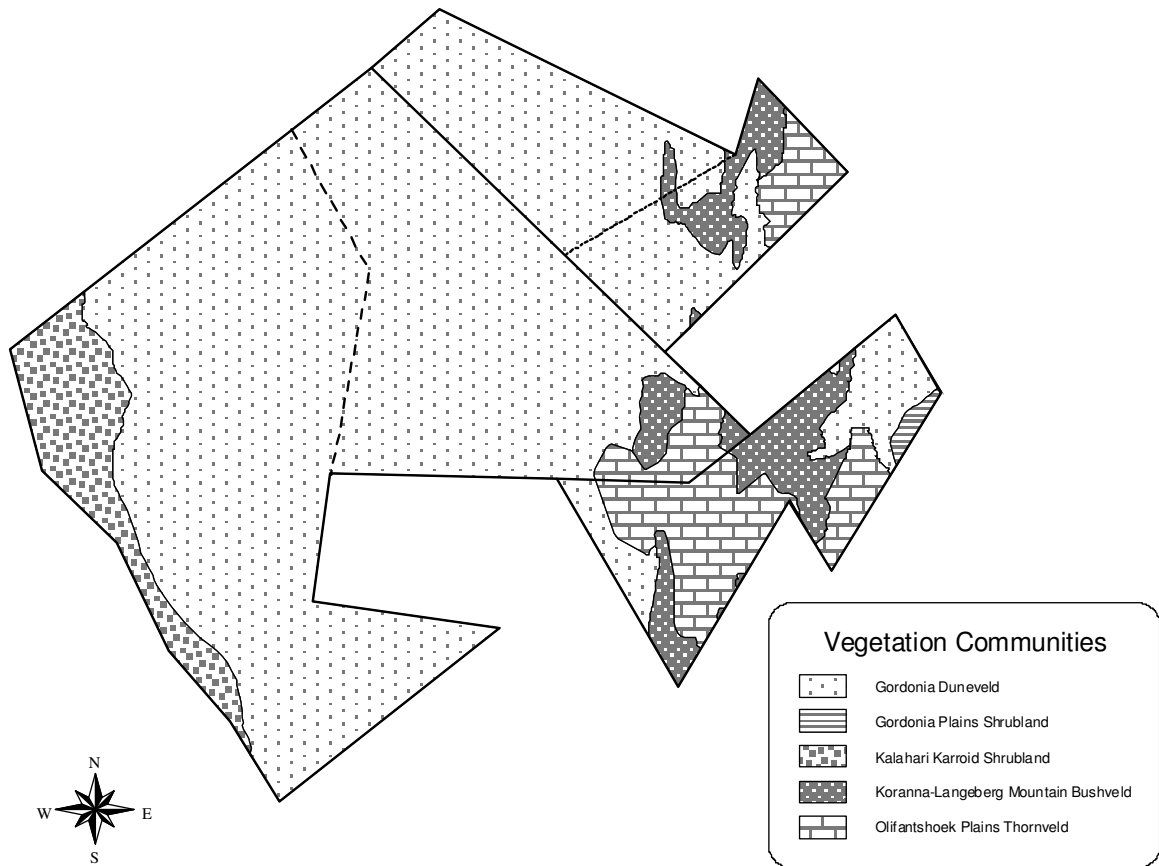


Figure 2.4. Vegetation communities identified at the study site (Adapted from Mucina & Rutherford 2006).

Within these communities, the vegetation at the study site can be further divided into nine types (Figure 2.5). The Gordonia Duneveld is comprised of *Acacia*

haematoxylon Savannah, Mixed Savannah and Duneveld Grassland. All three these vegetation types are characterised by stable, parallel dunes of unstructured and easily drained Aeolian sands that are raised 3 – 8 m above the surrounding plains. Olifantshoek Plains Thornveld occurs along the margins of the mountains as well as on some low-lying rocky areas between the mountains. This vegetation type is represented locally by *Acacia mellifera* Thickets, *Acacia erioloba* Veld, *Acacia mellifera* - *Rhigozum trichotomum* Veld (in the east) as well as elements of *Acacia haematoxylon* Savannah, Mixed Savannah and Dwarf Karroid Shrubland. Koranna-Langeberg Mountain Bushveld is typified by rugged mountainous regions, with the sole local representative being Mountain Veld. The Kalahari Karroid Shrubland is dominated by low-growing shrubs on undifferentiated, structureless soils of calcareous origin with isolated trees that are generally below 3 m in crown height. This community can be sub-divided into Grassy Dwarf Shrubland and *Acacia mellifera* - *Rhigozum trichotomum* Veld (in the west). Gordonia Plains Shrubland is present only in the extreme east of the study site, where it is represented by Dwarf Karroid Shrubland on calcareous soils, or shallow Aeolian sands overlying calcrete.

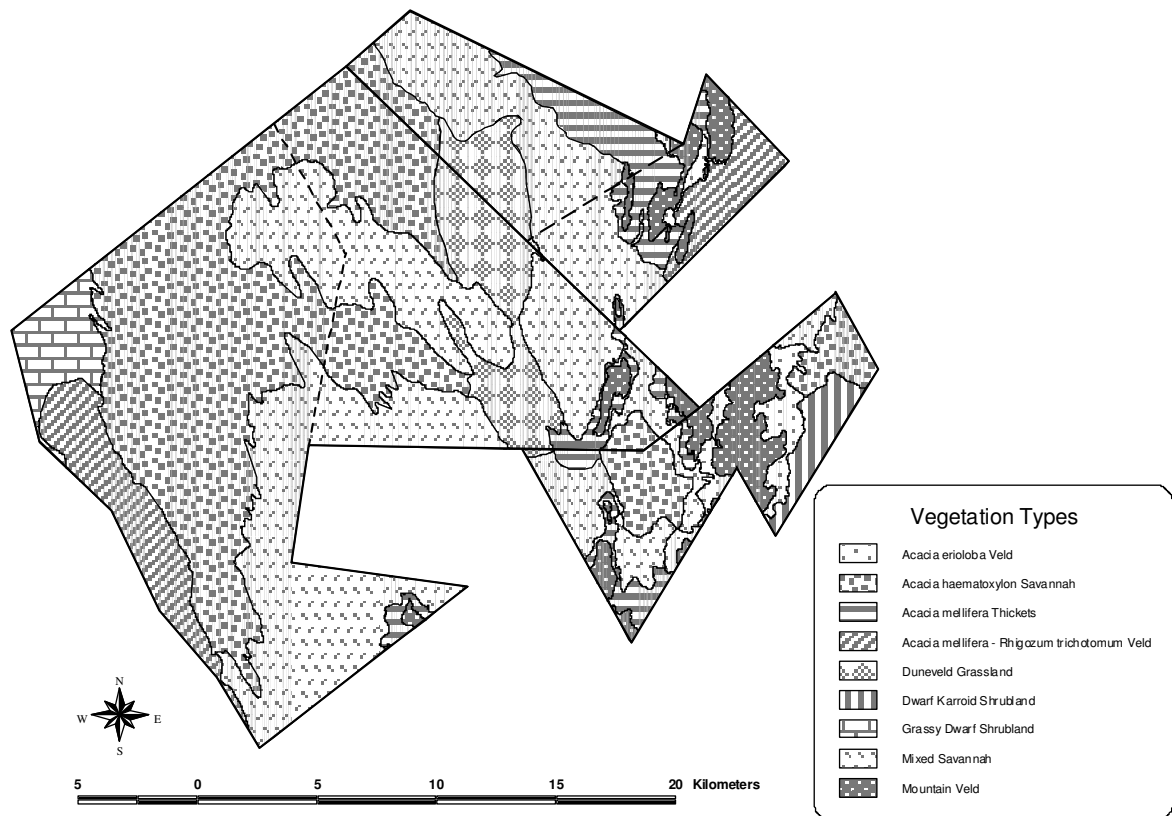


Figure 2.5. Vegetation types present at the study site (Adapted from the base map of Birch & Birch 2007).

Each vegetation type is discussed in more detail below. The description of each vegetation type is largely based on the descriptions of Mucina & Rutherford (2006) and Birch & Birch (2007), with ground-proofing and modifications where required.

2.4.1 *Acacia erioloba* Veld

This vegetation type is found at the base of mountains and in the narrow valley floors between mountains, where the clay content of the soil is slightly higher. Although tree cover is generally fairly good, the grass cover varies from areas with good cover to large open patches where the grass has been over-utilised by game. The dominant tree species is *Acacia erioloba* and these vary in size from smallish trees of 2 – 3 m to large mature trees exceeding 6 m in height. Other common trees and shrubs

include *Ziziphus mucronata*, *Acacia mellifera*, *Boscia albitrunca*, *Phaeoptilum spinosum*, *Lycium cinereum*, *L. hirsutum* and *Monechma incanum*. The grass layer is comprised mainly of *Stipagrostis u. uniplumis*, *Eragrostis l. lehmanniana*, *Aristida stipitata*, *Schmidtia kalahariensis*, *Schmidtia pappophoroides*, *Aristida c. congesta*, *Eragrostis trichophora* and *Centropodia glauca*. Forbs are dominated by *Eriocephalus spinescens*, *Barleria rigida*, *Plinthus karrooicus*, *Hermbstaedtia linearis*, *Sarcostemma viminale*, *Protasparagus africanus*, *P. racemosus*, *P. suaveolens*, *Chrysocoma ciliata*, *Eriocephalus spinescens*, *E. ericoides*, *Helichrysum argyrosphaerum*, *Cleome angustifolia*, *Acanthosicyos naudinianus*, *Citrullus lanatus*, *Elephantorrhiza elephantina*, *Indigofera alternans*, *Senna italica arachoides*, *Harpagophytum p. procumbens* and *Hermannia vestita*. *Tribulus terrestris* and *Tribulus z. zeyheri* are common in the over-utilised areas, where they often form dense carpets after the first good summer rains. A portion of this vegetation type on Glen Ruby has been invaded by the exotic tree species *Prosopis g. glandulosa*.

2.4.2 *Acacia haematoxylon* Savannah

This veld type is found predominantly on the undulating duneveld. It is characterised by a fairly high percentage of grass cover (60 – 80 %) and a low tree density (5 – 10 %). The dominant tree species is *Acacia haematoxylon*, which are usually quite short (2 – 3 m) in stature. The forb community contains mainly *Monechma incanum*, *Elephantorrhiza elephantina*, *Hermannia tomentosa*, *Gnidia polycephala* and *Crotalaria spartioides*. Common grass species include *Centropodia glauca*, *Stipagrostis u. uniplumis*, *Eragrostis l. lehmanniana*, *Aristida meridionalis*, *Stipagrostis ciliata*, *S. obtusa*, *Schmidtia pappophoroides*, *Aristida c. congesta*, *Eragrostis micrantha*, *Eragrostis pallens*, *Antheophora argentea* and *A. pubescens*. *Stipagrostis amabilis* is more common on the dune crests, while the similar *S.*

namaquensis forms dense stands in dune valleys, especially in areas that appear to contain more moisture. *Schmidtia kalahariensis* and *Tribulus z. zeyheri* are common in areas that have been overgrazed, as well as around drinking troughs, where the trampling effect of visiting game largely limits the establishment and growth of perennial grass species. The exotic tree species *Prosopis g. glandulosa* has invaded this vegetation type in areas, especially around waterholes and in isolated pockets in dune streets where it may form dense stands.

2.4.3 *Acacia mellifera* Thickets

As the name implies, this veld type is dominated by *Acacia mellifera*, which occurs either as dense stands or as more open savannah. Tree density ranges from 10 to > 20 %, and grass coverage is moderate at 50 – 60 %. This vegetation type usually occurs near mountains, where the sands have a higher clay content, and often abuts between the Mountain Veld or *Acacia erioloba* Veld and the sandy duneveld vegetation types. Other tree and shrub species occurring in this vegetation type include *Acacia erioloba*, *Grewia flava*, *Boscia albitrunca*, *Rhigozum trichotomum*, *Parkinsonia africana* and *Ehretia rigida*. Grass cover is dominated by *Eragrostis l. lehmanniana*, *Aristida c. congesta*, *A. meridionalis*, *A. vestita*, *Stipagrostis u. uniplumis*, *S. ciliata*, *Eragrostis trichophora*, *Centropodia glauca*, *Schmidtia pappophoroides*, *Enneapogon cenchroides* and *Panicum maximum*. *Schmidtia kalahariensis* and *Tribulus z. zeyheri* occur in disturbed and overgrazed areas. The dominant forbs are *Elephantorrhiza elephantina*, *Indigofera alternans*, *Lebeckia linearifolia*, *Senna italica arachoides*, *Monechma incanum*, *Protasparagus africanus*, *P. racemosus*, *P. suaveolens*, *Helichrysum argyrosphaerum*, *Acanthosicyos naudinianus*, *Pentzia incana*, *Lycium cinereum*, *Hermannia vestita* and *Chrysocoma ciliata*. *Boophane disticha* are also present in small numbers.

2.4.4 *Acacia mellifera* - *Rhigozum trichotomum* Veld

The *Acacia mellifera* - *Rhigozum trichotomum* veld is most prevalent on flat areas of red sand. These areas usually have a higher clay content, resulting in more moisture being retained in the soil and resultantly a sweeter veld. This in turn leads to grazers concentrating on this veld, consequently leading to over-utilization and degradation of this veld and ultimately invasion by poorly palatable pioneer species such as *Rhigozum trichotomum* which often form dense, impenetrable stands. Grass cover is generally minimal. The only other shrub that occurs with any frequency in this vegetation type is *Searsia tridactyla*. Grass species are dominated by *Aristida c. congesta*, *Schmidtia kalahariensis*, *Eragrostis l. lehmanniana*, *Aristida stipitata*, *Stipagrostis u. uniplumis*, *S. obtusa*, *S. ciliata*, *Enneapogon cenchroides* and *Centropodia glauca*. Trees consist of *Acacia mellifera*, *A. erioloba* and *Boscia albitrunca*. The few forbs that are present are *Monechma incanum*, *Eriocephalus spinescens*, *Protasparagus africanus*, *Chrysocoma ciliata*, *Ehretia rigida*, *Acanthosicyos naudinianus*, *Senna italica arachoides*, *Harpagophytum p. procumbens*, *Hermannia vestita* and *Tribulus z. zeyheri*.

2.4.5 Duneveld Grassland

This vegetation type occurs in the fossil duneveld and is characterised by a vegetation structure that is nearly entirely devoid of any trees or large shrubs. The trees and shrubs that are present comprise < 5 % of this vegetation type and are typically of a dwarf (< 1.5 m) growth form. The dominant grasses are *Centropodia glauca*, *Stipagrostis u. uniplumis*, *S. obtusa*, *S. ciliata*, *S. amabilis*, *Aristida meridionalis*, *A. c. congesta*, *A. stipitata*, *Panicum c. coloratum*, *Schmidtia pappophoroides*, *Anthephora pubescens*, *A. argentea*, *Eragrostis l. lehmanniana*,

Eragrostis micrantha and *E. pallens*. The forb layer is dominated by *Elephantorrhiza elephantina*, *Monechma incanum*, *Hermannia tomentosa*, *H. vestita*, *Gnidia polycephala*, *Crotalaria spartioides*, *Acanthosicyos naudinianus*, *Senna italica arachoides*, *Indigofera alternans* and *Thesium* sp. The few stunted trees that are present are usually *Boscia albitrunca*, *Acacia haematoxylon* or *A. mellifera*.

2.4.6 Dwarf Karroid Shrubland

The Dwarf Karroid Shrubland is characterised by a very low (< 0.5 m) growth form occurring on flats on calcareous soils. As the name implies, the plant species that occur here are mainly of karroid origin and grow at very low densities, resulting in a lot of bare ground. The dominant plant species are *Eriocephalus ericoides*, *E. spinescens*, *Monechma incanum*, *Pentzia calcarea*, *P. incana*, *P. lanata*, *Barleria rigida*, *Plinthus karrooicus*, *Chrysocoma ciliata*, *Felicia f. filifolia*, *F. m. muricata*, *Geigeria ornativa*, *Helichrysum argyrosphaerum*, *Pteronia glauca*, *Cleome angustifolia*, *Indigofera alternans*, *Lebeckia linearifolia*, *Senna italica arachoides*, *Harpagophytum p. procumbens*, *Thesium* sp., *Aptosimum spinescens*, *Sutera halimifolia*, *S. virgulosa*, *Walafrida saxatilis*, *Lycium spinosum*, *Hermannia vestita* and *Gnidia polycephala*. *Phaeoptilum spinosum* is present at low densities. The dominant grass is *Eragrostis* cf. *truncata*, but other species such as *Eragrostis l. lehmanniana*, *Aristida c. congesta*, *Schmidtia pappophoroides*, *Stipagrostis u. uniplumis* and *Centropodia glauca* are also present, especially towards the edge of this community. The exotic tree species *Prosopis g. glandulosa* has invaded this vegetation type to a minimal extent, but is mainly restricted to the vicinity of dry drainage lines.

2.4.7 Grassy Dwarf Shrubland

This vegetation type also occurs on calcareous plains, although the calcrete may be shallowly covered with red sand. This vegetation type also has a low growth form (typically < 0.5 m) consisting mainly of dwarf karroid shrubs, while bare patches of calcrete are a common sight where this vegetation type has been overgrazed. The dominant shrubs are *Monechma foliosum*, *M. incanum*, *Chrysocoma ciliata*, *Zygophyllum* sp., *Barleria rigida*, *Plinthus karrooicus*, *Eriocephalus spinescens*, *E. ericoides*, *Pentzia calcarea*, *Pteronia glauca*, *Indigofera alternans*, *Lebeckia linearifolia*, *Senna italica arachoides*, *Thesium* cf. *lineatum*, *Aptosimum spinescens*, *Sutera halimifolia*, *Phaeoptilum spinosum*, *Walafrida saxatilis*, *Lycium spinosum* and *Hermannia vestita*. The grasses are dominated by *Stipagrostis ciliata*, *Eragrostis trichophora*, *Aristida c. congesta*, *A. meridionalis*, *Centropodia glauca*, *Eragrostis l. lehmanniana*, *Schmidtia pappophoroides* and *Stipagrostis u. uniplumis*. *Schmidtia kalahariensis*, *Tribulus terrestris* and *T. z. zeyheri* dominate in overgrazed and disturbed areas. In patches this area has been invaded by the exotic tree *Prosopis g. glandulosa* which occurs either as small shrubs or large, scattered trees.

2.4.8 Mixed Savannah

The Mixed Savannah is found in the undulating duneveld and is characterised by a high percentage grass cover (60 – 80 %) and a fairly high tree and shrub diversity with a moderate (10 – 20 %) tree cover. Common tree species include *Boscia albitrunca* and *Acacia mellifera*, but fair numbers of *Acacia erioloba*, *A. haematoxylon* and the shrubs *Grewia flava*, *Ziziphus mucronata* and *Phaeoptilum spinosum* are also present. *Parkinsonia africana* is relatively common in the west and south of the study site, but occurs sporadically elsewhere. Other shrubs include *Searsia burchelli* and *S. tridactyla*. The most common grass species are *Eragrostis l. lehmanniana*,

Stipagrostis u. uniplumis, *S. ciliata*, *S. obtusa*, *Aristida meridionalis*, *A. stipitata*, *Panicum c. coloratum*, *Anthephora pubescens*, *Aristida c. congesta*, *Eragrostis trichophora*, *Centropodia glauca*, *Schmidtia pappophoroides*, *Eragrostis pallens*, *Enneapogon cenchroides*, *Eragrostis aspera* and *Pogonarthria squarrosa*. *Stipagrostis amabilis* is present on the dune crests while the similar *S. namaquensis* is occasionally found in dune streets and in low-lying areas, and is particularly common in and bordering dry watercourses. *Panicum maximum* and *Cenchrus ciliaris* occur in shaded environments, while *Schmidtia kalahariensis*, *Tribulus z. zeyheri* and *T. terrestris* are common in disturbed and overgrazed areas. The dominant shrubs, in addition to *G. flava*, are *Ziziphus mucronata*, *Monechma incanum*, *Rhigozum trichotomum*, *Ehretia rigida*, *Acacia h. hebeclada* and *Euphorbia mauritanica*. The forbs are dominated by *Elephantorrhiza elephantina*, *Lebeckia linearifolia*, *Senna italica arachoides*, *Helichrysum argyrosphaerum*, *Lycium cinereum*, *Hermannia tomentosa*, *Crotalaria spartioides*, *Cleome angustifolia*, *Gnidia polycephala*, *Acanthosicyos naudinianus*, *Protasparagus africanus*, *P. racemosus*, *Cyperus usitatus* and *Thesium hystrix*. *Nerine laticoma* occurs in the south of the study site. The exotic tree species *Prosopis g. glandulosa* has invaded this veld type in some places, especially around waterholes and in dune streets, where it may form dense stands or less frequently occurs as solitary trees.

