Ecology and morphology of the Kalahari tent tortoise, *Psammobates oculifer*, in a semi-arid environment.

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor Philosophiae, in the Department of Biodiversity and Conservation Biology, Faculty of Science, University of the Western Cape

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KEYWORDS

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ABSTRACT

Ecology and morphology of the Kalahari tent tortoise, *Psammobates oculifer*, in a semi-arid environment.

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Ph.D. thesis, Department of Biodiversity and Conservation Biology, University of the Western Cape.

Southern Africa harbours one-third of the world's Testudinid species, many of which inhabit arid or semi-arid areas, but ecological information on these species is scant. I studied the habitat, morphology and ecology of Kalahari tent tortoises over 13 months in semi-arid Savanna at Benfontein farm, Northern Cape Province, South Africa. In order to allow continuous monitoring of individuals, I attached radiotransmitters to males and females, split equally between two habitats, sites E (east) and W (west), with apparent differences in vegetation structure. Results of the study were based on data obtained from 27 telemetered tortoises and 161 individuals encountered opportunistically. Female Kalahari tent tortoises were larger than males and the sex ratio did not differ from 1:1. Based on person-hours to capture tortoises, the population appeared to have a low density, with more time required to capture a juvenile (35 hours) than an adult (10-11 hours). The frequency distribution of body size ranges was indicative of recruitment. Relative age, based on annuli counts, suggested that males were younger than females, perhaps because males as the smaller sex are more predation-prone than females. Linear relationships between annuli counts and shell volume indicated that, after reaching sexual maturity, female body size increased faster in volume than did male body size, possibly because a larger volume may enhance female reproductive success. Body condition differed between sites, sexes and among seasons. The hot and dry summer may account for low summer body condition, whereas vegetation differences and size effects, respectively, may account for the low body condition of tortoises in site W and in males. Site E was sandy with grasses, particularly *Schmidtia pappophoroides*, being the prevalent growth form. This habitat resembled a Savanna vegetation type *Schmidtia pappophoroides – Acacia erioloba* described for a neighbouring reserve. Site W was stonier, dominated by shrubs, and was reminiscent of Northern Upper Karoo vegetation (NKu3). Neither site resembled Kimberley Thornveld (SVk4), the designated vegetation type of the area. Differences in substrate and grazing intensity may have contributed to site vegetation differences. Rainfall had an important influence on seasonal vegetation. Short grass abundance

correlated with rainfall and annual plants sprouted after spring rain. Refuge use changed according to season and sex. Males selected denser refuges than females did, perhaps because males were smaller and more vulnerable to predation and solar heat. Tortoises selected sparse, short grass as refuges in cool months, probably to maximise basking whilst remaining in protective cover. During hot periods, mammal burrows were preferred to vegetation as refugia. The smaller males spent more time in cover than females, which may be related to predator avoidance or thermoregulation. Females spent more time basking than males, perhaps due to their larger size and to facilitate reproductive processes. Tortoises did not brumate, but through a combination of basking, and orientation relative to the sun in their refuges, managed to attain body temperatures that allowed small bouts of activity. Body temperature for active tortoises was similar among seasons, and was higher for more specialised active behaviours, such as feeding and socialising, than for walking. Increased activity by males in spring could relate to mating behaviour while females were more active in autumn, when they foraged more than males, perhaps due to the high cost of seasonal reproductive requirements. Males displaced further per day than did females, but home range estimates did not differ between sexes. Annual home range estimates varied substantially among individuals: 0.7–306 ha for minimum convex polygons and 0.7–181 ha for 95% fixed kernel estimates. The ability to cover large areas would assist tortoises in finding resources, e.g., food, in an area where resource distribution may be patchy. Differences among seasonal home ranges and movements probably reflect seasonal climatic change; activity areas shrinking when temperatures were extreme. In order to assess the effects of a semi-arid environment on the morphology of *P. oculifer*, I compared its morphology to that of its 'cool-adapted' sister taxon *Psammobates geometricus*, using live and museum specimens. Both *P. oculifer* and *P. geometricus* are sexually dimorphic and differences between the two species could indicate environmental or sexual selection effects, or a combination of the two. The shorter bridge length, which allowed more leg space, and wider front feet in *P. oculifer* cohorts probably represent traits for manoeuvring in a sandy habitat, while wider heads in *P. oculifer* possibly relate to interspecific differences in diet. The flatter shell in female *P. oculifer*, relative to *P. geometricus*, may represent a trade-off between space for reproductive structures, e.g., eggs, and the need to fit into small refuges, e.g., mammal burrows. Male *P. oculifer* had wider shells, more space around their hind legs, and wider hind feet than *P. geometricus* males had, all characteristics which may assist males to fight and mate in a sandy environment.

March 2012

DECLARATION

I declare that *Ecology and morphology of the Kalahari tent tortoise, Psammobates oculifer, in a semi-arid environment* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.
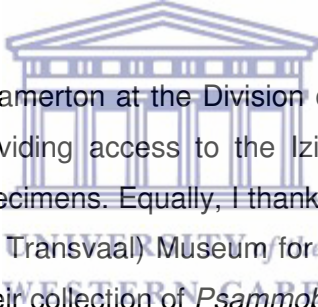
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1   GENERAL INTRODUCTION

1.1   THE ECOLOGY OF ARID/SEMI-ARID HABITATS

Arid and semi-arid zones are largely defined by two environmental factors: temperature and rainfall. Rainfall in these regions is both limited and unpredictable. Annual rainfall in the Kalahari Desert ranges from below 200 mm (arid) to 500 mm (semi-arid), it is stochastic, occurring between 10 and 50 days per year, and can be subject to spatial variability (Noy-Meir, 1973). Temperatures are seasonally extreme in arid zones, e.g., the Mojave Desert temperatures range from 54 °C in summer to -9 °C in the winter (Woodbury & Hardy, 1948). Soils in arid or semi-arid regions tend to be relatively nutrient poor (Pianka, 1989) and while lack of nutrients may negatively affect seasonal pulses in ephemeral growth, water is often the limiting factor (Noy-Meir, 1974). Thus, food (primary productivity) in arid areas may be rain dependent and consequently, only available sporadically.

Arid zone organisms employ a variety of tactics, both physiological and behavioural, to cope with environmental fluxes. Animals may aestivate to reduce metabolism and water loss or they may have physical adaptations, like heat reflecting surfaces, to assist in thermoregulation (Cloudsley-Thompson, 1999). An animal may change its seasonal behaviour to cope with climate extremes; oscillating between nocturnal or crepuscular activity to avoid the heat of the day in summer and diurnal activity in winter as temperatures decrease (Noy-Meir, 1974; Cloudsley-Thompson, 1999). Ectotherms are particularly well-suited to arid environments. Their low, metabolic resting rates (compared to endotherms) allow them to remain inactive for long periods when resources are scarce (Pough, 1980; Cloudsley-Thompson, 1999).

1.2   ADAPTATIONS OF TESTUDINIDS IN ARID AND SEMI-ARID ZONES

Similar to many other arid zone ectotherms, tortoises' seasonal choice of microclimates helps regulate their body temperature (Judd & Rose, 1977; Bailey et al., 1995; Hailey & Coulson, 1996a; McMaster & Downs, 2006a) as does decreasing activity in a seasonally adverse environment. Even within seasons with relatively benign climates, activity patterns may change daily. Activity tends to be unimodal when daily temperatures are moderate but switches to a bimodal pattern with the advent of midday heat (Rose & Judd, 1975; McRae et al., 1981; Nagy & Medica, 1986; Kazmaier et al., 2001a; Lagarde et al., 2002). Seasonal climate fluctuations may affect resource

availability and consequently influence tortoise movements in arid and semi-arid areas. Limited resources may require tortoises to range wider (Geffen & Mendelssohn, 1988; Barret, 1990; O'Connor et al., 1994; Lagarde et al., 2003), although drought can decrease movements as water and forage become increasingly depleted (Duda et al., 1999).

As well as behavioural adaptations, tortoises have evolved morphological and physiological traits that allow them to persist in arid environments. Females often produce smaller clutches of larger eggs, a large egg being less prone to desiccation and a larger hatchling having a greater probability of survival in a harsh environment (Hofmeyr et al., 2005). To produce such large eggs, a tortoise needs to be large-bodied (Bonnet et al., 2001; and see review in Hofmeyr et al., 2005). However, in the arid zone tortoise, *Homopus signatus signatus*, where natural selection favours a flat body shape, this species is still able to lay large, single eggs through the mechanism of pelvic kinesis (Hofmeyr et al., 2005). One aspect of a harsh climate is a short mating season (Lagarde et al., 2002), and this may favour certain morphological traits in a tortoise. In *Testudo horsfieldii*, the leg space afforded by a shorter and narrower plastron conveys additional mobility, perhaps assisting males in mate searching, particularly important when time is limited (Bonnet et al., 2001). Tortoises may occur in low densities in arid environments (Berry, 1986; Freilich et al., 2000; Berry et al., 2006; McMaster & Downs, 2006b) and extra mobility would also be an advantage for males' searching for females when they are scarce. Equally, the additional costs of sexual reproduction in testudinid females, compared to males, may be more pronounced in a harsh environment; a female needing to increase activity to forage in autumn to replenish reserves before brumation in the cold, dry season (Lagarde et al., 2002).

Generally, restricted and unpredictable water supply requires tortoises to have physiological adaptations not only to survive the long periods between rainfall events but also to reproduce when water, and hence forage, are limited (Peterson, 1996; Henen, 1997). Changes in the physiology of arid zone tortoises are closely linked to rainfall, both directly through drinking and indirectly by foraging following rain-related plant growth (Nagy & Medica, 1986; Henen, 2002a). Tortoise body condition may thus change seasonally, low body condition coinciding with periods of drought (Loehr et al., 2007). Like all ectotherm populations, ultimately arid zone tortoises must forage and digest food, find mates, and avoid predators within the constraints of regulating their body temperature (Dunham et al., 1989).

1.3 THE GENUS *PSAMMOBATES*

Psammobates ('sand loving'), a genus endemic to southern Africa, contains three species: *P. geometricus*, *P. oculifer* and *P. tentorius*, the latter having three subspecies, *P. t. tentorius*, *P. t. trimeni* and *P. t. verroxii* (Branch, 1988). *Psammobates* is an arid or semi-arid dwelling genus with the exception of *P. geometricus*, for which mean annual rainfall within its range is 500-750 mm (Hofmeyr et al., 2005). The Critically Endangered *P. geometricus* (Baard & Hofmeyr, in press) is endemic to the Western Cape Province, South Africa. Its fidelity to specific vegetation types, Shale Renosterveld and Alluvial Fynbos (Baard, 1993; Baard, 1995a; Cunningham et al., 2002) has left it in a fragmented habitat as much of its former range is now farmland (Baard, 1990). Extreme habitat fidelity in *P. geometricus* may be a consequence of diet preferences and appropriate vegetation cover, e.g., to conceal it from predators (Baard, 1995a). *Psammobates geometricus* is found in areas where soil nutrients are relatively high (Rebelo et al., 2006) and this combined with higher annual rainfall and lower summer temperatures in the area suggest *P. geometricus* may not be under the same resource constraints as other *Psammobates* species. Clutch sizes tend to be larger in *P. geometricus* than other members of the genus (Hofmeyr et al., 2005), and this is possibly resource related.

Psammobates tentorius trimeni inhabits the western Succulent Karoo, and its range extends from Namaqualand in South Africa to southern Namibia. *Psammobates t. tentorius* is found in the southeast corner of South Africa, between Grahamstown and Colesberg, where Succulent and Nama Karoo biomes overlap (Boycott & Bourquin, 2000). The reproductive strategy of *P. t. tentorius* reflects their arid habitat. Clutch frequency correlates with body condition, but they do not follow the 'large egg in an arid zone' strategy; tortoises rather increase fecundity by having more clutches in a reproductive season (Leuteritz & Hofmeyr, 2007). *Psammobates t. verroxii* occurs in the Nama Karoo, between the ranges of the other two subspecies (Boycott & Bourquin, 2000). Female *P. t. verroxii* from a population in southern Namibia has small home ranges and tortoise activity is bimodal in summer. They consume grass and geophytes, and largely use trees as refugia (Cunningham & Simang, 2009) but sample size in this study was small and it may be regarded as a preliminary investigation.

As is generally true of the genus *Psammobates*, research on *P. oculifer* is limited. Much of what is known about *P. oculifer* is published in field guides and occasional anecdotal accounts; only one full-length article has been published on *P. oculifer*,

comparing its diet with the sympatric *Stigmochelys pardalis* (Rall & Fairall, 1993). *Psammobates oculifer* has a large range, inhabiting arid and semi-arid areas north of the Orange River in South Africa, and in and around the Kalahari Desert in Namibia and Botswana (Branch, 1988). Recently, specimens were also found in Zimbabwe (Broadley et al., 2010). *Psammobates oculifer* frequents Kalahari Thornveld and arid savannah (Branch, 1988). It is sexually dimorphic; female *P. oculifer* are larger than males, while males are flatter with longer tails than females (Branch, 1988; Boycott & Bourquin, 2000). *Psammobates oculifer* has been recorded as being mainly active in summer (particularly after rain; Boycott & Bourquin, 2000). Mating has been recorded in November, while females from the Kimberley area were found to be gravid and to lay single, large eggs between December and March (Rall, 1990). *Psammobates oculifer* digs shallow refuges in sand and aestivate in these refuges during dry winter (Milstein, 1968), while it may also use animal burrows as 'ready-made' retreats (Branch, 1988). Similar to other arid zone herbivores (see Noy-Meir, 1974), *P. oculifer* has a 'generalised specialist' diet, it is able to eat a broad range of plant species when compelled to by drought, but specialises when certain species become available after increases in rainfall (Rall & Fairall, 1993). Although sympatric with *S. pardalis* in part of its range, the differences in diet between *P. oculifer* and *S. pardalis* do not appear to be a result of competition between the two species (Hailey, 1995). Predators of *P. oculifer* include jackals, honey badgers, hyenas, mongooses, secretary birds and eagles (Boycott & Bourquin, 2000).

1.4   PURPOSE, HYPOTHESES AND THESIS ORGANISATION

The genus *Psammobates* is indicative of studies of other southern African, arid zone testudinids; with the exception of *Homopus signatus signatus* (Hofmeyr et al., 2005; Loehr, 2008), they are in their infancy. This is despite a third of the world's testudinid species occurring in southern Africa (Branch, 1988; Boycott & Bourquin, 2000), of which many inhabit arid or semi-arid areas (Branch, 1988; Boycott & Bourquin, 2000; Hofmeyr et al., 2005). Historical research of southern African testudinids is in stark contrast to the study of the largely arid and semi-arid dwelling genus *Gopherus* of North America and *G. agassizii* in particular. The ecology of *G. agassizii* was comprehensively studied by Woodbury and Hardy (1948) i.e., over 60 years ago, and they in turn, referenced works that are now 80 years old. Since 1948, there has been long term studies of all aspects of this species' ecology (e.g., Berry, 1986; Longshore et al., 2003; Berry et al., 2006), as well as landmark studies of its ecophysiology (e.g., Nagy & Medica, 1986; Peterson, 1996; Henen, 1997). Although completed over a

shorter period, this study is more akin to that of Woodbury and Hardy (1948). The baseline ecology for *P. oculifer* is lacking, and before one can ask increasingly 'complex' questions and provide answers as to 'why', you have to find out 'what' an organism does and how it does it (Altmann & Altmann, 2003). Thus this study attempts to provide the 'what' but does so in context of the existing literature on arid zone tortoises – i.e., is the ecology and behaviour of *P. oculifer* typical of other arid zone tortoise species? Concurrently, by expanding the knowledge of the ecology of *P. oculifer*, I will contribute to the global understanding of arid and semi-arid testudinids from a region that represents a 'hot spot' for such species.

The sister taxon of *P. oculifer*, *P. geometricus*, may allow us to gain greater insight into morphological, and other, arid zone adaptations of *P. oculifer*. Although the molecular data published is insufficient to estimate when these two species diverged (and hence find the mechanism of their divergence), a morphological comparison of these taxa, given their very different habitats, should help us evaluate if they differ and if so, how they differ. Using novel ecological knowledge of *P. oculifer* from this study and contrasting it with the available ecological literature of its 'cool adapted' sister taxon, *P. geometricus*, I will highlight some of the aspects of each species' morphology that may reflect environmental differences. I have asked the following questions to help achieve this end:

1. **Population characteristics including body condition:** What is the sex ratio, size at maturity, size and age structure, and density of a population of *P. oculifer*, and how do the these characters relate to the environment? To what extend is body condition influenced by seasonal changes in the environment and is the effect similar for males and females? (Chapter 3)

2. **Environmental and habitat characteristics:** What characterises the environment of *P. oculifer* and does that change seasonally with reference to climate, vegetation and substrate? (Chapter 4)

3. **Habitat Utilisation:** Which microhabitats do the tortoises select on a seasonal basis and are they selective in their choice? Do males and females have the same requirements? (Chapter 5)

4. **Activity and behaviour:** How do activity and behaviour change with season, and with daily, temporal patterns? How do specific environmental fluctuations, e.g., temperature, influence their activities and their thermoregulatory behaviour in

particular? How do these activities and movements relate to the biology of males and females? (Chapter 6)

5. **Space requirements:** How do movement patterns relate to the environment and biology of the species, and how much space do males and females require on a seasonal basis? (Chapter 7)

6. **Morphology:** Which morphological characters distinguish males and females of *P. geometricus* and *P. oculifer*? Are there any regional (geographic) environmental effects on *P. oculifer*? How do the morphologies of *P. oculifer* and *P. geometricus* differ and how may these differences reflect environmental effects? (Chapter 8)

Chapter 2 describes the study site and outlines the fieldwork whereas Chapter 9 draws conclusions from the data presented in Chapters 3-8, and considers the impact this information may have on the conservation of *P. oculifer*.

2 STUDY DESIGN AND GENERAL METHODS

2.1 FIELDWORK

2.1.1 Study area, field periods and radio-tracking

The study area was at Benfontein, a cattle and game farm of approximately 10,000 ha located near Kimberley, in the Northern Cape Province, South Africa (Fig. 2.1). Benfontein is within the Kimberley Thornveld vegetation unit, which forms part of the Eastern Kalahari Bushveld Bioregion in the Savanna Biome (Rutherford et al., 2006a). The study area was in a fenced-off cattle ranching area, of approximately 2,700 ha, divided by a fence running approximately north to south. For the purposes of this study, the two areas split by the dividing fence were called sites E (east) and W (west) respectively (Fig. 2.1). I chose the separate sites as the vegetation structure and cover between the two appeared to differ.
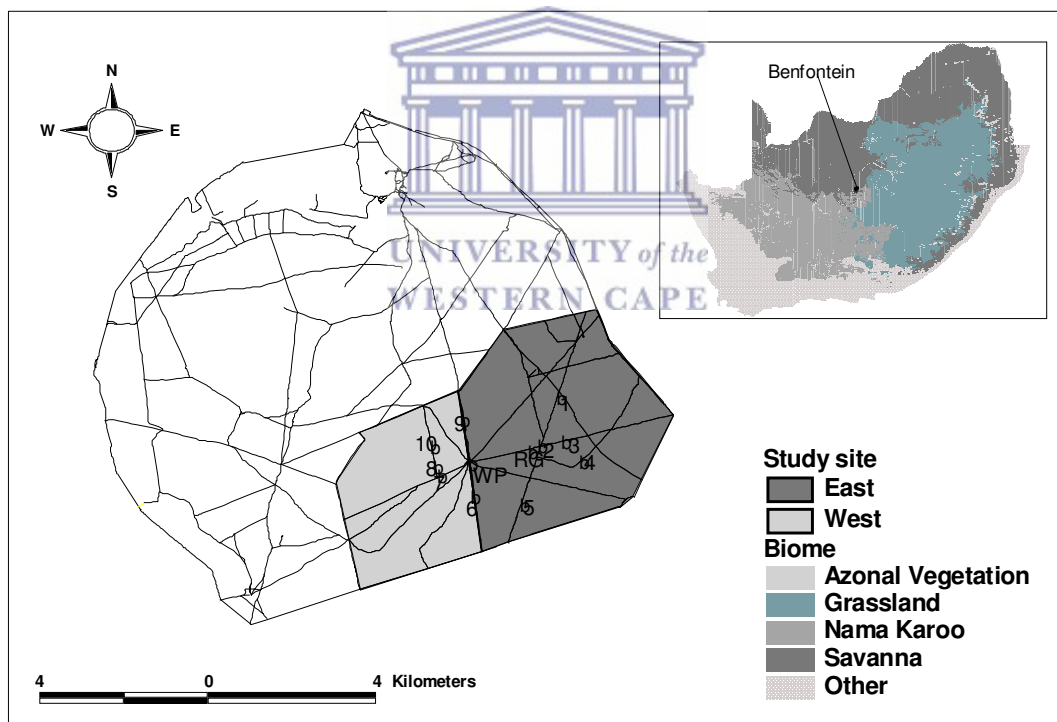
Figure 2.1 The position of Benfontein farm amongst the biomes of South Africa (inset), modified from Rutherford et al. (2006b), and a map of Benfontein showing the study area, which was divided into site W (light grey) and site E (dark grey). The position of 10 vegetation plots (25 m^2 each) are marked in the study area, together with the position of the electronic rain gauge (RG) and a water pump (WP). Black lines within the perimeter indicate farm tracks.

The study duration was 13 months, from March 2006 to April 2007 (Table 2.1). Tortoises were found during March and April 2006 using structured searches involving one to five people. The field study was initially based around 25 tortoises (13 females, 12 males), split relatively evenly between the study sites, and equipped with radio transmitters (mass < 12% of body mass; AVM Instrument Company Limited, Colfax, USA) that were attached to either the anterior or the posterior vertebral and costal scutes, whichever was less obstructive. To monitor seasonal changes in vegetation cover and characteristics, I randomly chose five 5 x 5 m plots demarcated with fence posts in each site (Fig. 2.1). After the release of animals fitted with transmitters (by 11th April 2006), field trips consisted of recording data from radio-tracked tortoises and tortoises captured opportunistically while tracking, as well as seasonally monitoring vegetation plots (Table 2.1). During winter, there were fewer field days (n = 23) compared to other seasons as tortoise activity was low during the cold, dry season.

Table 2.1 The starting and finishing dates of each field excursion and the total number of sample days for each trip. Dates in bold denotes trips that included vegetation plot surveys.

Year	Start	Finish	Field days	Season
2006	**20th March**	**16th April**	**26**	**Autumn**
	10th May	**27th May**	**18**	**Autumn**
	3rd July	16th July	11	Winter
	7th August	**20th August**	**12**	**Winter**
	11th September	25th September	15	Spring
	16th October	**5th November**	**18**	**Spring**
	28th November	17th December	19	Summer
2007	**5th January**	**17th January**	**12**	**Summer**
	1st February	5th February	5	Summer
	13th February	22nd February	10	Summer
	10th March	**25th March**	**16**	**Autumn**
	14th April	**1st May**	**17**	**Autumn**

2.1.2 Rainfall and temperature

I took a suite of temperature records from tortoises that were encountered opportunistically and from telemetered tortoises when they were being weighed. A digital thermometer (± 0.1 °C) with a thin thermocouple was used to take inguinal

temperature, as well as air and ground temperatures in the immediate vicinity of the tortoise. In addition, records of air temperature and rainfall for the study period, as well as long-term records, were obtained from the South Africa Weather Service (SAWS) for a weather station at Kimberley airport, approximately 5 km from the study area. Because rainfall in the Northern Cape is often localised, as rain is produced in bursts by sporadic thunderstorms, I also recorded rainfall with an electronic range gauge (Rain Collector II, Davis Instruments Corporation, California and HOBO Event Logger, Onset Computer Corporation, Massachusetts), which was erected in April 2006, approximately half-way between sites E and W (Fig. 2.1).

2.2 MORPHOMETRIC STUDIES

The choice of morphometric measurements was aimed at providing detailed morphological descriptions of *P. oculifer* and *P. geometricus* and evaluating their sexual dimorphism. Available sources were both live captures (Benfontein for *P. oculifer* and the south-western Cape for *P. geometricus*) and preserved museum specimens (South African Iziko Museum for both species, and Transvaal Museum for *P. oculifer* only, Chapter 8). Measurements chosen to illustrate sexual dimorphism corresponded with those taken in similar studies (Bonnet et al., 2001; Hofmeyr et al., 2005; Loehr et al., 2006; Mann et al., 2006) but incorporated novel measurements, e.g., supracaudal scute (distal) width (Chapter 8). In addition, a subset of morphometric measurements (e.g., feet width that may be affected by substrate) were chosen to best represent the effect of habitat on morphology, both regionally (*P. oculifer*) and interspecifically (*P. oculifer* versus *P. geometricus*).

3   POPULATION ECOLOGY AND BODY CONDITION

3.1   INTRODUCTION

In ectotherms, a population is comprised of individuals that must forage and digest food, find mates and avoid predators, within the constraints of regulating their body temperature. The ability of an individual to do this is affected by both biophysical changes, e.g., climate flux, and intraspecific social interaction such as fighting over resources, both of which may culminate in immigration, emigration, or mortality, the latter three impacting on population density (Dunham et al., 1989).

Most long-term population studies of testudinids in arid areas involve the desert tortoise, *Gopherus agassizii*. Intraspecific variation in population densities of *G. agassizii* is high; densities range from 0.0078 to 1.84 individuals per ha (Berry et al., 2006). Density of testudinid populations in mesic areas can be considerably higher than densities recorded for G. *agassizii*, e.g., *Chersina angulata* has a density of 38.3 individuals per ha in the Eastern Cape of South Africa (Branch, 1984). However, densities are not always easy to estimate accurately. Density estimates may fluctuate depending on sampling techniques used and biases can occur due to habitat type, size of tortoises (both may affect ease of capture) and seasonal behaviour favouring the capture of one sex (Stubbs et al., 1984; Hailey, 1988; Kazmaier et al., 2001b).

Sex ratios may be an artefact of seasonal sampling, but skewed sex ratios may occur naturally in a population. Sex can be determined by nest temperature (Bull & Charnov, 1989) and this may increase births of a specific sex (Ewert & Nelson, 1991). Equally, predation on the smaller sex may increase the proportion of the larger sex found in a population (Hellgren et al., 2000). The relationship between body size and age in chelonian populations are often monitored by studying the relationship between the number of growth rings (annuli) on an individual's scutes and its straight carapace length (SCL; Germano, 1992). Annuli counts in wild testudinid populations rely on the assumption of there being a set number of growth periods (and thus a set number of annuli deposited) per annum (Zug, 1991). Annuli counts have been shown to be effective for age-growth analyses in some instances (Swingland et al., 1989; Germano, 1994; Hellgren et al., 2000), but not in others (Zug, 1991). Ultimately, accurate ageing via growth ring counts involves monitoring individual tortoises more than once a year over several years to relate growth ring deposition to causative factors (Wilson et al., 2003). However, the size of a testudinid may be more important than its age, both in

terms of sexual maturity (Germano, 1994) and its ability to survive; smaller individuals being more vulnerable to predation than larger ones (Hill, 1999). Thus, morphological demographics indicate a populations' ability to persist.

A tortoise's mass relative to its size is a surrogate measure of the body condition of an individual, and hence the health of a population and its general reproductive potential (Hofmeyr et al., 2005; Loehr et al., 2007). Body condition in testudinids can be measured as a ratio of mass to shell volume (Loehr et al., 2004) or body mass scaled to shell volume (Loehr et al., 2007). Tortoise body condition has been studied in context of reproduction (Henen, 1997; Hofmeyr et al., 2005), rainfall (Henen, 2002a; Loehr et al., 2007), activity and food availability (Willemsen & Hailey, 2002). Body mass (condition) may be important in females for egg production; tortoises with better body condition produce larger eggs and thus larger offspring (Hofmeyr et al., 2005). In an arid environment, larger eggs and hatchlings are less prone to desiccation and more likely to survive (Hofmeyr et al., 2005). Seasonal rainfall increases tortoise body mass both directly through drinking and indirectly via consumption of plants that germinate after rainfall (Nagy & Medica, 1986; Henen, 2002a; Loehr et al., 2007).

This chapter represents the first attempt to describe population characteristics of a wild population of Kalahari tent tortoises, *Psammobates oculifer*. As such, the purpose of this study was to quantify fundamental aspects of the population, notably: age and sex structure, morphological demographics, growth-age analyses, and approximate size at maturity. I also monitored body condition in both sexes and habitats and evaluated how it varied over time (seasons).

3.2   MATERIALS AND METHODS

3.2.1 *Study area and field methods*

I studied population characteristics of *P. oculifer* at Benfontein farm over 13 months, from March 2006 to April 2007. There were 12 field excursions covering five seasons; autumn 2006, winter, spring, summer and autumn 2007 (see Chapter 2). The study area of approximately 2,700 ha was divided into sites E (east) and W (west), because of an apparent difference in vegetation (see Chapter 4). During March and April 2006, searches were made to find male and female tortoises for a radio-telemetry study. Searches involved one to five people and were either done on foot, particularly in the site W where vegetation was less dense, or by driving on farm tracks, particularly in the site E where vegetation was denser. Driving was a more effective search method in

areas of dense cover because *P. oculifer* is cryptic and animals were easier to detect when active and in the open (i.e., on farm tracks). The last tortoise to be captured for the radio-telemetry study was on 13 April 2006, up to which date there were incidental captures of female and juvenile tortoises not used for telemetry. After 13 April 2006, the search effort relating to incidental capture/recapture of tortoises was limited to the time spent in the field radio-tracking tortoises (usually one person), both on foot and in a vehicle. Hourly search effort per day was relatively consistent within seasons, as the telemetered tortoises were typically tracked from early morning, before they became active, until late afternoon, after activity finished.

Upon capture, I immediately weighed animals with a digital balance (±0.1 g) to limit the chance that spontaneous urination or defecation upon handling may affect body mass. Apart from weighing, I measured the straight carapace length (SCL, mm), shell width at the middle (SWM, at the sixth marginal scute; mm) and shell height (SHM, at the apex of the highest dorsal scute; mm) for each tortoise with vernier callipers (±0.01 mm) so shell volume (SV, cm^3) could be calculated. I calculated shell volume using a modified formula for an ellipsoid: SV = π * SCL * SHM * SW / 6000 (Loehr et al., 2004; Hofmeyr et al., 2005; Loehr et al., 2007). Scute rings (annuli) were counted using a hand lens and scutes were selected on both the dorsal and ventral sides – no specific scute was targeted as annuli clarity of individuals varied among scutes (ventral scutes were often easier to count than dorsal scutes). I also took digital photographs of dorsal and ventral surfaces, which helped verify annuli counts made in the field. I classified each tortoise as male, female or juvenile; males were distinguished from females by their flatter shell, longer tail, and large, incurved supracaudal scute (Branch, 1988; Boycott & Bourquin, 2000) whereas small individuals with no sexual dimorphic characteristics were classified as juveniles. Prior to releasing a tortoise, I notched the marginal scutes of the tortoise (Honegger, 1979) for future identification.

Apart from weighing tortoises on first capture, I also weighed (with the exception of winter) each telemetered tortoise on the first and last day of each field excursion (see Table 2.1). Regular weighing allowed a consistent evaluation of seasonal changes in body condition. Because two short field excursions were done during February, the tortoises were weighed at the start of the first excursion and at the end of the second excursion. As from 17 April 2006, rainfall data was collected using an electronic rain gauge erected in the study area. Rainfall prior to 17 April 2006 was taken from the

South African Weather Service's (SAWS) weather station approximately 5 km from the study area (see Chapter 2 for details).

3.2.2   Data and statistical analyses

To calculate the search time catching tortoises, I took the number of hours, or pro rata thereof, spent searching and multiplied it by the number of people involved in each search. Searches made by car or by radio-tracking did not involve more than one person. The number of search hours per day while radio-tracking was taken as the difference between the time of locating the first and the last tortoise each day. On days when more than one trip was made to the study area, daily time spent searching was the sum of all trips.

I evaluated hours per unit capture (HPUC) within each of the 12 field excursions (see Chapter 2), thus if no tortoise was caught at the end of a field excursion, that time was not 'carried forward' to the next field excursion. Trips were usually daily, but sometimes, particularly in summer, two trips were made in one day, in which case each trip was treated individually. The amount of time that passed between arriving in the field and the capture of the first tortoise was the HPUC for that tortoise. Time then accumulated until the capture of the next tortoise, and this process was repeated across days until the end of a field excursion. I calculated HPUC per season and HPUC was calculated for males, females and juveniles separately as well as for cohorts combined. No tortoises were found opportunistically from 17 May to 20 August 2006 (34 days in the field), thus although time was recorded, it was not included in HPUC analyses. I did not analyse HPUC as time spent in each site (E and W) in any one day, as this varied on an hourly basis and it was not feasible to filter out actual time spent per site.

To test that the sex ratio did not differ from 1:1 and for the effect of season on sex ratios, I used goodness of fit tests (χ^2). Contingency table analyses (χ^2) were used to analyse the effect of site on sex ratios and the differences in frequencies among size categories (SCL, mass and volume) and annuli categories, with a Yates correction for continuity where the degrees of freedom equalled one. For analyses of SCL categories, the lowest category chosen was less than 70 mm and the highest more than 120 mm, with categories increasing in 10 mm increments between the two. Similarly, mass and volume increments started at <150 g or cm^3 and increased in 50 g or cm^3 increments up to >400 g or cm^3. In each case, categories were chosen to give a relatively even

spread of the data. In all instances where contingency table analyses were used, mean expected frequencies (n/rc, where n = total count, r = the total for each row and c = the total for each column) were more than or equal to six (Zar, 1999).

After testing if data were parametric, before or after transformation ($\log_{10}$), I used multifactor ANOVAs (*F* statistic), followed by Student-Newman-Keuls (SNK) post hoc tests, to compare HPUC among cohorts and seasons. I used simple regressions (r^2) to evaluate the dependency of the number of scute annuli on SCL and SV. If data were parametric and regressions significant (before or after $\log_{10}$ transformation), I used analysis of covariance (ANCOVA) to compare a) regression slopes of annuli counts on both SV and SCL (mm), and b) regression slopes of body mass (BM) on SV. In the latter case, the comparison of BM between sexes, while accounting for differences in body size (SV), was to assess differences in body condition (Hofmeyr et al., 2005; Loehr et al., 2007). If, after a homogeneity of slopes test (Quinn & Keough, 2002), regression slopes differed, I used a Zerbe test (Zerbe et al., 1982) to see for which regions of the independent variable the dependent variable differed. As tortoises' BM was measured more than once per season for radio-tracked and recaptured animals, I used the mean BM per season for the relevant individual when doing seasonal analyses. Seven radio-tracked tortoises died during the course of the study (see Chapter 7, Table 7.1) from unknown causes. Hence, before calculating seasonal mean BM for these seven tortoises, I first plotted the body condition indices (BCI; BM/SV) of all tortoises against time. After scrutinising the plots, I identified the point at which the BCI for each of the seven tortoises deviated from the general pattern and then excluded this BM and all subsequent BMs from the calculation of that tortoise's mean seasonal BM.

In all analyses, whenever I used multiple tests, I adjusted alpha with a sequential Bonferroni procedure (Holm, 1979). Statistical analyses were performed using SigmaStat 2.03 and PASW 18 (SPSS Inc., Chicago, USA), and in the case of ANCOVA and Zerbe tests, Microsoft Excel. For sake of simplicity and ease of comparison, I always reported means (± standard deviations) even when non-parametric tests were used.

3.3 RESULTS

3.3.1 Animals captured and sex ratios

The proportion of each cohort captured (including juveniles) was independent of site (Contingency table, P = 0.29, Table 3.1). However, the proportion of individuals captured between sites was not even (Goodness of fit test, χ^2_1 = 9.8, P = 0.0017, Table 3.1); more tortoises were captured in site W than in site E. The male to female ratio, excluding recaptures, was 1.00:0.90, not significantly different from 1:1 (Goodness of fit test, P = 0.54 Table 3.1). I included recaptures when calculating seasonal sex ratios to indicate relative abundance of males and females encountered within season. Male to female ratios differed from 1:1 in autumn 2006 and spring (Goodness of fit test, $\chi^2_1 \geq$ 4.2, P < 0.04) but not in other seasons (P > 0.08, Fig. 3.1).

Table 3.1 All Female (F), male (M) and juvenile (J) tortoises captured (including first captures used for telemetry but not including recaptures of marked tortoises) at Benfontein from March 2006 to April 2007 in sites E, W and combined sites.

Sex	E	W	Total
F	26	55	81
J	8	9	17
M	38	52	90
Total	72	116	188

Male to female ratios differed among seasons (Contingency table, χ^2_3 = 16.2, P = 0.0010. Spring ratios differed from ratios in autumn 2006 (χ^2_1 = 9.8, P = 0.0018), but ratios among remaining seasons did not differ after application of a sequential Bonferroni (P = 0.014 > adjusted α = 0.010). Ratios between juveniles and either gender did not differ among seasons (Fisher's exact test P > 0.065 Fig. 3.1). Among seasons, the proportion of total captures of males, females and all tortoises were not even (Goodness of fit test, χ^2_3 > 15.4, P < 0.0015). Proportionately more tortoises were captured in spring than in any other season and catches in autumn 2006 were higher than they were in autumn 2007 ($\chi^2_1 \geq$ 5.96, P < 0.015), but summer catches did not differ from autumn 2006 and 2007 and (P > 0.10). No tortoises were caught in winter (Fig. 3.1). Female captures were higher in spring than in summer and autumn 2007 ($\chi^2_1 \geq$ 8.48, P < 0.004), but did not differ among other seasons (P > 0.026 > 0.012 = adjusted α). Male captures peaked in spring and were higher in summer than they were in autumn 2007 ($\chi^2_1 \geq$ 8.04, P < 0.005) but captures among remaining seasons did not differ (Fig. 3.1).
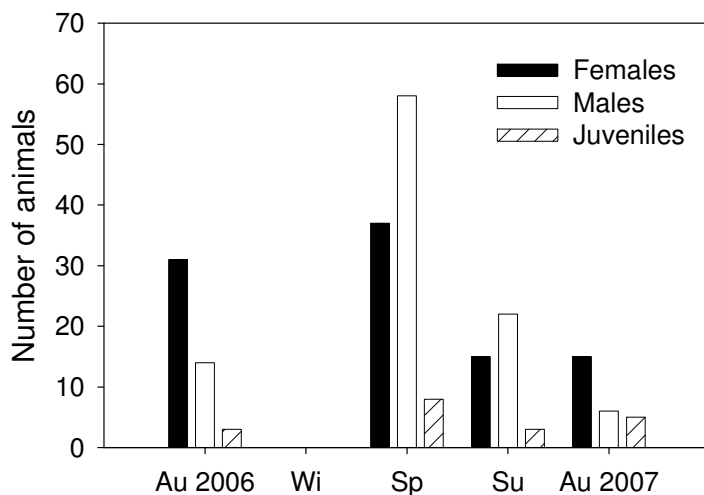
Figure 3.1 Number of tortoises captured per season at Benfontein, including first capture of telemetered tortoises and recaptured individuals.

3.3.2 *Tortoise captures/recaptures and hours per unit capture*

Days and person-hours spent in the field were 182 and 1,463 respectively (Table 3.2). Including the first capture of tortoises for a telemetry study and all opportunistic captures/recaptures of tortoises while radio-tracking, 98 females, 100 males and 19 juveniles (n = 217) were captured/recaptured during the study (Table 3.2). Of tortoises recaptured, 41% of female recaptures (n = 7) and 70% of male recaptures (n = 7) occurred within a month. In addition, 58% of males captured/recaptured were done so within September, October and the first five days in November (spring; Table 3.2). One female was recaptured three times, four females and one male were recaptured twice, while the remainder were recaptured once. The sampling was widespread and uneven between areas, thus it was not possible to estimate population size.

Hours per unit capture for females, males, juveniles, and all cohorts combined were 10.18±11.08, 10.69±15.83, 34.94±34.56 and 5.13±6.55 hours per tortoise. There was a significant difference in HPUC among cohorts (2 Way ANOVA, data $\log_{10}$ transformed, $F_{2,205}$ = 7.63, P = 0.0005) with juveniles being harder to catch than females or males, and there being no difference between the latter two. Hours per unit capture also varied among seasons (winter excluded; data $\log_{10}$ transformed, $F_{3,205}$ = 6.20, P = 0.0006) and sex and season interacted (data $\log_{10}$ transformed, $F_{6,205}$ = 2.94, P = 0.009). Tortoises were harder to find in all seasons than they were in spring (Fig. 3.2). Within females and juveniles, seasons did not affect HPUC, but males were harder to find in all seasons than they were in spring (Fig. 3.2). In spring, juveniles were the

hardest to catch and males were easier to catch than females. Juveniles had a higher HPUC than females in autumn 2007 and HPUC did not differ among cohorts in autumn 2006 or summer (Fig. 3.2).

Table 3.2 Seasonal summary for number of field days, person-hours (hours per day multiplied by the number of searchers), and the number of *Psammobates oculifer* captured at Benfontein. Total captures for females, males, juveniles and all cohorts combined are indicated as the numbers captured + recaptures = total. Tortoise captures include the first capture of telemetered tortoises (13 females and 12 males in autumn 2006 and 2 females in summer).

Month	Days	Hours	Females	Males	Juveniles	All
Au-06	44	386.6	31 + 0 = 31	14 + 0 = 14	3 + 0 = 3	48 + 0 = 48
Wi	23	174.7	0 + 0 = 0	0 + 0 = 0	0 + 0 = 0	0 + 0 = 0
Sp	35	324.8	29 + 8 = 37	50 + 8 = 58	8 + 0 = 8	87 + 16 = 103
Su	47	321.0	9 + 6 = 15	20 + 2 = 22	2 + 1 = 3	31 + 9 = 40
Au-07	33	255.7	12 + 3 = 15	6 + 0 = 6	4 + 1 = 5	22 + 4 = 26
Total	182	1462.6	81 + 17 = 98	90 + 10 = 100	17 + 2 = 19	188 + 29 = 217
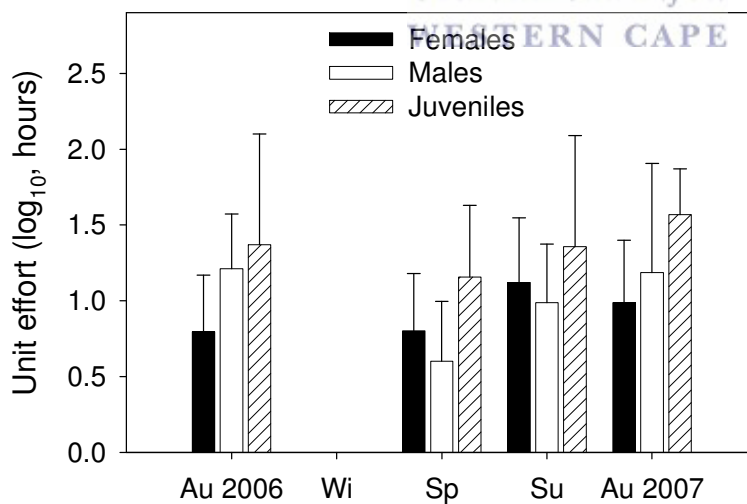
Figure 3.2 Seasonal changes in hours per unit capture (hours, ±SD) for *Psammobates oculifer* cohorts at Benfontein. No tortoises were caught during winter. Hours per unit capture was based on the cumulative number of hours between a capture of each cohort.

3.3.3 Growth rings (annuli)

Females had the highest mean number of annuli (17.68±2.78) followed by males (15.02±3.05) and juveniles (9.24±2.63). The minimum and maximum numbers of annuli were 12 and 23 for females, 10 and 24 for males, and 2 and 13 for juveniles. There was a significant difference between males and females in the frequencies of animals occurring in each annuli category (Contingency table, $\chi^2_5 = 34.4$, $P < 0.0001$; Fig 3.3). Females had more annuli than males had; 79.2% ($n = 57$) of females had 16 or more annuli, whereas 69.8% ($n = 44$) of males had 15 annuli or fewer (Fig. 3.3). Juveniles had the lowest annuli counts; 71% ($n = 12$) of the juveniles had ten or fewer annuli.
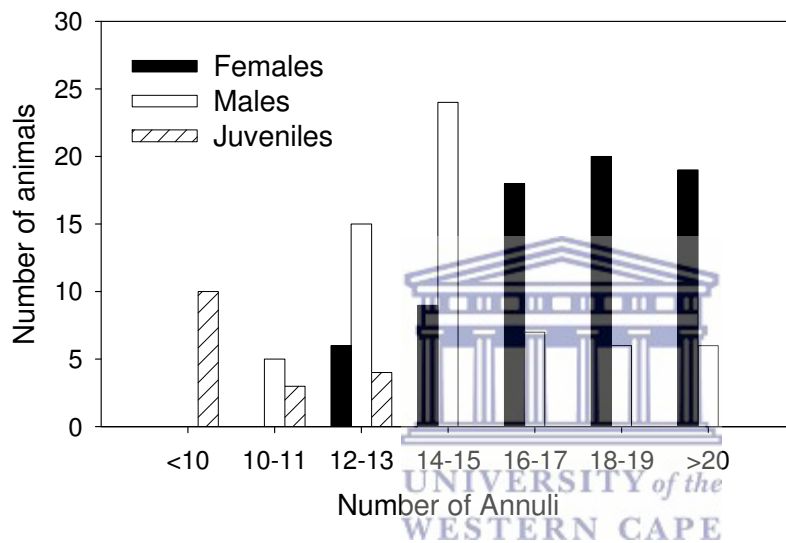
Figure 3.3 Frequencies for the number of annuli counted for male, female and juvenile *Psammobates oculifer* at Benfontein.

Regressions for number of annuli on SCL or SV were significant for males ($F_{1,61} \geq$ 30.47, $P < 0.0001$, $r^2 \geq 0.33$), females ($F_{1,70} \geq 21.82$, $P < 0.0001$, $r^2 \geq 0.24$) and juveniles ($F_{1,15} \geq 14.70$, $P \geq 0.0011$, $r^2 = 0.49$; Fig. 3.4). An analysis of covariance between males, females and juveniles with SCL as the covariate showed no difference between slopes or elevations among cohorts ($F_{2,146} = 0.98$, $P = 0.38$). The regression equation for cohorts combined was: annuli = 0.209 SCL − 5.824, relating to the formation of two annuli per 10 mm SCL growth. When shell volume was used as the covariate, slopes of the regressions differed ($F_{2,146} = 5.17$, $P = 0.0068$); the male and juvenile slopes were steeper than that of females, and the male slope diverged from the female slope at 249.9 cm^3 (Fig. 3.4). The regression equation for males and juveniles combined was: annuli = 0.056 SV + 3.666, relating to the formation of 2.78 annuli per 50 cm^3 growth. The equation for females was: annuli = 0.024 SV + 9.794, relating to 1.18 annuli per 50 cm^3 growth. Phrased in terms of annuli formation,

juveniles and males grew 17.9 cm³/annulus whereas females grew 41.7 cm³/annulus; females thus accumulated 2.33 times the volume per annulus than males did.
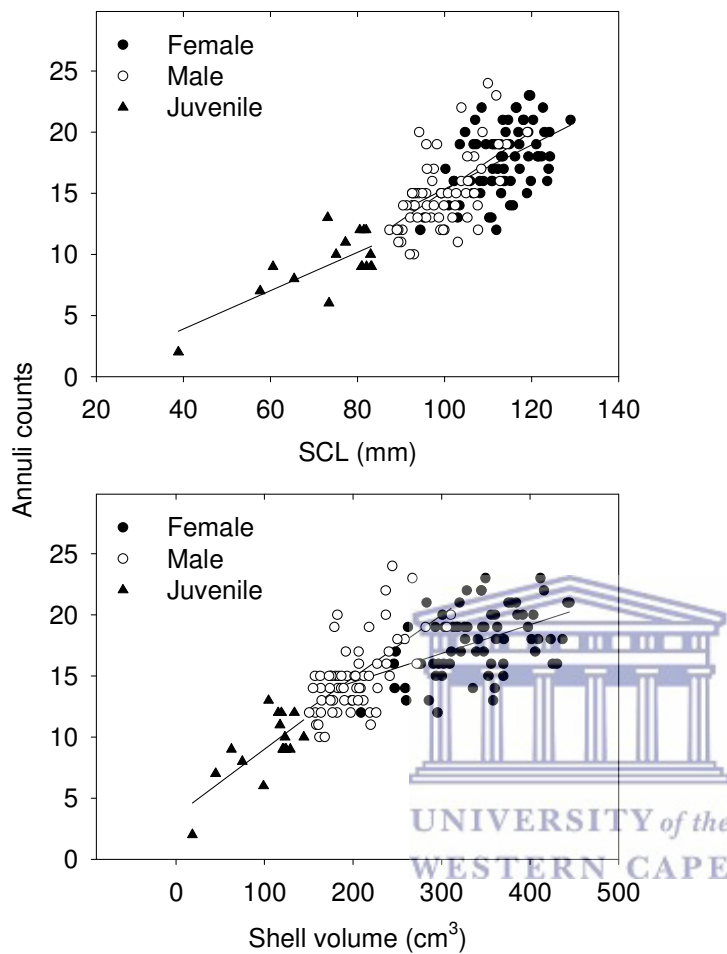
Figure 3.4 Linear regressions of number annuli on straight carapace length and shell volume for female, male and juvenile *Psammobates oculifer* at Benfontein.

At the end of the study, I recounted the number of growth rings of 10 males and 6 females that I had used for a telemetry study. At least one year had passed since the first capture of each tortoise. I counted one additional annulus for five of the 10 males, two additional annuli on one male, whereas no new growth rings formed on the remaining four males. Three of the females had one extra growth ring but no additional annuli developed on the other three females.

3.3.4 Size categories and size at maturity
All juveniles had a straight carapace length (SCL) below 89 mm. Large juveniles (24%) overlapped with small males (6%) in the 80 to 89 mm category but the SCL of most males were between 90 and 99 mm (55%), and males were larger than juveniles

(Contingency table, χ^2_5 = 71.18; Fig. 3.5 A). Males (33%) overlapped with females (24%) in the 100-109 mm category, but the majority of females were larger than males (Contingency table, χ^2_4 = 81.67, P < 0.0001), with 70% of females exceeding 110 mm (Fig. 3.5 A).

The categories body mass and shell volume had similar distributions to each other. All juveniles had a shell volume of less than 150 cm^3 and most weighed less than 150 g (96%). Males' shell volume (87%) and mass (84%) were predominately between 150 and 249 cm^3 or g, greater than juvenile volume or mass (Contingency table, $\chi^2 \geq$ 66.57, df $\geq$ 3, P < 0.0001; Figs. 3.5 B and C). Females had a larger shell volume and mass than males (Contingency table, $\chi^2_4 \geq$ 93.17, P < 0.0001), and the proportions across size categories were more evenly spread in females than seen for juveniles or males. Female shell volumes within each 50 cm^3 category, 250 cm^3 and upwards, were 20, 32, 25 and 16% respectively. Similarly, within each 50 g mass category, beginning with 250 g, the proportional distributions were 25, 33, 21, 11% respectively (Figs. 3.5 B and C).

Based on the exhibition of courting behaviour (12 males and 10 females; Chapter 6) the smallest 'sexually mature' male had an SCL of 87.35 mm and the smallest female found with a male was 92.88 mm. The smallest female also had a plastral scute arrangement consistent with other females (see Chapter 8). The smallest of five gravid females encountered was 109.53 mm.
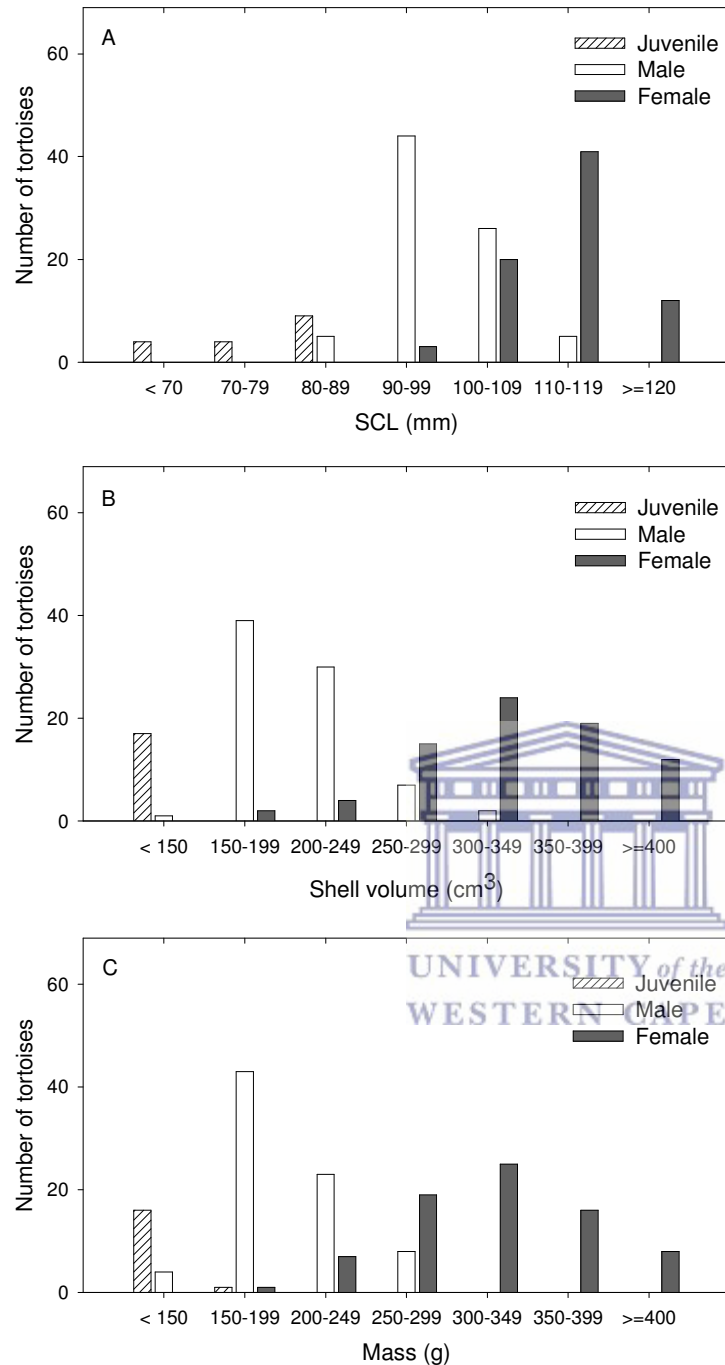
Figure 3.5 Size distributions of juvenile, male and female tortoises at Benfontein by a) straight carapace length (mm); b) shell volume (cm^3) and c) body mass (g).

3.3.5 Seasonal changes in body mass (body condition)

The regression slopes of BM on SV between sites, sexes and among seasons did not differ (data log$_{10}$ transformed, three factor ANCOVA, *P* = 0.538) but regression elevations differed between all three factors *(F ≥ 6.81, df 1 ≥ 1, df 2 = 248, P < 0.003)* although there was no interaction among factors (*P* > 0.079). Female body condition (BC) was higher than that of males, as was that of tortoises in site E compared with

those in site W. Among seasons, regression elevations of BM on SV (body condition) was lowest in summer but did not differ among other seasons (Fig. 3.6). There was no correlation between body mass and rainfall and body mass and rainfall with a one-month delay ($P > 0.25$).
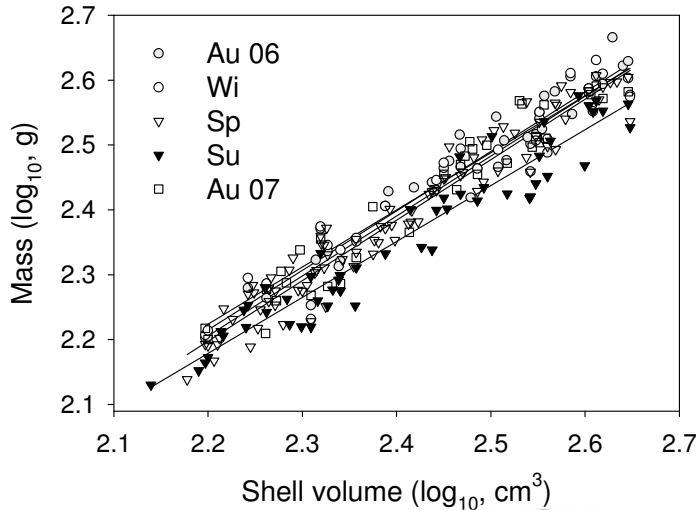
Figure 3.6 Linear regressions of individuals' seasonal mean mass (g) on shell volume (cm^3) for *Psammobates oculifer* at Benfontein. Regression slopes were similar among seasons as were regression elevations except summer, which had the lowest elevation.