2.4.9 Mountain Veld

The Mountain Veld is one of the most diverse vegetation types on the study site and also varies the most in topography. Rock cover is relatively high at 50 – 60 %, but grass cover between the rocks is near 100 %. There are also numerous shrubs growing in between the rocks and in the rock crevices and succulents are fairly common. The shrub component consists of *Acacia mellifera*, *Rhigozum obovatum*, *R.*

trichotomum, *Croton gratissimus*, *Searsia burchelli*, *S. lancea*, *S. pyroides*, *S. tridactyla*, *Boscia albitrunca*, *Euclea undulata*, *Ehretia rigida*, *Euphorbia mauritanica*, *Ziziphus mucronata* and *Grewia flava*. *Barleria rigida*, *Justicia thymifolia*, *Plinthus karrooicus*, *Sarcostemma viminale*, *Protasparagus africanus*, *P. suaveolens*, *Rumohra* spp., *Geigeria ornativa*, *Helichrysum argyrosphaerum*, *Hertia pallens*, *Putterlickia pyracantha*, *Indigofera sessilifolia*, *Senna italica arachoides*, *Pelargonium* sp., *Salvia* sp., *Thesium* sp., *Lycium hirsutum*, *L. spinosum*, *L. cinereum* and *Hermannia vestita*. The bulbous *Boophane disticha* is also common. Common grasses include *Cenchrus ciliaris*, *Heteropogon contortus*, *Digitaria seriata*, *Aristida meridionalis*, *Anthephora argentea*, *Brachiaria nigropedata*, *Enneapogon cenchroides*, *Eragrostis l. lehmanniana*, *E. micrantha*, *Melinis nerviglumis*, *Eustachys paspaloides*, *Stipagrostis u. uniplumis* and *Centropodia glauca*.

CHAPTER THREE

REVIEW OF THE ANTHROPOGENIC THREATS FACED BY GROUND PANGOLINS *SMUTSIA TEMMINCKII* IN SOUTHERN AFRICA

3.1 INTRODUCTION

The ground pangolin *Smutsia temminckii* is an elusive, poorly-studied mammal occurring in the northern regions of South Africa and throughout the remainder of southern Africa (Sweeney 1956; Smithers 1971; Swart 1997). Their dorsal and lateral surfaces are covered in overlapping hard, plate-like scales (Smithers 1983; Swart 1997) which afford them protection from most predators and renders them unmistakable. When threatened, ground pangolins roll into a tight ball with the vulnerable head and soft underbelly covered by the broad, muscular tail, thus presenting the attacker with a nearly impenetrable barrier of armour (Kingdon 1971; Smithers 1971; Heath 1992; Richer *et al.* 1997; Swart 1997; Heath & Coulson 1998).

Due to the secretive nature and low population densities of this species, relatively little is known about the threats that it faces. All pangolin species are widely revered for their traditional healing powers (Kingdon 1971; Coulson 1989; Heath 1992; Bräutigam *et al.* 1994; Swart 1996; Heath & Coulson 1997b; Kyle 2000; Friedmann & Daly 2004; Soewu & Ayodele 2009; Manwa & Ndamba 2011; Whiting *et al.* 2011) and are also utilised as a source of protein (van Aarde *et al.* 1990; Ansell 1960; Kingdon 1971). Electrified game fences are known to pose a threat to ground pangolins (van Aarde *et al.* 1990; Friedmann & Daly 2004; Beck 2008) while other known threats identified in the literature are habitat destruction (Coulson 1989; Friedmann & Daly 2004) and a high susceptibility to chemicals (van Ee 1966, 1978;

Heath 1992; Friedmann & Daly 2004). Bräutigam *et al.* (1994) also make mention of the threat posed by the illicit export of pangolins for the Asian cuisine and traditional medicine markets and recent studies (Challender 2011; Challender & Hywood 2012) suggest that this threat is steadily increasing.

Ground pangolins are listed as *Vulnerable* in South Africa (Friedmann & Daly 2004), although most assessment criteria for this species are data deficient. Globally, this species is listed as *Least Concern* although the population is believed to be decreasing (Hoffmann 2008) and most assessment criteria are data deficient. Of the four African pangolin species, the ground pangolin has been studied most intensively, enabling us to review and consolidate the known threats that this species faces. No comprehensive threat review has previously been undertaken for this species, with even the most recent Red Data assessments relying on a limited amount of available data. Here the available literature pertaining to threats faced by ground pangolins in southern Africa is consolidated and new threats which have recently come to light are highlighted. New empirical data are also presented, primarily on mortality associated with electric fences. This review is intended to facilitate future threat assessments for this species, utilising a comprehensive dataset and ensuring that the assessment is as comprehensive as possible.

3.2 MATERIALS AND METHODS

Fence electrocution data were extracted from the records held by Kalahari Oryx Private Game Farm (KO), a 52 000 ha farm located at 28°30'S, 22°02'E in the southern Kalahari Desert in the Northern Cape Province of South Africa. As part of KO's fence monitoring protocol, fences were monitored three times per week and all

fence-related mortalities recorded. Data for the period 1 September 2009 – 31 August 2012 along a 93 km stretch of intensively monitored fence were used for the mortality rate calculation, while electrocutions from the entire farm were used to infer age, gender and seasonal electrocution characteristics. The farm is fenced as per the Northern Cape Nature Conservation Act 9/2009 (NCNCA 9/2009) specifications for large predators, *viz.* a 2.4 m high, 21-strand game fence with wire mesh extending 950 mm up the fence and buried to a depth of 250 mm. There are six electrified live strands and five earth strands offset from the fence with insulated brackets, and a double-strand live : earth (inside) or single-strand live (outside) tripwire offset 500 mm from the fence and set at a height of 200 mm. It should be noted that the farm is fenced as per the specifications of the draft Northern Cape Nature Conservation Act, which requires a single live strand on the outside tripwire. The updated NCNCA 9/2009 requires that both internal and external tripwires consist of an upper live and a lower earth strand.

Road mortalities were recorded from *ad hoc* monitoring of the N14 national road for 80 km between KO and the nearest town (Upington). Additional road mortalities were inferred from study skins present at KO that originated along a 15 km stretch of the N14 between 2003 and 2008.

Additional threats faced by ground pangolins were identified by reviewing relevant literature, as well as during informal interviews with landowners in the Northern Cape in an attempt to identify and quantify threats faced by ground pangolins in this region, as well as the extent to which livestock are predated by the two main predators of livestock, *viz.* caracal *Felis caracal* and black-backed jackal *Canis mesomelas* (hereinafter referred to as ‘damage-causing predators’).

3.3 THREATS

3.3.1 Electrified Fences

Ground pangolins are bipedal, walking on their hind legs with the front legs and tail held off the ground, which results in their unprotected underbellies being exposed while walking. When a ground pangolin comes into contact with an electrified fence the head or underbelly usually receives the initial shock. This results in the animal adopting its defence of rolling into a ball, often inadvertently wrapping itself around the electrified wire in the process. Once wrapped around the wire each successive shock causes the trapped animal to curl even tighter around the wire, until the repeated electrical pulses eventually kill it. Individuals found on electrified fences frequently display epidermal burns (including holes burnt through their scales), while internal injuries may also be significant. On occasions the electric pulses are too weak to kill an individual outright, but strong enough to invoke the defence response of remaining curled up in a ball (straddling the wires). In these instances individuals eventually succumb to exposure and / or starvation. If found in time, ground pangolins can often be removed from electric fences and released unharmed. However, after prolonged exposure to the electric current individuals may develop debilitating, apparently neurological disorders. Although these individuals may walk off after being removed from the fence, they do not move far before collapsing and ultimately dying from exposure and starvation.

The specifications for game fences stipulated in Provincial Nature Conservation Regulations depend on the type of game animals contained on a farm. In the Northern Cape, all fences for dangerous game include a two-strand offset tripwire on

either side of the fence set at a height of 200 mm, and a lowest electrified strand on the main fence also set at a height of 200 mm above the ground (NCNCA 9/2009). There is also a growing trend amongst livestock farmers to place an electrified wire on either side of their livestock fences at a height of 100 – 300 mm in an attempt to prevent damage-causing predators from gaining access to their farms (see also Beck 2008).

Fences *per se* do not pose a significant threat to ground pangolins or their movements, although reports were received of ground pangolins becoming entangled and dying in mesh livestock fences. When a ground pangolin reaches a fence, it usually walks along this structure, periodically testing the fence for any weak spots through which it can pass and often covering a considerable distance in the process. Weak spots in fences usually take the form of a hole dug underneath the fence by another species, or a spot where the fence has rusted through (particularly with older fences). In the case of a non-electrified fence, ground pangolins may resort to climbing over such an obstruction (Smithers 1971) and have been known to climb over fences in excess of 2 m in height (M. Booysen, *pers. comm.*).

Various authors have raised concerns over the numbers of ground pangolins electrocuted on fences (van Aarde *et al.* 1990; Friedmann & Daly 2004; Beck 2008), although only Beck (2008) gives quantitative data on the prevalence of electrocutions. During a year-long study at Tswalu Kalahari Reserve in the Northern Cape Province, Beck (2008) recorded an electrocution rate of 0.033 individuals.km⁻¹.yr⁻¹. This translates to one ground pangolin electrocuted per year for every 30 km of electrified fence.

Between 1 September 2009 and 31 August 2012, 21 ground pangolins were found electrocuted on the 93-km stretch of fence at KO and an additional four individuals were removed from this fence and released alive. These data (including individuals that were found alive and removed but which would have died otherwise) indicate a mortality rate of $0.09 \text{ individuals.km}^{-1}.\text{yr}^{-1}$, which is substantially higher than the mortality rate $0.033 \text{ individuals.km}^{-1}.\text{yr}^{-1}$ recorded by Beck (2008). Of the 29 electrocutions for which gender data are available, 55 % ($n = 16$) were male, 34 % ($n = 10$) were female and 10 % ($n = 3$) could not be sexed. These results suggest a slight male-biased fence mortality, which can be partially explained by the results of the biological study. Preliminary results suggest that male ground pangolins reach sexual maturity later than females and also establish a fixed home range at a later age (Chapter 4). Thus males traverse greater distances than females do and consequently stand a greater chance of encountering an electrified fence.

An analysis of the 25 electrocutions for which reliable morphometric data are available indicates a higher proportion of mortalities in the 3.0 – 7.0 kg (840 – 1110 mm) size range (Figure 3.1). There are two potential explanations for this finding: 1) This pattern represents the proportion of this size class in the greater population; and 2) Individuals in this size class are juveniles and young adults and many (especially males) appear to be floaters, i.e. wandering over large distances in search of a vacant territory (Chapter 4). Larger (i.e. older) animals tend to be sedentary with a fixed home range that may or may not include an electrified fence. In this latter instance, mature individuals largely appear to recognise the threat posed by these barriers and are able to negotiate them safely.

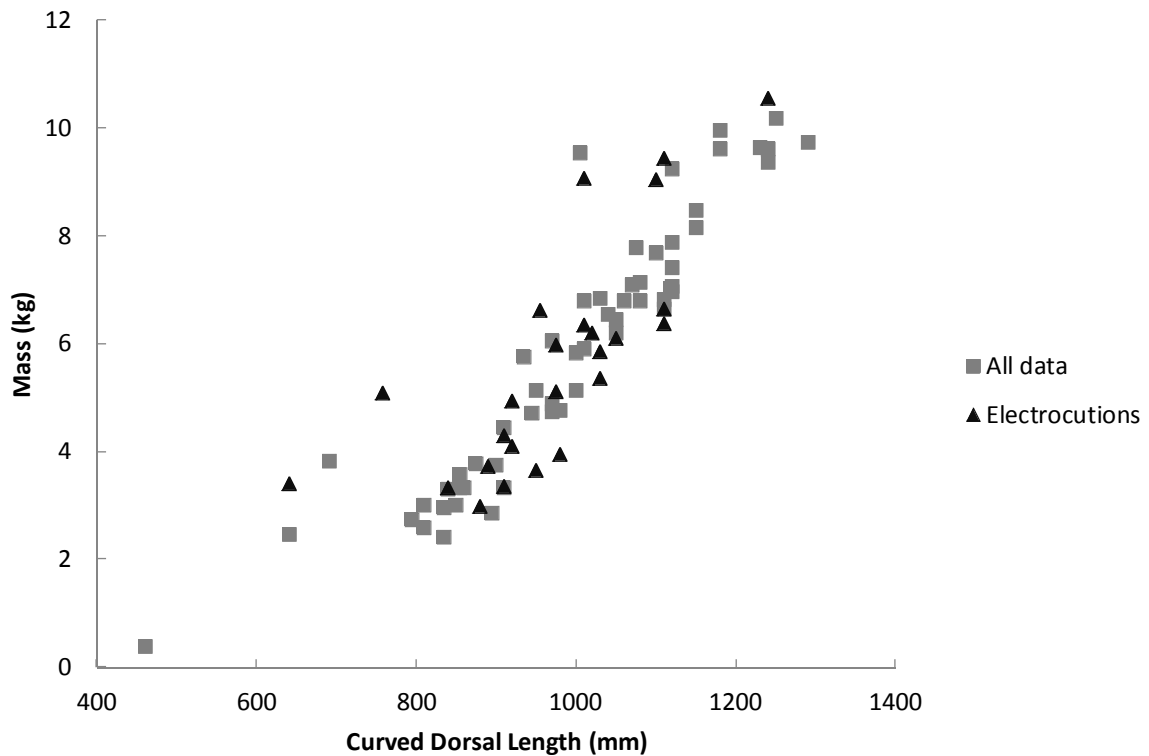


Figure 3.1. Morphometric data for 25 ground pangolins found electrocuted at Kalahari Oryx Private Game Farm between September 2009 and August 2012, compared to the morphometric data for all ground pangolins recorded at this site.

There was a peak in electrocutions between January and April, while no electrocutions were recorded between August and October (Figure 3.2). This summer peak coincides with a peak in rainfall and may reflect a period of greater activity and movement as this is also when the previous years' pups start dispersing. It is interesting to note that no mortalities were recorded during what appears to be the peak breeding season (August – October).

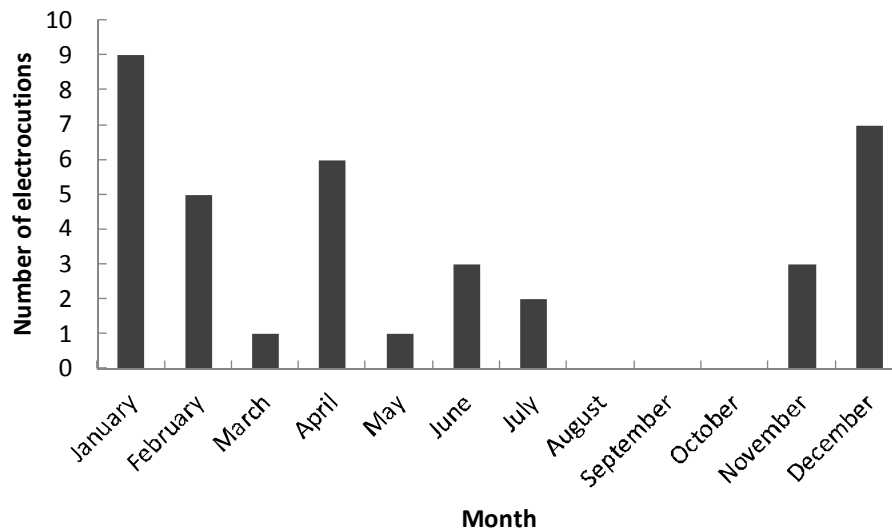


Figure 3.2. Total numbers of ground pangolin electrocutions recorded between December 2007 and July 2012 on Kalahari Oryx Private Game Farm, shown per month.

3.3.2 Traditional Medicine and the Bushmeat Trade

Another threat faced by ground pangolins is their use in traditional medicine (*muthi*) and as a source of food (Ansell 1960; Kingdon 1971; Coulson 1989; van Aarde *et al.* 1990; Heath 1992, and references therein; Bräutigam *et al.* 1994; Swart 1996; Heath & Coulson 1997b; Friedmann & Daly 2004; Whiting *et al.* 2011; R. Bruyns, *pers. comm.*). Ground pangolins are revered for their perceived medicinal and magical powers and are also killed out of ignorance, as well as to obtain their scales for inclusion in traditional dresses and ornamentations (Kingdon 1971; Heath & Coulson 1997b, and references therein; Kyle 2000; Soewu & Ayodele 2009; Manwa & Ndamba 2011). Nearly all parts of ground pangolins are used in *muthi* and ceremonies, including those intended to produce rain, seek favour from higher authorities and cure various ailments (Kingdon 1971; Heath & Coulson 1997b, and references therein; Kyle 2000; Soewu & Ayodele 2009). Jacobsen *et al.* (1991) record three instances of ground pangolins being killed for food, while a fourth individual was shot for no apparent reason. In the Kalahari, many farm workers will

eat ground pangolins that are found dead, although very few profess to actively seeking them as food. The extent to which ground pangolins are being used in the local *muthi* trade and as a source of food has not yet been quantified. There is also a growing tendency for ground pangolins to be exported to the Asian markets (Bräutigam *et al.* 1994; Challender 2011; Challender & Hywood 2012), which is likely to place an even greater strain on this species.

3.3.3 Gin Traps

A third threat faced by ground pangolins, and one that predominantly occurs in areas where commercial farming with small livestock is prevalent, is their capture in gin traps. Gin traps consist of two spring-loaded metal jaws that snap together when a central pressure plate is triggered, effectively trapping any animal that steps in it. A number of gin trap designs exist, including traps with serrated jaw edges; jaws that fit tightly together once triggered; and traps that leave a small space in between the two jaws when closed, purportedly to prevent injury to the trapped animal (as required by the National Environmental Management: Biodiversity Act: Norms and standards for the management of damage-causing animals in South Africa [NEMBA]). For the purposes of this review, the term 'gin trap' is used in reference to all three these varieties as well as 'neck-traps' (larger gin traps that are baited and capture the predator around the neck). Gin traps are widely used on most livestock farms in an attempt to control damage-causing predators (*pers. obs.*) despite their use being prohibited without a valid permit (NEMBA). Ground pangolins are often caught in gin traps that are indiscriminately set for damage-causing predators, especially when set underneath or near fences. These traps are infrequently checked and ground pangolins that are caught in gin traps often die from exposure and starvation, although if found timeously many can be released unharmed. The continued use of

gin traps is spurred on by the heavy losses experienced by farmers as a result of damage-causing predators (reportedly 30 – 80 % of annual natality) and the resultant bounties paid by farmers for every damage-causing predator caught. The extent of the threat posed by gin traps needs to be determined more accurately, but based on available data appears to be far less than electrocutions at present.

3.3.4 Habitat Loss

Coulson (1989) found ground pangolins to be absent from areas used for crop agriculture and areas of dense human habitation. Habitat loss probably has a pronounced effect on the current distribution of ground pangolins, however as quantitative data on this species' past and present distribution are lacking, it is difficult to estimate the magnitude of the effect of land transformation (see also Friedmann & Daly 2004). Land suitable for crop agriculture and human habitation is particularly prone to transformation and changes in ground pangolin densities and distribution are believed to be most pronounced in these areas.

3.3.5 Road Mortalities

Five ground pangolins were found killed by vehicles on the N14 between KO and Upington between 1 September 2009 and 31 August 2012, while a further two mortalities were recorded on the N14 east of KO. In the five years prior to this study, at least four ground pangolins were killed on this same stretch of road, as evidenced by study skins retained by KO. A report was received of a ground pangolin being killed on the railway tracks south of KO while crossing the Sishen-Saldanha railway tracks. The *ad hoc* nature of the road monitoring, coupled with some road mortalities being removed by unknown persons, suggests that the magnitude of this threat may be higher than reported here.