3.4 DISCUSSION

3.4.1 *Population characteristics*

At Benfontein, the sex ratio for *P. oculifer* did not differ from 1:1. Testudinid populations are known both to deviate from and conform to a 1:1 sex ratio, even within the same species (Berry, 1986), but studies of other South African testudinid populations also recorded parity between sexes (Branch, 1984; Van Heezik et al., 1994; Loehr, 2002; McMaster & Downs, 2006b). Although the overall sex ratio was 1:1, catches of tortoises at Benfontein differed seasonally as did the HPUC. Inactive tortoises were hard to locate and capture frequency was related to the level of seasonal activity. Males were most active in spring and early summer and females were most active in autumn 2006 (Chapter 6) with corresponding high catches in these seasons. The male activity bias in spring, particularly in October was greater than the female activity bias in autumn 2006 (April, Chapter 6), hence the significant difference in ease of male captures in spring that was not reflected in female captures during autumn 2006.

Site also affected tortoise captures; captures in site W exceeded those in site E. Possible reasons for this are higher tortoise densities in site W and/or that tortoises were easier to capture there. A higher tortoise density in site W may suggest it was a preferred habitat, possibly due to it having a greater abundance of preferred plant refuge types (see Chapter 5) and/or available forage. However, this seems unlikely on both accounts. Site E was more similar to the species' savanna habitat where grasses dominate (Chapter 4) and grass is their preferred refuge (Chapter 5). Body condition for tortoises in site E was also greater than it was for tortoises in site W (this chapter), perhaps indicating that forage was better there. The more plausible suggestion for high capture rates in site W is that tortoises were easier to locate in site W. Vegetation cover was more sparse in site W than it was in site E (Chapter 4), rendering tortoises more visible (and easier to capture) than they were in site E. Ultimately, I did not record temporal search effort within each site and thus could not assess within site HPUC (discussed in context of combined sites below) that may indicate site differences in tortoise density.

I could not derive a population estimate for *P. oculifer* in this study due to inconsistencies in sampling design, thus HPUC was the only indicator of tortoise density at Benfontein. The hours per unit capture in this study (five hours / tortoise) was slightly higher than that recorded in a six year study of *Gopherus agassizii* (four hours average; Freilich et al., 2000) where densities of *G. agassizii* were estimated at 42 individuals per km^2 (0.42 individuals per ha). Freilich et al., (2000) may have reduced HPUC by sampling in spring every year, a time of year when tortoises may have been more active and thus easier to catch. The high capture rate of *G. agassizii* in burrows, 39%, probably reflects the more substantial and more visible burrows inhabited by *G. agassizii*. Captures of inactive *P. oculifer* in this study (without the assistance of radio-telemetry) were negligible as refuges were usually small and well concealed (T Keswick, unpublished data). Despite a relatively high percentage of tortoises caught in burrows, drought-induced inactivity was still a suggested cause of low annual capture rates of *G. agassizii*. Assuming that *P. oculifer* 'catchability' is similar to that of *G. agassizii*, HPUC may indicate that tortoise densities were relatively low at Benfontein. This would be expected, as tortoise populations in arid areas tend to have low densities, as low as 0.015 tortoises per ha (Berry, 1986; Berry et al., 2006; McMaster & Downs, 2006b), whereas in less extreme climates, densities as high as 38.3 individuals per ha have been recorded, when adjusted for unused habitat (Branch, 1984). Branch's (1984) study took place near Port Elizabeth in the Eastern Cape where rainfall is higher than it is at Benfontein. Depending on temperature, net primary

productivity is known to correlate with rainfall (Cao et al., 2004) and thus the Port Elizabeth area may be an area of higher production than Benfontein and more able to sustain high tortoise densities.

At Benfontein, the cohort that was most difficult to catch was juveniles, particularly small ones (less than 50 mm SCL). Two likely reasons for this were increased predation and difficulty of detection. Juveniles were small and cryptic, and potential predators such as the jackal (*Canis mesomelas*), yellow mongoose (*Cynictis penicillata*) and secretary bird (*Sagittarius serpentarius*) were all present at Benfontein. Portions of tortoise scutes were found in jackal scats at Benfontein (Klare et al., 2010), and the colour and pattern looked to belong to *P. oculifer* (T Keswick, personal observation). In a study of *Stigmochelys pardalis* and *Chersina angulata* in the Eastern Cape, Mason et al., (2000) also cited predation and/or detection difficulties as reasons for low juvenile catches in both species.

Despite limited numbers of very small specimens, size frequency distributions for *P. oculifer* at Benfontein indicate that recruitment occurred. Females were larger (SCL) than males but relative to size, distributions between size classes within genders were similar. *Psammobates oculifer* at Benfontein appeared to have more mid-sized animals than a population of *Chersina angulata* in the Eastern Cape, where a high proportion of large individuals indicated low recruitment (Branch, 1984).

As well as looking at size distributions, I attempted to gain insight into the age of the population by counting scute growth rings, or annuli. There was evidence of increases in annuli over the study year in animals that were radio-tracked. I recounted annuli at the end of the study and fifty percent of animals had added extra annuli. The sample size and the period were insufficient to use this recount of annuli to calibrate growth over time. I did not find a decrease in the annuli from the recounts, which should have been equally likely as finding additional annuli; and this may suggest that additionally annuli were deposited rather than being added through counting error. Despite this, one tortoise had two extra annuli, which is likely due to counting error. Generally, counting annuli became more difficult after approximately 19, as growth rings became compacted. The carapace, and to a lesser degree the plastron, often became worn in large animals (T Keswick, personal observation), which made it difficult to count annuli. A possible reason for a worn carapace is sand abrasion over time, which may be worse in large (older) individuals. Whatever the reason for worn carapaces, they negatively

affect analyses of annuli and size relationships, particularly in the larger sex, females. In a few individuals (less than ten animals), the scute boss appeared to have been shed (T Keswick, personal observation), a phenomenon that also should be considered when evaluating age-size relationships in *P. oculifer* (see Zug, 1991). An additional factor affecting annuli number is that severe climatic conditions (e.g. drought) may limit growth and, hence, annuli deposition. Thus tortoises may be older than their annuli suggests, particularly in a semi-arid environment where droughts may occur relatively often (see Chapter 4).

Females were older than males based on the mean number of annuli. Factors for age bias between sexes include increased longevity in females (e.g., males may be more predation prone than females) and temperature-dependent sex determination that is relatively common in turtles (Janzen & Paukstis, 1991). Temperature-dependent sex determination (TDSD) may produce an age bias in the population by periods of constant temperatures favouring the birth of a specific sex (Ewert & Nelson, 1991). I had no means of testing TDSD, but small male size compared to females, would render males more vulnerable to predators than females are, reducing their longevity. As well as being small, males spent more time in cover than females did (Chapter 6) and predator avoidance is a reason for doing so. In a population of another southern African arid zone endemic, *Homopus signatus signatus*, females were also found to be older than males although it was not known why this was the case (Loehr, 2002).

Although it was not possible to age the population accurately, regressions allowed me to do relative comparisons of age-size relationships between males and females. There were no cohort differences when using SCL as the covariate, but slopes differed when I exchanged SCL for SV. The slope of annuli on SV was steeper for juveniles and males than for females, indicating that when females and males had the same number of growth rings, females had larger SV than the males. If both sexes accumulate one growth ring per year, it means that females grow faster in volume than males after reaching sexual maturity, perhaps because a large size is important in female fecundity (Hofmeyr et al., 2005).

3.4.2 *Body condition*

This study allowed evaluation of body condition (BC) based on mass scaled on shell volume in context of seasonal changes in rainfall and food availability (food availability is linked to rainfall – see Chapter 4). However, there was no correlation between body

mass and rainfall in this study. The lack of a correlation between mass and rainfall may be due to changing patterns in seasonal rainfall combined with a short sampling period. Most of the rain fell in the second autumn (64.2 mm and 74.6 mm in March and April 2007 respectively, Chapter 4), while in 2006 rain was mainly in summer (179 mm in February, SAWS), nearly two months prior to the commencement of this study. Rain between these times was sporadic and it is not surprising that there was no correlation between BC and rainfall. Despite no statistical relationship between BC and rainfall, season affected BC, which is likely rainfall related.

Body condition was lower in summer. Low, summer body condition may be due to a delay in seasonal rainfall. December, January and February are the hottest months at Benfontein (Chapter 4), but rainfall usually peaks in mid to late summer (46 year mean to 2006: 63, 67 and 70 mm for January to March respectively, SAWS) and is a mitigating factor for tortoise BC in these hot months as tortoises can rehydrate, and food availability would increase after rain. Although March 2007 rainfall was close to the long-term mean (64 mm at the study site), January (26.8 mm) and February (6.2 mm) were much drier than usual, and it is likely that this negatively affected tortoise BC at Benfontein in summer 2007. Low seasonal rainfall is a probable cause of poor body condition in other arid zone testudinids (Nagy & Medica, 1986; Henen, 1997; Loehr et al., 2007) due to depleted energy and protein reserves (Loehr et al., 2007) or dehydration (Henen, 1997).

Tortoises in site E had a better body condition than those in site W perhaps because of differences in vegetation between the sites. Site E was more typical of the semi-arid savanna with which *Psammobates oculifer* is associated (Branch, 1988), while site W was more similar to the more shrubby Northern Upper Karoo vegetation (see Chapter 4 for site vegetation descriptions). Tortoises selected grass refuges (as one may expect from a 'savanna species') in both sites while they did not select shrubs in either (Chapter 5). In addition, cover was sparser in site W than it was in site E (Chapter 4). Concurrently, tortoises' body temperatures in site W were higher than they were in site E, as were ground and air temperatures (Chapter 6). Less vegetation cover in site W combined with a reduction in favoured microhabitats (grass) may have affected tortoises' ability to thermoregulate. In turn, this may have resulted in water loss and /or control over their metabolism, thereby negatively affecting tortoise mass (e.g., see Cloudsley-Thompson, 1999). Greater abundances of palatable grasses, such as *Eragrostis lehmanniana*, in site E (than in site W; Chapter 4), which I observed

tortoises eating (and see Rall & Fairall, 1993) may also have positively affected tortoise body condition in site E. Additionally, the cover of herbaceous plants, the preferred food of *P. oculifer* (Rall & Fairall 1993) was more than double in site E than in site W. As well as an effect of site, there was also an effect of sex – males had lower body condition than females did. The fact that it was a general effect, and not specific to a season, e.g. mating season, makes this difficult to explain. Males were smaller than females (Chapter 8) and despite using denser refuges than females did (Chapter 5) they still had a higher mean body temperature than females did (Chapter 6). Thus low body condition in males could again be associated with thermoregulation and consequent increases in metabolic rates and/or water loss. Alternatively, the formula used to calculate SV may have overestimated male body size, which would have resulted in an apparent lower body condition for males relative to females.

3.5   CONCLUSIONS

This study represents the first attempt to record population parameters for *Psammobates oculifer*. The sex ratio did not differ from 1:1 and although sex did not affect ease of location, juveniles were harder to find than adults were. A bias in favour of the number of tortoises located in site W was probably related to the lower percentage of vegetation cover in that site; vegetation cover in site E was greater which impaired visibility. Although I did not derive a population estimate, the hours per unit capture indicates that population density was relatively low. The spread of size classes are indicative of recruitment, but annuli counts suggested that females may live longer than males, perhaps because the smaller male is more predator-prone than the larger females. Generally, annuli may underestimate age, as tortoises may not deposit annuli during periods when the climate is unfavourable e.g., during a drought. The relationship between annuli and shell volume may indicate that females invest more energy into growth than males do after reaching maturity, perhaps because a large size holds benefits for females in terms of reproductive success. Tortoises' body condition was lowest in the dry summer, which may reflect a dearth of water and rain related forage. Lower body condition of animals in site W compared to site E and in males compared to females may be related to difficulties in thermoregulation due to unsuitable habitat in site W and small male body size respectively.

4 HABITAT

4.1 INTRODUCTION

Climatic and edaphic factors are major determinants of vegetation cover, plant community structure (Kassas, 1953; Leistner & Werger, 1973; Vorster & Roux, 1983; Ringrose et al., 1998; Rutherford et al., 2006b) and, consequently, animal distributions (McNaughton, 1985; McNay et al., 1994). In arid and semi-arid regions, water is often the limiting resource in plant communities and rainfall is seasonal and sporadic (Noy-Meir, 1973; Ringrose et al., 2003). Thus, vegetation cover and composition may vary temporally and spatially in response to available water (Noy-Meir, 1973; Fourie & Roberts, 1977). Vegetation composition can be characterised in terms of plant species, growth forms (e.g., shrubs and grasses), or plant life cycles (e.g., annuals and perennials), whereas vegetation structure can be defined by horizontal, vertical and temporal arrangements. Mucina et al. (2006a) and Rutherford et al. (2006b) combined plant communities into vegetation units, based on dominant ecological gradients and factors (e.g., salt content of soil), floristic similarities, and dominant vegetation structure.
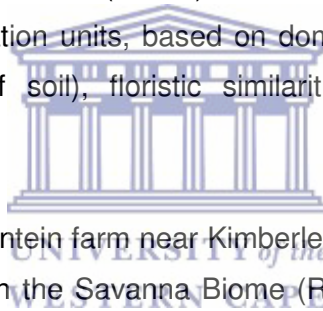
This study took place at Benfontein farm near Kimberley, which falls within the Eastern Kalahari Bushveld Bioregion in the Savanna Biome (Rutherford et al., 2006b). In this Bioregion, mean annual rainfall is 362 mm with a coefficient of variation of 34%, mean annual temperature is 17.8 °C, frost occurrence averages 33 days per annum, and soil moisture stress (% days when evaporation is more than double the supply) averages 83% (Rutherford et al., 2006a). Vegetation in the Kimberley district encompasses four vegetation units: Kimberley Thornveld (SVk4) and Vaalbos Rocky Shrubland (SVk5), two Savanna vegetation units; Northern Upper Karoo (NKu3), a Nama-Karoo vegetation unit; and Highveld Salt Pans (AZi10), an Inland Azonal vegetation unit (Mucina et al., 2006b; Mucina et al., 2006c; Rutherford et al., 2006a).

Kimberley Thornveld is found on plains of sandy to loamy soils (Hutton soil form, Ae and Ah land types), and is characterised by scattered trees (e.g., *Acacia erioloba*), a substantial shrub layer, and grasses. Vaalbos Rocky Shrubland is prominent in elevated areas adjacent to Kimberley Thornveld and comprises of evergreen shrubs (e.g., *Diospyros lycioides*) on a predominantly rocky, dolerite substrate or calcrete soils in low-lying areas (Rutherford et al., 2006a). Northern Upper Karoo vegetation consists mainly of dwarf, karoid shrubs (e.g., *Chrysocoma ciliata*) and grasses (e.g., *Aristida*

spp.), with occasional low trees (e.g., *Acacia mellifera*) on shallow to deep soils (Mucina et al., 2006b). Highveld Salt Pans are temporary to permanent water bodies on Ecca shales that become progressively saline over dry periods. Low shrubs and grasses, particularly in grazed areas, surround the pans. Common shrubs of Highveld Saltpans include *Pentzia incana* and *Lycium cinereum* (Mucina et al., 2006c).

Grassland and Nama-Karoo Biomes border the study site to the east and south, respectively; transitional or ecotonal (Low & Rebelo, 1996) effects may thus influence habitat heterogeneity (Rutherford, 1997). Anthropogenic related effects, such as livestock grazing (Todd & Hoffman, 1999; Todd, 2006), can also have a profound influence on localised habitat. The creation of 'piospheres' by livestock in areas surrounding artificial watering holes (seen particularly in arid areas), is one such example (Jeltsch et al., 1997; Todd, 2006).

The purpose of this study was to characterise the habitat of *Psammobates oculifer* in order to assess the species' functional ecology. The objectives of the habitat assessment were to (1) characterise the climate, substrate, soil and vegetation communities of the study area, (2) link the vegetation communities at the study site to the newly recognised vegetation units for this region, and (3) characterise seasonal changes in vegetation composition and structure. The results of this study can be used to assess the requirements of animals other than tortoises, and should contribute significantly to our understanding of vegetation dynamics in the Savanna Biome.

4.2   MATERIALS AND METHODS

4.2.1 Study area and weather data

The study site at Benfontein farm was in a cattle ranching area of approximately 2,700 ha, divided by a fence running approximately north to south. For the purposes of this study, the two areas split by the dividing fence were called sites E (east) and W (west), respectively (see general methods and Fig. 2.1 for details). Both sites were on Kalahari aeolian sand; site E contained mainly grasses, interspersed thinly with trees, whereas site W comprised of tussock grasses, small shrubs and bare, calcrete patches. Temperature and rainfall data collection are described in the general methods section (Chapter 2).
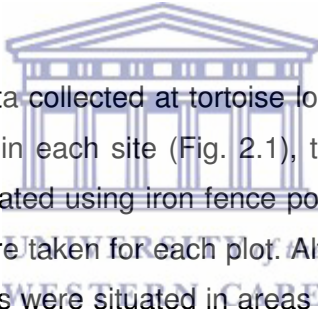
4.2.2 Habitat assessment

I assessed vegetation and substrate of the study site throughout the study period (22 March 2006 to 30 April 2007) at tortoise location/relocation sites, and made seasonal assessments of 10 vegetation plots (Fig. 2.1). For the first method, I radio-tracked 15 female and 12 male tortoises over the study period (see Chapters 2 & 7 for details). Each time I located a tortoise, I assessed the tortoise's habitat within an estimated radius of 5 m of the tortoise's location. I ranked the substrate from 1 to 5; 1 being 100% sand, 2 being sand and < 25% small stones, 3 being sand and < 25% small and medium stones, 4 being 25-50% small and medium stones and 5 being more than 50% small and medium stones. I estimated percentage plant cover in 5% gradations by comparing the percentage of live and dead vegetation cover, rooted to the ground, relative to bare substrate. Percentage plant cover was evaluated also at four height categories; < 10 cm, 10-60 cm, 61-100 cm and > 100 cm; their sum equalling the percentage total plant cover estimate. Height classes were selected because they represented the vegetation structure at the study site and were relevant to tortoises' biology. *Psammobates oculifer* is a small tortoise (mean height 53.7±13.2 mm) and plants of height class <10 cm were at a tortoise's foraging height. The height classes 10-60 cm and 61-100 cm were chosen because they were representative, respectively, of short versus tall shrubs/grasses at the sites. Most plants were shorter than 1 m in height so those above 1 m were lumped. Plants were placed in a plant press and identified to species level, where possible, by herbarium staff at the McGregor Museum in Kimberley.

To assess proportional abundance of plant species (from 20th September 2006), species were ranked from 1 to 5: 1 being merely present and 5 being the most abundant. This allowed calculation of relative cover indices (RCI; Joshua et al., 2005). The traditional method of estimating abundance of species is to assign a specific percent cover range to each rank. This method becomes problematic, however, when locations have a whole range of species. In this instance, I first summed all the rank values for the location and then expressed the rank value of each species as a proportion of the sum of the ranks. This proportion was then multiplied by percent total cover for the location to obtain a RCI of the species. A species with a rank of 5 would represent 100% of the plant cover when only one species was present, but may represent only 25% of the plant cover, even though it was the most abundant species, when the sum of the ranks of all species was 20. Plant species could tie ranks on the basis that they contributed in equal proportions to the vegetation cover. Unless there were obvious differences in vegetation, vegetation details were treated as being the

same (i.e., one record) when a tortoise had moved a short distance (< 10 m) from its previous location.

Plant species were subsequently collated into two different groups for analysis. In the first group, plant species were divided into growth forms namely: trees, shrubs, grasses, herbs, geophytes, sedges and others (e.g., unidentified seedlings, moss, algae and cryptogamic soils). Shrubs and grasses were subdivided into short shrubs or grasses (≤ 60 cm) and tall shrubs or grasses (> 60 cm), respectively. Grass forms also included the categories dead grass and unknown grass (species and height not recorded). In the second group, plant species were categorised into plant types based on their life cycle, namely: annuals, perennials, and unknown (e.g., plant species identified to genus level, non-flowering plants, and other ground cover). All species were a 'form' and a 'type' based on relevant botanical literature (Shearing & van Heerden, 1997; van Rooyen, 2001; Germishuizen & Meyer, 2003; van Oudtshoorn, 2004).

As a supplement to habitat data collected at tortoise locations, I located 10 vegetation plots of 25 m^2 (5 x 5 m), five in each site (Fig. 2.1), to monitor seasonal changes in vegetation. Plots were demarcated using iron fence posts or bamboo canes and GPS locations (accurate to 5 m) were taken for each plot. Although the location of each plot was randomly chosen, the plots were situated in areas where I had found tortoises. As part of the initial survey, I assessed the substrate in each plot. At subsequent surveys, each vegetation plot was monitored at least once per season (see Table 2.1 in Chapter 2). Percentage cover and vegetation ranking was executed using the same methods as at tortoise relocations described above.

At the end of the study, I took soil samples from each of the 10 vegetation plots. Soil samples were randomly collected in each plot and consisted of five cores of 10 cm depth, which were mixed in a bucket to get an even mix of the plot soil profile. Subsequently, a 500 g subsample was placed in a zip-lock bag, which was marked with the plot's number. The soil samples were analysed at BemLab (Pty) Ltd in Somerset West, South Africa for: electrical resistance (Ω) (Soil and plant analysis Council, 1999a), pH (Eksteen, 1969; Soil and plant analysis Council, 1999b), percentage Na, K, Ca, Mg and exchangeable cations (cmol+/kg) (The Non Affiliated Soil Analysis Work Committee, 1990a; Soil and plant analysis Council, 1999c), P (mg/kg) (The Non Affiliated Soil Analysis Work Committee, 1990b; Soil and plant analysis Council, 1999d), total nitrogen (%; Hornek & Miller, 1998), total carbon (%;

Soil and plant analysis Council, 1999e) and percentage sand/silt/clay (Day, 1956; van der Watt, 1966). Soil analysis may provide insight into differences in vegetation type and percentage cover between the two sites, and may affect plant nutrient content and, perhaps, the tortoises' body condition.

4.2.3   Data and statistical analyses

Because March 2006 contained only 10 records for site E, I included March with April data for analyses. Similarly, records for the first and last few days in November 2006 were combined with October and December data, respectively. To avoid pseudo-replication in tortoise relocation samples, I used data from only the first record when the same tortoise was found at the same location consecutively. When tortoises were found mating or in mating related behaviour (see Table 6.1), I noted the vegetation data in context of the female only, thus as one record.

In order to express rank values for plant species in terms of percent cover, I calculated a relative cover index (RCI; Joshua et al., 2005) for each plant species in vegetation plots and at tortoise relocation sites. All rank values within a plot or relocation site were summed and the rank value of each species was expressed as a proportion of the total. The proportion was then multiplied by percent total cover for the plot or relocation site. The sum of the species' relative cover indices (RCIs) thus equalled the percent total plant cover of the plot or relocation site. Relative cover indices of growth forms or plant types were calculated in a similar way.

I used Margalef's index (d) for species richness ($d = (S-1) / \ln N$, where S = number of species and N = the sum of all frequencies of the plant species in a month or site) to allow for differences in sample size when assessing temporal and spatial patterns in species richness (Clarke & Warwick, 2001). To compare species diversity amongst months and between sites, I used (a) Shannon-Wiener's index of diversity (or entropy): $H' = -\Sigma\ n_i/N \ln n_i/N$, where n_i is the frequency of the ith species in a month or site and N is the sum of all frequencies of the plant species in a month or site (Zar, 1999), and (b) Simpson's index of diversity (or entropy): $D' = 1-D$, where $D = \Sigma(n / N)^2$ (Peet 1974). The Shannon-Wiener index is sensitive to changes in the abundance of rare species, whereas Simpson's index is sensitive to changes in abundant species. I also compared equitability of abundance, using the Shannon-Wiener index of evenness, $J' = H' / H'_{max}$, where H'_{max} is the ln of the species count (Zar, 1999). Values of J' near to 1 suggest a more homogeneous species distribution; those nearing 0 indicate species dominance.

I compared habitat data of vegetation plots and tortoise relocation sites visually and statistically, by Mann-Whitney tests (MW; T statistic) with sequential Bonferroni adjustments, to decide if the data should be analysed separately or as a combined data set. This comparison included all data sets for plots, but only included tortoise relocation data that matched the months when plots were sampled.

I used two-way ANOVAs (F statistic), followed by Student-Newman-Keuls (SNK) post hoc tests, to compare monthly and inter-site means of vegetation categories that met parametric assumptions, before or after transformation ($\log_{10}$, ranks or arcsine square root). When data did not satisfy the requirements of normality or equal variance, I used Kruskal-Wallis ANOVAs (KWAs; H statistic), followed by Dunn's post hoc comparisons, to evaluate differences in sample medians amongst months, both total and within sites, and I used MW tests or Student's t tests (t statistic) for inter-site comparisons. In all instance, I applied a sequential Bonferroni procedure on all families of tests to control for Type I errors (Holm, 1979). I used Friedman's repeated measures ANOVA (FRMA, χ^2 tests), followed by SNK post hoc tests, to compare the RCIs of plant species and growth forms within sites and within months.

Simple regressions were used to estimate the variance in percent cover of vegetation, growth form and plant type RCIs, and diversity indices that were attributable to rainfall. When data were non-parametric, I used Spearman's rank correlation (r_s) to correlate vegetation data with rainfall data to assess environmental effects on plant cover. Both rainfall data of corresponding months and rainfall data of the previous month were used in regressions and correlations to accommodate a delayed effect of rainfall on plant growth. Pearson correlations were also used to compare relationships between soil categories (e.g., sand) and soil elements (e.g., % nitrogen per kg of soil) and r was squared to report correlation coefficients in each case (Zar, 1999).

Statistical analyses were done in SigmaStat 2.03 or SigmaPlot 11 (SPSS Inc., Chicago, USA), whereas diversity indices were compared by t-tests in Microsoft Excel. Variances for Shannon-Wiener (H') diversity indices were calculated according to Zar (1999) using the equation $s^2_H = (\Sigma n \ln^2 n - (\Sigma n \ln n)^2 / N) / N^2$ with degrees of freedom as $v = (s^2_{H1} + s^2_{H2})^2 / ((s^2_{H1})^2 / N_1 + (s^2_{H2})^2 / N_2)$. Variances for Simpson's diversity indices (D') were calculated according to Brower et al. (1998) using the equation $s^2 = 4[\Sigma(n/N)^3 - (\Sigma(n/N)^2)^2] / N$ with degrees of freedom for $D' = \infty$. All differences were considered significant at $P \leq 0.05$ except when the use of multiple tests required the application of a sequential Bonferroni procedure.

The need to use a combination of parametric and non-parametric tests complicated reporting of summary data in figures and tables. Consequently, for sake of simplicity and ease of comparison, I always reported means (±standard deviations) even when non-parametric tests were used. However, where significant differences were unclear in graphs or tables, because of reporting some non-parametric data as means, I provided medians with 25th and 75th percentiles in the text.

4.3 RESULTS

4.3.1 *Temperature and rainfall*

South African Weather Services (SAWS) rainfall of 323 mm for April 2006 to March 2007 was lower than the long-term average (415±135 mm) of 46 years (1960-2005) for the corresponding period. Based on SAWS long-term rainfall, the coefficient of variation for annual rainfall was 32%. Rainfall recorded from April 2006 to March 2007 at the study site was 301 mm, marginally lower than that recorded by SAWS. Summer months (December, January and February) were exceptionally dry with rainfall well below the long-term average (Fig. 4.1). In contrast, rainfall in April 2007 was substantially higher than the long-term average. Although annual rainfall recorded by SAWS and at the study site was broadly similar, the spatial heterogeneity of rainfall was evident in April 2007, when 69.1 mm more rain was recorded by SAWS than at the study site.