3.3.6 Poisoning

Two adult and a juvenile ground pangolin at the Bloemfontein Zoo died after being treated with a dichlorodiphenyltrichloroethane (DDT) solution to treat a tick infestation (van Ee 1966). A second pair of ground pangolins procured by this zoo also died after being moved to a new enclosure that had been treated with a soluble Lindane solution (containing benzene hexachloride) a month prior to them taking up residence (van Ee 1966). Heath (1992), based on the reports of van Ee (1966, 1978), first proposed that ground pangolins may be highly susceptible to chemicals, especially those used on crops. Subsequently Friedmann & Daly (2004) proposed that ground pangolins are susceptible to pesticides, particularly those used to control locusts. No primary source citing the origin of this latter argument could be traced, but it is believed to also originate from the reports of van Ee (1966, 1978), especially considering that benzene hexachloride is used as an agricultural insecticide (Milstein 1966). Poisoning is not believed to pose a significant threat to ground pangolins and this species' absence from croplands is most likely due to the higher human population in these areas resulting in greater persecution, the altered habitat no longer harbouring suitable prey species, and the land transformation removing suitable refuges, rather than as a direct result of poisoning. Furthermore, the high ground pangolin densities encountered in the Northern Cape Province (0.11 reproductively active adult individuals/km², Chapter 4), where spraying of insecticides to combat brown locust swarms is fairly common-place, suggests that the threat posed by poisoning is negligible, if a threat at all. The sensitivity of ground pangolins to chemicals may have been exaggerated and is based on limited observations of *ex situ* circumstances that do not reflect the *in situ* situation.

3.3.7 Pet Trade

Although not likely to be a significant threat, one report was received of a ground pangolin being sold as a pet. This individual almost certainly died, as ground pangolins are notoriously difficult to keep in captivity and even with specialist care display a high mortality rate (van Ee 1966, 1978; Heath & Coulson 1997b).

3.4 POSSIBLE MITIGATION MEASURES

Electrified fences arguably pose the greatest threat to this species, although the extent to which ground pangolins are used in the *muthi* trade still needs to be determined. There is an estimated 90 000 km of game fences in South Africa (Beck 2008), excluding livestock fences, and if even half of these fences are electrified this poses a significant threat to ground pangolins.

Various mitigation measures have been proposed to reduce fence-induced vertebrate mortalities, including 1) raising the height of the offset tripwire, 2) increasing the distance that the offset tripwire is placed from the fence, 3) packing a rock apron along the base of the fence and 4) duty cycling of the electrified fence (Beck 2008). The former two suggestions have been incorporated into the NCNCA 9/2009, while packing a rock apron is employed by some farms (where rocks are prevalent). The use of duty cycling (the electrified fence being switched on only at night to exclude damage-causing predators from a farm) has limited applicability, can only be used on livestock farms, and is only likely to be effective in reducing chelonian mortalities, as many other species that are prone to electrocution, including ground pangolins, are nocturnal or both diurnal and nocturnal (Beck 2008; Chapter

4). Furthermore, many of these mitigation measures are only effective for certain species, or not at all (R. Satekge, *pers. comm.*; *unpubl. data*).

During the course of this study a new 14.2 km-long internal fence was erected on KO for managerial purposes. In an attempt to reduce electrocutions, a three-strand tripwire (rather than the standard single- or double-strand tripwire) was erected along this new fence. The total height of the tripwire array remained the same, but an additional live strand was added to the configuration, which now has a live-earth-live configuration. In the 30 months since its erection, only a single ground pangolin has been electrocuted on this fence, a mortality rate of $0.028 \text{ pangolins km}^{-1}.\text{yr}^{-1}$. This is substantially lower than the rate of $0.09 \text{ pangolins km}^{-1}.\text{yr}^{-1}$ recorded for an established electrified fence at the same site and, considering that newly erected fences are characterised by a disproportionately high mortality rate, may suggest that this configuration is effective in reducing electrocutions.

A second potential solution to electrocutions is to develop an in-line monitoring unit for electrified fences. Such a unit should be suitable for attachment to an existing fence and continually monitor the current drawn. When the unit registers an increase in the current drawn (i.e. when an animal is trapped on the electrified fence, thus creating a short-circuit), the monitoring unit registers this and cuts the power to this portion of the fence for a pre-determined period. The unit should be able to re-initiate itself after this pre-determined period, and if the fault persists should be able to switch off again. After a pre-defined number of restarts, an error message could be sent via GSM signal to alert the management staff of a persistent fault on the line. Having the electricity flow to the affected strand stopped for a period of time should allow the ground pangolin to uncurl itself and move away from the fence.

Whenever possible, electrified strands should be placed at a minimum height of 300 – 400 mm above the ground. This should ensure that these wires are high enough for ground pangolins to pass unharmed underneath and has proved effective in reducing fence-associated electrocutions of chelonians in the Eastern Cape Province (A. Fisher, *pers. comm.*). Although such a fence would remain effective on farms where large herbivores are present, it may not effectively contain large predators, as these latter species have a tendency to dig underneath fences. This design would also likely allow damage-causing predators to pass underneath unhindered and would thus result in tensions between game farmers and adjoining livestock farmers. Ultimately any mitigation measures would need to be both cost-effective while still maintaining the integrity and function of the fence in keeping predatory animals either in (conservation areas) or out (livestock farms).

A final possible mitigating measure is to purposefully introduce breaches into a fence. This can be achieved by leaving the smaller holes that are dug underneath a fence open, especially if there is evidence that they are being used by ground pangolins. Alternatively, a suitable opening such as a concrete pipe, welded mesh tunnel or open metal frame could be inserted into the fence at intervals. Such openings would need to be carefully designed to exclude damage-causing predators while permitting ground pangolins and other non-target species unrestricted passage.

The losses incurred by livestock farmers due to damage-causing predators are substantial and costly. Van Niekerk (2009) conducted structured telephonic interviews with farmers in the five main small livestock producing provinces of South Africa, three of which (the Northern Cape, Mpumalanga, and marginally the Free

State Provinces) have populations of ground pangolins. Van Niekerk's results suggest that total predation losses average 4 % (range: 3 – 6 %) per province per annum and losses of lambs / kids younger than six months of age average 7 % (range: 6 – 13 %) per province per annum. Predation resulted in an estimated annual loss of R 1.4 billion across the five provinces (van Niekerk 2009). Given the generally low profit margins inherent in livestock farming, these losses are potentially crippling and many farmers will thus go to great lengths to eradicate damage-causing predators from their farm. The only reasonable measure to counteract the threat of gin traps at present is to educate the public, and farmers in particular, as to the plight of ground pangolins. Livestock farmers will continue to use gin traps for the foreseeable future, but if found and released in time ground pangolins that are caught in these traps can often be released unharmed. Developing more effective ways to control the movements of damage-causing predators and to reduce livestock mortalities would go a long way towards ground pangolin conservation in that it would reduce the need for other control measures such as the indiscriminate use of gin traps.

Despite habitat loss being viewed as a potential threat to ground pangolins, one positive indication is that ground pangolin densities on well-managed livestock (and private game) farms appear to be similar to densities in adjacent conserved areas. With private reserves alone covering 13 % of South Africa (Berger 2006), compared to the 5 % covered by National Parks (Falkena & van Hoven 2000), private reserves represent a large additional potential habitat for this species. If livestock farms are added to this figure, the area of potentially suitable habitat for ground pangolins increases dramatically. In addition to providing substantial additional habitat, these areas would also provide effective migratory corridors to sustain gene flow between

purportedly isolated populations. Privately owned land may, however, expose ground pangolins to various anthropogenic threats, including persecution for *muthi* and food. The private sector should be actively engaged to determine the current occurrence of ground pangolins on their property, the potential for this species to occur on their property, and what can be done to protect individuals on their property. In effect, private landowners need to be recruited as the custodians of this species.

3.5 CONCLUSIONS

Based on current data, fence electrocutions pose the greatest threat to ground pangolins in southern Africa and methods to reduce or even prevent these electrocutions should be sought as a matter of urgency. Further research should be undertaken to assess how widespread these electrocutions are, as well as how electrocution rates vary regionally. Future research should also aim to quantify the prevalence of ground pangolins in the *muthi* trade, as well as to compare this species' historical and current distribution to assess whether there has been a change. A formal study to ascertain the prevalence of ground pangolins as road mortalities and as gin trap victims should also be undertaken to assess the magnitude posed by these threats. Lastly, landowners should be directly engaged to ascertain the extent of occurrence and densities of ground pangolins on private land.

CHAPTER FOUR

HOME RANGE SIZE, ACTIVITY PERIODS AND REFUGE SITE SELECTION OF AN ARID-ZONE POPULATION OF GROUND PANGOLINS *SMUTSIA TEMMINCKII*

4.1 INTRODUCTION

A home range is defined as “that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as [being] part of the home range” (Burt 1943). Thus a home range represents the smallest area needed to sustain an individual by providing all the required key resources such as food, shelter and breeding opportunities (Fielden 1991) and determination of an animal's home range provides insights into that species' foraging ecology and social structure (Getty 1981; Mares *et al.* 1982). Having information available on the extent of an individuals' home range also allows researchers to approximate the densities and thus absolute numbers of a species, which is particularly useful for elusive species where traditional techniques are inappropriate to determine population sizes.

Ground pangolins *Smutsia temminckii* are scarce, mostly nocturnal mammals that occur from the northern portions of South Africa in the south to Chad and southern Sudan in the north (Heath 1992). Yet despite their wide distribution, ground pangolins remain poorly studied. Jacobsen *et al.* (1991) were the first to publish data on the home range sizes of individuals in the former Transvaal (present-day Mpumalanga, Limpopo, Gauteng and North-West Provinces) while Heath & Coulson (1997a,b) reported on the home range size and relocation success of ground pangolins in Zimbabwe. Most recently Swart (1996; see also Swart *et al.* 1999) undertook an

ecological study of this species in the Sabi Sand Game Reserve in north-eastern South Africa. Various authors have also reported on aspects of ground pangolin ecology (Coulson 1989; van Aarde *et al.* 1990; Richer *et al.* 1997), although most of these studies are characterised by small sample sizes.

Individuals of a species living in an arid environment tend to have larger home ranges than do their congeners in mesic environments (Attuquayefio *et al.* 1986; Fielden 1991). This is attributed to the lower primary productivity in arid environments which results in fewer available food resources (Fielden 1991). However, all of the previous studies on ground pangolins have been restricted to mesic savannahs in the eastern regions of South Africa and Zimbabwe and, as yet, no studies have been undertaken in the more arid areas of this species' distribution. Thus arid-zone biological and ecological data are currently lacking for this species, which precludes comparisons being drawn between arid and mesic populations.

Ground pangolins are described as being predominantly nocturnal (Wilson 1994; Gaubert 2011) or crepuscular (van Aarde *et al.* 1990; Jacobsen *et al.* 1991) although certain authors make mention of some diurnal activity (Smithers 1971; Smithers & Wilson 1979; Coulson 1989; Jacobsen *et al.* 1991; Swart 1996; Heath & Coulson 1997a; Richer *et al.* 1997). Swart (1996) suggested that the apparent crepuscular activity recorded by some authors may be due to an increase in observer activity at this time rather than a true reflection of ground pangolin activity, and also recorded individuals emerging from their burrows significantly earlier in winter.

Ground pangolins are currently listed as *Least Concern* by the IUCN, although many assessment criteria are data deficient and the population is believed to be declining

throughout its range (Hoffmann 2008). The ecological attributes of this species are required from across its range to enable conservationists to better understand the species and to assist with developing conservation strategies for the long-term protection of this species. This study represents the first ecological study of ground pangolins in an arid environment.

4.2 MATERIALS AND METHODS

Home ranges were determined for 13 ground pangolins at Kalahari Oryx Private Game Farm between October 2009 and October 2012. The study site is situated in the Kalahari biome of the Northern Cape Province in South Africa, between latitudes 28°21'S – 28°42'S and longitudes 21°55 'E – 22°15'E (Figure 4.1). The study site is at the western edge of this species' distribution in South Africa.

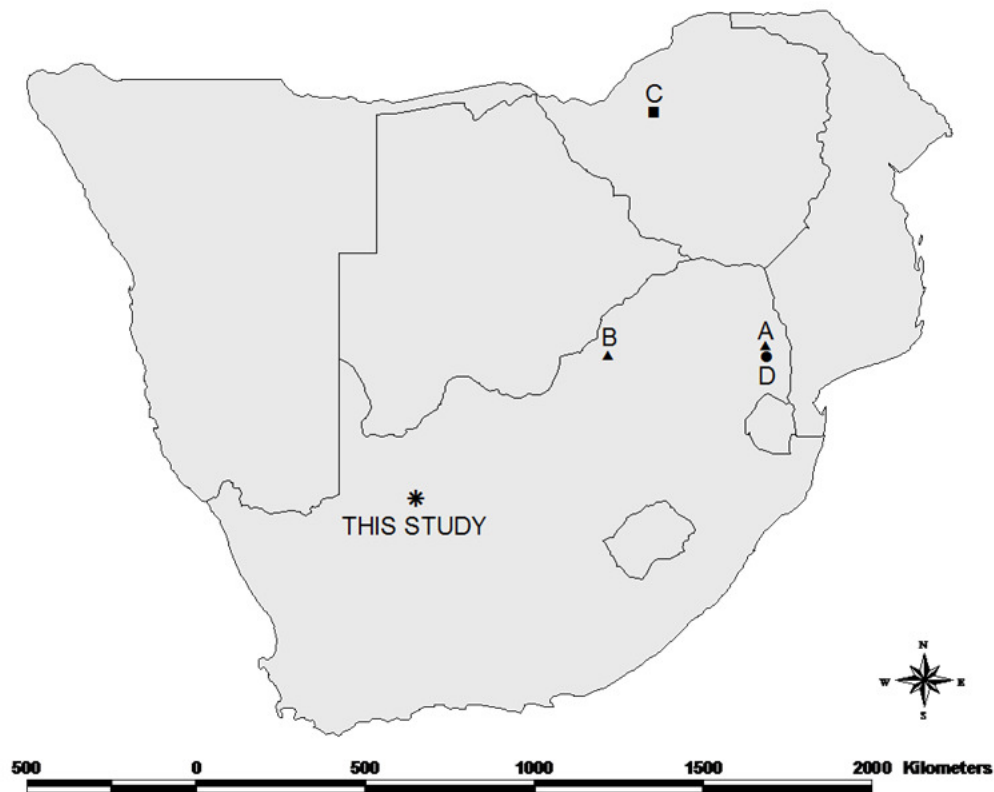


Figure 4.1. Location of the present study in relation to previous ground pangolin research. (A) Hans Hoheison Wildlife Research Station and (B) Thabazimbi: van Aarde *et al.* 1990, Jacobsen *et al.* 1991; (C) Sengwa Wildlife Research Station: Heath & Coulson 1997a,b, 1998, Richer *et al.* 1997; and (D) Sabi Sand Game Reserve: Swart 1996, Swart *et al.* 1999.

Study animals were located by following their tracks or by chance encounters. Once located, a custom-built Very High Frequency (VHF) transmitter (Africa Wildlife Tracking, Pretoria, South Africa) was attached to a single median dorsal scale at the level of the pelvic region and secured with a 3 mm machinery bolt on either side of the transmitter and Pratley® Quickset Epoxy underneath the transmitter. Bolts were inserted from beneath the scale to ensure a flush fit and prevent any projections that could potentially injure the animal. Once the epoxy had dried, the exposed bolts and any gaps between the transmitter and the scale were covered with Pratley® Quickset Putty to prevent vegetation snagging on the transmitter or pangolin mites *Manitherionyssus heterotarsus* Vitzthum, which commonly occur on ground

pangolins, to shelter under the transmitter and potentially cause discomfort. Once the putty had dried the animal was released at the capture site. The VHF transmitters, including the Pratley® Quickset Putty, weighed 100 – 120 g, representing $\leq 4\%$ of body mass.

Study animals were visually located on a daily basis for the first month to determine the approximate home range. After this period individuals were located as often as was feasible and typically at least twice a week. Study animals were tracked at various times of the day and night, depending on their activity periods. Due to the presence of high densities of large carnivores in a portion of the study site and the resultant limitations imposed by the study site managers, some study animals were only located during the day when they were typically resting in their refuges (see also Heath & Coulson 1997a).

Once located, a Global Positioning System (GPS; Garmin GPS V, Kansas, USA) with a stated accuracy of 4 – 7 m (depending on satellite reception) was used to manually record the animal's geographic location. These data were downloaded to a computer using the program DNR Garmin 5.04 (Minnesota Department of Natural Resources, Minnesota, USA) and viewed in the geographical information system ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California, USA). Four ground pangolins were fitted with custom-designed GPS loggers (Ecotone, Poland) to determine fine-scale movements after an initial VHF tracking period of one month confirmed that they were resident. The GPS loggers weighed 200 g and were thus only used on larger individuals weighing > 6 kg to ensure that the transmitter did not exceed 5 % of the animal's body mass. GPS loggers were programmed to record the animal's location every hour, and took six consecutive locality readings to ensure a

high degree of accuracy and to identify any incorrect localities. GPS logger accuracy was determined by comparing the localities recorded by these loggers to co-ordinates manually recorded with a handheld GPS at known locations. These results indicated that the loggers were accurate to within 20 m, and often to within ≤ 10 m, depending on satellite reception. GPS logger data were downloaded in the field with an Ecotone Remote Download Base Station that stored the data on a non-volatile memory card and erased the logger's memory once downloaded. Data stored on the Base Station were downloaded to a computer via a download cable and were visualised in Google™ Earth prior to being converted to ArcView format using DNR Garmin 5.04. Outlying co-ordinates identified in Google™ Earth were manually removed when the data were viewed in ArcView GIS.

Prior to analysis the GPS logger data were edited by removing duplicate co-ordinates, retaining only one of the six co-ordinates recorded each hour. This ensured that no artificial weighting of localities occurred when the data were analysed. All co-ordinates were converted to Universal Transverse Mercator co-ordinates and input into the software program Ranges 7 v. 2.9 (Anatrack Ltd., Wareham, UK). Three measures of home range were calculated for each individual: Minimum Convex Polygon (MCP), 95 % Harmonic Mean (using default settings) and 95 % Kernel (with default settings). Kernel home range estimates most accurately reflect the true home range extent, as MCP estimates include all data points, including outliers, and thus include a lot of additional area that is not utilised by the study animal. Likewise, Harmonic Mean home range estimates are highly sensitive to outlying data points and thus result in the inclusion of many additional grid points (i.e. area) that are not utilised by the study animal. The result is that both MCP and Harmonic Mean analyses tend to overestimate home range size whereas Kernel

analyses are well defined and tractable and thus provide a better estimate of home range extent (Seaman & Powell 1996). However, as MCP is the most often used measure of home range size, both MCP and Kernel home range characteristics were statistically investigated.

An Incremental Area Analysis was performed on the Kernel home range to determine the number of localities required to predict the 95 % core home range. Seasonal differences in home range size and habitat use were assessed by assigning the localities recorded for each individual to summer (November – February) and winter (May – August) localities. Home range data were statistically analysed using GraphPad InStat v 3.0 (GraphPad Software, San Diego, California, USA) to determine whether there was any correlation between calculated home range size and biological factors such as mass, sex, age class and the number of observations for each individual.

Emergence and return times were determined for three individuals fitted with GPS loggers. The loggers were only able to record a geographic location when above ground and thus the first recorded position for each day occurred within one hour of the study animal emerging from its refuge. The loggers thus provided an unbiased representation of emergence and returning times as these were not influenced by the presence of an observer and were recorded in the same manner for each individual. Because the loggers recorded locations hourly, emergence times were likewise assigned to 1-hour intervals based on the 24-hour clock. Thus 00:00 represents 00:00 – 00:59, 01:00 represents 01:00 – 01:59, and so forth. When study animals took refuge in exposed sites, continuous satellite coverage was possible which resulted in continuous hourly positions. These data were visible as a cluster of

successive points in a very small area when viewed in Google™ Earth. In these instances the first position in this cluster (based on time) was viewed as the return time of the previous day and the first position leaving this cluster was viewed as the emergence time of the following day. A multiple regression analysis was performed on the emergence times using GraphPad InStat v 3.0 to determine whether these were affected by minimum and maximum temperatures.

Habitat selectivity was investigated with a modified selectivity index S (McNaughton 1978):

$$S_j = \sum | P_{Hi} - P_{Li} | / 2$$

where P_{Hi} is the proportional abundance of the i -th habitat in the study area and P_{Li} is the proportional abundance of locality records in the i -th habitat for ground pangolin j . A selectivity value of zero denotes no habitat selectivity, while a value of one denotes maximum habitat selectivity.

Upon completion of this study all transmitters that had not yet been removed were removed, with the exception of four animals with which contact was lost during the course of this research and which could not be relocated after exhaustive searching.

4.3 RESULTS

4.3.1. Home Range Extent

Home range extent was estimated for seven adult (≥ 6 kg) and six juvenile (< 6 kg) ground pangolins. Of these, two adults and three juveniles had fewer than 50 locations each and were thus excluded from statistical analyses. Home range size varied depending on the size, and thus in effect the age, of the individual (Table 4.1).

MCP home ranges for adults averaged $10.0 \pm 8.9 \text{ km}^2$ (mean \pm SD). The 95 % Harmonic Mean and Kernel home ranges for adults averaged $4.1 \pm 4.2 \text{ km}^2$ and $6.5 \pm 5.9 \text{ km}^2$, respectively. Juveniles had an average MCP home range of $7.1 \pm 1.1 \text{ km}^2$. The 95 % Harmonic Mean and Kernel home ranges for juveniles averaged $1.63 \pm 0.3 \text{ km}^2$ and $6.1 \pm 4.0 \text{ km}^2$, respectively. Electrified game fences occasionally influenced the location (and possibly the size) of home ranges by creating an impassable barrier. However, some study animals were regularly seen passing through electrified fences, sometimes on a nightly basis, without any hindrance and these effects are thus believed to be negligible.

Table 4.1. Three measures of home range size for seven adult ($\geq 6 \text{ kg}$) and six juvenile ($< 6 \text{ kg}$) ground pangolins. Field numbers marked with an asterisk indicate individuals for which a 95 % Incremental Area Analysis indicated that home range stationarity had been reached and that the entire home range had thus likely been mapped.

Animal ID	Gender	Average mass (kg)	Number of observations	Minimum Convex Polygon (km^2)	95 % Harmonic Mean (km^2)	95 % Kernel (km^2)
STEM 35	Male	10.0	53	12.89	2.81	11.91
STEM 5*	Female	9.7	210	23.90	10.98	13.76
STEM 20*	Female	7.7	43	3.40	0.33	2.45
STEM 38*	Male	7.5	241	7.63	4.93	3.32
STEM 22*	Female	7.1	82	3.95	0.85	2.67
STEM 39	Female	6.8	128	1.45	0.73	0.69
STEM 40	Female	6.2	18	1.92	0.03	2.60
STEM 18*	Male	4.4	98	8.34	1.70	8.37
STEM 23	Male	3.8	90	1.29	0.69	1.11
STEM 19*	Female	3.5	51	6.94	1.26	8.50
STEM 46	Male	3.3	24	0.20	0.02	0.07
STEM 70	Female	2.8	18	1.99	0.08	2.49
STEM 21	Male	2.6	10	0.90	0.01	2.61

Neither the Kernel home range nor the MCP home range were correlated with mass (Spearman rank correlation $r = 0.429$, $P = 0.299$, $df = 7$ and $r = 0.524$, $P = 0.197$, $df = 7$, respectively) or the number of observations ($r = -0.143$, $P = 0.752$, $df = 7$ and $r = 0.143$, $P = 0.752$, $df = 7$, respectively). There was no significant difference in average home range size between sexes (unpaired t-test Kernel: $t = 0.038$, $P = 0.971$, $df = 6$; MCP with Welch correction: $t = 0.060$, $P = 0.959$, $df = 3$) or between age classes (Kernel: $t = 0.093$, $P = 0.929$, $df = 6$; MCP with Welch correction: $t = 0.703$, $P = 0.521$, $df = 4$).

The degree of home range overlap could be determined for two adult pairs. The respective home ranges of STEM 22 and STEM 35 overlapped by 12.65 %. In comparison, the home range of adult male STEM 38 was entirely encompassed by the home range of adult female STEM 5.

Only two individuals, an adult female (STEM 5) and adult male (STEM 38), had sufficient data to compare seasonal differences in home range size. The trends are opposite for these two individuals, with the female utilising a larger area in summer and the male utilising a larger area in winter (Figure 4.2). This contradicting trend may be owing to the relatively small sample size, especially for STEM 5.

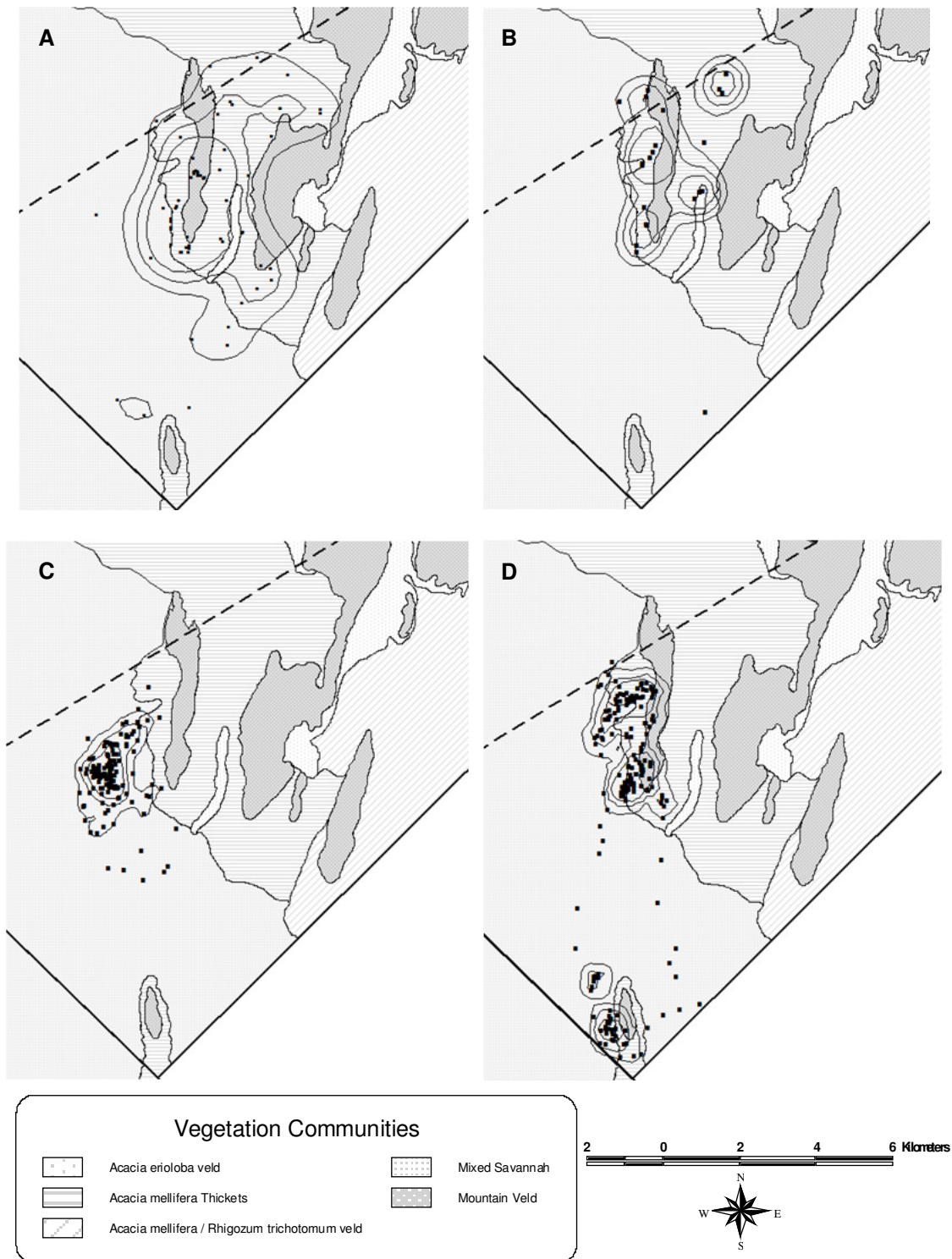


Figure 4.2. Summer (Nov – Feb) and winter (May – Aug) home ranges for an adult female (STEM 5) and adult male (STEM 38) ground pangolin. (A) STEM 5 summer home range (n = 61); (B) STEM 5 winter home range (n = 24); (C) STEM 38 summer home range (n = 154); (D) STEM 38 winter home range (n = 210). The 50th, 75th & 95th percentile Kernel home ranges are displayed for each season. Solid dark lines show electrified game-proof fences; the dashed dark line indicates an electrified fence that was removed during this study.

Four adult and two juvenile ground pangolins had additive home range graphs that reached a plateau during the Incremental Area Analysis, suggesting that additional points were unlikely to significantly alter the calculated home range size. An analysis of these six individuals indicated that 88 ± 67.7 (mean \pm SD) locations (i.e. tracking days) were required to reliably predict 95 % of the Kernel home range at this study site. The remaining seven individuals had home ranges that had not reached stationarity, suggesting that the entire home range had not yet been determined.

4.3.2 Habitat Use

Five adult and six juvenile ground pangolins' home ranges were analysed to determine whether habitat use was random or whether particular habitats were favoured. There was no apparent habitat selectivity amongst any of the individuals (Table 4.2). Only two adult individuals had enough data to meaningfully investigate seasonal variations in habitat use, neither of which showed any habitat selectivity during either of the seasons or overall (Table 4.2).

Table 4.2. Habitat selectivity values for 12 ground pangolins. A value of zero represents no habitat selectivity, whereas a value of one represents maximum habitat selectivity.

Animal ID	Overall Selectivity	Summer	Winter
STEM 35	0.122	-	-
STEM 5*	0.182	0.164	0.247
STEM 20*	0.155	-	-
STEM 38*	0.075	0.067	0.142
STEM 22*	0.142	-	-
STEM 39	0.370	-	-
STEM 18*	0.322	-	-
STEM 23	0.068	-	-
STEM 19*	0.122	-	-
STEM 46	0.046	-	-
STEM 70	0.203	-	-
STEM 21	0.330	-	-
OVERALL	0.081		

4.3.3 Dispersal

Dispersal was defined as young animals leaving the boundaries of their natal home range without returning to it, or older individuals that were not resident in any particular area, indicating that they had no fixed home range. Three individuals were observed dispersing during this study. A young female (STEM 19, 3.5 kg) that was originally located in her natal home range remained in this home range for the first six months of tracking (28 June 2010 – 30 December 2010). She then started to disperse northwards, following the bases of successive mountains and moved a straight-line distance of 31 km (following her daily path this distance is 36 km) in 11 days. Contact was lost when she entered mountainous terrain and despite extensive

aerial and ground searching she was not located again until 3 October 2011, when her signal was again located during routine scanning. She was located on a farm 24.5 km north-east of her natal home range and 17.5 km south-east of her last known location. A labourer interviewed at this site stated that he had first noticed her in the same vicinity as where she currently was during September 2011. This suggests that she covered a minimum distance of 48.5 km in nine months, although this distance may have been much greater.

A young male (STEM 23, 3.8 kg) was followed for four months in his 0.9 km² MCP natal home range before he started dispersing during December 2010. He established a small (0.4 km² MCP) home range 5 km north of his natal home range and remained here for at least 2.5 months before contact was lost.

A young adult male (STEM 47, 6.7 kg) was located in the home range of female STEM 5 and resided in a 2.1 km² MCP home range for the first month of monitoring before he started to disperse on 6 October 2011, initially travelling northwards along the same mountain range that STEM 19 had followed. Upon reaching the northern tip of this range, the GPS logger had to be replaced, thus interrupting his dispersal for a day. After release, he continued dispersing north-eastward, travelling another 16 km before establishing a small home range (0.5 km² MCP) which he occupied for seven days. He then continued dispersing north-eastward, travelling a further 11 km before the transmitter was removed. In total this individual travelled a minimum distance of 32 km in 20 days. A second young adult male (STEM 31, 6.5 kg) was tracked for 18 days between 22 December 2010 and 11 January 2011, before contact was lost when he entered an extensive mountain range. During this time he showed no fixed directional movements, travelling 81 km and covering an area of 154 km² MCP.

4.3.4 Activity Periods

Activity periods varied according to the season and the individual study animal. An adult male (STEM 38, 7.5 kg) tracked between 11 August 2011 and 23 June 2012 emerged at various times of the day and night, the emergence times being dependant on season. During autumn and winter he emerged most frequently in the early afternoon, whilst during summer he emerged in the late afternoon to early evening (Figure 4.3). Emergence time was highly dependent on both the minimum and maximum temperatures, although minimum temperature ($t = 2.701$, $P = 0.008$, $df = 175$) was more important than maximum temperature ($t = 2.121$, $P = 0.035$, $df = 175$). A young adult female (STEM 39, 6.8 kg) that was tracked during late winter and early spring was predominantly diurnal (Figure 4.3). A young adult male (STEM 47, 6.7 kg) that was studied during spring while he was dispersing emerged in the late afternoon to early evening (Figure 4.3). Emergence times were unaffected by the lunar cycle.

Activity periods averaged 5.7 ± 2.0 hours (mean \pm SD, range 1 – 12 hours). Winter foraging times averaged 5.6 ± 1.6 hours (range 2 – 10 hours) while summer foraging bouts averaged 5.7 ± 2.2 hours (range 1 – 12 hours). There was no significant difference in the length of foraging bouts between winter and summer (Student's t-test $t = 0.11$, $P = 0.91$, $df = 197$).

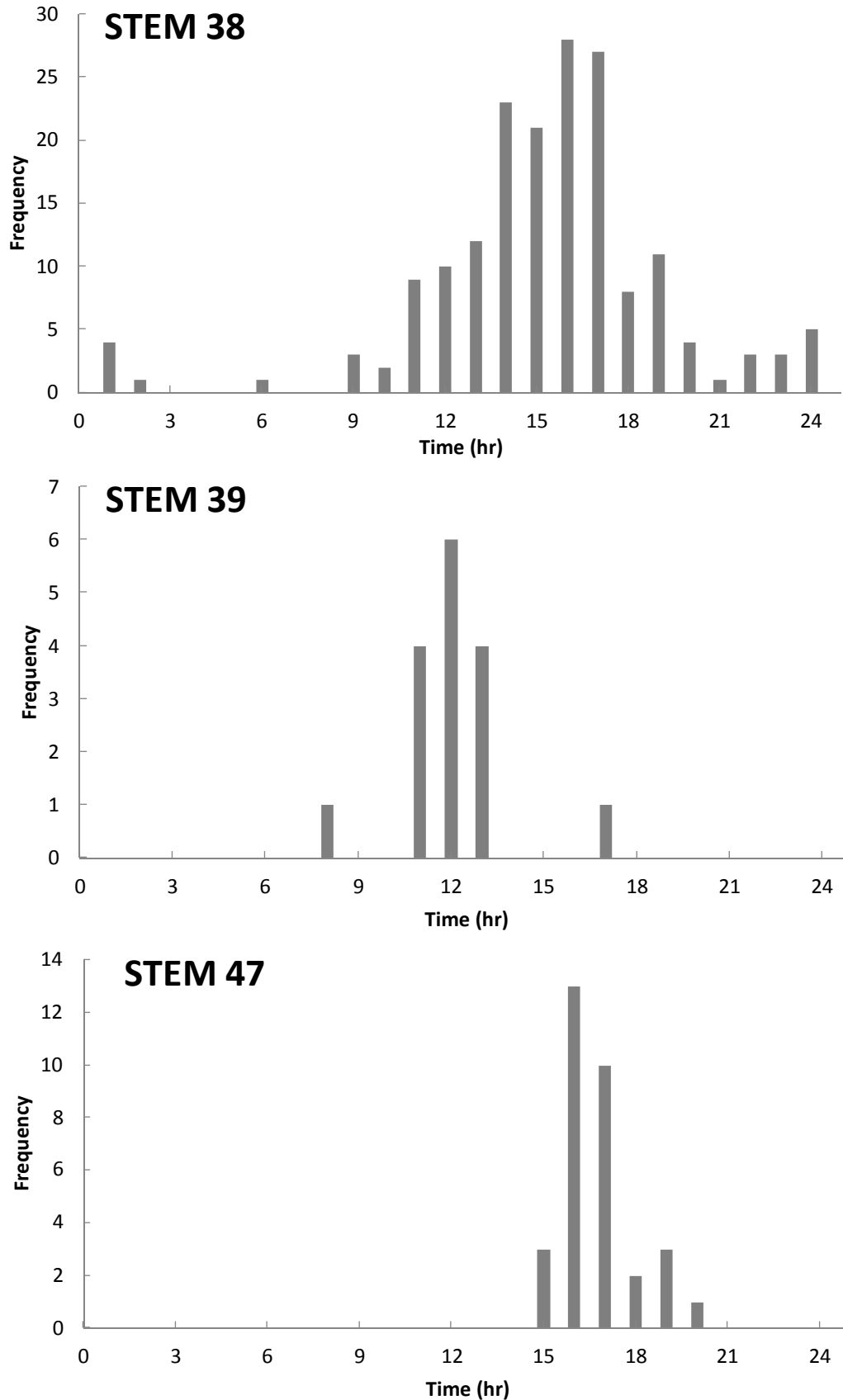


Figure 4.3. Emergence times of two adult male (STEM 38 & STEM 47) and a young adult female (STEM 39) ground pangolin. Emergence times are based on 1-hour intervals according to the 24-hour clock.

4.3.5 Refuge Site Selection

A total of 492 refuges were recorded being used during this study (Table 4.3). Burrows, and especially aardvark *Orycteropus afer* burrows, were the most favoured refuges (89.6 %, n = 441). Porcupines *Hystrix africaeaustralis* also periodically utilised aardvark burrows as refuges, thus complicating the assignment of a burrow to a particular species. For the purposes of this study, burrows were deemed to be dug by porcupines based on external characteristics (an extended 'entrance tunnel' leading up to the burrow; a deeper burrow often with multiple entrances; presence of bones and horns dragged in by porcupines and a proliferation of porcupine tracks). Only juvenile ground pangolins used vegetation as cover and were also more likely to take refuge between rocks, usually squeezing themselves in between two rocks. Only one adult, a dispersing male (STEM 31), was seen to dig his own burrow, which was < 1 m in depth. Refuge selection did not differ significantly between adults and juveniles (Student's t-test $t = 0.005$, $P = 1.0$, $df = 7$).

Table 4.3. The type and proportion of refuges utilised by 16 ground pangolins between September 2009 and October 2012. N is the total number of times ground pangolins were seen utilising each refuge type and % is the proportional use of each refuge type.

Refuge Type	Overall		Adults		Juveniles	
	n	%	n	%	n	%
Aardvark burrow	343	69.7	237	74.8	106	60.6
Springhare warren	68	13.8	48	15.1	20	11.4
Cave	32	6.5	15	4.7	17	9.7
Porcupine warren	30	6.1	13	4.1	17	9.7
Rocks	13	2.6	2	0.6	11	6.3
Vegetation	3	0.6	0	0	3	1.7
Termite mound	2	0.4	1	0.3	1	0.6
Self-excavated burrow	1	0.2	1	0.3	0	0
TOTAL	492		317		175	

4.3.6 Densities

Ground pangolins were recorded fairly uniformly across the study site, although sightings were closely associated with the road network (Figure 4.4). Individuals were most frequently sighted around mountains, although interpretation of this trend is confounded by the more extensive road network around mountains and this habitat type occurring in close proximity to the farm headquarters which resulted in a higher observer density.

Each adult male's home range closely mirrored the home range of an adult female, suggesting that there is a single pair of sexually mature adults in each home range. Furthermore, as these home ranges are stable across successive years it may indicate that ground pangolins in the Kalahari are monogamous. Home ranges

between adjoining individuals of the same sex did not appear to overlap, although there are too few data to test this statistically.

The maximum MCP home range sizes of adult male and female ground pangolins at the study site were 13 km² and 24 km², respectively. Thus the average maximum home range size for a pair of ground pangolins was 18.5 km², suggesting a density of 0.11 reproductively active adult individuals/km². In addition to the adult breeding pair, each home range usually also supported the previous year's offspring as well as at least one transient dispersing sub-adult individual. Thus the overall density of ground pangolins at the study site may be as high as four ground pangolins per home range, or 0.22 individuals/km².