Mean maximum temperatures ranged from a low of 19.1 °C in May 2006 to a high of 34.5 °C in February 2007 (SAWS). The mean minima temperatures ranged from a low of 0.9 °C in June 2006 to a high of 18.5 °C in February 2007 (Fig. 4.1). Temperature extremes recorded at the study site were approximately -4 °C and 40 °C in the shade.
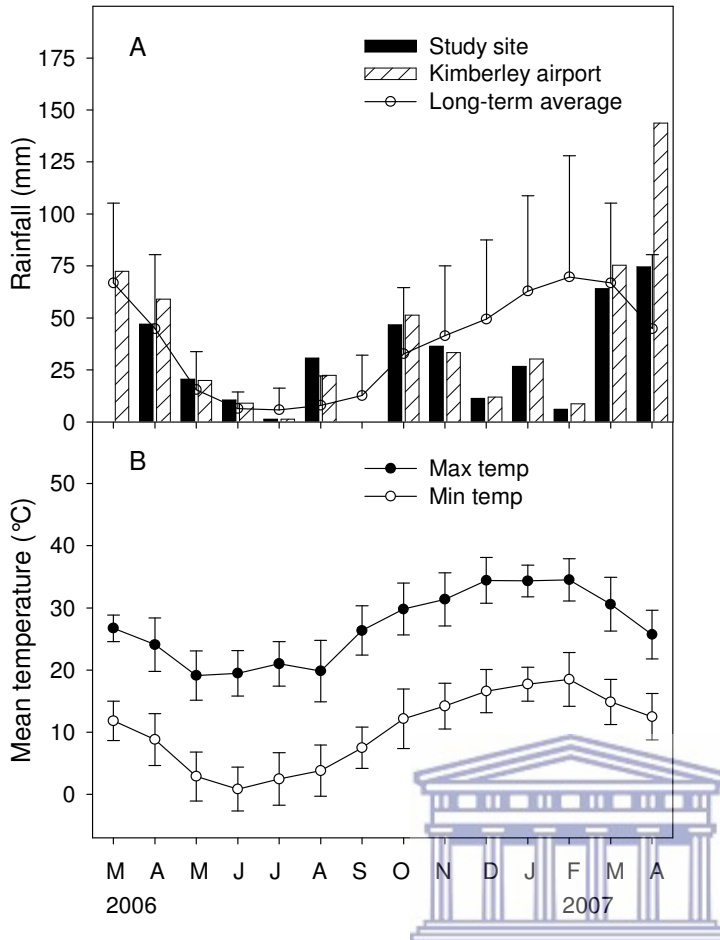
Figure 4.1 A. Monthly rainfall at the study site and at Kimberley airport ca. 5 km from the study site (South African Weather Services; SAWS), and the long-term rainfall average (±SD) at Kimberley airport. The long-term rainfall averages were determined over 46 years, from 1960 to 2006. B. Mean monthly maxima and minima temperatures (°C; ±SD) for the study period recorded at Kimberley airport (SAWS).

4.3.2 Substrate and soil

The substrate in the study area was ranked as sandy with a low occurrence of small stones. Soil texture was predominantly that of sand (96.26±0.85%) with some clay (2.34±0.59%) and silt (1.40±0.43%; Table 4.1).

Table 4.1 Substrate properties for site E ($n = 667$), site W ($n = 687$) and the two sites combined ($n = 1354$); and soil properties recorded for the same sites ($n = 5$, 5 and 10 except for H$^+$ where $n = 5$, 4 and 9, respectively). The substrate means (±SD) and ranges are based on the recorded ranks (1-5).

	Total		East site		West site	
Substrate:	1.44 ±	0.81	1.05 ±	0.27	*1.82 ±	0.97
Range of ranks	1-5		1-3		1-5	
Soil properties:						
pH (KCl)	5.67	± 0.33	5.48	± 0.13	5.86	± 0.38
Resistivity (Ω)	3024	± 679	*3462	± 404	2586	± 628
H$^+$ (cmol/kg)	0.36	± 0.05	0.38	± 0.02	0.34	± 0.06
P (mg/kg)	3.90	± 4.28	2.40	± 0.55	5.40	± 5.94
K (mg/kg)	143.00	± 15.60	144.80	± 15.51	141.20	± 17.28
Na (cmol(+)/kg)	0.02	± 0.01	0.02	± 0.00	0.03	± 0.01
K (cmol(+)/kg)	0.37	± 0.04	0.37	± 0.04	0.36	± 0.04
Ca (cmol(+)/kg)	2.49	± 0.56	2.33	± 0.42	2.66	± 0.68
Mg (cmol(+)/kg)	1.06	± 0.13	1.07	± 0.14	1.05	± 0.12
N (%)	0.04	± 0.01	0.05	± 0.01	0.04	± 0.00
C (%)	0.21	± 0.09	0.20	± 0.10	0.22	± 0.08
Na (%)	0.55	± 0.13	0.49	± 0.09	0.60	± 0.16
K (%)	8.59	± 0.62	8.88	± 0.52	8.30	± 0.62
Ca (%)	57.86	± 5.56	55.49	± 5.00	60.23	± 5.53
Mg (%)	25.05	± 3.02	25.85	± 4.12	24.24	± 1.38
CEC (cmol/kg)$^\#$	4.27	± 0.53	4.17	± 0.38	4.37	± 0.68
Clay (%)	2.34	± 0.59	2.64	± 0.43	2.04	± 0.61
Silt (%)	1.40	± 0.43	1.60	± 0.51	1.20	± 0.24
Sand (%)	96.26	± 0.85	95.76	± 0.75	96.76	± 0.65

*Significant site differences, $P \leq 0.05$
#Cation exchange capacity (CEC)

The substrate differed between sites; site W was slightly stonier than site E ($T_{659,637} = 320005$, $P < 0.0001$). Despite having a more stony substrate, soil in site W tended to have a higher percentage of sand ($t_8 = 2.241$, $P = 0.055$). The variation in total phosphorus concentration in site W was substantially higher than in site E (variance ratio test: $F_{4,4} = 118$, $P < 0.001$). This was due to one plot in site W having a phosphorus concentration more than six-fold higher than the mean for the other plots.

Additionally, site W had lower soil resistivity than site E (t_8 = 2.624, P = 0.030). There were affinities between soil textures (sand, silt and clay) in the study area and certain soil properties. Percentage sand was inversely correlated to the soil's hydrogen ion concentration (r^2 = 0.53, df = 7, P = 0.026) and percentage nitrogen (r^2 = 0.66, df = 8, P = 0.0047). In contrast, there was a positive relationship between percentage nitrogen and percentage silt (r^2 = 0.72, df = 8, P = 0.0018), and between hydrogen ion concentration and percentage clay (r^2 = 0.77, df = 7, P = 0.0020). Furthermore, percentage clay was inversely related to the soil's phosphate concentration (r^2 = 0.48, df = 8, P = 0.027), and was directly correlated to percentage potassium (r^2 = 0.52, df = 8, P = 0.019). The pH of soils had a positive relationship with both cation exchange capacity (CEC; r^2 = 0.69, df = 8, P = 0.0032) and combined base cations (r^2 = 0.76, df = 8, P = 0.0012).

4.3.3 Percentage plant cover

4.3.3.1 Percentage cover in vegetation plots and tortoise relocation sites

I collected vegetation data from plots to provide a consistent measure of seasonal changes in vegetation at sites E and W. However, the vegetation data from plots covered a relatively small area in comparison with vegetation data collected while radio-tracking tortoises. Thus, a more complete characterisation of vegetation would be gained by combining the two data sets. Furthermore, combining the data allow a more robust presentation of plant composition at the sites. Both data sets contained species unique to their set. To justify combining plot data with relocation data, I compared percentage cover, both total and for different height categories, between the two data sets. There were no differences between plots and tortoise relocations in percentage total cover and percentage cover of plants > 100 cm (all P > 0.09), but there were significant differences in percentage cover categories for H < 10 cm ($T_{70,899}$ = 26602, P = 0.0011), H 10-60 cm ($T_{70,899}$ = 40178, P = 0.0058) and H 61-100 cm ($T_{70,899}$ = 27566, P = 0.0047). However, when comparing the data graphically, the statistical differences appeared to be a function of the large sample size (relocation data, n = 899; plot data, n = 70). Differences between means for particular months averaged 3.5%, and varied from 0.2% to 8.2%. Average differences for H < 10 cm, H 10-60 cm and H 61-100 cm were 3.0%, 4.8% and 3.3%, respectively. In view of the inaccuracies associated with estimating percentage cover in 5% intervals, these differences were considered insignificant and the data for the two sampling methods were combined.

4.3.3.2 Percentage cover, height categories and inter-site differences

Percent plant cover at the study site averaged 71% and was higher for site E than for site W ($T_{664,692}$ = 616003, P < 0.0001; Table 4.2). Plant cover for the different height categories differed significantly in site E, site W and both sites combined (Friedman's RMA, all χ^2 > 1586, df = 3, P < 0.0001); the 10-60 cm height class provided most cover, followed by the categories < 10 cm, 61-100 cm and > 100 cm (Table 4.2). Site E had greater cover than site W had for plants with heights < 10 cm and 10-60 cm (all MW rank sum tests, $T_{664,692}$ > 516918, P < 0.0001), and although site E appeared to have greater cover for plant height > 100 cm it was not significant after applying a sequential Bonferroni procedure (P = 0.025 > 0.002 = adjusted α). Site W had higher cover than site E had for the plant height category 61-100 cm ($T_{664,692}$ = 421683, P < 0.0001; Table 4.2).

Table 4.2 Mean (±SD) vegetation cover (%) for total cover and cover of height classes <10 cm, 10-60 cm, 61-100 cm and >100 cm of site E (n = 664), site W (n = 692) and the two sites combined (n = 1356).

	Total		Site E		Site W	
Total cover	70.9	± 9.0	*75.5	± 9.0	66.5	± 6.5
Cover H < 10 cm	12.2	± 8.1	*13.3	± 6.9	11.0	± 8.9
Cover H 10-60 cm	49.3	± 13.2	*53.2	± 14.2	45.6	± 10.9
Cover H 61-100 cm	8.9	± 8.6	8.0	± 8.7	*9.8	± 8.5
Cover H > 100 cm	0.5	± 3.3	1.0	± 4.6	0.1	± 0.6

*Indicates significant difference between sites, P < 0.0001

4.3.3.3 Seasonal effects on vegetation cover

Season (month) had a significant effect on total plant cover for the combined sites (KWA, H_{10} = 31.33, P = 0.00051), but not at a post hoc level. Total cover within site E also changed over time (H_{10} = 84.72, P < 0.0001), with a higher plant cover in April to October 2006 than in February and March 2007. Unlike site E, cover within site W did not change with season (P = 0.11). Within all months, site E had a higher total cover than site W had (all $T \geq 567$, $n1 \geq 25$, $n2 \geq 32$, P < 0.0001; Fig. 4.2).
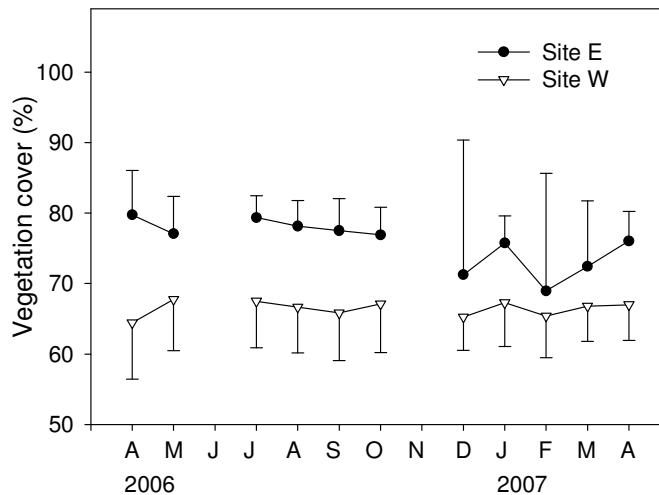
Figure 4.2 Percent plant cover (mean ±SD) recorded over 13 months at the East (E) and West (W) sites on Benfontein farm, near Kimberley. No data were recorded in June 2006 and data recorded the first and last days of November were combined with October and December data, respectively.

In the combined sites, cover for plants < 10 cm in height varied amongst months (H_{10} = 99.56, P < 0.0001), with lower cover in July than in all other months. Cover in October, December, January and March was greater than in May with October cover higher than that in September. Cover in this height category also differed among month within site E (H_{10} = 143.8, P < 0.0001; Fig. 4.3A). October had a higher cover than all months except August, and August cover exceeded that of the remaining months except September, December and January. September and December cover was higher than that of May, July and February. Monthly cover of plant height < 10 cm also differed at site W (H_{10} = 92.2, P < 0.0001; Fig. 4.3A). Cover in January and March was higher than in August and September, with July having lower cover than all the other months except August. Plants cover with height < 10 cm was greater in site E than in site W in the months May to October (t_{61} = 6.72, all T ≥ 615, $n1$ ≥ 30, $n2$ ≥ 43, P < 0.0001) but not in the remaining months (after applying a sequential Bonferroni procedure, P ≥ 0.04 > 0.002 = adjusted α).

Percentage cover of the height category 10-60 cm tended to decrease from winter to summer (H_{10} = 92.9, P < 0.0001; Fig. 4.3B). The cover from May through September and April 2007, was higher than in April 2006 and December. May to August cover was higher than in October and January, whereas July cover was higher than the cover in February and March. Similarly, seasonal changes for site E peaked also in winter (H_{10} = 95.4, P < 0.0001; Fig. 4.3B) with cover in July higher than all months but September

and May. Cover in May and September was higher than it was in April 2006, October, December, February and March. August had higher cover than in December (Fig. 4.3B). Although there was a significant difference amongst months within site W (H_{10} = 49.6, P < 0.0001; Fig. 4.3B), it was not discernible at a post hoc level (P > 0.05). Site E had a higher cover of plants of the height category 10-60 cm than site W had within all months except December (all t ≥ 2.97, df ≥ 61; all T ≥ 902, n1 ≥ 25, n2 ≥ 43, P < 0.008; Fig. 4.3B).

Percentage cover of plants with heights of 61-100 cm differed amongst months (H_{10} = 51.93, P < 0.0001). Cover for April to July exceeded that of August and September. Similarly, cover varied monthly at site E (H_{10} = 70.04, P < 0.0001; Fig. 4.3C), with a higher cover in April 2006 than in May to October and in February and March. April 2007 cover was higher than in August and September whereas December, January and March cover exceeded that of August (Fig. 4.3C). The trend for cover variation at site W (H_{10} = 52.85, P < 0.0001; Fig. 4.3C) differed from that of site E. May and July had higher cover than in September and April 2007, while July cover was also higher than the cover in April 2006, August to January and March (Fig. 4.3C). From May to August, and in October and February, cover was greater in site W than in site E (t_{71} = 2.79; all T ≥ 648, $n1$ ≥ 30, $n2$ ≥ 32, P < 0.0068).

There were differences in the cover of plants over 100 cm tall amongst months in site E (H_{10} = 44.89, P < 0.0001) and in both sites combined (H_{10} = 50.07, P < 0.0001; Fig. 4.3 D) but the differences were not significant at the post hoc level. Percentage plant cover did not differ amongst seasons in site W (P = 0.57) or between sites within months (P > 0.08; Fig. 4.3D).

4.3.3.4 *Effect of rainfall on vegetation cover*

Percent plant cover in the height category 61-100 cm at site E was positively influenced by rainfall from the previous month ($F_{1,9}$ = 7.82, P = 0.021, r^2 = 0.47), but no other percentage cover category was significantly effected by rainfall (P > 0.08).
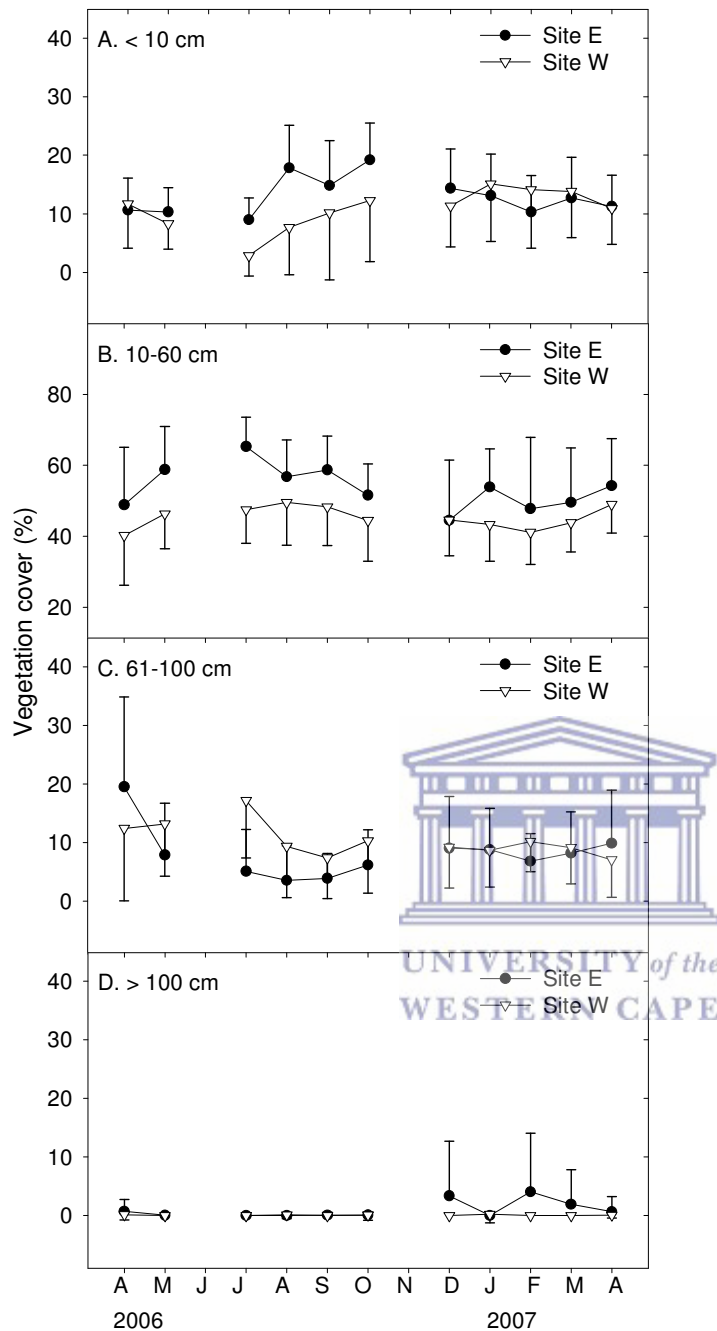
Figure 4.3 Monthly mean percentage vegetation cover (±SD) at different height categories for (A) < 10 cm, (B) 10-60 cm, (C) 61-100 cm, (D) > 100 cm. Percentage cover was not recorded for June, and data collected the first and last few days of November were added to October and December, respectively.

4.3.4 Abundance of plant species and other ground cover

4.3.4.1 Species composition of sites

There were 98 plant/other ground cover records, of which 74 were identified to species level and 14 to genus level, all genera representing 30 families. Additional records included five unidentified grasses, one unidentified herb, seedlings, moss, algae and cryptogamic soil (Table 4.3). The most common families were the grasses (Poaceae) with 14 species, the daisy family (Asteraceae) with 13 species, and the legumes (Fabaceae) with nine species. Four families (Hyacinthaceae, Scrophulariaceae, Solanaceae and Sterculiaceae) contributed five species each, two families contributed three species each, seven families contributed two species each and 14 families were represented by a single species (Table 4.3). Site E had 79 records, with 28 families, of which Poaceae (12 species), Asteraceae (11 species), Fabaceae (7 species) and Scrophulariaceae (5 species) were dominant. Site W had 78 records, with 24 families, of which Poaceae (14 species), Asteraceae (13 species), Fabaceae (7 species) and Hyacinthaceae (5 species) were dominant.

Analysis for relative cover indices (RCIs) of plants was based on 94 instead of 98 items, because four plants were not recorded subsequent to the date when I started ranking plant species at relocation sites. These plants were *Babiana hypogaea*, *Hermannia erodioides* and *Melolobium* sp. from site W, and *Searsia lancea* from site E (Table 4.3). The RCIs of plants within site E (FRMA, $\chi^2 \geq$ 17082.4, df = 93, $P <$ 0.0001), site W (FRMA, $\chi^2 \geq$ 14882.0, df = 93, $P <$ 0.0001) and the two sites combined (FRMA, $\chi^2 \geq$ 27955.5, df = 93, $P <$ 0.0001) differed significantly. Post hoc tests for the combined sites showed that the RCIs of 23 plant items differed from each other and were higher than the RCIs of all remaining plant items. Similarly, 17 records, three of which tied, in site E and 17 records in site W could be ranked according to SNK post hoc results for these sites (Table 4.3).

Schmidtia pappophoroides (a short grass) was the most abundant species in site E and the two sites combined but it was only the third most abundant species in site W, where *Stipagrostis uniplumis* (a tall grass) was the most abundant plant (Table 4.3). *Chrysocoma ciliata* was the most abundant shrub in site E (ranked second) and the two sites combined (ranked third), but not in site W where *Pentzia incana* (ranked second) was the most abundant shrub. *Hermannia tomentosa* was the most abundant herb in site W (ranked fifth) and the two sites combined (ranked fourth), but *Selago paniculata* (ranked fourth) was the most abundant herb in site E (Table 4.3).

Table 4.3 Mean relative cover index of plant items for site E, site W and combined sites (total) ranked in accordance with SNK post hoc test results of Friedman's repeated measure ANOVAs (hence a species may be ranked higher than another species despite having a lower mean RCI, e.g., *S. uniplumis* is ranked higher than *C. ciliata* in combined sites). Asterisks next to the RCI of site E or W indicate significant site differences. Zeros indicate absence of species at a site. The four last entries have no RCIs and are included for completeness. Plant types were partitioned into Annuals (A), Perennials (P), and Unknown (U). Growth forms were divided into GS (grass, short), GT (grass, tall), G (geophyte), H (herb), SS (shrub, short), ST (shrub, tall), T (tree), and U (unknown).

Family	Species	Plant type	Growth form	Total (RCI)	Rank	Site E (RCI)	Rank	Site W (RCI)	Rank
Poaceae	*Schmidtia pappophoroides*	P	GS	10.545	1	14.741*	1	6.225	3
Poaceae	*Stipagrostis uniplumis*	P	GT	5.764	2	6.281*	3	5.231	1
Asteraceae	*Chrysocoma ciliata*	P	SS	5.924	3	7.936*	2	3.852	7
Sterculiaceae	*Hermannia tomentosa*	P	H	5.240	4	5.448	5	5.026	5
Asteraceae	*Pentzia incana*	P	SS	5.355	5	4.290	6	6.451*	2
Asteraceae	*Eriocephalus ericoides*	P	SS	3.102	6	1.112	13	5.150*	4
Poaceae	*Stipagrostis obtusa*	P	GS	3.011	7	2.513	8	3.523*	8
Asteraceae	Amphiglossa triflora	P	SS	2.695	8	1.351	11	4.079*	6
Scrophulariaceae	*Selago paniculata*	P	H	3.742	9	6.960*	4	0.430	
Molluginaceae	*Plinthus karooicus*	P	SS	2.051	10	1.456	9	2.664*	9
Poaceae	*Eragrostis lehmanniana*	P	GS	2.077	11	2.761*	7	1.372	14
Thymelaeaceae	*Gnidia polycephala*	P	SS	1.851	12	0.889	14	2.841*	11
Sterculiaceae	*Hermannia comosa*	P	H	1.290	13	1.289	10	1.292	12
Asteraceae	*Rosenia humilis*	P	SS	2.089	14	0.422		3.805*	10
Campanulaceae	*Wahlenbergia androsacea*	A	H	1.622	15	2.944*	8	0.261	
Fabaceae	*Senna italica*	P	H	0.804	16	1.243	10	0.352	
Fabaceae	*Melolobium macrocalyx*	P	SS	0.792	17	0.377		1.219	17
Poaceae	*Cymbopogon pospischilii*	P	GT	0.916	18	0.126		1.728*	13
Unidentified	Seedlings	U	U	1.051	19	1.515	12	0.573	
Poaceae	*Eragrostis trichophora*	P	GS	0.854	20	1.263	14	0.434	
Poaceae	Grazed grass	U	U	1.038	21	0.257		1.842*	16
Solanaceae	*Lycium cinereum*	P	SS	0.660	22	0.000		1.340*	15
Solanaceae	*Solanum incanum*	P	ST	0.496	23	0.775		0.209	
Apiaceae	*Deverra denudata*	P	ST	0.627		0.532		0.725	
Poaceae	*Aristida adscensionis*	A	GT	0.353		0.487		0.216	
Fabaceae	*Acacia erioloba*	P	*T*	0.466		0.893		0.026	
Poaceae	*Aristida diffusa*	P	GT	0.439		0.198		0.686	
Scrophulariaceae	*Zaluzianskya violacea*	A	H	0.418		0.608		0.222	
Asteraceae	*Ifloga* sp.	A	H	0.391		0.412		0.369	
Molluginaceae	*Limeum sulcatum*	A	H	0.375		0.508		0.239	

Table 4.3 continued

Family	Species	Plant type	Growth form	Total (RCI)	Rank	Site E (RCI)	Rank	Site W (RCI)	Rank
Scrophulariaceae	*Nemesia fructicans*	A	H	0.341		0.432		0.248	
Poaceae	*Themeda triandra*	P	GT	0.285		0.483		0.081	
Solanaceae	*Lycium hirsutum*	P	ST	0.278		0.549		0.000	
Convolvulaceae	*Convolvulus ocellatus*	P	SS	0.241		0.088		0.398	
Fabaceae	*Acacia* sp.	P	T	0.230		0.333		0.124	
Asteraceae	*Pentzia calcarea*	P	SS	0.202		0.154		0.251	
Solanaceae	*Solanum capense*	P	SS	0.178		0.252		0.103	
Poaceae	Grass shoots	U	U	0.178		0.074		0.284	
Scrophulariaceae	*Peliostomum leucorrhizum*	P	H	0.174		0.070		0.282	
Iridaceae	*Moraea pallida*	P	G	0.170		0.184		0.156	
Asteraceae	*Helichrysum argyrosphaerum*	A	H	0.167		0.196		0.138	
Asteraceae	*Dicoma macrocephala*	P	H	0.155		0.148		0.162	
Poaceae	*Pogonarthria squarrosa*	P	GT	0.155		0.297		0.009	
Campanulaceae	*Wahlenbergia nodosa*	P	SS	0.147		0.116		0.179	
Asphodelaceae	*Trachyandra* sp.	P	G	0.140		0.180		0.100	
Poaceae	*Oropetium capense*	P	GS	0.121		0.055		0.189	
Poaceae	Grass sp. 1	U	U	0.117		0.042		0.194	
Eriospermaceae	*Eriospermum* sp. 1	P	G	0.117		0.124		0.109	
Euphorbiaceae	*Euphorbia inaequilatera*	A	H	0.111		0.041		0.183	
Ebenaceae	*Diospyros lycioides*	P	ST	0.104		0.000		0.210	
Unidentified	*Cryptogamic soil*	U	U	0.097		0.000		0.196	
Hyacinthaceae	*Ledebouria leptophylla*	P	G	0.071		0.059		0.083	
Boranginaceae	*Heliotropium ciliatum*	P	H	0.068		0.117		0.017	
Asteraceae	*Felicia muricata*	P	SS	0.067		0.088		0.044	
Commelinaceae	*Commelina africana*	A	H	0.057		0.015		0.101	
Poaceae	Dead grass	U	U	0.045		0.089		0.000	
Poaceae	Grass sp. 2	U	U	0.045		0.000		0.091	
Eriospermaceae	*Eriospermum* sp. 2	P	G	0.034		0.019		0.049	
Asteraceae	*Senecio consanguineus*	A	H	0.033		0.040		0.025	
Unidentified	Algae	U	U	0.027		0.000		0.054	
Asteraceae	*Felicia* sp.	U	SS	0.025		0.000		0.051	
Cyperaceae	*Fuirena* sp.	U	S	0.021		0.030		0.012	
Solanaceae	*Datura stramonium*	A	ST	0.019		0.038		0.000	
Iridaceae	*Syringodea* sp.	P	G	0.018		0.020		0.017	
Hyacinthaceae	*Schizocarphus nervosus*	P	GS	0.016		0.019		0.013	
Anacardiaceae	*Searsia* sp.	P	T	0.016		0.032		0.000	
Fabaceae	*Acacia tortilis*	P	T	0.016		0.031		0.000	
Oxalidaceae	*Oxalis semiloba*	A	H	0.015		0.029		0.000	
Hyacinthaceae	*Dipcadi glaucum*	P	G	0.013		0.000		0.027	
Poaceae	*Tragus racemosus*	A	GS	0.013		0.000		0.026	
Capparaceae	*Cleome gynandra*	A	H	0.012		0.024		0.000	