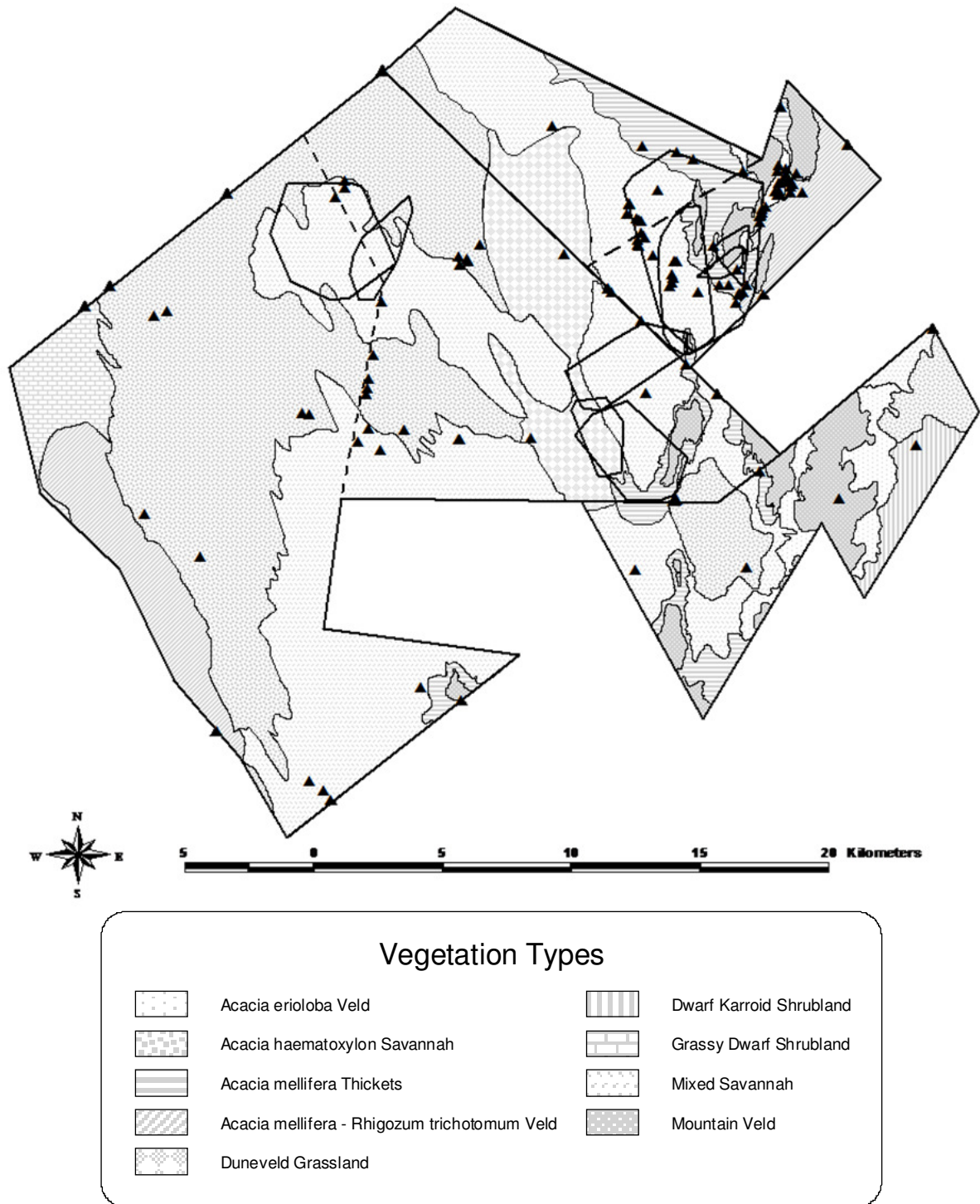


Figure 4.4. Distribution of ground pangolin sightings at the study site between September 2009 and October 2012. Solid boundary lines indicate electrified game-proof fences, the dashed line indicates a new electrified fence that was erected during the course of this study and the dotted line indicates an electrified fence that was removed during the course of this study. Dark triangles indicate ground pangolin sightings and solid lines indicate the MCP home ranges of study animals.

4.4 DISCUSSION

4.4.1 Home Range Extent

The home range sizes recorded during this study are similar to the 0.17 – 23.38 km² MCP recorded by Heath & Coulson (1997a) in Zimbabwe but are slightly larger than the range of 1.3 – 7.9 km² MCP recorded by van Aarde *et al.* (1990) in mesic north-eastern South Africa. However, as van Aarde *et al.* (1990) only studied five individuals for 52 nights, they may have underestimated home range size. This finding that arid-zone home range sizes are similar to those of mesic populations is surprising as animals in arid environments typically have larger home ranges than do individuals of the same or similar species in areas of higher rainfall where productivity is higher (Mares *et al.* 1976; Fielden 1991). However, ground pangolins in the Kalahari are 25 – 30 % smaller than individuals from north-eastern South Africa and Zimbabwe (*unpubl. data*) and smaller animals tend to have smaller home ranges than do larger individuals of the same species (Mohr 1947; McNab 1963). It is therefore possible that these two factors (body size and primary productivity) act in opposing directions, thus explaining the apparent similarity in home range size between these climatically different study sites.

Heath & Coulson (1997a) recorded adult male ground pangolins to have larger home ranges than adult females, and male and female home ranges to overlap by 1.5 – 20 %. These authors also reported that a male's home range overlapped the home ranges of a number of females and report an instance where an adult male moved 12 km from his home range into the home range of a female, presumably to mate (Heath & Coulson 1997a). This is in contrast to the findings of this study, in which adult males were found to be resident in a territory that sometimes wholly overlapped the

territory of only a single female. Furthermore, no movements of males into adjoining female's home ranges were observed, except for floating males (see below).

Ground pangolins use their entire home range on a continuous basis, moving between successive refuges on an *ad hoc* basis. This is in agreement with the findings of Heath & Coulson (1997a) but is in contrast to the results of van Aarde *et al.* (1990) who suspected that although ground pangolins may have a home range of ca. 20 km², they only use a small portion of this home range for periods of up to three months at a time before moving to a different, often adjoining, portion. Van Aarde *et al.*'s (1990) conclusions were largely drawn from intermittent observations of two adult males over a period of 18 months but only 52 tracking nights, which may explain these apparently conflicting results.

All juvenile ground pangolins that were fitted with telemetry during this study (n = 6) initially established home ranges within their natal home range. Of these six individuals, two died of natural causes before dispersing, three lost their transmitters and one was successfully followed through dispersal until a new home range was established (STEM 19). These results confirm the findings of Heath & Coulson (1997a) who recorded a newly weaned pup initially establishing its home range within its natal home range and suspected that juvenile dispersal thus occurred at a later stage.

An analysis of seven individuals' home ranges suggests that 88 ± 67.7 locations (i.e. tracking days) are required to reliably predict 95 % of the Kernel home range of an individual. This is similar to the 90 tracking days which Heath & Coulson (1997a) calculated would reliably estimate 95 % of MCP home range size for two adult

females in Zimbabwe. However, the large standard deviation cautions that substantially more observations may occasionally be required to predict home range size.

4.4.2 Habitat Use

The lack of habitat selectivity observed during this study is in sharp contrast to the high habitat selectivity recorded by Swart (1996) in the Sabi Sand Game Reserve. This may be attributable to the uniform geology and climate at the Kalahari study site resulting in a fairly uniform ant community (Chapter 5) which would nullify habitat selectivity as there would be no energetic gain in selecting specific habitats if all have similar prey communities. The lack of habitat selectivity may also be attributable to the vegetation communities in the Kalahari being more extensive than those in the Sabi Sand Game Reserve and thus the home ranges of individual ground pangolins in the Kalahari generally incorporating fewer habitat types than do those in more mesic regions. *Anoplolepis steingroeveri*, the species numerically most frequently preyed on by ground pangolins at the study site, was most common in the Mixed Savannah (Chapter 5), suggesting that ground pangolins should also preferentially select this habitat while foraging. However, two species of *Crematogaster* had higher standardised forage values (Chapter 5), suggesting that ground pangolins preyed on these two species more often than their proportional abundance would suggest. This reinforces the hypothesis that all five ant and termite species preyed on by ground pangolins at the study site are equally important constituents of the diet (see Chapter 5), which would also explain the apparent lack of habitat selectivity as all prey species are present in all habitat types, albeit at varying proportions.

The only habitat that showed a markedly different ant fauna, specifically in terms of lower prey species density, was the Dwarf Karroid Shrubland (Chapter 5). This vegetation type was the only community to occur on calcrete soils and was the only habitat not included in the home range of any study animal. However, one of the dispersing individuals (STEM 19) established her new home range in short Karroid Grassland on calcareous soils on a neighbouring farm, thus it is believed that the exclusion of this habitat type from the home ranges of individuals at the study site is an observational artefact that is confounded by the limited extent of this habitat at this site and its location in areas not often traversed during this study.

4.4.3 Dispersal

The data suggests that male ground pangolins may disperse further than females and may also remain floaters (i.e. without a fixed home range) for longer. Ground pangolins are probably able to disperse much further than the 36 km recorded during this study. Van Aarde *et al.* (1990) record a young male fitted with a VHF transmitter at Olifantshoek in the Northern Cape Province being recaptured four months later in the North-West Province, 300 km from the release site. The inferred dispersal rate of 2.5 km a day is within the range of 2 – 7 km recorded during the present study. Van Aarde *et al.* (1990) also report on a young adult male (7.1 kg) that was fitted with a VHF transmitter and translocated ca. 30 km before being released. The behaviour that they describe suggests that this could have been a dispersing male or floater, although accurate interpretation of the results is confounded by this individual having been translocated and that it may thus have been trying to establish a new home range rather than true dispersal. Nonetheless, these authors report that this male occupied successive home ranges of ca. 2.0 km² each for 2 – 3 months and moved 10 – 18 km between successive home ranges, suggesting true dispersal. This

behaviour is similar to that recorded for a young adult male (6.8 kg) tracked during this study which established home ranges of 2.1 km² and 0.5 km² and occupied them for 1 month and 7 days, respectively, while dispersing. A second young adult (6.5 kg) that was followed ranged over an area of 154 km² MCP in 18 days, which is much larger than van Aarde *et al.*'s (1990) value of 68 km² in five months. These data suggest that dispersal can be extensive and has implications for recolonization and gene flow. Furthermore, it suggests that dispersal may be directional, at least initially, later changing to 'floating' behaviour. A comprehensive study is required to further investigate the timing and nature of natal dispersal and the distances that are travelled.

4.4.4 Activity Periods

Activity periods varied seasonally, as well as according to the age (size) of the individual. Juvenile and sub-adult ground pangolins were more diurnal than were adults. However, there were marked seasonal differences with both juveniles and adults being active by day during winter and inclement weather. These results differ from those of Richer *et al.* (1997) and Swart (1996), who considered juveniles to be more crepuscular than adults, but that adults were occasionally active during the day in winter. This higher proportion of diurnal activity in the Kalahari is likely due to the more extreme climatic conditions at this study site. Pangolin scales are poor thermal insulators (McNab 1984; Heath & Hammel 1986; Weber *et al.* 1986; Swart 1996; Chapter 6) and thus ground pangolins need to resort to behavioural methods to control their body temperature (Chapter 6). Furthermore, winter is a nutritionally stressful time as more energy is expended to maintain a constant body temperature and ant activity decreases (Swart 1996; Chapters 5 & 6). By becoming more diurnal during winter, ground pangolins are able to avoid the low nightly ambient

temperatures, thus conserving energy. Conversely, by being nocturnal during summer individuals are able to avoid the extreme heat of the day, thus conserving moisture. Furthermore, as ant activity remains consistently low during winter regardless of the diel cycle (Chapter 5), ground pangolins do not need to take prey activity periods into consideration during this time. These findings suggest that ground pangolins may be more diurnal than previously thought, although diurnal activity probably depends on age class and geographic location. Furthermore, the contention that ground pangolins are mainly crepuscular (Coulson 1989; Jacobsen *et al.* 1991) probably relates to an increase in observer activity at this time of day rather than an increase in ground pangolin activity *per se* (see also Swart 1996).

The activity period lengths recorded in this study are similar to previously reported values. Heath & Coulson (1997b) recorded average activity periods of 6.30 hours (range 2.75 – 10.50 hours) and 5.35 hours (range 2.95 – 8.25 hours) for two adult females. Jacobsen *et al.* (1991) recorded activity periods of 5 – 6 hours while Swart (1996) recorded average activity periods of 3.85 ± 1.90 hours (range 0.58 – 8.33) for adults and 3.70 ± 1.43 hours (range 2.45 – 5.28) for juveniles. In agreement with Swart (1996) there were no seasonal differences in the lengths of activity periods.

4.4.5 Refuge Site Selection

Aardvark burrows were the most frequently used refuges, although other earthen burrows, caves and rock piles were also opportunistically used. The majority of observations of individuals seeking refuge in exposed positions (under vegetation, wedged between rocks or under small overhanging rocks) were of juveniles and dispersing individuals. This may be ascribable to juveniles lacking an extensive knowledge of their home range, or individuals finding themselves in unfamiliar

territory during dispersal. The proportional use of the various refuge types appeared to depend on their relative availability, although this was not specifically investigated. These findings are consistent with those of previous authors (Smithers 1971; van Aarde *et al.* 1990; Jacobsen *et al.* 1991; Heath & Coulson 1997a) but are contrary to Smithers (1971) who reported ground pangolins to preferentially take refuge in vegetation during the day. Van Aarde *et al.* (1990) reported individuals to return to the same burrow every 3 – 5 nights. During the current study, the length of time spent occupying any particular burrow varied considerably between individuals, ranging from one to ca. 30 nights. New burrows were continuously added and old burrows abandoned owing to some burrows collapsing while new burrows were continuously created through the digging actions of aardvark and porcupines.

Sweeney (1974) reports on a single burrow used by a ground pangolin that had an entrance diameter of 20 – 25 cm and a depth (length) of 3 – 5 m that sloped steeply downwards, with the end located 1 m below the soil surface. Although burrow characteristics were not specifically investigated during this study, notes were made for a number of burrows. Burrow entrances varied from 20 cm to > 1 m in diameter, and from < 1 m deep (aardvark foraging holes) to 7 m deep (a porcupine warren that was extended by a springhare *Pedetes capensis*). The end chamber ranged from < 30 cm to 6 m below the soil surface. Ground pangolins were frequently heard and seen 'modifying' existing burrows by digging them deeper and / or presumably increasing the size of the sleeping chamber. Burrows that were frequently used were periodically dug deeper, resulting in a large volume of sand and faeces being ejected at the burrow entrance.

4.4.6 Densities

Based on the maximum MCP home range values, densities at the study site are estimated at 0.11 reproductively active individuals/km² and overall densities are estimated at 0.22 individuals/km². Swart (1996) does not explicitly state densities or home range sizes at his study site. However, based on his data (18 individuals located in his 150 km² study site) the overall density can be estimated at 0.12 individuals/km², assuming that all individuals were recorded and that none immigrated into or emigrated from the study site. Using the MCP values of Heath & Coulson (1997a) the total density at Sengwa Wildlife Research Institute in Zimbabwe is 0.11 individuals/km². Thus densities in the Kalahari appear to be nearly twice as high as densities in mesic savannahs. Due to the sandy geology and the increased diurnal activity in winter in the Kalahari, ground pangolins are easier to locate, which might account for the higher calculated densities. Despite this, the higher densities calculated for the Kalahari are believed to be accurate, although further research is required to determine why densities are higher in arid environments.

CHAPTER FIVE

DIET AND PREY SELECTIVITY OF GROUND PANGOLINS *SMUTSIA TEMMINCKII* (SMUTS, 1832) IN THE SOUTHERN KALAHARI DESERT

5.1 INTRODUCTION

Ants (Hymenoptera: Formicidae) and termites (Isoptera) have colonised nearly all terrestrial ecosystems (Schoeman & Foord 2012), are a diverse and abundant constituent of biomass (Hölldobler & Wilson 1994) and an important food source to many vertebrate species. Ant and termite assemblages often vary considerably both seasonally and spatially and are closely linked to habitat complexity (Samways 1990; Andersen 1993; Swart 1996; Lindsey & Skinner 2001; Schoeman & Foord 2012). Ant species richness does not appear to show any clear geographical pattern, although this is probably partly because of a paucity of studies on this family (Marsh 1990), while the tendency of ant communities to change seasonally (P. Hawkes, *pers. comm.*) and differences in study design further confounds this. Termites, by contrast, tend to dominate the soil macrofauna in arid environments (Zeidler *et al.* 2002a,b) although their subterranean habits make them more difficult to sample.

Ground pangolins are wholly myrmecophagous (Coulson 1989; Jacobsen *et al.* 1991; Swart 1996) and selective in their prey choice, selecting specific ant and termite species rather than merely foraging on the most common species (Swart 1996). Swart (1996) recorded ground pangolins consuming 15 ant and five termite species in the Sabi Sand Game Reserve. Jacobsen *et al.* (1991) recorded 13 ant and three termite species in the diets of ground pangolins in north-eastern South Africa whilst

Coulson (1989) recorded five ant and four termite species in the stomachs of ground pangolins from Zimbabwe.

All of these studies were based in mesic environments, with no previous studies focussing on ground pangolins in arid environments. Thus at present data are lacking on the dietary preferences of this species in arid environments. Furthermore, overall prey diversity and abundance may be expected to be lower in arid environments due to lower primary productivity (Kaspari *et al.* 2000; Parr *et al.* 2004) and comparative habitat simplicity (Samways 1990; Andersen 1993; Swart 1996; Lindsey & Skinner 2001; Schoeman & Foord 2012). These predictions have implications for ground pangolin diets in arid environments, as they suggest that ground pangolins may utilise a greater suite of species than they do in mesic environments. This study is the first to investigate the dietary preferences of ground pangolins near the most arid edge of this species' range.

5.2 MATERIALS AND METHODS

5.2.1 Study Site

This study was conducted on Kalahari Oryx Private Game Farm (KO), situated in the Kalahari Biome in the Northern Cape Province of South Africa between latitudes 28°21'S – 28°42'S and longitudes 21°55'E – 22°15'E (Figure 5.1). Summer air temperatures may exceed 40 °C, with an average maximum summer temperature of 34 °C and an average minimum temperature of 17 °C. Winter temperatures may drop as low as -14 °C, and average a minimum of 3 °C and a maximum of 19 °C. The majority of rain falls between October and April with a peak from December to March,

predominantly in the form of thunderstorms. There is, however, some rainfall recorded throughout all months of the year (Figure 5.2).

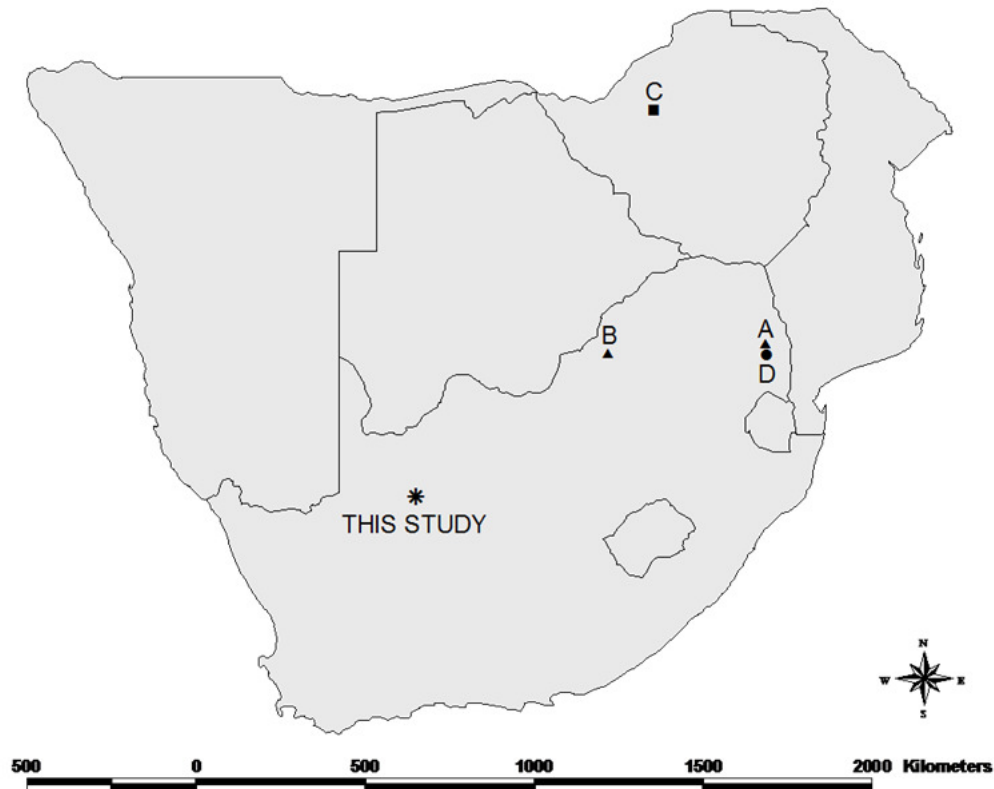


Figure 5.1. Location of the present study in relation to previous ground pangolin research. (A) Hans Hoheison Wildlife Research Station and (B) Thabazimbi: van Aarde *et al.* 1990, Jacobsen *et al.* 1991; (C) Sengwa Wildlife Research Station: Heath & Coulson 1997a,b, 1998, Richer *et al.* 1997; and (D) Sabi Sand Game Reserve: Swart 1996, Swart *et al.* 1999.