Table 4.3 continued

Family	Species	Plant type	Growth form	Total (RCI)	Rank	Site E (RCI)	Rank	Site W (RCI)	Rank
Sterculiaceae	*Hermannia coccocarpa*	A	H	0.012		0.005		0.019	
Pedaliaceae	*Harpagophytum procumbens*	P	H	0.011		0.012		0.011	
Scrophulariaceae	*Chaenostoma caeruleum*	A	H	0.010		0.020		0.000	
Unidentified	Moss	U	U	0.010		0.000		0.020	
Hyacinthaceae	*Dipcadi gracillimum*	P	G	0.008		0.005		0.011	
Anacardiaceae	*Searsia pyroides*	P	T	0.005		0.010		0.000	
Sterculiaceae	*Hermannia* sp.	U	H	0.005		0.010		0.000	
Cyperaceae	*Kyllinga alba*	P	S	0.005		0.000		0.010	
Lamiaceae	*Acrotome inflata*	A	H	0.004		0.008		0.000	
Unidentified	Herb sp. 1	U	H	0.004		0.008		0.000	
Fabaceae	*Rhynchosia confusa*	P	H	0.004		0.008		0.000	
Amaranthaceae	*Sericorema remotiflora*	P	H	0.004		0.008		0.000	
Asteraceae	*Gazania krebsiana*	A	H	0.004		0.000		0.008	
Brassicaceae	*Heliophila affinis*	A	H	0.004		0.008		0.000	
Fabaceae	*Indigofera* sp.	U	H	0.003		0.000		0.007	
Gentianaceae	*Sebaea exigua*	A	H	0.003		0.000		0.007	
Amaryllidaceae	*Boophone disticha*	P	G	0.003		0.006		0.000	
Hyacinthaceae	*Dipcadi* sp.	P	G	0.003		0.000		0.006	
Lamiaceae	*Stachys burchelliana*	A	H	0.003		0.006		0.000	
Fabaceae	*Rhynchosia minima*	P	H	0.003		0.006		0.000	
Amaranthaceae	*Hermbstaedtia fleckii*	A	H	0.003		0.000		0.006	
Brassicaceae	*Heliophila* sp.	U	H	0.003		0.005		0.000	
Iridaceae	*Hibiscus marlothianus*	P	H	0.002		0.000		0.005	
Sterculiaceae	*Babiana hypogaea*	P	G	x		0.000		x	
Fabaceae	*Hermannia erodioides*	P	H	x		0.000		x	
Anacardiaceae	*Melolobium* sp.	P	SS	x		0.000		x	
Malvaceae	*Searsia lancea*	P	T	x		x		0.000	

Vegetation composition was dominated by a few species that provided the bulk of the cover, for example, the cover of six, five and seven species, respectively, provided more than 50% cover for the site overall, site E and site W. The number of species that contributed more than 90% cover was 24 for the site overall, and 21 for each of sites E and W (Fig. 4.4).
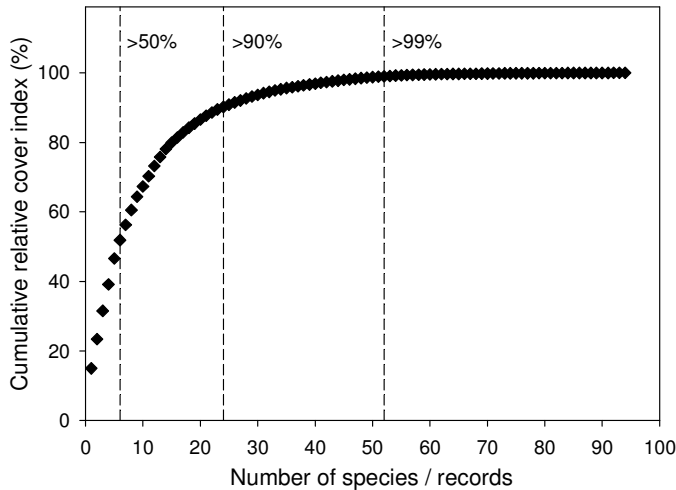
Figure 4.4 Cumulative percent cover for plant taxa at Benfontein farm. Vertical lines indicate the number of taxa that provided more than a specified percentage cover.

4.3.4.2 Site differences in species abundance

The grass species *Schmidtia pappophoroides*, *Stipagrostis uniplumis* and *Eragrostis lehmanniana* were more abundant in site E than in site W ($T_{444,457} \geq 123537$, $P < 0.0001$), whereas *Cymbopogon pospischilii*, *Stipagrostis obtusa*, and grazed grass were more abundant in site W than in site E ($T_{444,457} \geq 213350$, $P < 0.0001$; Table 4.3). Shrub species more abundant in site W than site E included *Pentzia incana*, *Eriocephalus ericoides*, *Amphiglossa triflora*, *Plinthus karooicus*, *Gnidia polycephala*, *Rosenia humilis* and *Lycium cinereum* ($T_{444,457} \geq 219517$, $P < 0.0001$; Table 4.3). *Chrysocoma ciliata*, a shrub, as well as 2 herbs, *Selago paniculata* and *Wahlenbergia androsacea*, had a higher abundance in site E than they had in site W ($T_{444,457} \geq 143760$, $P < 0.0001$; Table 4.3).

4.3.4.3 Seasonal effects on species abundance

Data on species abundance (RCI) for April, May and August 2006 were available only for vegetation plots, thus sample size ($n = 10$) was low for these months. Nevertheless, the RCIs of plant species differed within each monthly data set (all FRMAs, $\chi^2 \geq 93.279$, df ≥ 93, $P < 0.0001$; Table 4.4). There were no post-hoc differences in the RCIs of plants within April and August 2006 but in May, one species, the grass *Eragrostis lehmanniana*, had a higher RCI than other plants had. From September 2006 onwards, sample sizes for monthly records were larger ($n \geq 57$) because I recorded RCIs of plants at tortoise relocation sites. Plant items that had higher RCIs than others within that month were assigned a rank. The number of plant items that were ranked

(including ties) for the months September 2006 to April 2007 were 7, 18, 9, 7, 9, 15 and 17, respectively (Table 4.4).

Six plant species that were ranked highest for the study sites combined (Table 4.3) were ranked within each month from September 2006 to April 2007 (Table 4.4). These plants included two grasses, *Schmidtia pappophoroides* and *Stipagrostis uniplumis*; three shrubs, *Chrysocoma ciliata*, *Pentzia incana* and *Eriocephalus ericoides*; and one herb species, *Hermannia tomentosa*. *Schmidtia pappophoroides* was the most abundant plant species in October, December, March and April 2007 whereas *Stipagrostis uniplumis* was the most abundant plant species in September and January; the two species tied the top rank in February (Table 4.4).

Table 4.4 Seasonal changes in the presence/absence of plant items, the monthly rank of the plant and the mean RCI of the two sites. A plant received a rank when the SNK post hoc tests of a Friedman's repeated measures ANOVA showed that the plant's RCI was significantly greater than that of the other items within the same month. Data for April to August 2006 were derived from vegetation plots only (all $n = 10$), whereas data from September 2006 onwards included tortoise relocation data (all $n \geq 57$). An 'x' indicates that the plant was present, but not ranked, whereas a blank indicates that the plant was not recorded. Plant items in the table are arranged according to overall rank (first 23, see Table 4.3).

Species	Apr 06	May 06	Aug 06	Sep 06	Oct 06	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07	Total RCI
Schmidtia pappophoroides	x	x	x	2	1	1	2	1	1	1	10.545
Stipagrostis uniplumis	x	x	x	1	2	3	1	1	2	2	5.764
Chrysocoma ciliata	x	x	x	3	3	2	3	3	4	10	5.924
Hermannia tomentosa	x	x	x	x	4	4	4	3	2	5	5.240
Pentzia incana	x	x	x	4	5	5	5	3	6	2	5.355
Eriocephalus ericoides	x	x	x	7	8	7	7	6	12	11	3.102
Stipagrostis obtusa		x	x	x	7	x	x	x	9	4	3.011
Amphiglossa triflora	x	x	x	x	10	8	6	8	7	12	2.695
Selago paniculata	x	x	x		18	6	x	7	5	8	3.742
Plinthus karooicus	x	x	x	x	14	x	x	x	8	7	2.051
Eragrostis lehmanniana	x	1	x	x	17	x	x	x	11	6	2.077
Gnidia polycephala	x	x	x	x	11	x	x	x	10	14	1.851
Hermannia comosa	x	x	x	x	11	x	x	x	15	15	1.290
Rosenia humilis				6	8	9	x	x	x	x	2.089

Table 4.4 continued

Species	Apr 06	May 06	Aug 06	Sep 06	Oct 06	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07	Total RCI
Wahlenbergia androsacea				x	6	x	x	x			1.622
Senna italica	x				x	x	x	x	13	x	0.804
Melolobium macrocalyx				x	x		x	x	13	16	0.792
Cymbopogon pospischilii	x	x	x	x	15	x	x	x		x	0.916
Seedlings	x	x	x	5	13	x			x	x	1.051
Eragrostis trichophora		x							x	9	0.854
Grazed grass				x	16	x	x`	x	x	x	1.038
Lycium cinereum				x	x	x	x	x	x	x	0.660
Solanum incanum	x	x	x		x	x	x	x	x		0.496
Deverra denudata					x	x	x	x	x	x	0.627
Acacia erioloba				x	x	x		x	x	x	0.466
Aristida diffusa	x	x	x				x	x	x	x	0.439
Zaluzianskya violacea		x	x	x	x	x	x	x			0.418
Ifloga sp.			x	x	x		x				0.391
Limeum sulcatum									x	13	0.375
Aristida adscensionis	x	x	x	x	x	x			x	17	0.353
Nemesia fructicans				x	x	x					0.341
Themeda triandra	x	x	x	x	x	x		9	x	x	0.285
Lycium hirsutum				x	x	x	x		x	x	0.278
Convolvulus ocellatus					x	x	x	x	x	x	0.241
Acacia sp.		x	x		x	x	x	x	x	x	0.230
Pentzia calcarea	x	x	x						x	x	0.202
Grass shoots									x	x	0.178
Solanum capense	x								x	x	0.178
Peliostomum leucorrhizum				x	x	x			x	x	0.174
Moraea pallida				x	x			x			0.170
Helichrysum argyrosphaerum				x	x	x	x		x	x	0.167
Dicoma macrocephala	x	x	x						x	x	0.155
Pogonarthria squarrosa	x	x	x						x	x	0.155
Wahlenbergia nodosa							x		x	x	0.147
Trachyandra sp.									x	x	0.140
Oropetium capense									x	x	0.121
Eriospermum sp. 1			x							x	0.117
Grass sp. 1					x		x		x	x	0.117
Euphorbia inaequilatera	x				x				x	x	0.111
Diospyros lycioides	x	x	x	x	x	x	x		x	x	0.104

Table 4.4 continued

Species	Apr 06	May 06	Aug 06	Sep 06	Oct 06	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07	Total RCI
Cryptogamic soil					x	x	x	x	x	x	0.097
Ledebouria leptophylla									x	x	0.071
Heliotropium ciliatum									x	x	0.068
Felicia muricata				x	x				x	x	0.067
Commelina africana									x	x	0.057
Dead grass								x	x		0.045
Grass sp. 2					x		x		x		0.045
Eriospermum sp. 2		x								x	0.034
Senecio consanguineus				x						x	0.033
Algae										x	0.027
Felicia sp.									x	x	0.025
Fuirena sp.	x	x	x								0.021
Datura stramonium									x		0.019
Syringodea sp.				x							0.018
Acacia tortilis	x			x						x	0.016
Searsia sp.								x			0.016
Schizocarphus nervosus								x	x		0.016
Oxalis semiloba										x	0.015
Dipcadi glaucum									x	x	0.013
Tragus racemosus	x								x		0.013
Cleome gynandra										x	0.012
Hermannia coccocarpa									x	x	0.012
Harpagophytum procumbens									x	x	0.011
Moss										x	0.010
Chaenostoma caeruleum									x		0.010
Dipcadi gracillimum										x	0.008
Hermannia sp.		x	x								0.005
Kyllinga alba									x		0.005
Searsia pyroides									x		0.005
Acrotome inflata	x										0.004
Gazania krebsiana				x							0.004
Heliophila affinis									x		0.004
Herb sp. 1	x										0.004
Rhynchosia confusa						x					0.004
Sericorema remotiflora									x	x	0.004
Boophone disticha									x		0.003

Table 4.4 continued

Species	Apr 06	May 06	Aug 06	Sep 06	Oct 06	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07	Total RCI
Dipcadi sp.	x		x								0.003
Heliophila sp.									x		0.003
Hermbstaedtia fleckii										x	0.003
Indigofera sp.			x								0.003
Rhynchosia minima										x	0.003
Sebaea exigua		x	x								0.003
Stachys burchelliana				x							0.003
Hibiscus marlothianus	x										0.002
Babiana hypogaea				x							x
Hermannia erodioides				x							x
Melolobium sp.			x								x
Searsia lancea		x									x

Because the data did not satisfy the requirements for parametric tests, I could not simultaneously test all plant items for seasonal effects. Multiple tests on the full data set were not feasible, thus I selected the 10 most abundant species at each site (see Table 4.3) to test if their RCIs changed with month.

There were significant differences amongst months for all ten species in site E (all KWAs, $H_9 \geq 20.99$, $P \leq 0.012$), but only six were significant at a post hoc level. Of the grasses, *Schmidtia pappophoroides* was more abundant in May than it was in September or April 2007 whereas *Stipagrostis uniplumis* was more abundant in January (mid summer) than it was in May. The cover for *Eragrostis lehmanniana* was higher in May, August, and April 2006 and 2007 than it was in January or February 2007 (mid summer months). Additionally, May cover exceeded the cover in October, December and March, while cover in August was higher than that in October and December. The cover of two perennial herbs in site E changed with season. *Hermannia tomentosa* was more abundant in October, February and March than it was in September whereas The RCI of *Selago paniculata* was higher from December to April 2007 than it was in September. The annual herb *Wahlenbergia androsacea* had a greater abundance in October than it had in all other months except September and its abundance in September and December were higher than it was in March and April 2007.

In site W, month had no effect on the RCI of *Pentzia incana* but the effect was significant for nine of the top ten plant species (all KWAs, $H_9 \geq 20.99$, $P \leq 0.013$); only three species had significant differences at a post hoc level. *Amphiglossa triflora* was more abundant in January than September; *Chrysocoma ciliata* was more abundant in December and January than it was in April 2007, while *Eriocephalus ericoides* was more abundant in December than September.

4.3.4.4 Species richness and diversity

I recorded 91 different angiosperms (excluding seedlings, grass shoots, grazed grass and dead grass), as well as moss, algae and cryptogamic soils at the study site. Site E had 79 angiosperms and no other group, whereas site W had 73 angiosperms as well as moss, algae and cryptogamic soils. For calculations of species richness and diversity, I did not include moss, algae and cryptogamic soils with the angiosperms. There was little difference in species richness between site E and site W and this did not change after allowing for sample size differences (Margalef's index; Table 4.5). There was no difference between sites in Shannon-Weiner diversity indices ($P > 0.12$) but there were differences between sites in Simpson's diversity indices, which was greater in site W than in site E ($t_{10284} = 4.32$, $P < 0.001$; Table 4.5).

Table 4.5 Diversity indices for combined sites ($n = 901$), site E ($n = 457$) and site W ($n = 444$) derived from angiosperm species counts in vegetation plots and at tortoise relocation sites.

Index	Total	Site E	Site W
Species richness	91	79	73
Margalef's index (*d*)	9.733	9.153	8.388
Shannon-Wiener (*H*)	3.401	3.293	3.325
Simpson's (*D*')	0.953	0.945	0.951
Evenness (*J*)	0.754	0.754	0.775

Species richness and adjusted species richness (Margalef's index) were high at both sites in September–October 2006, and March–April 2007 (Fig. 4.5A, B). Similarly, both the Shannon-Wiener indices (*H*') and Simpson indices (*D*') in combined sites were high in August–September 2006 and March–April 2007, higher than in July, and December–February ($t \geq 3.45$, $v \geq 811$, $P < 0.001$ and $t \geq 3.16$, $n \geq 1269$, $P < 0.0016$ for *H*' and *D*' respectively; Fig. 4.5C, D). In sites E and W, the peak month for *H*' indices was April 2007 when it was higher than all other months (all *t* tests, $t \geq 3.31$, $v \geq 81$, $P < 0.001$).

D' indices were also highest in both sites in April 2007; they were higher than they were in May, July and October-February ($t \geq 4.467$, $n \geq 1146$, $P < 0.001$). Additionally, *D'* indices in April 2007 were higher than August and September in site W, and March in site E ($t \geq 3.68$, $n \geq 1359$, $P < 0.001$). Diversity indices were lowest in May in both sites, *H'* and *D'* indices being lower in May than they were in August-October and in March and April 2007 (all *t* tests, $t \geq 4.29$, $v \geq 651$, $P < 0.001$ and $t \geq 3.7$, $n \geq 721$, $P < 0.001$ for *H'* and *D'* respectively). Within site W, *H'* indices were also lower in May than they were in April 2006 and January (all *t* tests, $t \geq 2.81$, $v \geq 188$, $P < 0.0025$) and *D'* indices were lower in May than in January ($t_{745} = 3.16$, $P \leq 0.0016$ and $t \geq 3.16$, $n \geq 721$, $P \leq 0.0016$). In site E, May's *D'* indices were also lower than they were in July and February (all *t* tests, $t \geq 3.35$, $n \geq 655$, $P < 0.001$). Evenness in both sites decreased markedly from April to May 2006, but increased again in winter, with low values subsequently recorded in October and March (Fig. 4.5E).
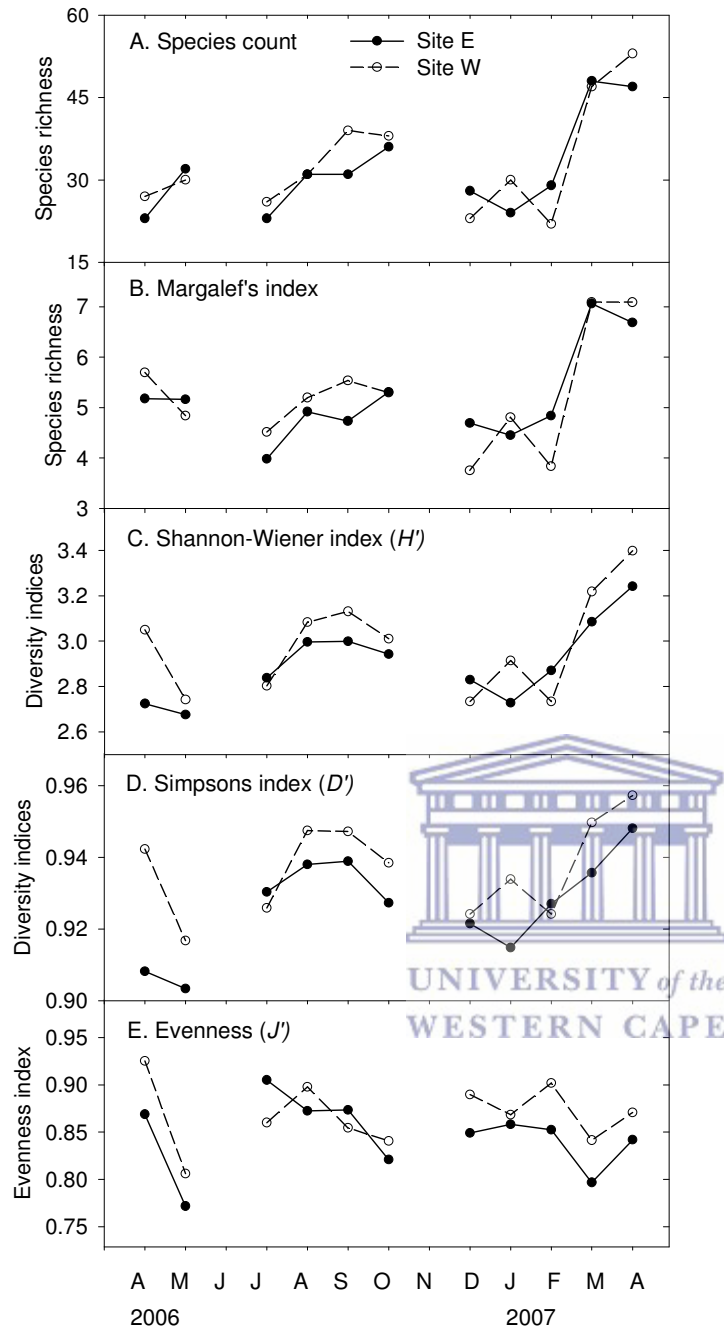
Figure 4.5 Seasonal changes in species richness and diversity at sites E and W on Benfontein farm. No data were collected in June 2006 and data of the first and last days of November were added to October and December, respectively.

4.3.4.5 The effects of rainfall on species richness and diversity

Species richness and adjusted species richness were positively influenced by rainfall in sites E, W and the two sites combined ($F_{1,9} \geq 6.25$, $P \leq 0.034$, $r^2 \geq 0.41$). Regressions between the Shannon entropy (H') and rainfall were also significant in site W ($F_{1,9} = 10.53$, $P = 0.01$, $r^2 = 0.54$) and the two sites combined ($F_{1,9} = 7.25$, $P = 0.025$, $r^2 = 0.45$) but not in site E ($P > 0.16$). Rainfall did not significantly affect species evenness (J') in

either site or the sites combined ($P > 0.23$). Rainfall also had no effect on the Simpson's entropy (D') in site E or the two sites combined ($P > 0.28$) but it did effect D' in site W ($F_{1,9} = 7.16$, $P = 0.025$, $r^2 = 0.44$). Species richness, adjusted species richness and diversity indices were not affected by rainfall that fell the previous month ($P > 0.26$).

4.3.5 Growth forms

4.3.5.1 Growth form abundance

The major growth forms did not have an equal distribution in the habitat overall (FRMA, $\chi^2_6 = 4333$, $P < 0.0001$; Table 4.6). Grass was the most abundant growth form, followed by shrubs, herbs and other. The RCIs of trees and geophytes did not differ, and both RCIs were higher than the RCI of sedges. Growth forms within site E were also unevenly distributed ($\chi^2_6 = 2171$, $P < 0.0001$; Table 4.6). The RCI of grass was highest, while the cover of shrubs and herbs did not differ but exceeded the RCIs of the remaining growth forms. All other growth forms differed significantly in the sequence: trees, other, geophytes and sedges. Within site W, growth form distributions differed ($\chi^2_6 = 2292$, $P < 0.0001$; Table 4.6). In this instance, shrubs were the dominant growth form, followed by grasses, herbs, other and geophytes; there was no difference in the cover of trees and sedges. Within major growth forms in site E, W and combined sites, short grass was most abundant of the grass subcategories, followed by tall and unknown grasses ($\chi^2_2 > 259$, $P < 0.0001$), while short shrubs had a higher abundance than tall shrubs ($t > 32$, df = 456, 443 and 900, respectively, $P < 0.0001$; Table 4.6).

4.3.5.2 Site and seasonal effects on growth forms

There were no RCIs collected in June or July 2006 and growth form data for April, May and August 2006 were derived from vegetation plots only; hence sample size was small ($n = 10$) in these months. Statistical results (after applying a sequential Bonferroni adjustment) for differences in growth form RCIs between sites were not affected after adjusting RCIs for differences in total cover within sites.

Both site and month influenced grass abundance, and the two factors interacted (site: $F_{1,881} = 85.52$; month: $F_{9,881} = 12.19$; interaction: $F_{9,881} = 6.40$; all $P < 0.0001$; Table 4.6; Fig 4.6A). In all months but September and February, grass was more abundant in site E than it was in site W (Fig. 4.6A). Grass abundance in April and May 2006 was greater than in all other months, and grass RCI in April 2007 exceeded that of September, December and February. The same pattern was apparent in site E, but

here grass abundance in April 2007 also exceeded that of October, January and March. There were no differences amongst months within site W (Fig. 4.6A).

Table 4.6 Mean (±SD) relative cover indices of plant growth forms for both sites combined (*n* = 901), and sites E (*n* = 457) and W (*n* = 444), respectively. Number superscripts denote growth form rankings (with ties) based on the results of KW one-way ANOVAs (*P* < 0.00001) and Dunn's post hoc tests (*P* < 0.05), hence in some instances a growth form maybe ranked higher than another growth form within a site, despite having a lower mean RCI, e.g., grass was ranked higher than shrubs in combined sites. Ranked growth forms, within the two sites and Total, were more abundant than all other forms below them (except 'other' in the 'total' column where it was higher than sedges only).

Growth Form	Total	Site E	Site W	Difference
Grasses, all	25.95^1 ± 9.99	29.67^1 ± 10.36	22.13^2 ± 7.96	E > W#
Grasses, short	16.62 ± 9.95	21.33 ± 9.01	11.77 ± 8.43	E > W*
Grasses, tall	7.91 ± 5.33	7.87 ± 5.30	7.95 ± 5.36	E = W
Grasses, unknown	1.42 ± 3.70	0.46 ± 2.25	2.41 ± 4.55	W > E*
Shrubs, all	27.08^2 ± 12.21	20.49^2 ± 10.75	33.85^1 ± 9.66	W > E#
Shrubs, short	25.55 ± 12.15	18.60 ± 10.01	32.71 ± 9.77	W > E*
Shrubs, tall	1.52 ± 3.57	1.89 ± 4.22	1.14 ± 2.69	E = W
Herbs	14.93^3 ± 10.78	20.56^2 ± 10.05	9.13^3 ± 8.11	E > W*
Trees	0.73^5 ± 2.57	1.30^4 ± 3.33	0.15 ± 1.14	E > W*
Geophytes	0.59^5 ± 1.91	0.62^6 ± 1.90	0.57^5 ± 1.93	E = W
Sedges	0.03^7 ± 0.39	0.03^7 ± 0.48	0.02^6 ± 0.27	E = W
Other	1.18^4 ± 3.15	1.52^5 ± 3.66	0.84^4 ± 2.48	E = W

Determined by two-way ANOVA

* Determined by *t*-test or Mann Whitney rank sum test and sequential Bonferroni procedure

Short grass comprised 72% and 53% of the total grass cover in sites E and W, respectively, and its RCI in all months was greater in site E than in site W ($F_{1,881}$ = 160, *P* < 0.0001). The RCIs of short grasses differed amongst months ($F_{9,881}$ = 19; *P* < 0.0001) and the interaction between month and site was significant ($F_{9,881}$ = 2.42, *P* = 0.01). Cover in May was higher than in all other months but April 2006 (site E and overall), whereas cover in April 2006 was higher than all months but August (site E and overall) and April 2007. Overall, the RCI of short grass in April 2007 was higher than all remaining months but August. February values in site E were lower than in August,

October, March and April 2007. In site W, short grass had higher cover in May and April 2007 than in December to March.
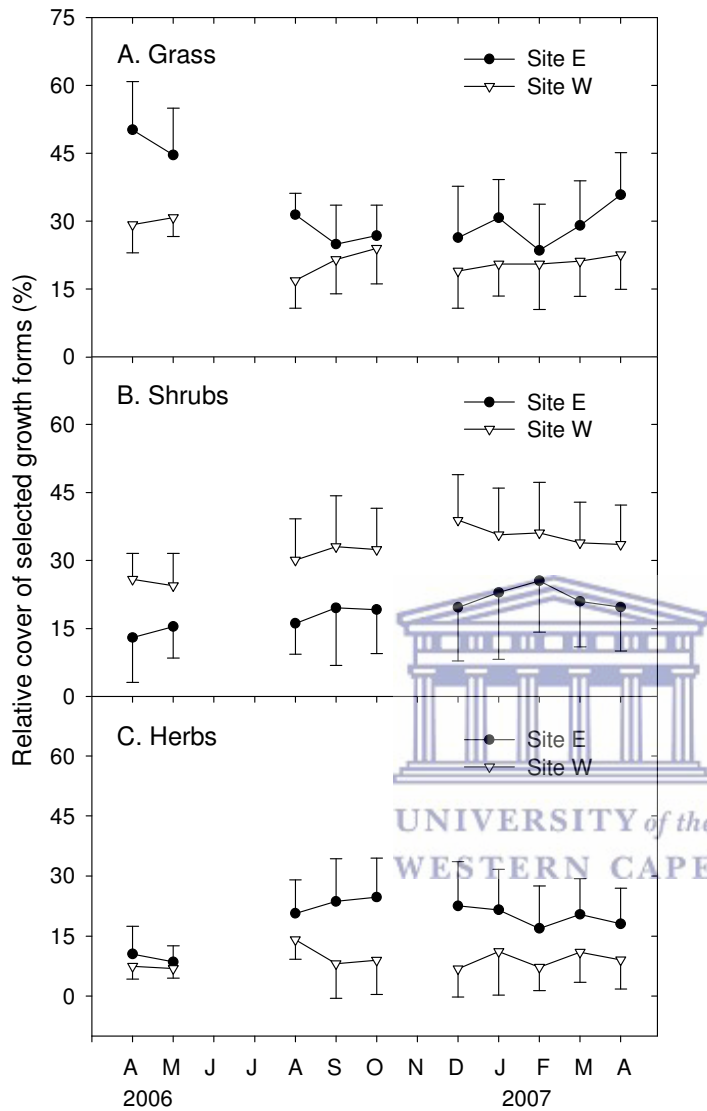
Figure 4.6 Monthly RCIs (mean ±SD) for shrubs (A), grasses (B) and herbs (C) in sites E and W. April, March and August 2006 data were derived from vegetation plots only, thus sample sizes were low (*n* = 10). From September 2006 onwards, plot data were combined with tortoise relocation data (*n* ≥ 59). No data were collected in June and July while small datasets collected at the beginning and end of November were added to October and December data, respectively.

Tall grass made up 36% of the grass cover in site W compared to 27% in site E but the overall difference between sites was not significant (*P* = 0.9; Table 4.6). Nevertheless, tall grass was more abundant in site E, than in site W in April 2007 ($T_{105,107}$ = 9226, *P* < 0.0001). Tall grass RCIs differed amongst months within sites E and W (H_9 ≥ 25, *P* <

0.003) but the post hoc tests were not significant and there was no difference amongst months when the two sites were combined (after using a sequential Bonferroni adjustment, P = 0.01 > 0.0007 = adjusted α). The RCI for unknown grass was greater in site W than in site E (overall: $T_{457,444}$ = 220,578; October: $T_{94,116}$ = 8275; March: $T_{61,99}$ = 5991; all P < 0.0001). The abundance of unknown grasses changed seasonally in site W and the two sites combined (H_9 ≥ 34.76, P < 0.0001), but there were no differences at a post hoc level. Month did not affect unknown grass abundance within site E (P > 0.10).

Shrubs were more abundant in site W than in site E ($F_{1,881}$ = 113.4, P < 0.0001; Table 4.6). The RCI in February was higher than in April 2006 and May ($F_{9,881}$ = 3.66, P = 0.00016; Fig. 4.6B), with no interaction between site and month. Short shrubs comprised 97% of the shrub cover in site W compared to 91% in site E and the difference between sites was significant ($F_{1,881}$ = 123.8, P < 0.0001). Their abundance was higher in February than in April 2006 ($F_{9,881}$ = 3.08, P = 0.0012) with no interaction between site and month. The abundance of tall shrubs did not differ between sites (P > 0.19, Table 4.6), but differed among months for site E (H_9 = 29.27, P = 0.00058) although there were no differences at the post hoc level. There was no difference amongst months in site W after the application of a sequential Bonferroni (P = 0.007 > 0.0007 = adjusted α).

Herb RCIs differed between sites ($F_{1,881}$ = 78.6, P < 0.0001), site E having higher herb RCIs than site W and there was a significant interaction between month and site ($F_{9,881}$ = 3.63, P = 0.00019) with higher herb abundance in site E than in site W in all months but April to August (Fig. 4.6C). The RCI of herbs differed amongst months ($F_{9,881}$ = 4.08, P < 0.0001) with significant post hoc differences only in site E; October had a higher herb cover than April and May 2006, and February to April 2007. Additionally, cover in December and January was higher than in May.

The RCI of geophytes did not differ between sites (Table 4.6), within months or overall (t tests and MW rank sum tests, df ≥ 8, P ≥ 0.40). Geophyte abundance in combined sites was highly seasonal (H_9 = 101.57, P < 0.0001); RCIs were highest in August (2.7±2.3) and April 2007 (1.3 ± 2.6), but were sparse in October (0.33±1.34), and were not encountered during December and January. Differences amongst months within sites E (H_9 = 54.63, P < 0.0001) and site W (H_9 = 57.88, P < 0.0001) were not significant at a post hoc level.

Trees were more abundant in site E than in site W overall ($T_{457,444}$ = 183,799, P < 0.0001; Table 4.6), but not in particular months. Tree RCIs for combined sites appeared to differ seasonally (H_9 = 24.45, P = 0.0036; adjusted P = 0.0038), but it was not significant at a post hoc level. There were no differences in the monthly RCIs of trees, within sites E or W.

There was no difference between sites in sedge abundance (MW rank sum tests, df ≥ 8, P ≥ 0.69) but sedge RCIs differed among months (all H_9 ≥ 89.60, P < 0.0001), with no post hoc differences for site E, site W or combined sites. The category 'other' (89% of which were unidentified seedlings) was more abundant in site E than in site W during September ($T_{19,38}$ = 719.5, P < 0.0044) and October ($T_{94,116}$ = 11661, P < 0.0001) but not within the remaining months or overall (after application of a sequential Bonferroni, P = 0.004 > 0.0006 = adjusted α; Table 4.6). In combined sites, the category 'Other' was affected by month (H_9 = 219.8, P < 0.0001) and had a greater RCI in August to October (late winter/spring), than in December to April 2007, i.e., the summer and autumn. 'Other' plant forms also differed amongst months within site E (H_9 = 197.6, P < 0.0001), with higher cover in August to October than in February, and site W (H_9 = 63.19, P < 0.0001), with no significant differences at a post hoc level.

4.3.5.3 The effect of monthly rainfall on growth forms

Of all growth form categories and sub-categories, only tall shrubs in site W had a significant relationship with monthly rainfall ($F_{1,9}$ = 7.76, P = 0.024, r^2 = 0.49), any significant effects of rainfall on other growth forms being after a one month delay. Grass abundance was significantly related to rainfall in sites E and W and the sites combined ($F_{1,9}$ ≥ 6.44, P < 0.04, r^2 ≥ 0.45). Furthermore, RCIs of short grass in site E and combined sites were positively influence by rainfall as was short grass in site W, but not significantly (P = 0.052). However, unknown grass in site W decreased with rainfall ($F_{1,9}$ ≥ 5.51, P < 0.047, r^2 ≥ 0.41) and there was no significant relationship between rainfall and tall grass (P > 0.12). In combined sites, there was a significant regression between sedge abundance and rainfall ($F_{1,9}$ = 6.03, P = 0.04, r^2 = 0.43) and sedges positively correlated with rainfall in site E (r_s = 0.62, P = 0.048) but not in site W (P > 0.49). The only major growth form category negatively related to rainfall was herbs. Herb RCIs decreased with rainfall in sites E, W and the sites combined ($F_{1,9}$ ≥ 5.7, P < 0.044, r^2 ≥ 0.42). Regressions between combined and short shrub RCIs and rainfall were not significant (P > 0.10), nor were they significant with RCIs of geophytes or trees (P > 0.54).

4.3.6 Vegetation types

4.3.6.1 Vegetation type abundance and site differences

The RCI for perennials overall was 63.9% (Table 4.7), which translates to 90% of the total plant cover. The perennial RCI was 66.4% in site E and 61.3% in site W (Table 4.7), equating to 88% and 92% of the plant cover in sites E and W, respectively. There were spatial differences in plant type cover: annuals and perennials had higher RCIs in site E than in site W ($T_{444,457}$ = 173683 and 160789, respectively, $P < 0.0001$), and 'unknown' types had a higher RCI in site W than in site E ($T_{444,457}$ = 215932, $P < 0.0001$). After adjusting for differences in total cover of the two sites, the proportion of annuals to total cover was still higher in site E than in site W ($T_{444,457}$ = 174588, $P < 0.0001$) and unknown types remained higher in site W ($T_{444,457}$ = 217039, $P < 0.0001$) but there was no difference in perennial cover of the two sites (P = 0.27).

Table 4.7 Total RCIs (mean ±SD) in sites E and W for annuals, perennials and "unknown" plants/ground cover. The "unknown" category included plants not identified to the species level that also included algae, mosses and cryptogamic soil.

Plant type	Total	Site E	Site W
Annual	3.9 ± 6.5	5.8 ± 7.8	2.1 ± 4.1
Perennial	63.9 ± 10.9	66.4 ± 12.9	61.3 ± 7.6
Unknown	2.7 ± 4.8	2.0 ± 4.3	3.3 ± 5.2

4.3.6.2 Vegetation type abundance and seasonal differences

Vegetation type data for April, May and August 2006 were derived from vegetation plots only; hence sample sizes were small in these months (n = 10). Abundance (RCIs) of annuals in combined sites varied amongst months (H_9 = 193.6, $P < 0.0001$). Abundance of annual plants in August was greater than most months, with the exception of September, October and April 2006. The RCIs in April 2006, September, October and April 2007 were greater than they were in February and March 2007, with December also being higher than February. Within site E there was also an effect of month on the abundance of annuals (H_9 = 243.4, $P < 0.0001$, Fig. 4.7A). The RCI from August to October (median ≥ 12.8, 25th ≥ 8.6 75th ≥ 17.1) was greater than it was in February and March (median, 25th, 75th = 0.0). September annual abundance in site E was also higher than May and December 2006, and January and April 2007 (median ≤ 2.3, 25th = 0.0 75th ≤ 7.4; Fig. 4.7A). The seasonal effect on annuals was weaker in site W although there were differences (H_9 = 75.7, $P < 0.0001$). The RCI in August (median = 8.8, 6.6-12.3) and April 2006 (median = 6.0, 3.9-6.6) was greater than it was in

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December and February (median = 0.0, 25th = 0.0 75th = 0.0), with August also being greater than March 2007 (median = 0.0, 0.0-0.0; Fig. 4.7A). Within months, annuals were significantly more abundant in site E than they were in site W during September-December (MW rank sum tests, $T_{19,38} \geq 845.5$, $P < 0.0001$; Fig. 4.7A).
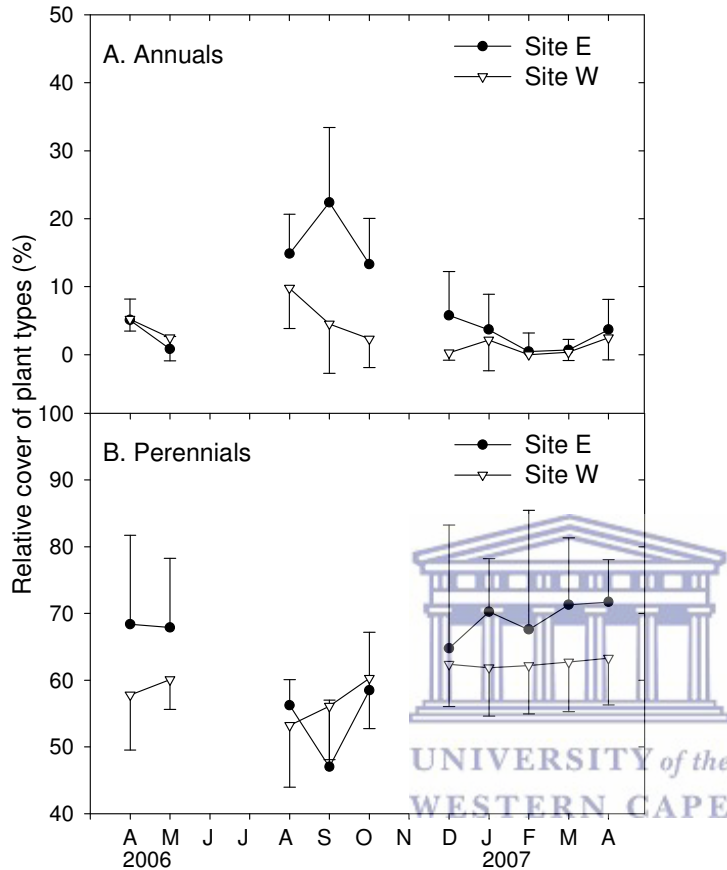
Figure 4.7 Monthly plant type RCIs (mean ±SD) for annuals (A) and perennials (B) for site E and site W. April, March and August 2006 data were derived from vegetation plots only, thus sample sizes were low (*n* = 10). From September 2006 onwards, plot data were combined with tortoise relocation data (*n* ≥ 59). No data were collected in June and July, and the small datasets collected at the beginning and end of November were added to October and December data, respectively.

The relative cover of perennials in combined sites varied amongst months (H_9 = 186.5, $P < 0.0001$), it was greater in December and February to April 2007 than it was in August to October 2006. Although January and December medians (65.0 and 65.3 respectively) were similar, the difference between January ranks and the ranks of all other months were not sufficient for differences to be significant. There were differences in perennial cover within site E (H_9 = 155.2, $P < 0.0001$), it was higher in December to April 2007 than it was in September, and higher in March 2007 than it

was in August and October (Fig. 4.7B). There were differences in perennial cover amongst months within site W (H_9 = 35.4, P < 0.0001) but not at a post hoc level. Within months, perennial RCIs were greater in site W than in site E in September ($T_{19,38}$ ≥ 346.5, P < 0.0001; Fig. 4.7B), but were greater in site E than in site W from December to April 2007 (all t tests and MW rank sum tests, df ≥ 57, P ≤ 0.003). Although December means were similar between sites, the median in site E (69.3, 63.3-75.0) was greater than it was in site W (64.3, 60.0-68.8).

In combined sites, the monthly pattern indicated seasonal changes in the abundance of "unknown" plants (H_9 = 143.05, P < 0.0001), which was higher in August to October than in April 2007, December and March. Monthly differences in unknown plants within site E (H_9 = 135.51, P < 0.0001) and site W (H_9 = 42.9, P < 0.0001) were not significant at a post hoc level. Within March 2007, "unknown" plants were more abundant in site W than in site E, after adjusting for differences in the total cover of each site ($T_{61,99}$ = 5992, P < 0.0001).

4.3.6.3 The effect of monthly rainfall on plant types

The previous month's rainfall negatively influenced unknown plant type abundance (of which 55% was grazed or dead grass; $F_{1,8}$ = 8.37, P < 0.04, r^2 = 0.51). Monthly rainfall did not affect any other plant types in sites E and W or the sites combined (P > 0.13).

4.4   DISCUSSION

4.4.1 *Climate and soil*

Temperature and rainfall are the main drivers of ecosystems within the range of *Psammobates oculifer* (Noy-Meir, 1973; Veenendaal et al., 1996; Scholes et al., 2002; Ringrose et al., 2003). With an annual rainfall of less than 500 mm, Benfontein is a semi-arid area. At 68%, rainfall predictability for Benfontein falls within the range experienced by other arid-zone, southern African testudinids (Hofmeyr et al., 2005). In this study, the majority of rainfall occurred during the late summer and autumn months, typical of the area, but the summer was drier than the long-term average, which may have had a corresponding effect on plant growth.

Although water may be the limiting factor for plant growth in arid and semi-arid savannas, nutrients become relevant in periods when sufficient soil water is available (Scholes, 1990). Dystrophic, dry, southern African savannas can be characterised as areas that are predominately sandy with a kaolonitic or quartzitic base that are low in

organic carbon (0.2 – 1%) and base cations (< 20 cmol (+)/kg; Scholes, 1990). Soil was only sampled once in this study which may affect the veracity of the results (Hartemink, 2006), but study area soil fertility was low, comprising a mean 96% sand with 0.21% organic carbon and base cations of 0.9 (cmol (+)/Kg). Similarly, Hutton and Clovelly soil forms in the Kalahari are also known to be infertile (van Rooyen, 1984) and mean organic carbon along the top soil of the Kalahari transect is 0.26% (Ringrose et al., 1998). Apart from general soil infertility in the study area, there was a large difference between variances of phosphate (P) concentration between sites. The difference in standard deviations of P concentrations was largely due a plot in site W where the concentration was six times that of the mean P concentrations of other plots. I checked this plot result with the laboratory (Bemlab) who confirmed that the P concentration for this plot was correct. It is possible that a dead animal or rotting plant matter in the plot contributed to the high phosphate levels there (see Bridges, 1997).

The study area's soil properties were broadly similar to those published for similar soils within southern Africa. The study area soil texture (96.26±0.85 sand) corresponds with other southern African arenosols (91%±8% sand) and the cation exchange capacity (CEC) of 4.27±0.53 is within those expected for the area (3±2; Hartemink & Huting, 2008). Study site soil pH (5.67 ± 0.33) was close to the 5.1 to 6.1 range recorded for four Kalahari sand sites in Botswana (Aranibar et al., 2004), which may be comparable to Benfontein as soil physical properties in Kalahari sands are similar over a wide area (Wang et al., 2007).

Soil profile and depth are important determinants of plant community structure within the southern Kalahari and the environs of Kimberley. Trees are found in areas of deeper sand (root space) while shrubs are able to colonise limestone outcrops where their roots can penetrate between rocks (Leistner, 1967; Bezuidenhout, 1994). The grass *Schmidtia pappophoroides* is also associated with sites on deep, red sand (Leistner, 1967; Bezuidenhout, 1994). Certainly, site W was stonier than site E. Shrubs, particularly *Pentzia incana* were dominant in the latter area, while in site E, where it was loose sand with few stones, trees (particularly *A. erioloba*) and *S. pappophoroides* were more abundant. Although I did not test soil depth, the occurrence of large (some in excess of 5 m high) *A. erioloba* indicate that soil was deep in site E. Soil depth and substrate appear to be important factors determining plant community structure in the study area.

As well as affecting angiosperm communities, soil structure may affect other communities such as cryptogams (see Thomas & Dougill, 2006 and references therein). Presence of cryptogams were recorded in site W but not in site E. Thomas & Dougill (2006) suggest that large-grained Kalahari sand (which is loose and easily disturbed) inhibits cryptogam crust formation compared with more consolidated soils in, inter alia, calcrete areas. This appeared to be true in this study, with cryptogams only being noticed in the area with greater surface calcrete, site W. Soil in site W also appeared to be more 'compact' than it was in site E (T Keswick, personal observation) although I did not measure sand grain size in the two sites to confirm this. Cryptogams can be important as a component of a tortoises' diet (Henen, 2002b) but I did not witness cryptogam consumption by *P. oculifer*.

4.4.2 *Vegetation cover and composition*

Vegetation cover between the two sites differed, 76% versus 66% for sites E and W respectively. There was no visible difference in topography between sites E and W, suggesting edaphic or anthropogenic-related (e.g., grazing) factors were influencing inter-site vegetation differences. Cattle grazed on both sites during the study period but separate stocking records for sites E and W were not available to evaluate differences in grazing intensity between sites. The stonier substrate at site W may account for some of the differences in vegetation cover; thinner soil making it harder for vegetation to colonise.

The digital map of South African bioregions has fine scale resolution, 100 m or less, depending on available data (Mucina et al., 2006a). When I overlaid a digital map of the study area on this digital map, the study area is located within the Kimberley Thornveld (SVk4) vegetation unit, although small patches of Northern Upper Karoo (NKu3) and High Veld Saltpan (AZi10) are located 2 to 3 kilometres from the study area. I observed fine scale differences in species abundance patterns and vegetation structure between sites E and W, but neither sites' species composition was typical of SVk4. In fact, the eight species in site W and E that corresponded with SVk4 taxa provided a RCI of only 4.4% and 6.1%, respectively.

Asteraceae, Poaceae and Fabaceae were the most commonly represented families in the study area, which is typical of arid and semi-arid ecosystems (Mucina et al., 2006b). Dominant (ranked) species in site W that are listed as important taxa in the NKu3 (Mucina et al., 2006b) included eight shrubs (*Pentzia incana*, *Eriocephalus ericoides*, *Amphiglossa triflora*, *Chrysocoma ciliata*, *Plinthus karooicus*, *Rosenia*

humilis, *Gnidia polycephala*, and *Lycium cinereum*), two grasses (*Stipagrostis obtusa* and *Eragrostis lehmanniana*) and one herb (*Hermannia comosa*). In addition, eight unranked species in site W (four grasses, two shrubs, one herb and one geophyte) corresponded with the taxa that characterize NKu3. The mean RCI in site W was 67%, of which 38% consisted of plants listed as important taxa in NKu3 (Mucina et al., 2006b). This suggests that site W might be classified as NKu3, although some important taxa in site W (e.g., *Pentzia incana*, *Eriocephalus ericoides*, *Amphiglossa triflora*, *Stipagrostis obtusa*, *Plinthus karooicus* and *Rosenia humilis*) are not listed as typical NKu3 taxa.

Vegetation composition in site E showed some correspondence to NKu3 (17 taxa with a RCI of 25.7%), but important taxa of site E are not listed as NKu3 species (Mucina et al., 2006b). Site E was largely dominated by the grass *Schmidtia pappophoroides* (RCI = 14.7%), and the vegetation at site E appears to be more similar to the vegetation community *Schmidtia pappophoroides – Themeda triandra* at Vaalbos National Park and Rooipoort Nature Reserve (RNR; Bezuidenhout, 1994; Bezuidenhout, 2009), and the community *Schmidtia pappophoroides – Acacia erioloba* at RNR (Bezuidenhout, 1994; Bezuidenhout, 2009). Vaalbos and RNR are approximately 60 km north and west, respectively, from the study site. Site E taxa that corresponded with the RNR communities *S. pappophoroides – T. triandra* and *S. pappophoroides – A. erioloba,* had a RCI of 42.3% and 40.9%, respectively. Ranked taxa at site E that occurred in both communities included *S. pappophoroides*, *C. ciliata*, *Stipagrostis uniplumis*, *Hermannia tomentosa*, *E. lehmanniana*, *Senna italica* and *G. polycephala*. In addition, the taxon *H. comosa* occurred in the *S. pappophoroides – T. triandra* community. An important difference between site E and the *S. pappophoroides – T. triandra* community at RNR is that the latter community has a poorly developed shrub cover of only 1%. In contrast, the *S. pappophoroides – A. erioloba* community at RNR has a shrub cover of 13%, which corresponds better to the shrub cover of 20.5% at site E. Site E is thus best characterised by the *S. pappophoroides – A. erioloba* community, as described at RNR.

4.4.3 Vegetation structure

Vegetation height structure was similar in both sites; it was predominantly 10-60 cm, followed by categories less than 10 cm, 61-100 cm and over 100 cm respectively. Site similarities in vegetation height structure belie the difference in vegetation form composition within the two sites. Whereas in site W, vegetation 10-60 cm was dominated by short shrubs (e.g., *Pentzia incana* and *Eriocephalus ericoides*) with some

short grasses (e.g., *S. pappophoroides* and *Stipagrostis obtusa*), vegetation at site E consisted mainly of short grass (particularly *S. pappophoroides*), herbs (e.g., *Selago paniculata*) and small shrubs (particularly *C. ciliata*).

In the vegetation cover < 10 cm category, the most abundant species was *Hermannia tomentosa*, a common creeping herb (ranked 5 in both sites). Vegetation cover < 10 cm was greater in site E than site W, partially due to the abundance of the small annual *Wahlenbergia androsacea*. Unfortunately, no RCIs were recorded before September (when annuals were common; T Keswick, personal observation) making it difficult to quantify remaining site differences in this height category. Tall grass constituted a large proportion of vegetation cover between 61 and 100 cm high in both sites, of which *Stipagrostis uniplumis* was the largest contributor, as well as *Cymbopogon pospischilii* in site W. Vegetation taller than 100 cm consisted of mainly trees (*A. erioloba*) in site E and tall shrubs (e.g., *Diospyros* lycioides) in site W. There was no difference in this category between site (probably due to low sample size), but trees were more common in site E than in site W.
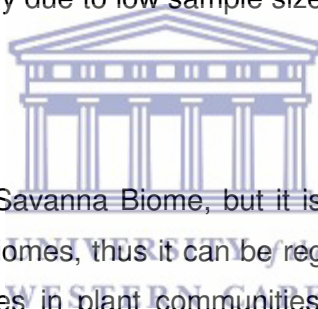
4.4.4 Habitat heterogeneity

The Kimberley area is in the Savanna Biome, but it is close to the confluence of the Nama Karoo and Grassland biomes, thus it can be regarded an ecotone, which partly explains small-scale differences in plant communities at the study area. However, what both the Nama Karoo and Savanna share is a tendency to have low plant species diversity, at least at the beta or gamma scale, when compared to other southern African biomes (Bezuidenhout, 2009). In the case of the Nama Karoo, this may be a function of lack of environmental and geological variation (Mucina et al., 2006b). Equally, the red sands of the Kalahari are relatively homogeneous (Wang et al., 2007), thus a lack of niche separation may result in limited species diversity there (Skarpe, 1986). Scholes (1997) also suggests that, despite having low beta and gamma diversity, alpha diversity in Savanna is not dissimilar to that of any other southern African biome, although there is no reference to particular Savanna types, e.g., semi-arid savannas, when diversity is discussed.

The average number of species per vegetation plot over the study period was 10.2 (±1.85 SD) per 25 m^2, or 41 species per 0.01 ha. The total number of species was 63 in the combined plots (250 m^2), which equates to 25 species per 0.01 ha, and is comparable to the southern Kalahari, where van Rooyen & van Rooyen (1998) used data from Leistner & Werger (1973) and calculated species richness of twelve plant

communities which ranged from 23 to 32 species per 0.01 ha. There was little difference in species richness or adjusted species richness between sites. Both sites had several dominant plant species, with *S. pappophoroides* having a particularly high RCI in site E. After converting Simpson's dominance index to the effective number of species, according to Jost (2006), site E and W respectively, had 18 and 20 equally common species, representing 23% and 27% of the sites' species richness. This difference in species diversity between sites appears minor, despite statistical tests showing that Simpson's indices differed significantly between sites. Conversion of Shannon-Wiener indices (Jost, 2006) to effective number of species for site E and W, provided values of 27 and 28 equally common species, respectively. It thus seems clear that diversity at the two sites was quite similar. Van Rooyen and van Rooyen (1998) calculated *H'* value for plant communities in the southern Kalahari ranging from 0.36-1.48 on clay soils, and 2.59-3.04 on red sand, which equate to ranges of 1-5 equally common species on clay, and 13–21 equally common species on sand, according to Jost (2006). Common species in sites E and W in this study (both on red sand) are higher than the latter range, perhaps because sampling in this study was done over a number of seasons.

Apart from ecotonal effects, grazing had visibly affected vegetation cover in the study site. An area of approximately 200 m radius surrounding a watering point (WP; Fig. 2.1) was trampled by cattle creating something similar to 'piospheres' described for other arid or semi-arid areas (Jeltsch et al., 1997; Todd, 2006). An estimate of 7.8 – 10 ha/LSU (large stocking unit) was given for stocking rates at Benfontein in the vicinity of this study area (Seymour, 2008). Recommended stocking rates for Kalahari Sandveld are 6 to 7 large animal units per 100 ha, which equates to about to 14.3 to 16.6 ha/LSU (Bothma, 2002), i.e., Benfontein stocking levels exceed those recommended. As historic stocking rates were not available, I could not fully evaluate grazing impact on cover although grass species can act as an indicator of veld condition. The most abundant grass, *Schmidtia pappophoroides* is considered a decreaser grass on red sand (Bancroft et al., 1998) as is *Stipagrostis obtusa* in general (van Oudtshoorn, 2004), suggesting that overgrazing at Benfontein has not reached critical levels. However, several increaser grass species have high ranks, e.g., *Stipagrostis uniplumis* (2nd), *Eragrostis lehmanniana* (11th) and *Cymbopogon pospischilii* (18th), indicating some level of overgrazing (van Oudtshoorn, 2004). This impression is supported by the abundance of *Chrysocoma ciliata* (3rd) and *Pentzia incana* (5th), which are regarded as invader species (Roux & Vorster, 1983; Rutherford & Westfall, 1986; Acocks, 1988) that increase under high grazing pressure. Nevertheless, assessing the effect of

livestock grazing is difficult without allowing for fluxes in rainfall patterns (O'Connor & Roux, 1995; Bancroft et al., 1998).