The study site was divided into nine vegetation types based on dominant plant species, structure and geology. These were: Grassy Dwarf Shrubland, Dwarf Karroid Shrubland, *Acacia mellifera* - *Rhigozum trichotomum* Veld, *Acacia erioloba* Veld, *Acacia mellifera* Thickets, *Acacia haematoxylon* Savannah, Mixed Savannah, Duneveld Grassland and Mountain Veld. The *Acacia haematoxylon* Savannah, *Acacia mellifera* Thickets, Mixed Savannah and Duneveld Grassland jointly comprise the Gordonia Duneveld (SVkd 1) of Mucina and Rutherford (2006); the *Acacia*

mellifera Thickets, *Acacia mellifera* - *Rhigozum trichotomum* Veld (in the east), *Acacia erioloba* Veld and elements of the *Acacia haematoxylon* Savannah, Mixed Savannah and Dwarf Karroid Shrubland can be assigned to Olifantshoek Plains Thornveld (SVk 13). Mountain Veld is synonymous with Mucina and Rutherford's (2006) Koranna-Langeberg Mountain Bushveld (SVk 15), while Kalahari Karroid Shrubland (NKb 5) is locally represented by Grassy Dwarf Shrubland and *Acacia mellifera* - *Rhigozum trichotomum* Veld (in the west). Dwarf Karroid Shrubland is synonymous with Gordonias Plains Shrubland (SVk 16).

5.2.2 Ant and Termite Sampling

Invertebrate sampling was conducted monthly from March 2011 – February 2012 in eight of the nine habitat types (Grassy Dwarf Shrubland was excluded due to logistical constraints). Ant and termite assemblages were sampled with non-lipped plastic bottles with a mouth diameter of 45 mm and a depth of 64 mm. A single pitfall array consisting of a 3 x 4 grid of pitfall traps, with traps placed 10 m apart, was placed randomly in each habitat type. Traps were buried flush with the ground with minimal disturbance to surrounding vegetation. Whenever possible, equal numbers of pitfall traps were placed in sunny and shaded locations to sample both of these microhabitats (Swart 1996). Each pitfall trap was filled to a depth of 20 – 35 mm with a 50 % propylene glycol solution as preservative, with more solution being added in summer to compensate for the greater evaporation rates. To overcome the 'digging-in' effect (Joesse 1965; Greenslade 1973) traps were buried two weeks prior to the onset of sampling. Traps were activated for 48 consecutive hours every month and sampled at dawn and dusk daily, following the time recommended for a standard ant sampling protocol (Agosti & Alonso 2000). When inactive, empty bottles with their lids

fitted were left in position to mark the sampling sites and to prevent unnecessary disturbance during the next round of sampling.

Termite richness was additionally assessed with two bait varieties. Baits were placed in a 6 x 6 grid, placed 5 m apart, and consisted of 18 toilet paper rolls (each roll held together with a single strip of clear plastic tape) and 18 pine stakes (300 mm x 35 mm x 35 mm). Baits were buried vertically, covered with 50 mm of soil and marked by placing a stone on top of them. Owing to a large proportion of the toilet rolls being dug up by bat-eared foxes *Otocyon megalotis*, and initial observations indicating that termites only form a small proportion of ground pangolin diets at the study site, monitoring of termite baits was discontinued after the first month and excluded from all analyses.

Pitfall samples were sorted macroscopically (and microscopically where doubt existed) into orders and stored separately in absolute ethanol. Samples from each site were pooled according to the sampling period, resulting in a final sample size of four samples per site per month (two day samples, two night samples). Samples were sorted microscopically into morphospecies based on external morphological characteristics, the number of individuals of each morphospecies in each sample was recorded, and a reference collection established. Traps disturbed by animals were excluded from the analyses and were statistically corrected for.

As certain ant species travel in armies, a single pitfall trap may trap disproportionately high numbers of these species. Likewise, if a trap is inadvertently placed near an active ant nest, this particular trap may induce biases (Swart 1996). In order to make the data more representative, in instances where more than 50 % of individuals from

a morphospecies in a sample were collected in a single pitfall trap, this trap was excluded from the analysis and statistically corrected for (provided that ≥ 10 individuals of that morphospecies were captured in the entire sample). A representative sample of each morphospecies was sent to an ant taxonomist (Peter Hawkes, AfriBugs, Onderstepoort, Pretoria) for identification to the lowest taxonomic level possible. If the species could not be determined, the specimen was assigned an AfriBugs morphospecies code (AFRC-za code) matched to the AfriBugs collection.

5.2.3 Feeding Observations

Fourteen habituated ground pangolins were followed throughout this study for various periods of time. Observations were made in all habitat types and at various times of the day and night, depending on the activity periods of the study animals. Study animals were observed from a distance of 1 – 5 metres, depending on the individual and how it reacted to the presence of the observer. After an individual had fed at a specific site, a sample of the prey was collected and stored in absolute ethanol for later identification. These samples were microscopically compared to the reference collection and a subset sent to AfriBugs for verification.

To assess whether any particular prey species was preferentially selected for, each ant and termite species was assigned a forage ratio based on the equation of Manly *et al.* (1993):

$$\dot{W} = o_i / \pi_i$$

where o_i is the proportion of prey type i observed in the diets of ground pangolins and π_i is the proportion of prey type i that is available to ground pangolins as prey (i.e. the proportion of each ant and termite species recorded in pitfall traps during this study). These ratios were then standardised by dividing the individual forage ratio for each

species by the sum of all forage ratios (Minnaar *et al. submitted*). This results in a value between zero and one, with zero indicating that the species was not fed on at all and one indicating that this species was exclusively fed on.

5.2.4 Statistical Analyses

Nonparametric repeated measures ANOVA was used to test for any significant difference in ant and termite species richness and abundance between sites and a Dunn's Multiple Comparisons test was applied to determine which sites contributed to influence this significance, if observed. A Kruskal-Wallis test was employed to assess whether the ant and termite species selected for by ground pangolins were equally distributed across all study sites. A Mann-Whitney U' test was used to test if ant activity showed any significant relationship to seasons and a Spearman Rank correlation test was applied to determine if ant and termite activity was associated with monthly temperatures. A Wilcoxon Matched-pairs Signed-rank test was used to test whether ant and termite activity was associated with day or night photoperiods. A Chi-squared test was used to determine whether ground pangolins selected specific prey species or whether prey selection was random. All Statistical analyses were performed with the software program Statistica (StatSoft 2009).

5.3 RESULTS

5.3.1 Ant and Termite Richness and Abundance

Fifty-three ant species, representing seven subfamilies and 22 genera, were recorded with an additional species (*Aenictus* AFRC-za03) being actively sampled (Table 5.1). The subfamily Myrmicinae was the most speciose, representing 63 % of all taxa recorded, followed by Formicinae (22 %). The most species-rich genera were

Tetramorium (13 species), *Monomorium* and *Camponotus* (six species each). Four termite species were recorded, representing two subfamilies. Ant and termite species richness was similar between all eight vegetation types, ranging from 35 – 41 species (Table 5.1). The Mountain Veld had the highest species richness (41 species) while the Dwarf Karroid Shrubland and *Acacia mellifera* Thickets had the lowest (35 species each).

Table 5.1. Epigaeic ant and termite species collected in each of the eight vegetation types at the study site between March 2011 and February 2012. The photoperiod in which most activity occurred is also indicated for each species. Numbers in non-boldface indicate species that form part of a morphospecies complex and although its presence at the study site was confirmed, it may not occur in all vegetation types indicated. Totals for these species are for the entire morphospecies complex. Vegetation type codes are: DKS = Dwarf Karroid Shrubland; AMRT = *Acacia mellifera* - *Rhigozum trichotomum* Veld; AE = *Acacia erioloba* Veld; AM = *Acacia mellifera* Thicket; MV = Mountain Veld; MS = Mixed Savannah; DG = Duneveld Grassland; AH = *Acacia haematoxylon* Savannah. AFRC-za = AfriBugs collection morphospecies code.

ANT AND TERMITE SPECIES	VEGETATION COMMUNITY								ACTIVITY PERIOD
	DKS	AMRT	AE	AM	MV	MS	DG	AH	
FORMICIDAE									
Aenictinae									
<i>Aenictus furibundus</i> Arnold				3					Nocturnal
* <i>Aenictus</i> AFRC-za03									
Cerapachyinae									
<i>Cerapachys coxalis</i> Arnold		2							Diurnal
Dolichoderinae									
<i>Technomyrmex pallipes</i> (F. Smith)		1	24	22	146	330	2	233	Nocturnal
Dorylinae									
<i>Dorylus</i> AFRC-za05	4				1			2	Nocturnal
Formicinae									
<i>Anoplolepis steingroeveri</i> (Forel)	131	59	38	1		795	156	246	Both
<i>Camponotus fulvopilosus</i> (de Geer) [savannah form]		56	11	47	2	28	39	25	Diurnal
<i>Camponotus mystaceus kamae</i> Forel	8	51	12	86	44	172	84	30	Nocturnal
<i>Camponotus namacola</i> Prins	2								Diurnal

Table 5.1 continued

ANT AND TERMITE SPECIES	VEGETATION COMMUNITY								ACTIVITY PERIOD
	DKS	AMRT	AE	AM	MV	MS	DG	AH	
<i>Camponotus</i> AFRC-za20						1			Diurnal
<i>Camponotus (Myrmosericus)</i> AFRC-za34					10				Diurnal
<i>Camponotus</i> AFRC-za50 sp. nov.						7			Diurnal
<i>Lepisiota imperfecta</i> (Santschi)		2		1	2	12	18	8	Diurnal
<i>Lepisiota</i> AFRC-za15		2		1	2	12	18	8	Diurnal
<i>Lepisiota</i> AFRC-za19					23	4			Diurnal
<i>Lepisiota</i> AFRC-za20		5	66	5		22	13	23	Diurnal
<i>Tapinolepis</i> AFRC-za02	30	101	2	7	8	111	60	6	Diurnal
Myrmicinae									
<i>Cataulacus intrudens</i> (F. Smith)		5	6						Both
<i>Crematogaster</i> AFRC-za08		44	8	17	3	5			Both
<i>Crematogaster</i> AFRC-za12			2	1	119			1	Nocturnal
<i>Meranoplus glaber</i> Arnold	4	7	2		2	66	105	7	Nocturnal
<i>Meranoplus spininodis</i> Arnold	4	7	2		2	66	105	7	Nocturnal
<i>Messor capensis</i> (Mayr)		6	3						Diurnal
<i>Monomorium damarense</i> Forel	203	690	218	272	39	513	659	521	Diurnal
<i>Monomorium minor</i> Stitz	6	140	61	6	21	94	90	84	Diurnal
<i>Monomorium notulum</i> Forel	203	690	218	272	39	513	659	521	Diurnal
<i>Monomorium rufulum</i> Stitz	48	2	5	50	15	292	3	2	Diurnal
<i>Monomorium setuliferum</i> Forel	203	690	218	272	39	513	659	521	Diurnal
<i>Monomorium vaguum</i> Santschi	203	690	218	272	39	513	659	521	Diurnal

Table 5.1 continued

ANT AND TERMITE SPECIES	VEGETATION COMMUNITY								ACTIVITY PERIOD
	DKS	AMRT	AE	AM	MV	MS	DG	AH	
<i>Myrmicaria fusca nigerrima</i> Arnold				2	2				Both
<i>Nesomyrmex vannoorti</i> Mbanyana & Robertson	4	3	3		1		3	1	Diurnal
<i>Ocymyrmex cavatodorsatus</i> Prins				2		2	1	12	Diurnal
<i>Ocymyrmex hirsutus</i> Forel	13	77	33	29		99	76	76	Diurnal
<i>Oligomyrmex</i> AFRC-za01	4				1			2	Nocturnal
<i>Pheidole tenuinodis</i> Mayr	525	1023	410	112	7	393	1573	454	Both
<i>Pheidole</i> AFRC-za10	8		8						Diurnal
<i>Pheidole</i> AFRC-za17	8		8						Diurnal
<i>Pheidole</i> AFRC-za25	203	690	218	272	39	513	659	521	Diurnal
<i>Tetramorium argentopilosum</i> Arnold	4	3	3		1		3	1	Diurnal
<i>Tetramorium flaviceps</i> Arnold	65	69	79	72	73	171	103	47	Both
<i>Tetramorium inezulae</i> (Forel)	35	78	338	96	7	987	104	485	Both
<i>Tetramorium luteolum</i> Arnold	65	69	79	72	73	171	103	47	Both
<i>Tetramorium peringueyi</i> Arnold	1				3	1			Diurnal
<i>Tetramorium rufescens</i> Stitz	468	647	279	576	661	326	71	209	Diurnal
<i>Tetramorium sericeiventre</i> Emery	140	355	129	6	279	99	5		Diurnal
<i>Tetramorium sericium</i> Arnold	35	78	338	96	7	987	104	485	Both
<i>Tetramorium simulator</i> Arnold							10		Diurnal
<i>Tetramorium</i> AFRC-za12	203	690	218	272	39	513	659	521	Diurnal
<i>Tetramorium</i> AFRC-za21	35	78	338	96	7	987	104	485	Both
<i>Tetramorium</i> AFRC-za22	65	69	79	72	73	171	103	47	Both
<i>Tetramorium</i> AFRC-za23	65	69	79	72	73	171	103	47	Both

Table 5.1 continued

ANT AND TERMITE SPECIES	VEGETATION COMMUNITY								ACTIVITY PERIOD
	DKS	AMRT	AE	AM	MV	MS	DG	AH	
Ponerinae									
<i>Anochetus levaillanti</i> Emery			2		3	2	2		Diurnal
<i>Pachycondyla elisae</i> Forel			1		4				Both
<i>Hypoponera perparva</i> Bolton & Fisher	4				1			2	Nocturnal
TERMITIDAE									
Termitidae (unidentified sp.) 1		12	4	4		1	10	4	Both
Termitidae (unidentified sp.) 2				4	33	34	76	21	Both
Hodotermitidae									
<i>Hodotermes mossambicus</i> Hagen	17	49				20	7		Both
Nasutitermitinae									
<i>Trinervitermes trinervoides</i> Sjöstedt				3	12	13	16	3	Both
TOTAL NUMBER OF SPECIES	35	36	38	35	41	40	38	38	

Ant species richness and abundance differed significantly between the eight sites (Friedman Statistic $F_r = 18.251$, $P = 0.011$, $df = 27$). However, the post-test indicated that only the Dwarf Karroid Shrubland differed from the Mixed Savannah in terms of prey richness and abundance. Therefore it can be assumed that prey availability and species richness are equal across all vegetation types, except for the Dwarf Karroid Shrubland which only had 35 different species and 1 718 prey items trapped - the lowest of any of the sites.

Prey species presence did not differ significantly between sites ($P = 0.593$) although *Anoplolepis steingroeveri* was most prevalent in the Mixed Savannah (Table 5.1) and was the species most often preyed on by ground pangolins (47 % of observed foraging bouts, Table 5.2).

Ant activity showed pronounced seasonal variation, with significantly more species and individuals being captured in summer (Nov – Feb) than winter (May – Aug) (Mann-Whitney $U' = 16$, $P = 0.014$) (Figures 5.2 & 5.3). There was a significant correlation between the total number of ant and termite individuals caught each month and average monthly minimum (Spearman Rank-correlation $r = 0.923$, $P < 0.001$, $df = 11$) and maximum ($r = 0.874$, $P < 0.001$, $df = 11$) ambient temperatures. There was significantly more ant activity during the day (58.5 %, $n = 31$) compared to the night (17 %, $n = 9$) ($t = 1.803$, $P = 0.009$, $df = 39$) (Figure 5.2). The remaining 24.5 % ($n = 13$) of species could not be assigned to either photoperiod, either because the sample sizes were too small or because these species were crepuscular or genuinely active during both photoperiods. When only the five prey species were considered (excluding Termitidae sp., which was not often collected in pitfall traps), there was no significant difference in photoperiod activity ($t = 0.079$, $P = 0.087$, $df =$

4). This suggests that although prey species activity was higher during the day, this was not significantly so.

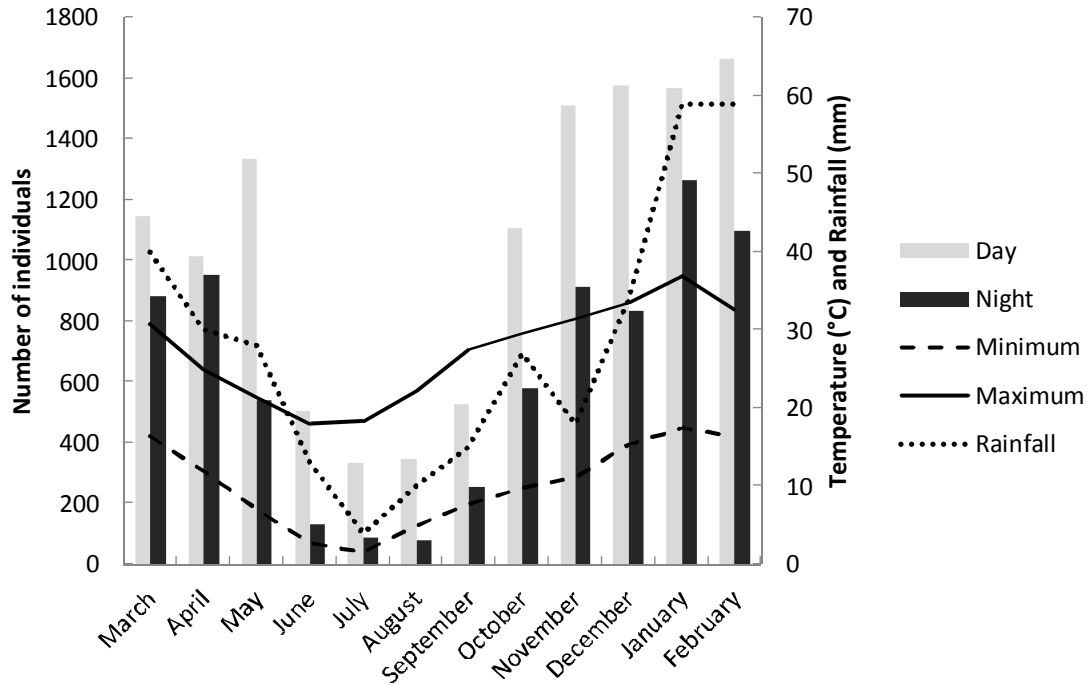


Figure 5.2. Absolute numbers of epigaeic ants and termites captured in day and night samples between March 2011 and February 2012. The average minimum and maximum temperatures as well as rainfall during this period are also shown.

5.3.2 Feeding Observations

A total of 146 feeding bouts by 14 individuals were observed, involving four ant and two termite species (Table 5.2). *Anoplolepis steingroeveri* was preyed on most frequently, followed by *Crematogaster* AFRC-za08 and *Crematogaster* AFRC-za12. Ground pangolins were recorded feeding on Termitidae sp. 1 on two occasions, although on both occasions the amount of time spent at the exposed subterranean nest suggests that they may have just excavated the nest and moved on without actually consuming any termites. If ground pangolins do indeed feed on this species it only forms a very small proportion of their diet at this site.

Table 5.2. Number of foraging bouts, proportion of foraging bouts and standardised forage ratio for each of the ant and termite species preyed on by ground pangolins at Kalahari Oryx Private Game Farm.

Species	Number of foraging bouts	% of total observations	Standardised Forage Ratio
<i>Anoplolepis steingroeveri</i>	69	47	0.063
<i>Camponotus fulvopilosus</i>	8	6	0.055
<i>Crematogaster</i> AFRC-za08	31	21	0.520
<i>Crematogaster</i> AFRC-za12	20	14	0.218
Termitidae sp. 1	2	1	0.104
<i>Trinervitermes trinervoides</i>	16	11	0.041

Ground pangolins did not prey on the most abundant ant and termite species but rather selected specific species (Chi-squared test $\chi^2 = 19.090$, $P < 0.001$, $df = 1$) (Figure 5.3). The standardised forage ratio values suggest that *Crematogaster* AFRC-za08 was preyed upon more frequently than its presence in pitfall traps would suggest, indicating that ground pangolins may have specifically selected this species. *Crematogaster* AFRC-za12 was also preyed on more frequently than its presence in pitfall traps would suggest. These results indicate that ground pangolins may be preferentially selecting the two *Crematogaster* species and that *Anoplolepis steingroeveri* is preyed on in relation to its absolute abundance.