4.4.5   Seasonal effects

The timing and quantity of rainfall is an important influence on seasonal plant growth in arid or semi-arid areas (Leistner & Werger, 1973; Noy-Meir, 1973; Veenendaal et al., 1996; Ringrose et al., 2003). In this study, vegetation with height 61 to 100 cm, as well as six growth form categories or subcategories (mainly grass) and two plant types correlated to rainfall or rainfall one month earlier, at the study area either overall or within a site. Despite the influence of rainfall on vegetation abundance at Benfontein, there was no effect of rainfall at the broad level of vegetation cover or vegetation between 10 and 60 cm, the most abundant height category. Total cover and cover between 10 and 60 cm were mainly perennials, consisting of shrubs, grasses and herbs, all of which may react to rainfall or utilise water differently and such reactions may be habitat dependent. For instance, in the semi-arid Nama Karoo, shrub growth (in response to rain) is less pronounced than that of grasses (Vorster & Roux, 1983), but in Botswana's Kalahari Transect, both grass and woody cover correlated to rainfall whereas forbs (herbs) did not (Ringrose et al., 2003).

Within vegetation cover between 10 and 60 cm high, short grass correlated with rainfall, but with a one-month lag. The most abundant, perennial short grass taxa were *S. pappophoroides*, *S. obtusa* and *E. lehmanniana*. Rainfall in March and April 2006 was 72.5 and 60 mm respectively (SAWS and this study). The sample size for the first two months of the study period was low (thus variance was high) because the data were generated from plots only. Despite this, the most abundant species (grass or otherwise) in May 2006 was *E. lehmanniana*, it was the only species to be ranked (no species was ranked in April). The peak abundance for *E. lehmanniana* was also the peak for short grass which then died back from September to February, a period which included the drier than average summer. Short grass RCIs increased again in March and April 2007 in response to an increase in rainfall. The increase in short grass in autumn 2007 coincided with an increase in the abundance of *E. lehmanniana* from February, when it was unranked, to being ranked 11th in March and 6th in April 2007 after 64 mm of March rain. *Eragrostis lehmanniana* is known for growing quickly in response to rain (Fourie & Roberts, 1977; O'Connor & Roux, 1995) and can become very abundant (Roux & Vorster, 1983). This suggests that it is an important contributor to increases in short grass abundance after rain at Benfontein. The only other common short grass (ranked 7th overall) whose abundance related to rainfall was *Stipagrostis*

obtusa, a perennial. *Stipagrostis obtusa* was first ranked in October (7th), coinciding with the first spring rains, but remained 'dormant' (unranked) through summer until, following rain in March and April 2007, it was ranked 9th and 4th respectively. Basal cover of *Stipagrostis obtusa* strongly correlated to annual rainfall ($r^2 = 0.90$) in the south-western Kalahari (van Rooyen & van Rooyen, 1998).

Unlike short grass, short shrubs did not correlate with rainfall. Short shrub cover tends to fluctuate less over the year than grass cover (Vorster & Roux, 1983), which was the case at Benfontein. O'Connor and Roux (1995), in their 23-year study in the Karoo, found no significant correlation within years between rainfall means and the corresponding basal cover mean of the short shrubs *P. incana*, *C. ciliata*, *R. humilis* and *E. ericoides*. This indicates that either these small shrubs appear to react slowly to rainfall, or their growth is harder to detect over a short period (see Hoffman et al., 1990). Three of these species were also the most abundant short shrubs in the Benfontein study area.

Contrary to short shrubs, tall (more than 60 cm) shrub cover correlated with rainfall in site W. The most prevalent tall shrub in site W was *Deverra denudata*, which despite being categorised as a perennial (Germishuizen & Meyer, 2003), behaved more like a weak annual, appearing quickly with rain in October, having previously gone unnoticed despite its size (T Keswick, personal observation). One vegetation plot in site W contained another tall shrub *Diospyros lycioides*, which had sparse foliage from May through August, the dry period, but regained its foliage from October onwards. The RCI of these two species, and their combined RCI correlated with rainfall ($r_s = 0.77$, $P = 0.009$ for combined) and they comprised 82% of the tall shrub mean RCI in site W, which partially explains why tall shrub abundance in site W correlated with rainfall.

The tall shrub, *Deverra denudata* may have also been a factor in vegetation cover 61 to 100 cm high correlating with rainfall in site E. This vegetation height category was dominated by tall grass, of which the most abundant species was *Stipagrostis uniplumis*, but tall grass cover did not correlate with rainfall. Lack of a relationship between rainfall and tall grass abundance may be due to phenology or sampling. The RCIs of both *Stipagrostis uniplumis* and the less abundant *Themeda triandra* were highest in mid summer (flowering time), i.e., their abundance was not attributable to recent rainfall. *Themeda triandra* may be able to endure without water – it is drought tolerant and less sensitive to rainfall than *E. lehmanniana* (Fourie & Roberts, 1977). *Stipagrostis uniplumis* was frequently used as a refuge by *P. oculifer* during hot

summer months (Chapter 5) which may have confounded its seasonal abundance patterns. However, other tall grasses such *Pogonarthria squarrosa* and *Aristida adscensionis* tended to be abundant after rain, and together with the apparent rain related abundance of *Deverra denudata*, may have contributed to vegetation 61 to 100 cm correlating with rainfall in site E.

Seasonal variability in the lowest vegetation height category (less than 10 cm) was largely linked to annuals. Although annual abundance did not correlate to rainfall, the sudden 'burst' of annuals from August to October, in both sites, suggests that their arrival was in response to late winter and spring rainfall. Rainfall was over 30 mm (long term SAWS mean = 8 mm) and over 47 mm (long term SAWS mean = 32 mm) for August and October, respectively, compared with a combined total of 12 mm for June and July. Annuals respond quickly to rainfall and when temperatures are seasonally low, evaporation is reduced and available soil moisture increases (Noy-Meir, 1973). *Wahlenbergia androsacea*, *Zaluzianskya violacea*, *Ifloga* sp. and *Nemesia fructicans* were the most abundant low-growing (< 10 cm) spring annuals at Benfontein. All of these annuals' abundance peaked between August and October. In combined sites, annuals contributed 17% to the RCI in August (the month of their greatest abundance) compared to 0.004% in February (the hottest month). Rainfall and reduced temperatures in autumn (April 2006 and 2007) may also favour annual growth and yet there was little increase in annual abundance during these months. Generally, seedlings of different species may have different responses to seasonal rain (van Rooyen & van Rooyen, 1998) and it is possible that Benfontein is an area where annual seedlings tend to respond to spring rainfall. Late summer and autumn are also times of seasonal perennial grass growth and competition (e.g., for light and space) from grass may hinder the growth of annuals at this time.

Seventeen out of 21 annuals recorded were herbs, and they contributed considerably to herb cover in spring, but the greatest contributor to herb cover was the perennial creeper, *Hermannia tomentosa* (fourth most abundant species overall). It was most abundant in February and March, but was generally abundant through all seasons and in both sites. This species is known to have a long taproot, and can access water in deep soils (Leistner, 1967), which may contribute to its temporal and spatial ubiquity here. Despite the aseasonal abundance of *H. tomentosa*, herbs were negatively correlated to rainfall. This is difficult to explain given the wide variety of herbs; both annual and perennial with diverse growth strategies (see Leistner, 1967 for example). A possible reason is that, as with shrubs, herb abundance tended to be lower when

grass abundance was high. Grasses increase quickly after rain and may 'out-compete' herbs for space and light. Thus, just as grass RCIs correlate positively with rainfall, herbs abundance may shrink accordingly.

The RCIs of the three relatively rare growth forms, trees, geophytes and sedges, differed amongst months, but only geophyte differences were evident at a post hoc level. Geophytes followed a similar seasonal pattern to annuals; their RCIs peaked in late winter/spring, with a second growth period in April 2007. Geophytes often bloom before or at the onset of seasonal rain (Lovegrove, 1993) as they did at Benfontein. Although sedges in site W correlated to rainfall with a one-month lag, the sample size was small and the trend was, perhaps, coincidental.

As well as vegetation categories, seasonal plant diversity also correlated to rainfall. Species richness and adjusted species richness positively correlated to rainfall in both sites and the sites combined. This stems from increases in ephemerals and geophytes related to spring and autumn rainfall. Shannon-Weiner (H') and Simpson's (D') indices both correlated to rainfall in site W but not in site E. During January, 27 mm rain fell at the study site and there was a small increase in grass in site E, while there was an increase in herbs in site W, mostly due to an increase in annuals. This appears to be one of the differences in seasonal diversity between the two sites. Annuals responded quickly to rainfall in the site of lower vegetation cover (W) while in site E, grass is abundant and quicker to react to rainfall, limiting opportunities for the establishment of annuals. This pattern is most succinct in January, when high temperatures limit soil moisture availability. Although site E had a greater abundance of annuals, one species, *Wahlenbergia androsacea*, dominated, comprising nearly 50% of the mean RCI of annual plants. The abundance of annual species in site W was more equitable (*Ifloga* sp. was the most abundant annual, 13% of the RCI) and they tended to 'pulse' in response to rainfall, which may further explain differences in seasonal diversity patterns between sites. Species evenness did not correlate with rainfall (in either site or the sites combined) despite a general trend for it to decline with increases in species richness.

4.4.6   Kalahari tent tortoise

Although vegetation plots were monitored seasonally, most vegetation data were collected when radio-tracking tortoises, which can create sampling bias due to tortoise habitat preference. As with all ectotherms, tortoise activity is lowest during colder months, July in particular in this study (Chapters 6 & 7). Thus, vegetation cover data

from July is probably the least reliable, particularly because no plot data/vegetation RCIs were recorded to supplement data gained from tortoise tracking. Equally, seasonal differences in vegetation more than 100 cm in height may reflect tortoises using vegetation, e.g., trees as shade when it was hot. Midday heat also restricts daily tortoise activity, although not to the same extent as cold in winter (Chapter 6). Plant availability versus plant use and seasonal changes in use, specifically as refuges, are the subject of Chapter 5.

A mitigating factor for seasonal bias in vegetation sampling (using tracked tortoises) is that the tortoises' inactivity (low coverage) coincided with seasons when soil moisture availability for plants was limited. Winter is the dry season and high midsummer temperatures (Fig. 4.1) increase evaporation of soil moisture. This restricts growth in many forms of herbaceous plants and negatively affects species richness/diversity (this study). Thus spring and autumn at Benfontein, when tortoises were most active (Chapter 6), coincided with periods of greatest activity in herbaceous plant growth, particularly grasses, annuals and geophytes. In addition, tortoises' largest home ranges were in spring and autumn 2007 (Chapter 7), thus sampling in these months was widespread.
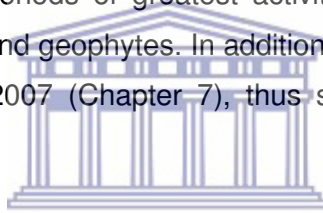
Other than data collected to evaluate tortoise refuge use (Chapter 5), information gathered on other aspects of tortoise-vegetation dynamics, such as feeding ecology, was limited. I did keep records of food plants where possible, but records were few due to the tortoises' being shy and difficult to observe while feeding (Chapter 6). Kalahari tent tortoises consumed annuals, particularly the annual *Wahlenbergia androsacea* (common in spring; T Keswick, unpublished data), which were most abundant in site E. Furthermore, I saw tortoises feeding on the grasses *Eragrostis lehmanniana* and *Schmidtia pappophoroides*, both more abundant in site E than they were in site W. This apparent abundance of food plant species in site E was perhaps reflected in tortoise body condition there; it was higher in site E than it was in site W (Chapter 3). Another possible effect of vegetation on tortoise body condition is the influence of vegetation cover and the prevalence of plant refuge species on the tortoises' thermal environment. Vegetation cover was lower in site W than it was in site E and there were fewer preferred plant refuge species in site W (it was predominantly shrubby). This may account for higher tortoise body temperatures, due to greater exposure, in this site (Chapter 6). A higher body temperature would be detrimental to tortoises if it increased their metabolism and/or promoted water loss, thereby depleting body condition (see Chapter 3). *Psammobates oculifer* is predominantly a savanna species (Branch 1988

and see Chapter 8) and hence site E is probably more typical of its habitat than is the shrubby site W. Possible overgrazing of the study area (discussed in section 4.4.4) may have contributed to increases in shrubby species, e.g. *Chrysocoma ciliata*, as well as certain grasses such as *Schmidtia pappophoroides* (see Acocks 1988). Tortoises feed on and hide in *S. pappophoroides*, but an invasion of Karoid shrubs linked to overgrazing may negatively influence the conservation of *P. oculifer*; specifically if such invasion reduces the abundance of food or refuge plants in an area.

4.5   CONCLUSIONS

Benfontein habitat is semi-arid; rainfall is less than 500 mm per annum. Rain fell in spring (October) but the highest rainfall recorded during the study period was late summer/autumn. The study area was split into site W, the stonier site and site E which was sandier and this may account for some of the differences in species abundance and vegetation structure between them. Site E was dominated by short grass, particularly *Schmidtia pappophoroides* coupled with intermittent *Acacia erioloba* and was similar to the *Schmidtia pappophoroides - Acacia erioloba* community at the Rooiport Nature Reserve but not SvK4 (Kimberley Thornveld). In site W, where it was stonier, short shrubs such as *Pentzia incana* were abundant and the site was broadly similar to Northern Upper Karoo vegetation (NKu3). The study area had similar species richness, but higher numbers of common species than the southern Kalahari Savanna. A major driver of seasonal flux in the study area was rainfall. Grass abundance correlated with rainfall but shrubs were less mutable, either because they react slower to rainfall than grasses, or because their growth is not perceptible over short periods. Although abundance of annuals did not correlate with rainfall, it was likely that their appearance was rain related, the biggest annual pulse coming in spring after the first rains. Possible bias in seasonal sampling caused by lack of tortoise movement in winter was perhaps mitigated by winter being a period of limited plant growth. Although not substantiated, increases in Karoid shrubs, perhaps linked to overgrazing, may negatively impact tortoises through a reduction in preferred food and refuge cover, and a consequential loss in body condition.

5   HABITAT UTILISATION

5.1   INTRODUCTION

Habitats can be described in terms of discrete categories such as marsh and heath, or continuous categories such as shrub density or percentage cover, and may be used on their own or in tandem (Manly et al., 2002). In ectotherms, a key criterion in habitat choice is that it affords strict control of thermoregulation, without which an individual cannot fulfil basic life requirements such as movement or feeding (Bogert, 1949; Grant & Dunham, 1988; Dunham et al., 1989; Huey, 1991). Use of microhabitats, such as rock clefts or burrows, plays an important role in ectotherm thermoregulation (Stevenson, 1985; Grant & Dunham, 1988). However, there may be trade-offs between a microhabitat's use for thermoregulatory purposes and its ability to help fulfil other life requirements, e.g., predator avoidance (Downes & Shine, 1998). Thermoregulatory requirements of individuals can vary both inter- and intra-specifically, which may lead to differences in microhabitat use by a group, e.g., females versus males (Singh et al., 2002).

As with other ectotherms, testudinid habitats must have adequate food, water (Nagy & Medica, 1986; Henen, 1997; Duda et al., 1999), and cover for shade or predation (Bourn & Coe, 1978; Coe et al., 1979; Luiselli, 2005), as well as suitable nesting sites for females (Auffenberg & Weaver Jr, 1969). Testudinid habitat assessments are often done at a species rather than a sex level (Coe et al., 1979; Barret, 1990; Longepierre et al., 2001; McCoy et al. 2006; Stevenson et al., 2007). Even studies that do compare sexes either find no difference between them (Wright et al., 1988; Kazmaier et al., 2001c) or when a difference is found, the reason for the difference is unclear (Gibson & Hamilton, 1983; Anadón et al., 2006).

A common feature of arid or semi-arid habitats is friable soil, which facilitates burrow excavation, a behaviour seen in the North American testudinids of the genus, *Gopherus* (Woodbury & Hardy, 1948; Auffenberg & Weaver Jr, 1969; Douglass & Layne, 1978). Woodbury and Hardy's (1948) study of *Gopherus agassizii* in south-west Utah reported seasonal temperature ranges between -9 °C and 52 °C. Exposure to such extreme temperatures over much of its range causes *G. agassizii* to construct burrows to avoid extreme heat in summer and to brumate (Nagy & Medica, 1986; Bailey et al., 1995; Nussear et al., 2007). However, burrow construction is not essential for arid zone tortoises. Burrowing behaviour is a common adaptive trait in arid zone

fauna (Noy-Meir, 1974; Lovegrove, 1993; Kinlaw, 1999) and a tortoise may be able to utilise burrows of other species; the small tortoise *Testudo kleinmanni* was observed aestivating in rodent burrows in the Negev Desert (Geffen & Mendelssohn, 1989). Tortoise use of microhabitats is not restricted to burrows. *Stigmochelys pardalis*, a much larger tortoise than *T. kleinmanni* and the largest of the southern African tortoises, uses a variety of shrubs and trees as refuges in the Northern Cape, South Africa (McMaster and Downs 2006a). Proportions of plant refuge species used by *S. pardalis* in this study changed seasonally and they occasionally used aardvark (*Orycteropus afer*) burrows, but burrow use was not seasonal (McMaster and Downs 2006a). *Stigmochelys pardalis* in the Free State, South Africa showed clear partitioning of both seasonal and diurnal/nocturnal plant refuge use (Douglas & Rall, 2006). In the same study, *S. pardalis* switched from less dense to more dense plant shelters in summer when diurnal temperatures increased. Douglas and Rall (2006) also noted that tortoises did not use dense refuges during winter, suggesting that these tortoises are more tolerant of cold (up to -11.7 °C) than they are of high temperatures. The choice of low-density refuges in winter (and the resulting exposure) ultimately may be a trade-off between exposure and maximisation of basking time.

There is little information about habitat use of the southern African testudinid genus *Psammobates* and much of it relates to diet. *Psammobates geometricus* is endemic to Renosterveld and Alluvial fynbos vegetation in the Western Cape, South Africa and its habitat fidelity is possibly a function of a specialised diet (Baard, 1995a). *Psammobates oculifer* is known to be a specialist herbivore, although it can broaden its diet when food becomes scarce (Rall & Fairall, 1993). In southern Namibia during summer, *Psammobates tentorius verroxii* used mainly trees and shrubs as refuges, while grass was rarely used, and burrows were not used. Grass was an important habitat component of *P. t. verroxii*, however, as it comprised half the diet of four telemetered females (Cunningham & Simang, 2009).

The purpose of this study was to evaluate habitat use of *P. oculifer* and more specifically, its use of microhabitats (refuges). I assessed the effect of seasonal weather patterns on habitat and/or microhabitat use, e.g., to see if an increase in seasonal diurnal temperatures would cause a switch from using plant refuges to burrows. I also investigated the effect of sexual dimorphism on type and structure of habitats used. For example, the small male may be prompted to use denser refuges

than females do for added concealment/protection. Additionally, I comment on the seasonal effect on the structure of plant refuges.

5.2 MATERIALS AND METHODS

5.2.1 Habitat and refuge data

I used habitat data of 27 telemetered tortoises (591 records from 12 males and 500 records from 15 females) to assess if males and females select similar habitat qualities within each site. The data assessed included substrate quality, total vegetation cover, and the percent plant cover by height category and growth form. Details of the study design, and the methods to record habitat characteristics, can be found, respectively, in Chapter 2, section 2.1.1, and Chapter 4, section 4.2.2 of this thesis.

Refuge data were collected from the 27 radio-tracked tortoises and from five opportunistic captures (see Chapter 2, sections 2.1 to 2.2 for general methods). *Psammobates oculifer* took refuge under vegetation or in burrows constructed by other animals. I identified the dominant plant species (section 4.2.2) of each refuge and used a tape measure to record the width and height of burrow openings and refuge plants. I also estimated plant refuge density based on the percentage of the tortoise visible from above. Refuge density was given a rank of one when more than 75% of the tortoise's body was visible, a rank of two indicated that 50-75% of the body was visible, a rank of three related to 25-50% visibility, a rank of four was given when only 5-25% of the tortoise was visible, whereas a rank of five indicated that the body was fully covered and that the refuge plant was very dense.

5.2.2 Data and statistical analyses

Before analysing refuge data, I combined March 2006 data with that of April because records for March were sparse (three records in site E and 11 records in site W). Similarly, records for the first and last few days in November 2006 were combined with October and December data, respectively. To avoid pseudoreplication in tortoise refuges (and habitat sites), I used data from only the first record when the same tortoise was found in the same refuge consecutively. When tortoises were found mating or in mating related behaviour (see Table 6.1), I noted the refuge data in context of the female only, thus as one record. Within all plant refuge and availability analyses, I combined the categories Grazed and Dead grass (see Table 4.3 for species lists) as Unknown grass, because the two categories had similar refuge characteristics. Dead grass referred to dry grass that lay flat whereas grazed grass was cropped and

broken. For analyses involving the refuge density of individual plant species/items, I used only 14 of the 23 species/items listed in combined sites. The remaining nine items were excluded because each species/item was recorded less than five times and none occurred more than twice in any one month.

When analysing ratio or interval scale data, I first tested if the data were parametric, before or after transformation, in order to use multifactor ANOVAs (*F* statistic), followed by Student-Newman-Keuls (SNK) post hoc tests, to compare monthly, inter-site and inter-sex means. When data did not satisfy the requirements of normality or equal variance, I used Kruskal-Wallis ANOVAs (KW ANOVA; *H* statistic), followed by Dunn's post hoc comparisons, to evaluate differences in sample medians amongst months, and I used Mann-Whitney tests (MW; *T* statistic) or Student's *t* tests (*t* statistic) for inter-site and inter-sex comparisons. This procedure was followed to: (a) assess if male and female habitats at the two sites differ in substrate, total plant cover, cover by the respective height categories, and composition of growth forms, and (b) evaluate the effects of site, sex and month on refuge width, height and density. Prior to analysing monthly refuge width, height and density data, I compared each monthly pattern graphically and where monthly patterns were similar, I combined sex and/or site data for subsequent analyses. Within each site, I ranked: (a) the percentage cover height categories and (b) growth form abundances (RCIs) in male and female habitats using Friedman's repeated measures ANOVA (FRMA, χ^2 tests), followed by SNK post hoc tests.

Analyses of the effect of site, sex and month on proportional burrow use (versus plant use) were done using chi-square tests (χ^2), or Fisher's exact tests where frequencies were low, with a Yates correction for continuity where the degrees of freedom equalled one. I also used chi-square tests to test for the effect of sex and/or site on the use of individual growth forms, and plant refuge species/items, and to analyse the effect of month on the use of growth form refuges. To do this I used multiple tests to contrast the frequency of each single species or growth form category with the sum of all remaining frequencies. When analysing growth forms amongst months, I used the subcategories short and tall grass and short shrubs only as they comprised more than 90% of the growth forms used in both sites. In all instances where chi-square analyses were used, mean expected frequencies were more than or equal to six in each case (Zar, 1999). I also estimated the dependence of daily proportional burrow use on maximum daily temperatures by first transforming (arcsine square root) proportional burrow use (Zar, 1999) and then finding the best fit curve for the data using the

Levenberg-Marquardt algorithm (Marquardt, 1963; Shrager, 1970; Shrager, 1972; Nash, 1979; Press et al., 1986). The data was fitted with a two parameter, single exponential curve, where the equation of the line is:

$$y = ae^{bx} \qquad\qquad \text{..…………….. [1]}$$

I then used linear regression (r^2) to establish the degree of influence of maximum daily temperature on proportional burrow use. In order to assess individual bias in number of refuge species/items, I used Spearman's rank order correlation (r_s) to test for the relationship between the number of refuge records (frequencies) per telemetered tortoise and the number of refuge species/items used per tortoise.

To evaluate preference or avoidance of plant refuge items, I first had to express availability and utilization in similar ways. Refuge items were expressed as a proportion of the total number of refuges used at a particular site, or for a particular group, and the sum of the parts was always 100%. In contrast, availability of particular plant items, as presented in Chapter 4.2.4, was expressed relative to total plant cover (RCI) of an area, with total plant cover and uncovered soil making up 100% cover. Consequently, I recalculated all RCI's relative to a 100% cover (divided by real total cover), to make the units for availability and utilization equitable.

To test if the proportional use of refuges differed significantly from expected use (according to availability), I constructed a set of simultaneous confidence intervals (CI's) around the proportional use with a continuity correction factor. When expected proportional usage fell outside the confidence intervals, the difference was treated as being significant – the items were either selected or avoided (Bailey, 1980; Cherry, 1996). Confidence intervals were constructed using the formulae:

$$\text{Lower limit CI} = \frac{[\sqrt{p'_{(i\text{-})}} - \sqrt{C\,(C+1-\,p'_{(i\text{-})})}]^2}{(C+1)^2} \qquad \text{..………….. [2]}$$

$$\text{Upper limit CI} = \frac{[\sqrt{p'_{(i\text{+})}} + \sqrt{C\,(C+1-\,p'_{(i\text{+})})}]^2}{(C+1)^2} \qquad \text{..………….. [3]}$$

Where $p_{(i\text{-})} = (n_i - 1/8) / (N + 1/8)$

   $p_{(i\text{+})} = (n_i + 7/8) / (N + 1/8)$

   $C = B/4N$ where B is the upper $(\alpha/k)100^{th}$ percentile of a chi-square
   distribution with one degree of freedom (Cherry, 1996).

Many plant items were available but never used as refuges. To test if these plant items were avoided, I constructed CI's around the expected use (based on availability) of the plant items (Zar, 1999) to determine if the CI's include or exclude zero. Active avoidance was assumed when the CI's excluded zero. I applied sequential Bonferroni adjustments when multiple tests were used (Holm, 1979).

SigmaStat 2.03 and TableCurve 2D 5.01 (SPSS Inc., Chicago, USA) was used for all statistical analyses except for chi-square calculations and calculation of confidence intervals, which were done in Microsoft Excel in accordance with Zar (1999) and (Bailey, 1980), respectively. For sake of simplicity and ease of comparison, I always reported means (±standard deviations) even when non-parametric tests were used.

5.3 RESULTS

5.3.1 Sex differences in habitat selection

Differences in vegetation composition between sites were evaluated in Chapter 4, thus I focus here on differences in habitat choice between males and females within sites. Although most data came from habitat assessments of tortoises found in refuges, a substantial proportion (25%) of the assessment represent the habitat of animals that were found in the open. The assumption was made that tortoises took refuge in the habitats they frequent and did not seek alternative habitats when they look for cover.

5.3.1.1 Substrate and percent vegetation cover

There was no effect of sex on habitat substrates ($P > 0.48$) or on total vegetation cover in site E ($P > 0.06$; Table 5.1). For both sexes, the height category 10-60 cm was the predominant vegetation in site E, with H < 10 cm contributing more to vegetation cover than did H 61-100 cm, and H > 100 cm contributing the smallest percentage cover (all FRMAs, $\chi^2 \geq 713.2$, df = 3, $P < 0.0001$; Table 5.1). Female habitats had a greater degree of H 10-60 cm cover than male habitats had (MW test, $T_{297,329} = 82451$, $P < 0.0001$; Table 5.1), whereas both the H < 10 cm and 61-100 cm categories were more abundant in male habitats than they were in female habitats ($T_{297,329} \geq 99637$, $P < 0.0039$; Table 5.1). There was no difference between sexes in abundance of vegetation higher than 100 cm ($P > 0.051$).