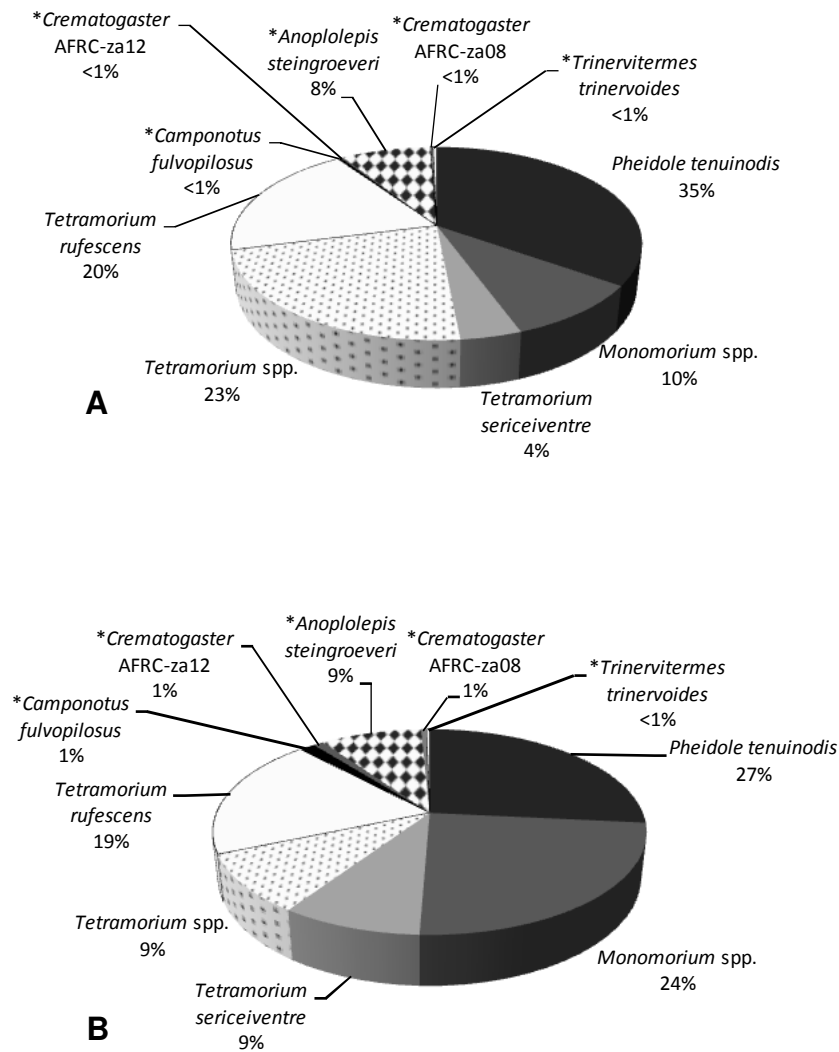


Figure 5.3. (A) Winter (May – Aug) and (B) Summer (Nov – Feb) variation in the relative abundance of the five most common ant species, and ant and termite species that were preyed on by ground pangolins, pooled for all eight sites. Species marked with a “*” were preyed on by ground pangolins.

Trinervitermes trinervoides formed an important component of the diet of those individuals that had access to mountains, where this species is prevalent. The Mountain Veld had the highest concentration of epigeal termitaria, the majority of which showed signs of predation. Epigeal termitaria were only rarely encountered in the Dwarf Karroid Shrubland, with fewer of these showing signs of having been fed on, and were completely absent from all other habitats. Although termites were present in all of the habitats sampled (Table 5.1), termitaria that were not in the

Mountain Veld or Dwarf Karroid Shrubland were subterranean. *Crematogaster* AFRC-za12 was most prevalent in mountains (Table 5.1), frequently occurring in moribund termitaria. In contrast, *Crematogaster* AFRC-za08 occurred almost exclusively in the dunes and plains, where it was particularly common at the base and on the stems of trees and logs. *Anoplolepis steingroeveri* and *Camponotus fulvopilosus* were almost exclusively encountered in the flatter areas of the study site, where they were particularly common at the bases of grass tufts.

5.4 DISCUSSION

Ground pangolins were recorded preying on only four ant and two termite species, representing 7.5 % and 50 % of the total species richness of each family, respectively. However, as the termite diversity at the site was not comprehensively sampled it is probable that this diversity is higher, which would suggest an even greater selectivity regarding termites than the current value suggests. These results are contrary to the findings of Swart *et al.* (1999) who recorded ground pangolins to feed on 15 ant and five termite species (30 % and 100 % of species richness, respectively) in the mesic Sabi Sand Game Reserve. However, five ant (10 %) and one termite (20 %) species constituted 97.7 % of the diet (Swart *et al.* 1999), which is similar to the current findings. Similarly, Jacobsen *et al.* (1991) recorded ground pangolins to feed on 13 ant and three termite species. These data suggest that ground pangolins selectively feed on a small number of ant and termite species, but that they will opportunistically forage on other species as well.

Although *Anoplolepis steingroeveri* was preyed on most frequently, the standardised forage values suggest that the two *Crematogaster* species were consumed more

frequently than their proportional abundance at the study site would suggest, which may indicate that ground pangolins specifically target these species. These results may also suggest, however, that *Crematogaster* are more sedentary and thus less likely to be sampled in pitfall traps, while the more active behaviour of *A. steingroeveri* makes them more likely to be sampled. This perceived lower abundance will in turn result in a higher perceived forage ratio, thus inflating these prey species' apparent importance in the diet.

This researcher does not believe that it is biologically relevant to designate one particular species as being the most important prey species for ground pangolins at the study site (cf. Swart 1996; Swart *et al.* 1999). Rather, it is this researcher's opinion that all five species preyed on (excluding Termitidae sp. 1) are equally important and that the observed differences in proportional consumption, and hence forage value, of the prey species may be attributable to observer bias (more observations made in certain habitat types) and the relative abundance of each species at the study site. Furthermore, the proportion of each prey species in the diet largely reflects the habitats that are available to individual ground pangolins, as many of the prey species also show habitat specificity.

Ground pangolins are selective in their prey choice, not foraging on the most abundant species but rather selecting specific species that often occur at lower abundances (see also Swart 1996). This selectivity does not appear to be based on the size of the prey alone, as the four most commonly collected ant species all have average body lengths of 3.2 – 3.9 mm, as do *Crematogaster* spp., the latter being regularly preyed on by ground pangolins. The chemical and mechanical defences of each species are likely to play a role in determining whether they are suitable as

prey, as would nest characteristics. If the nest chambers are deep underground they will be out of reach of foraging ground pangolins, which typically only dig shallow excavations while foraging (see also Swart 1996; Swart *et al.* 1999). Species with well-developed chemical and physical defences are also likely to be avoided, as are species that occur at low densities.

In order to be available as a viable food source ants and termites should be inactive in burrows, and thus concentrated, when ground pangolins are active (see also Swart 1996). This is nearly always the case with *T. trinervoides*, which are either clumped within their mounds or in foraging runs (Adam 1993; Taylor *et al.* 2002). Despite *Crematogaster* AFRC-za12 being predominantly nocturnal, large concentrations were still present in moribund termitaria at night, facilitating their availability as a prey source. All five prey species are virtually inactive during winter, thus representing a permanently clumped food resource. Many ground pangolins become diurnal during winter (Chapter 3) and are thus able to escape the cold night-time temperatures while still having a clumped food resource available. However, many ant species are presumed to hibernate deep underground in winter, thus effectively removing them as a food source. This appears to be confirmed by some ground pangolins, especially young animals, losing condition during winter and some even dying of starvation (Heath & Coulson 1998; Chapter 6), although increased energy requirements due to the colder temperatures may also account for this drop in mass.

The pitfall trapping data indicate that *A. steingroeveri*, which is most frequently preyed on by ground pangolins, is most prevalent in the Mixed Savannah, suggesting that ground pangolins should preferentially select this habitat type while foraging. This was not observed, however, and foraging ground pangolins showed no habitat

selection (Chapter 3). This may be explained by the fact that although *A. steingroeveri* was most preyed on, it was not the sole prey species. This further substantiates the contention that no single species can be designated the most important prey species and that all prey species play a role in determining habitat use by ground pangolins.

Contrary to the findings of Swart (1996) only termite mounds were regularly revisited, and no ant nests were recorded to be visited more than once. This may be an observational artefact, or it may be that ant nests are more prevalent or more evenly distributed in the Kalahari due to the softer sand being easier to dig in and it thus being easier to establish a new nest. In agreement with Swart (1996) and Jacobsen *et al.* (1991), study animals followed a zig-zag pattern while active, allowing them to effectively cover more ground while foraging.

Previous authors (Kingdon 1971; Swart 1996) suggested that mound-building termite species are not available to ground pangolins as a food source due to the hard mound crust being impenetrable to the pangolin's comparatively weak digging abilities. During this study ground pangolins frequently preyed on *T. trinervoides* and *Crematogaster* AFRC-za12 within active and moribund termitaria. In these instances they would enter the termitarium through an existing foraging hole, usually located on the side of the mound, and once inside the comparatively soft carton material was dug away to expose the ants and termites. It is unclear whether ground pangolins or another animal dug the initial foraging holes, as aardvark *Orycteropus afer* are reported to often feed in termitaria (Willis *et al.* 1992; Lindsey 1999) and is the only other species at the study site with claws strong enough to create the initial opening. Although only the aardvark has been recorded opening epigeal termite mounds, *T.*

trinervoides mounds at the study site occur almost exclusively in the mountains – a habitat that no aardvark was seen in, nor was any other sign of aardvark found here. In addition, termitaria at the top of the mountains often have foraging holes in them while Lindsey (1999) suggests that aardvark avoid rocky terrain due to their decreased mobility in this habitat and the increased difficulty of digging in between rocks. It is unlikely that aardvark would spend unnecessary energy to ascend to the top of a mountain to forage when there are no suitable refuges there and when more accessible prey sources are present on the flatter ground and mountain foothills. Ground pangolins, by contrast, do not require large refuges and often take refuge beneath bushes, in rock piles or between rocks (Chapter 3). They are also proficient climbers and can ascend a mountain with surprising ease. On one occasion a female ground pangolin was observed starting to dig into a termite mound following heavy rains that softened the hard outer crust. This researcher surmises that ground pangolins are capable of opening termite mounds, especially after rains, and that once opened a mound is regularly revisited to maintain the feeding port. This prevents the re-establishment of the hard outer crust and ensures a reliable food resource for those individuals that have access to mountains.

This study agrees with previous studies in that ground pangolins are wholly myrmecophagous and selective in their dietary habits, selecting specific ant and termite species rather than preying on the most abundant species. Contrary to what might be expected, ground pangolins in arid environments are just as selective as mesic populations with regards to prey species. This study also found ants to comprise the bulk of the ground pangolin's diet, but that termites remain an important food source as well.

CHAPTER SIX

CORE BODY TEMPERATURE OF A FREE-ROAMING GROUND

PANGOLIN *SMUTSIA TEMMINCKII*

6.1 INTRODUCTION

Heterothermy is widespread in mammals and is used by species from both tropical and temperate regions, although being more prevalent in smaller-bodied mammals (Geiser 1998, 2004; Lovegrove 2012). Recent years have seen an increased interest in determining the evolutionary origins of heterothermy, in part because of the implications for understanding the origins of endothermy in general. These endeavours have highlighted the paucity, and often complete lack, of data for a variety of mammalian taxa, many of which may shed light on the origins of heterothermy (Lovegrove 2012). Recent work in the Afrotheria, especially the tenrecs, has revealed that normothermy and heterothermy are in fact on a thermal continuum and that there is no distinct 'cross-over' point between these two states (Poppitt *et al.* 1994; Lovegrove & Génin 2008).

Pangolins belong to the Order Pholidota, which is most closely related to the Carnivora (Murphy *et al.* 2007). They are unique among mammals in that their bodies are covered in hard scales rather than hair, which although providing adequate protection against predators (Swart 1997; *pers. obs.*) offer minimal thermal insulation (McNab 1984; Heath & Hammel 1986; Weber *et al.* 1986; Swart 1996). Ground pangolins feed exclusively on ants and termites (Swart 1996; Swart *et al.* 1999; Chapter 5) and previous studies have found myrmecophagous placental mammals to have lower than average core body temperatures (T_b) (Eisenraut 1956; Jones 1973;

McNab 1984; Heath & Hammel 1986; Heath 1987). Previous authors using rectal measurements to study T_b in captive pangolins recorded values of 27.0 – 34.0 °C for three-cusped pangolins *Phataginus tricuspis* (Eisentraut 1956; Jones 1973; McNab 1984), 26.5 – 34.5 °C for giant pangolins *Smutsia gigantea* (Jones 1973), 27.5 – 37.5 °C for Sunda pangolins *Manis javanica* (McNab 1984), 33.0 – 34.0 °C for thick-tailed pangolins *M. crassicaudata* (McNab 1984) and 33.2 – 35.5 °C for short-tailed pangolins *M. pentadactyla* (Heath & Hammel 1986; Heath 1987). Jones (1973) reported that at ambient temperatures (T_a) below 26.0 °C, the T_b of giant pangolins would often become variable with some individuals displaying “precipitous” drops in T_b . Although these data provide initial insights into the physiology of captive pangolins, they cannot necessarily be viewed as representing the condition in the wild, as physiological patterns are often vastly different between captive and wild individuals (Geiser *et al.* 2000, 2007).

Patterns of thermoregulation have not yet been studied in free-roaming pangolins, owing largely to the difficulty in finding these secretive mammals and tracking individuals for any length of time. Furthermore, the African pangolin species are extremely difficult to keep in captivity and thus it is unlikely that any detailed physiological studies on captive individuals will be forthcoming. Despite the small sample size (a single animal), the current study provides insights into thermoregulation under free-ranging conditions in an entire mammalian order of which virtually nothing is known. The value of physiological data from single animals has been discussed previously. For instance, Withers *et al.* (2000) reported data from a single north-western marsupial mole *Notoryctes caurinus*, citing this species’ rarity and difficulty to obtain as validation for the small sample size. In that study, the marsupial mole was kept in captivity during experimentation and died shortly after

completion of the experiments (Withers *et al.* 2000). Nonetheless, the novelty of the data and the difficulty in obtaining such data validated its publication, and this researcher would argue that the same criteria apply here.

6.2 MATERIALS AND METHODS

A TidbiT v2 temperature data logger (Onset Computer Corporation, Massachusetts) was implanted into an adult female ground pangolin *Smutsia temminckii* (1120 mm, 7.08 kg) by a veterinary surgeon. She was anaesthetised with a cocktail of 0.62 ml (8.9 mg / kg) ketamine hydrochloride (Anaket V) and 0.62 ml (0.09 mg / kg) medetomidine hydrochloride (Domitor) injected intramuscularly into the *quadriceps femoris* muscle mass, the drugs taking effect within four minutes. The sterilised logger was implanted in the intraperitoneal cavity via a median incision. All tissue layers were individually sutured using permanent sutures and the epidermis was sutured with 'side-stitching' to ensure complete sealing of the wound, prevent any foreign bodies from entering the wound and to prevent the animal from being able to remove the sutures. 0.62 ml of Convenia (0.79 mg / kg) was administered as a long-acting antibiotic; the entire procedure lasting 20 minutes. She woke up 2.5 minutes after administration of 0.62 ml (0.44 mg / kg) of the reversal agent Antisedan and was transported back to the study site and released at the capture site 28 hours after being captured. Upon release, she purposefully walked off and was followed at a distance until she entered an abandoned aardvark *Orycteropus afer* burrow that she could use as a refuge.

A second logger was implanted into a young male (STEM 23), who was followed for 143 days after the procedure before contact was lost when he started to disperse

(Chapter 4). During this period he also displayed normal behaviour, suggesting that the procedure had no adverse effects on either individual. Due to the data logger needing to be retrieved in order for the data to be downloaded, no data could be obtained from this individual.

Prior to deployment, temperature loggers were calibrated against a mercury thermometer (accurate to 1 °C) by immersing them in incrementally heated water baths (15 – 45 °C, 5 °C intervals) and allowed to equilibrate for 20 minutes, recording the temperature at one-minute intervals. Air temperature (T_a) at the study site was recorded using a mercury minimum - maximum thermometer (Zhejiang, China) placed in a central location.

A non-parametric Spearman Rank Correlation test, corrected for ties, was used to test whether there was a correlation between T_a and T_b values. The Heterothermy Index (HI) proposed by Boyles *et al.* (2011) was used to interpret the overall variation and pattern of the T_b trace.

General body condition and the relative mass of ground pangolin armour was assessed by examining 18 individuals that were found dead, either as a result of electrocutions on electrified fences or as road mortalities. Only recently deceased individuals were used to preclude skewing of the data through desiccation and putrefaction-induced weight loss. Animals were skinned and the mass of the armour (scales and epidermis) and the remainder of the body were determined by weighing these components separately on an electronic scale. General body condition was scored using a sliding scale of 0 – 5, with 0 representing no body fat and 5 representing maximum body fat.

6.3 RESULTS

The adult female was followed for 34 days after the procedure before she died of natural causes. During this time she was followed regularly and her behaviour did not differ from what was observed prior to the surgery, or from other individuals that were observed concurrently at the study site.

The female's T_b followed a cyclical circadian pattern (Figure 6.1). Like other individuals in the study population she displayed predominantly diurnal activity during this study period, becoming active by mid-afternoon and retreating down a burrow by early evening. T_b 's were generally highest in the early afternoon, coinciding with the onset of activity. Following the initial rewarming spike, T_b decreased to a 0.8 – 1.2 °C lower 'activity temperature' while she foraged. During periods of activity, T_b was erratic, showing frequent small spikes and troughs. After retiring to a suitable refuge, T_b decreased gradually to a minimum value prior to rapid rewarming preceding the onset of activity. T_b ranged between 29.5 – 35.4 °C, although typically remaining between 32.0 – 35.0 °C. There was a rapid decrease in T_b from a peak of 35.4 °C at 14:00 pm on the 3rd of June to a low of 30.1 °C at 10:45 am on the 4th of June – a difference of 5.3 °C in less than 24 hours. From 8 – 10 June T_b remained low (29.5 – 32.3 °C), with temperatures peaking at midnight. No direct observations were available for this period and it is thus not known whether she became nocturnal during this period or completely inactive, although the latter is suspected.

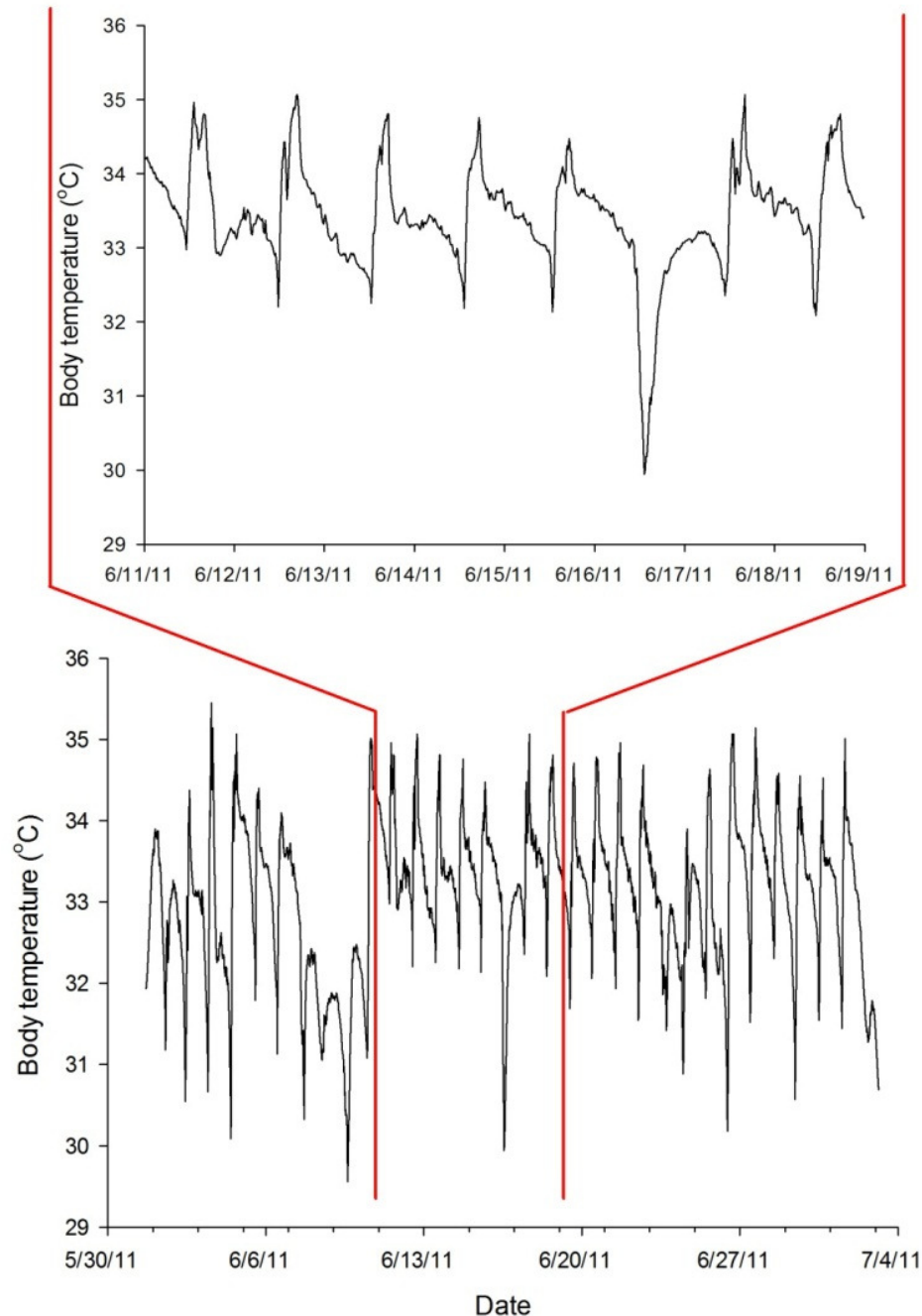


Figure 6.1. Core body temperature trace of a free-ranging adult female ground pangolin *Smutsia temminckii* measured between 31 May and 3 July 2011. The exploded section shows daily core body temperature variation between 11 and 19 June.

There was no correlation between daily $T_{a \text{ min}}$ and $T_{b \text{ min}}$ (Spearman's Rank Correlation $r = 0.194$, $P = 0.297$, $df = 30$) or the range of daily T_a and T_b values ($r = 0.221$, $P = 0.232$, $df = 30$), although there was a significant correlation between daily

$T_{a \max}$ and $T_{b \max}$ ($r = 0.505$, $P = 0.004$, $df = 30$). Daily HI values averaged $0.97 \text{ }^\circ\text{C}$ across the study period (range $0.45 - 2.36 \text{ }^\circ\text{C}$).

Body armour comprised $34.3 \pm 3.4 \%$ (mean \pm SD) of total mass.

6.4 DISCUSSION

These results suggest that ground pangolins are indeed heterothermic, although the HI value, extent of reduction in T_b and the pattern of the T_b trace are not consistent with torpor or hibernation. This is in line with recent studies which have found that a number of species previously thought to be homeothermic actually display temporal variations in T_b (Boyles *et al.* 2011). The average T_b and variation in daily amplitude recorded here are consistent with previous captive studies of pholidotes (Eisentraut 1956; Jones 1973; McNab 1984; Heath & Hammel 1986; Heath 1987). Furthermore, the T_b values recorded in this study are in the basoendothermic range as defined by Lovegrove (2012), i.e. in the lower 20 % of mammalian T_b 's measured to date.

The continuous small peaks and troughs in T_b while this female was active may reflect locomotory heat production and the inability of scales to provide thermal insulation. Pangolins cannot alter their insulation through piloerection as scales are poor insulators (McNab 1984; Heath & Hammel 1986; Weber *et al.* 1986; Swart 1996) and thus they need to rely on other means to control their T_b , including behavioural and physiological means.

This study found that adipose tissue is stored both subcutaneously and intra-abdominally and is used as an energy source at the onset of winter. 70.6% ($n = 12$)

of ground pangolins examined had fat scores of 4 or 5, while 29.4 % (n = 5) had fat scores of ≤ 3 . Of these latter animals, one was hit by a car while another was rescued from an electrified fence but showed severe neurological trauma – both of these individuals died of their injuries over several days, likely accounting for their low fat scores. One female was in the early stages of pregnancy. A 5-month old pup underwent a 19.8 % reduction in mass at the onset of winter and died two months later. The autopsy revealed that she had no fat reserves and general muscular dystrophy, suggesting that she starved to death and that winter may be a particularly stressful time for young individuals (see also Heath & Coulson 1998). Intra-abdominal fat reserves, especially fat deposits in the pelvic region, are used up first and subcutaneous fat reserves may still be present after these intra-abdominal reserves have been depleted. The persistence of subcutaneous fat suggests that these deposits may be used for insulation in addition to acting as an energy reserve.

Armour constitutes a large proportion of the ground pangolin's total mass, with the values recorded in this study being similar to the 33 % reported by Kingdon (1971). This suggests a high energetic investment in body armour, which in turn suggests that ground pangolins assimilate enough energy from their diet to enable them to carry this extra mass (see Lovegrove 2001) and that carrying this extra mass confers sufficient protection from predators to justify this energy expenditure (see Lovegrove 2000, 2001).

It remains to be determined whether daily heterothermy is seasonally employed by ground pangolins or whether it is employed year-round. It also remains to be determined whether young individuals and nursing females employ heterothermy – the latter being a period of extreme nutritional stress because of the need to

drastically increase weight before pupping (Swart 1996; Chin *et al.* 2011). Despite the small sample size, this paper presents the first sequence of T_b patterns in a free-roaming ground pangolin, including the first evidence that this species uses daily heterothermy. This research also demonstrated the effectiveness of the methods used in this study and provides baseline data on which future studies can build. It is suggested that future studies investigate T_b across all seasons, combining these data with activity-sensing telemetry to better understand the T_b fluctuations in relation to activity patterns. It would also be revealing to study metabolic rate variation across the seasons.

REFERENCES

- ADAM, R.A. 1993. Aspects of the biology of the harvester termite *Trinervitermes trinervoides* (Sjostedt) (Isoptera: Termitidae). Ph.D. thesis, University of the Orange Free State, Bloemfontein, South Africa.
- AGOSTI, D. & ALONSO, L.E. 2000. The ALL protocol: A standard protocol for the collection of ground dwelling ants. *In*: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (eds), *Ants. Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington DC. pp. 204–206.
- ANDERSEN, A.N. 1993. Ant assemblages in the gulf region of Australia's semi-arid tropics: Species composition, patterns of organisation, and biogeography. *Australian Journal of Zoology* 41: 399–414.
- ANSELL, W.F.H. 1960. *Mammals of Northern Rhodesia*, pp. 30–31. The Government Printer, Lusaka.
- ATTUQUAYEFIO, D.K., GORMAN, M.L. & WOLTON, R.J. 1986. Home range sizes in the wood mouse *Apodemus sylvaticus*: Habitat, sex and seasonal differences. *Journal of Zoology (London)* 210: 45–53.
- BECK, A. 2008. Electric fence induced mortality in South Africa. M.Sc. thesis, University of the Witwatersrand, Johannesburg, South Africa.
- BERGER, D. 2006. South Africa Yearbook 2005/2006. Government Communication and Information System. Pretoria, South Africa.
- BIRCH, N. & BIRCH, M. 2007. Breeding facility management plan for Kalahari Oryx Game Reserve. Unpublished report, 411 pp.
- BOYLES, J.G., SMIT, B & MCKECHNIE, A.E. 2011. A new comparative metric for estimating heterothermy in endotherms. *Physiological and Biochemical Zoology* 84(1): 115–123.

- BRÄUTIGAM, A., HOWES, J., HUMPHREYS, T & HUTTON, J. 1994. Recent information on the status and utilisation of African pangolins. *TRAFFIC Bulletin* 15(1): 15–22.
- BURT, W.H., 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346–359.
- CHALLENGER, D.W.S. 2011. Asian pangolins: Increasing affluence driving hunting pressure. *TRAFFIC Bulletin* 23(3): 92–93.
- CHALLENGER, D.W.S. & HYWOOD, L. 2012. African pangolins under increased pressure from poaching and intercontinental trade. *TRAFFIC Bulletin* 24(2): 53–55.
- CHIN, S-C., LIEN, C-Y., CHAN, Y-T., CHEN, C-L., YANG, Y-C. & YEH, L-S. 2011. Monitoring the gestation period of rescued Formosan Pangolin (*Manis pentadactyla pentadactyla*) with progesterone radioimmunoassay. *Zoo Biology* 30: 1–11.
- COULSON, M.H. 1989. The pangolin (*Manis temminckii* Smuts, 1832) in Zimbabwe. *African Journal of Ecology* 27: 149–155.
- EISENTRAUT, M. 1956. *Der Winterschlaf mit seinen physiologischen und oekologischen Begleiterscheinungen*. Gustav Fisher, Jena. As cited by Geiser 1998.
- FALKENA, H.B. & VAN HOVEN, W. 2000. Bulls, bears and lions: Game ranch profitability in southern Africa. SA Financial Sector Forum Publications, Rivonia.
- FIELDEN, L.J. 1991. Home range and movements of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology (London)* 223: 675–686.
- FRIEDMANN, Y. & DALY, B. (eds). 2004. *Red Data Book of the mammals of South Africa: A conservation assessment*, pp. 598–599. CBSG Southern Africa,

Conservation Breeding Specialist Group (SSC/IUCN), Endangered Wildlife Trust.
South Africa.

- GAUBERT, P., 2011. Family Manidae (Pangolins). IN: WILSON, D.E. & MITTERMEIER, R.A. (EDS). *Handbook of the Mammals of the World Vol. 2. Hoofed Mammals*. Lynx Edicions, Barcelona, Spain, pp. 82–103.
- GAUDIN, T.J., EMRY, R.J. & WIBLE, J.R. 2009. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: A morphology based analysis. *Journal of Mammalian Evolution* 16: 235–305.
- GEISER, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: Importance of body size. *Clinical and Experimental Pharmacology and Physiology* 25: 736–740.
- GEISER, F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology* 66: 239–274.
- GEISER, F., HOLLOWAY, J.C. & KÖRTNER, G. 2007. Thermal biology, torpor and behaviour in sugar gliders: A laboratory-field comparison. *Journal of Comparative Physiology B* 177: 495–501.
- GEISER, F., HOLLOWAY, J.C., KÖRTNER, G., MADDOCKS, T.A., TURBILL, C. & BRIGHAM, R.M. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G., Klingenspor, M. (eds.). *Life in the cold: 11th international hibernation symposium*. Springer, Berlin, pp. 95–102.
- GETTY, T. 1981. Structure and dynamics of chipmunk home range. *Journal of Mammalogy* 62: 726–737.
- GREENSLADE, P.J.M. 1973. Sampling ants with pitfall traps: Digging-in effects. *Insectes Sociaux* 20: 343–353.

- 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. & COULSON, I.M. 1997a. Home range size and distribution in a wild population of Cape pangolins, *Manis temminckii*, in north-west Zimbabwe. *African Journal of Ecology* 35: 94–109.
- HEATH, M.E. & COULSON, I.M. 1997b. Preliminary studies on relocation of Cape pangolins *Manis temminckii*. *South African Journal of Wildlife Research* 27: 51–56.
- HEATH, M.E. & COULSON, I.M. 1998. Measurements of length and mass in a wild population of Cape pangolins (*Manis temminckii*) in north-west Zimbabwe. *African Journal of Ecology* 36: 267–270.
- HEATH, M.E. & HAMMEL, H.T. 1986. Body temperature and rate of O₂ consumption in Chinese pangolins. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 250: 377–382.
- HOFFMANN, M. 2008. *Smutsia temminckii*. In: IUCN 2012. IUCN Red list of threatened species. Version 2012.2. Available online at www.iucnredlist.org. As viewed on 18 January 2013.
- HÖLLDOBLER, B. & WILSON, E.O. 1994. *The ants*. Belknap Press, Massachusetts, USA.
- JACOBSEN, N.H.G., NEWBERY, R.E., DE WET, M.J., VILJOEN, P.C. & PIETERSEN, E. 1991. A contribution of the ecology of the Steppe Pangolin *Manis temminckii* in the Transvaal. *Zeitschrift für Säugetierkunde* 56(2): 94–100.
- JONES, C. 1973. Body temperatures of *Manis gigantea* and *Manis tricuspis*. *Journal of Mammalogy* 54: 263–266.

- JOOSSE, E.N.G. 1965. Pitfall trapping as a method for studying surface dwelling Collembola. *Zeitschrift fuer Morphologie und Oekologie der Tiere* 55: 587–596.
- KASPARI, M., O'DONNELL, S. & KERCHER, J.R. 2000. Energy, density and constraints to species richness: Ant assemblages along a productivity gradient. *American Naturalist* 155: 280–293.
- KINGDON, J. 1971. *East African Mammals – An atlas of Evolution in Africa* Vol. 1. (Primates, Hyraxes, Pangolins, Protoungulates, Sirenians), pp. 365–369. London, Academic Press.
- KYLE, R. 2000. Some notes on the occurrence and conservation status of *Manis temminckii*, the pangolin, in Maputaland, Kwazulu/Natal. *Koedoe* 43: 97–98.
- LINDSEY, P.A. 1999. The feeding ecology and habitat use of the aardvark *Orycteropus afer*. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.
- LINDSEY, P.A. & SKINNER, J.D. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. *Journal of Arid Environments* 48: 551–568.
- LOVEGROVE, B.G. 2000. The zoogeography of mammalian basal metabolic rate. *The American Naturalist* 156: 201–219.
- LOVEGROVE, B.G. 2001. The evolution of body armor in mammals: Plantigrade constraints of large body size. *Evolution* 55: 1464–1473.
- LOVEGROVE, B.G. 2012. The evolution of endothermy in Cenozoic mammals: A plesiomorphic-apomorphic continuum. *Biological Reviews* 87: 128–162.
- LOVEGROVE, B.G. & GÉNIN, F. 2008. Torpor and hibernation in a basal placental mammal, the lesser hedgehog tenrec *Echinops telfairi*. *Journal of Comparative Physiology B* 178: 691–698.

- MANLY, B.F.J., MACDONALD, L. & THOMAS, D. 1993. Resource selection by animals: Statistical design and analysis for field studies. Chapman & Hall, London.
- MANWA, L. & NDAMBA, G.T. 2011. The language of dress among the subcultural group of the Dzimababwe people in Masvingo, Zimbabwe. *Journal of Emerging Trends in Educational Research and Policy Studies* 2(6): 436–442.
- MARES, M.A., LACHER, T.E., WILLIG, M.R., BITAR, N.A., ADAMS, R., KLINGER, A & TAZIK, D. 1982. An experimental analysis of social spacing in *Tamias striatus*. *Ecology* 63: 267–273.
- MARES, M.A., WATSON, M.D. & LACHER, T. 1976. Home range perturbations in *Tamias striatus*. *Oecologia Berlin* 25: 1–12.
- MARSH, A.C. 1990. The biology and ecology of Namib Desert Ants. In: Namib ecology: 25 years of Namib research, M.K. Seely (ed), pp. 109–114. Transvaal Museum Monograph No. 7, Pretoria, 230 pp.
- MCNAB, B.K. 1963. Bioenergetics and determination of home range size. *American Naturalist* 97: 133–139.
- MCNAB, B.K. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology (London)* **203**: 485–510.
- MCNAUGHTON, S.J., 1978. Serengeti ungulates: Feeding selectivity influences the effectiveness of plant defence guilds. *Science* 199: 806–807.
- MILSTEIN, P. LE S. 1966. Preliminary observations of white storks feeding on poisoned brown locusts. *Ostrich* 37(1): 197–215.
- MINNAAR, C., BOYLES, J., SOLE, C., MINNAAR, I. & MCKECHNIE, A. *Submitted*. Light pollution disrupts predator-prey dynamics in a bat-moth community. *Oecologia*.

- MOHR, C.O. 1947. Table of equivalent populations of North American mammals. *American Midland Naturalist* 37: 223–249.
- MUCINA, L. & RUTHERFORD, M.C. (eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- MURPHY, W.J., PRINGLE, T.H., CRIDER, T.A., SPRINGER, M.S. & MILLER, W. 2007. Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Research* 17: 413–421.
- PARR, C.L., ROBERTSON, H.G., BIGGS, H.C. & CHOWN, S.L. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* 41(4): 630–642.
- POPPITT, S.D., SPEAKMAN, J.R. & RACEY, P.A. 1994. Energetics of reproduction in the lesser hedgehog tenrec, *Echinops telfairi* (Martin). *Physiological Zoology* 67: 976–994.
- RICHER, R., COULSON, I. & HEATH, M. 1997. Foraging behaviour and ecology of the Cape Pangolin (*Manis temminckii*) in north-western Zimbabwe. *African Journal of Ecology* 35: 361–369.
- ROBINSON, P.T. 1983. The use of ketamine in restraint of a black-bellied pangolin (*Manis tetradactyla*). *Journal of Zoo and Animal Medicine* 14: 19–23.
- SAMWAYS, M.J. 1990. Species temporal variability: Epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* 84: 482–490.
- SCHOEMAN, C.S. & FOORD, S.H. 2012. A checklist of epigaeic ants (Hymenoptera: Formicidae) from the Marakele National Park, Limpopo, South Africa. *Koedoe* 54(1): 1–7.
- SEAMAN, D.E. & POWELL, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77(7): 2075–2085.

- SMITHERS, R.H.N. 1971. The mammals of Botswana. *Museum Memoirs of the National Museums and Monuments, Rhodesia* 4: 1–340.
- SMITHERS, R.H.N. 1983. *The mammals of the southern African subregion*. University of Pretoria Publishers, Pretoria. pp. 157–159.
- SMITHERS, R.H.N. & WILSON, V.J. 1979. *Check list and atlas of the mammals of Zimbabwe Rhodesia*. Museum Memoir no. 9. The Trustees of the National Museum and Monuments, Salisbury, Zimbabwe Rhodesia, pp. 66–67.
- SOEWU, D.A. & AYODELE, I.A. 2009. Utilisation of Pangolin (*Manis spp.*) in traditional Yorubic medicine in Ijebu province, Ogun State, Nigeria. *Journal of Ethnobiology and Ethnomedicine* 5: 39–49.
- STATSOFT INC. 2009. STATISTICA (Data Analysis Software System) version 9. Available online at www.statsoft.com.
- SWART, J. 1996. Foraging behaviour of the Cape pangolin *Manis temminckii* in the Sabi Sand Wildtuin. MSc Thesis, University of Pretoria, Pretoria, South Africa.
- SWART, J. 1997. Order Pholidota. In: MILLS, G. & HES, L. (eds), 1997. *The complete book of southern African mammals*. Struik Winchester Publishers, Cape Town. pp. 112–113.
- SWART, J.M., RICHARDSON, P.R.K. & FERGUSON, J.W.H. 1999. Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology* 247: 281–292.
- SWEENEY, R.C.H. 1956. Some notes on the feeding habits of the ground pangolin, *Smutsia temminckii* (Smuts). *Annual Magazine of Natural History, 12th series* 9: 893–896.
- SWEENEY, R.C.H. 1974. *Naturalist in the Sudan*. Taplinger Publishing Co., New York, 240 pp.

- TAYLOR, W.A., LINDSEY, P.A. & SKINNER, J.D. 2002. The feeding ecology of the aardvark *Orycteropus afer*. *Journal of Arid Environments* 50: 135–152.
- VAN AARDE, R.J., RICHARDSON, P.R.K. & PIETERSEN, E. 1990. Report on the behavioural ecology of the Cape Pangolin (*Manis temminckii*). Mammal Research Institute, University of Pretoria, Internal Report.
- VAN EE, C.A. 1966. A note on breeding the Cape Pangolin *Manis temminckii* at Bloemfontein Zoo. *International Zoo Yearbook* 6: 163–164.
- VAN EE, C.A. 1978. Pangolins can't be bred in captivity. *African Wildlife* 32: 24–25.
- VAN NIEKERK, H.N. 2009. The extent of predation in the five main small livestock producing provinces of South Africa. Unpubl. MSc. Thesis, University of the Free State, Bloemfontein, South Africa.
- WEBER, R.E., HEATH, M.E. & 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: 103–112.
- WHITING, M.J., WILLIAMS, V.L. & HIBBITTS, T.J. 2011. Animals traded for traditional medicine at the Faraday market in South Africa: Species diversity and conservation implications. *Journal of Zoology* 284: 84–96.
- WILLIS, C.K., SKINNER, J.D. & ROBERTSON, H.G. 1992. Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*. *African Journal of Ecology* 30: 322–334.
- WILSON, A.E. 1994. Husbandry of pangolins. *International Zoo Yearbook* 33: 248–251.
- WITHERS, P.C., THOMPSON, G.G. & SEYMOUR, R.S. 2000. Metabolic physiology of the north-western marsupial mole, *Notoryctes caurinus* (Marsupialia: Notoryctidae). *Australian Journal of Zoology* 48: 241–258.

ZEIDLER, J., HANRAHAN, S. & SCHOLES, M. 2002a. Termite species richness, composition and diversity on five farms in southern Kunene region, Namibia. *African Zoology* 37(1): 7–11.

ZEIDLER, J., HANRAHAN, S. & SCHOLES, M. 2002b. Land use intensity affects range condition in arid to semi-arid Namibia. *Journal of Arid Environments* 52: 389–403.