In site W, the substrate in male habitats was stonier than it was in female habitats ($T_{313,335} = 94149$, $P < 0.002$) but females were found in areas with higher percent

vegetation cover than males were ($T_{313,\ 335}$ = 113090, P < 0.0001; Table 5.1). As it was in site E, in site W the majority of vegetation cover was in the height category 10-60 cm in both female and male habitats. Proportional contributions of each height category in female habitats in site W mirrored those of site E, but male habitats showed a different pattern. The percentage vegetation cover in categories H < 10 and H 61-100 cm did not differ in male habitats, but both contributed more to percentage cover than H > 100 cm did (FRMAs, $\chi^2 \geq$ 713.2, df = 3, P < 0.0001; Table 5.1). Differences between sexes in site W were minimal; female habitats had a higher percentage of cover for H < 10 cm than male habitats had ($T_{313,\ 335}$ = 110928, P < 0.0001; Table 5.1).

Table 5.1 Mean (±SD) substrate rank, percent vegetation cover and height categories, and relative cover indices of major growth forms (see Chapter 4.4.2 for details) for female and male tortoise habitats in sites E and W respectively. Substrate was ranked 1-5, 1 being 100% sand and 5 being rocky terrain. An asterisk denotes a significant difference between sexes (MW tests, P < 0.004).

	East site		West site	
	Females	**Males**	**Females**	**Males**
Substrate	1.03 ± 0.23	1.07 ± 0.32	1.69 ± 0.93	*1.95 ± 1.00
Total cover	75.91 ± 8.42	75.02 ± 9.94	*67.73 ± 6.55	65.51 ± 6.26
H < 10	12.34 ± 6.11	*14.78 ± 7.61	*12.09 ± 9.36	10.05 ± 8.47
H 10-60	*54.75 ± 14.12	50.43 ± 14.03	45.91 ± 11.43	45.32 ± 10.40
H 61-100	7.11 ± 7.59	*9.53 ± 9.81	9.71 ± 9.15	10.12 ± 7.99
H > 100	1.71 ± 6.24	0.32 ± 1.91	0.00 ± 0.18	0.00 ± 0.27
Grasses	28.49 ± 10.11	29.92 ± 10.13	22.90 ± 7.91	21.56 ± 8.05
Shrubs	19.86 ± 12.16	21.31 ± 9.32	32.52 ± 11.03	*35.32 ± 8.32
Herbs	21.56 ± 11.11	20.05 ± 9.20	*10.99 ± 8.13	7.65 ± 7.94
Trees	*2.26 ± 4.42	0.56 ± 1.84	0.29 ± 1.74	0.07 ± 0.53
Sedges	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.28
Geophytes	0.72 ± 2.17	0.42 ± 1.52	0.78 ± 2.44	0.33 ± 1.24
Other	1.29 ± 3.43	1.68 ± 3.89	1.04 ± 3.15	0.71 ± 2.02

5.3.1.2 Growth forms

In site E, both male and female habitats were dominated by grass, 30% and 28% respectively. Shrubs and herbs were co-dominant over remaining growth forms. Trees ranked after herbs and shrubs in female habitats (but not in male's) with sedges being the least abundant growth form in the habitats of both sexes (all FRMAs, $\chi^2 \geq$ 906.4, df = 6, P < 0.0001; Table 5.1). Within site E, trees were more abundant in female habitats

than they were in those of males ($T_{203, 216}$ = 46556.5, P < 0.002; Table 5.1), but there was no effect of sex on the abundance of remaining major growth form categories (P > 0.056).

The composition of growth forms in site W was similar for the habitat of both sexes; shrubs were dominant, comprising over 30% of the habitat for both sexes, while grass was more abundant than all remaining growth forms. After grass, herb abundance ranked highest in habitats of both sexes. In male habitats 'other' growth forms also ranked higher than trees, sedges and geophytes (FRMAs, χ^2 ≥ 854.8, df = 6, P < 0.0001; Table 5.1). Between sexes, male habitats had a higher proportion of shrubs than female habitats had while female habitats had more herbs ($T_{168, 237}$ ≥ 30453, P < 0.0017; Table 5.1). There were no further differences in habitats between sexes within site W (P > 0.07).

5.3.2 Refuge frequencies of individuals

Of the 1091 refuge records (reflecting the removal of consecutive stays in the same refuge by an individual), all but five records were derived from radio-tracked animals (the remainder were caught opportunistically). Refuge records for the 27 telemetered tortoises ranged from 14 to 73 per tortoise, with a mean ±SD of 40±16 refuges per individual. The number of refuges per individual ranged from 17 to 53 (33±12) for the 15 females, and from 14 to 73 (49±17) for the 12 males. There was a positive correlation between the number of records per radio-tracked individual and the number of refuge species/items an individual used (r_s = 0.681, n = 1086, P < 0.0001) suggesting that the number of refuge species/items per individual was related to quantity of records, and that individual preferences did not bias the data.

5.3.3 Refuge types: plants and burrow use and site, sex and month effects

Plant refuges accounted for 78% of tortoise refuges recorded (n = 853) and the remainder were animal burrows (n = 238, 22%). There was no difference in the proportional use of animal burrows between sites or sexes (P ≥ 0.56), thus I combined sites and sexes for monthly analyses. Proportional use of burrows by tortoises was highest in February (55%) and lowest in April 2007 (1.5%; Fig. 5.1). Burrow use was significantly affected by month; it was greater in the summer months of December, January and February than it was in all other months (χ^2_1 ≥ 14.421, P < 0.0002; Fig. 5.1). In addition to summer months, March's burrow use was higher than that of May, and burrow use in March and October was higher than that of April 2007 (χ^2_1 ≥ 12.73, P

< 0.001; Fig. 5.1). After applying a sequential Bonferroni, there were no other monthly differences in the proportion of burrows used ($P \geq 0.003 > 0.0018$ = adjusted α).
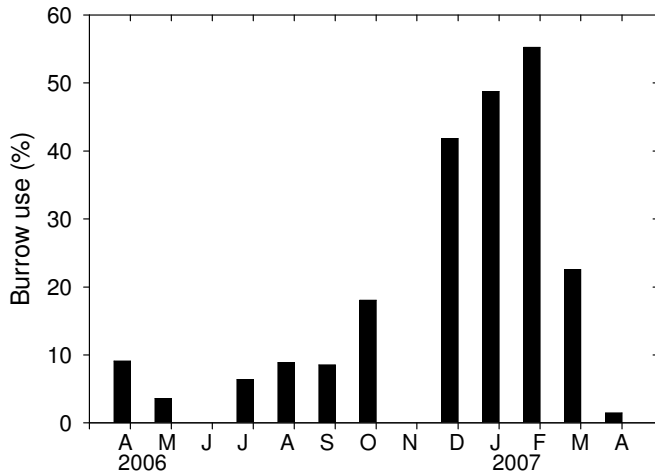
Figure 5.1 Monthly percentage use of burrows by tortoises. Data were not collected in June 2006 and the small number of records at the beginning and end of November was added to October and December, respectively.

Apart from tracking monthly changes in burrow use, I also assessed the effect of maximum temperature (°C) on proportional daily burrow use through regression analysis. There was an exponential increase in proportional burrow use with an increase in maximum daily temperature (arcsine square root transformed data, $r^2_{167} = 0.52$, $F = 181.6$, $P < 0.0001$; Fig. 5.2). Mean daily percentage burrow use was 12% of total refuges used on days when the maximum temperature was below 35 °C but increased to 48% on days when the maximum temperature was 35 °C to 39.7 °C (the maximum daily temperature recorded).
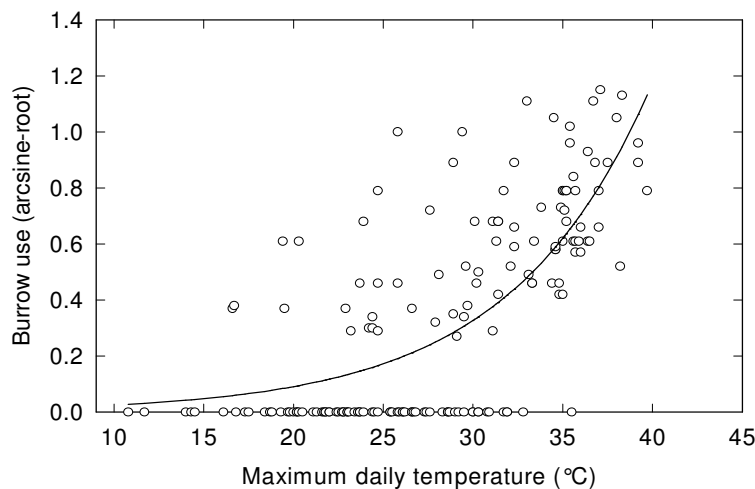
Figure 5.2 Maximum daily temperature (°C) and corresponding proportional use of burrows (arcsine square root transformed; $n = 167$) by tortoises during the study period ($r^2_{167} = 0.52$, $P < 0.0001$).

5.3.4 Burrow & plant characteristics

5.3.4.1 Site and sex differences in burrow dimensions

There was an effect of sex on both burrow width ($\log_{10}$) and burrow height ($\log_{10}$) as well as an effect of site on burrow height (all $F_{1,224} \geq 5.664$, $P \leq 0.018$). Female burrows were wider and higher than male burrows, and burrows in site W were higher than they were in site E (Table 5.2).

Table 5.2 Mean (±SD) width and height of all burrows measured for males (M) and females (F) within sites E and W. An asterisk denotes a difference between sexes within sites whereas a hatch indicates a difference between sites in burrow height (two-way ANOVAs, $P < 0.02$).

Site	Sex	Width (cm)			*n*	Height (cm)			*n*
E	F	*17.2	±	7.1	*(49)*	*12.2	±	5.1	*(49)*
E	M	14.9	±	5.7	*(69)*	10.7	±	3.6	*(69)*
W	F	*20.3	±	11.6	*(50)*	*15.2#	±	8.7	*(50)*
W	M	17.2	±	13.5	*(60)*	12.3#	±	8.2	*(60)*

5.3.4.2 Site and sex differences in plant refuge dimensions and density

Mean plant refuge heights were 42.3±21.42 cm, with no difference between sexes or sites, and no interaction of sex and site ($P > 0.35$). However, refuge widths ($\log_{10}$) differed between sites and between sexes ($F_{1,728} \geq 4.954$, $P \leq 0.027$) with no interaction between the two factors ($P = 0.54$; Table 5.3). Tortoises in site W used wider refuges than they did in site E and males used wider refuges than females did. Within both sites, males used denser refuges than those of females, and within sexes, refuges in site E were denser than refuges in site W (MW rank sum tests, $T \geq 34335$, $n1 \geq 196$, $n2 \geq 204$, $P < 0.024$; Table 5.3).

Table 5.3 Mean (±SD) plant refuge widths (cm) and densities (ranked 1 – 5, 1 when a tortoise was more than 75% visible and 5 when the tortoise was totally covered). Asterisks denote differences between sexes within sites (two-way ANOVAs, $P < 0.05$) whereas hatches indicate a difference between sites (MW rank sum tests, $P < 0.0001$).

Site	Sex	Width			*n*	Density			*n*
E	F	27.4	±	20.7	*(147)*	2.8#	±	1.2	*(196)*
E	M	*30.4	±	25.3	*(170)*	*3.5#	±	1.1	*(219)*
W	F	29.3#	±	16.4	*(193)*	2.5	±	1.2	*(204)*
W	M	*32.1#	±	17.6	*(222)*	*3.2	±	1.1	*(241)*

5.3.4.3 Seasonal effects on plant refuge measurements and density

Before analysing the seasonal effects on plant refuge width, height and density, I graphically compared seasonal patterns of each parameter between sites and sexes. Monthly pattern of refuge widths, heights and densities did not differ appreciably between sex and site in each case, thus I combined the data for temporal analyses.

There was a significant difference in plant refuge widths amongst months (H_{10} = 76.65, P < 0.0001). Generally, plant refuges were wider in summer months than they were in winter and spring: refuges in April 2006, May, January and February were wider than they were in July, August and September, while December refuges were also wider than those of August were. In April 2006 and February, refuges were wider than they were in April 2007 while April 2006 widths also exceeded those of October and March (Fig. 5.3A). The differences amongst months in plant refuge height (H_{10} = 74.56, P < 0.0001) related mostly to low height values for May, July and August when refuges were lower than they were in autumn months, April 2006 and March 2007. In August, refuges were lower than they were in all remaining months except May and July (Fig. 5.3B). As it was for width and height, so there was also an effect of month on plant refuge densities (H_{10} = 45.9, P = 0.0001). April 2007 refuge densities were lower than in April 2006, December and March. In December, refuges also had higher densities than in August and September.

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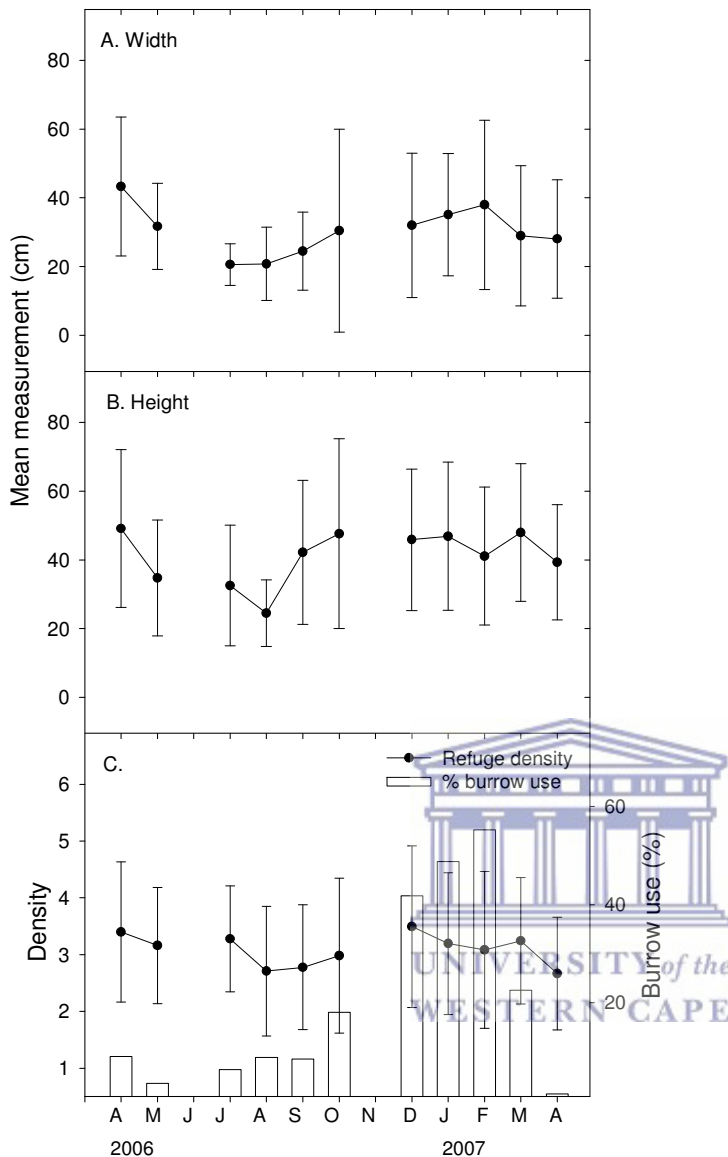
Figure 5.3 Mean monthly refuge widths (A), heights (B) and densities (C; all with SD bars). The bars (panel C) show monthly percent burrow use. Refuge densities were ranked from 1-5, 1 indicating that 75% or more of the tortoise was visible and 5 signifying the tortoise was 100% covered. No data were collected in June 2006 and data of the first and last days of November were added to October and December, respectively.

5.3.5 Refuge growth forms

5.3.5.1 Refuge frequencies and sex and site differences

There was no effect of sex on use of major growth forms, after applying a sequential Bonferroni correction ($P \geq 0.048 > 0.0125$ = adjusted α), thus I combined sexes for major growth form comparisons. Grass was the most commonly used growth form refuge in site E (77.5%); it was used more frequently than shrubs (20.6%), while the

remaining major growth forms, herbs and trees, were hardly used (chi-square tests, χ^2_1 ≥ 265.3, $P < 0.0001$; Table 5.4). In site W, tortoise use of grass (55.2%) and shrub (44.8%) refuges were more equitable than they were in site E, but grass was still used more frequently than shrubs were ($\chi^2_1 ≥ 9.205$, $P < 0.0024$); these were the only major growth forms used in site W (Table 5.4). Grass was used as a refuge more frequently in site E than it was in site W, while in site W shrubs were used more frequently than they were in site E ($\chi^2_1 ≥ 46.03$, $P < 0.0001$). There was no difference in the use of other major growth forms between sites ($P > 0.79$; Table 5.4).

Table 5.4 Percentage use of growth forms by female (F) and male (M) tortoises in sites E (female = 194 and 188, and male = 219 and 217 for major growth forms and subcategories, respectively), site W (female = 200 and male = 240), and for combined sexes. An asterisk denotes a significant difference between sexes and a hatch sign indicates a difference between sites (χ^2, $P < 0.0123$). Unknown grass includes dead and grazed grass.

	Site E		Site W		Site E	Site W
Growth form	**F (%)**	**M (%)**	**F (%)**	**M (%)**	**F+M (%)**	**F+M (%)**
Grass, all	80.4	74.9	58.0	52.9	77.5[#]	55.2
Grass, short	*52.6[#]	35.6[#]	*28.5	15.0	43.6	21.1
Grass, tall	27.8	35.6	29.5	36.7	32.0	33.4
Grass, unknown	0.0	3.7	0.0	1.3	1.9	0.7
Shrub, all	16.5	24.2	42.0	47.1	20.6	44.8[#]
Shrub, short	16.0	23.3	42.0[#]	47.1[#]	19.9	44.8
Shrub, tall	0.5	0.9	0.0	0.0	0.7	0.0
Herb	2.1	0.0	0.0	0.0	1.0	0.0
Tree	1.0	0.9	0.0	0.0	1.0	0.0

The proportional use of growth form subcategories differed between sites and sexes ($\chi^2 ≥ 14.213$, df ≥ 4, $P ≤ 0.0026$; Table 5.4), thus sites and sexes were analysed independently. Within site E, females used short grass refuges more than they did tall grass refuges, and both grass categories were used more often than short shrubs ($\chi^2_1 ≥ 24.201$, $P ≤ 0.0001$). Tall shrubs were rarely used by females in site E (Table 5.4). Unlike females, male tortoises used short and tall grass equally in site E, and both were used more often than short shrubs. In turn, males in site E used short shrubs more frequently than they did unknown grass and tall shrubs ($\chi^2_1 ≥ 7.457$, $P ≤ 0.0063$; Table 5.4). Females in site W used short shrubs more often than short and tall grass ($\chi^2_1 ≥ 6.269$, $P ≤ 0.0123$; Table 5.4) but there was no difference between the use of

these two grasses ($P > 0.91$). Contrary to females, male use of short shrubs and tall grass did not differ ($P = 0.0264 > 0.025$ = adjusted α). Males used both short shrubs and tall grass in site W more frequently than they did short and unknown grasses ($\chi^2_1 \geq$ 28.282, $P \leq 0.0001$; Table 5.4).

Within sites, proportional use of growth form subcategories (as refuges) differed between sexes; females used short grass more often than males did in both sites ($\chi^2_1 \geq$ 11.131, $P \leq 0.00032$; Table 5.4). There were no other differences in the use of growth form subcategories between sexes (χ^2 tests, $P > 0.021 > 0.0056$ = adjusted α). Within sexes, there were also differences in the use of growth form subcategories between sites; females and males used short grass as refuges more frequently in site E than they did in site W, while in site W they used short shrubs more often than they did in site E ($\chi^2_1 \geq 25.524$, $P < 0.0001$). There were no other differences in the use of growth form subcategories by either sex between sites ($P > 0.1$; Table 5.4).

5.3.5.2   Trends in monthly use of growth forms
Short and tall grasses and short shrubs constituted more than 90% of the refuges used in both sites E and W (Table 5.4), thus I limited temporal analyses to these subcategories. After application of a sequential Bonferroni procedure, monthly refuge use did not differ between sites or sexes ($P \geq 0.00423 > 0.00416$ = adjusted α), therefore I combined the data for monthly comparisons. Although use of short shrub refuges differed amongst months overall ($\chi^2_{10} \geq 18.608$, $P < 0.046$; Fig. 5.4) differences were not evident at an inter-month level after applying a sequential Bonferroni ($P = 0.0095 > 0.0009$ = adjusted α). Proportional use of short and tall grass, however, differed amongst months ($\chi^2_{10} \geq 43.166$, $P < 0.0001$; Fig. 5.4). Short grass was used more often in August than it was in October, December, January, February and March ($\chi^2_1 \geq 11.462$, $P < 0.0008$; Fig. 5.4). Use of short grass in May was also greater than it was in January, while use of short grass in April 2006, May and July was greater than it was in February and March ($\chi^2_1 \geq 11.273$, $P < 0.00079$; Fig. 5.4). There were no further differences in proportional use of short grass amongst months ($P \geq 0.0022 > 0.001$ = adjusted α). Proportional use of tall grass was highest in March when it was higher than it was in May, August and April 2007 ($\chi^2_1 \geq 12.191$, $P < 0.00049$; Fig. 5.4). There were no other differences in tall grass use amongst months ($P \geq 0.0019 > 0.0009$ = adjusted α).
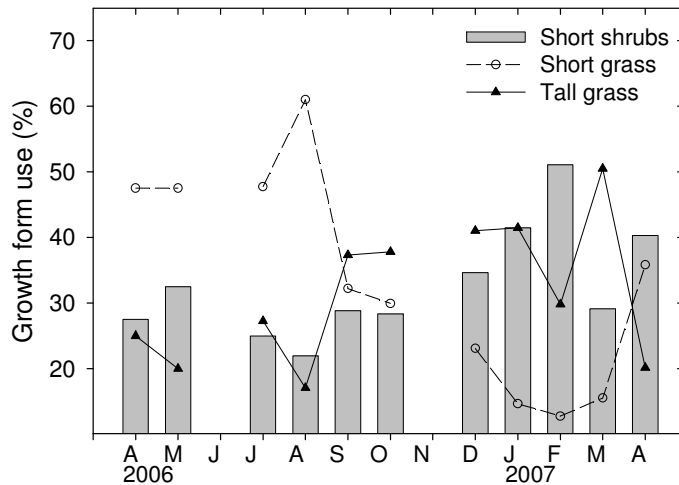
Figure 5.4 Monthly use of short shrubs, short grass and tall grass as a percentage of all plant refuges used each month by male and female tortoises in combined sites. Data were not collected in June 2006 and the small number of records at the beginning and end of November was added to October and December, respectively.

5.3.6 Refuge growth form use versus availability

When comparing the use versus availability of major growth forms, males and females at both sites showed strong selection for grass refuges, and avoided herbs and 'other' growth forms (Table 5.5). Both sexes at both sites used trees in proportion to availability, whereas the use of geophytes and sedges were avoided in site E, but used in proportion to availability in site W. Concerning grass and shrub subcategories, females and males in site E selected short and tall grass. Males also selected unknown grass, but females avoided it. Females avoided short and tall shrubs but males neither selected nor avoided them. In site W, both sexes selected tall grass. Females' selected short grass and avoided unknown grass whereas males neither selected nor avoided these subcategories. Males and females used short shrubs in proportion to their availability, but both avoided tall shrubs (Table 5.5).

Table 5.5 Growth form percentage availability and percentage use by female (F) and male (M) *Psammobates oculifer* in sites E and W. Selection (S), avoidance (A) or use in proportion to availability (N) were determined by constructing 95% simultaneous confidence intervals around proportional use (Neu et al., 1974; Byers et al., 1984).

Growth form	Site E					Site W				
	Avail	Use-F		Use-M		Avail	Use-F		Use-M	
Grass, all	38.7	80.4	S	74.9	S	32.9	58.0	S	52.9	S
Grass, short	27.3	52.6	S	35.6	S	17.1	28.5	S	15.0	N
Grass, tall	10.7	27.8	S	35.6	S	12.1	29.5	S	36.7	S
Grass, unknown	0.7	0	A	3.7	S	3.7	0.0	A	1.3	N
Shrub, all	28.4	16.5	A	24.2	N	51.9	42.0	N	47.1	N
Shrub, short	25.2	16	A	23.3	N	50.3	42.0	N	47.1	N
Shrub, tall	3.2	0.5	A	0.9	N	1.6	0.0	A	0.0	A
Herb	27.5	2.1	A	0.0	A	13.0	0.0	A	0.0	A
Tree	2.7	1.0	N	0.9	N	0.2	0.0	N	0.0	N
Other	1.9	0	A	0.0	A	1.2	0.0	A	0.0	A
Geophyte	0.7	0	A	0.0	A	0.8	0.0	N	0.0	N
Sedge	0.0	0	A	0.0	A	0.0	0.0	N	0.0	N

5.3.7 *Refuge species*

5.3.7.1 Site and sex differences and use versus availability

There were 23 plant refuge species recorded in the combined sites, with 22 and 16 in sites E and W, respectively. Females used 17 species in site E and 13 in site W and males used 16 species in site E and 15 species in site W. Refuges used in site E were dominated by five species: *Schmidtia pappophoroides* (short grass), *Stipagrostis uniplumis* (tall grass), *Pentzia incana* (small shrub), *S. obtusa* (short grass) and a small shrub, *Amphiglossa triflora*. These species, respectively, contributed 33.4%, 30.5%, 7.5%, 5.5%, 5.3% of species used, totalling over 80% of refuges used in site E (Fig. 5.5 and Table 5.6). In site W, the top five species, representing 70% of the refuges, were used more equitably than in site E: *S. uniplumis* (18.4%), *A. triflora* (15.7%), *P. incana* (12.7%), *S. obtusa* (12.5%) and *Cymbopogon pospischilii* (10.9%; tall grass) (Fig. 5.5 and Table 5.6).
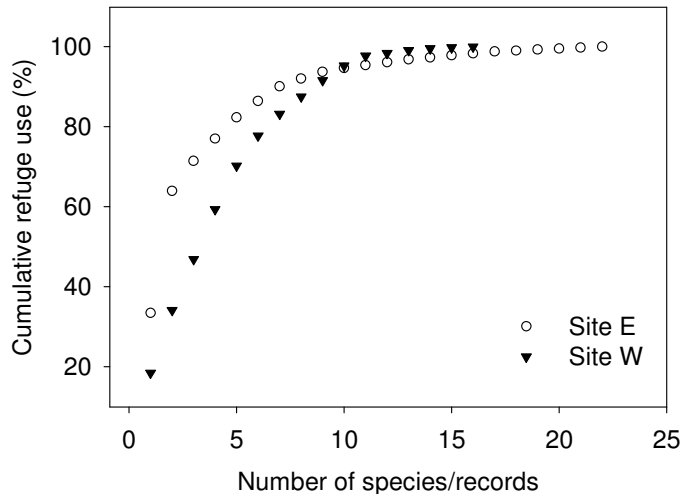
Figure 5.5 Cumulative percent usage of refuge species/items in sites E and W.

The use of refuge species overall differed between sexes within site E and site W ($\chi^2 \geq$ 43.335, df $\geq$ 15, P < 0.003; Table 5.6), but when use of individual species was compared, there was no differences between sexes in site E (chi-square tests, P > 0.02 > 0.0002 = adjusted α). In site W, females used the short grass *S. obtusa* more often than males did (χ^2_1 = 20.135, P < 0.00001; Table 5.6)*,* but there were no further differences in use of refuge species between sexes in site W (χ^2_1 $\geq$ 10.041, P $\geq$ 0.00153 > 0.00037 = adjusted α; Table 5.6).

Of species selected as refuges in site E, males selected four species in excess of their availability whereas females selected two species; *S. pappophoroides* and *S. uniplumis* were selected by both sexes, whereas males also selected *A. triflora* and Unknown grass (95% confidence intervals, (Bailey 1980); Table 5.6). Both sexes in site E avoided 10 species. In site W, males selected four and females three refuge species; *S. uniplumis* and *A. triflora* were selected by both sexes, whereas males also chose *Aristida diffusa* and *C. pospischilii*, and females chose *S. obtusa* (95% confidence intervals (Bailey 1980); Table 5.6). Five species were avoided by males and six by females. The remaining species in sites E and W were neither selected nor avoided.

Table 5.6 Percentage availability and use of plant species as refuges by male and female *Psammobates oculifer* in sites E and W. Selection (S), avoidance (A) or use in proportion to availability (N) was determined by constructing 95% simultaneous confidence intervals around proportional use (Bailey, 1980). Only species that were avoided or selected, or were more than 0.5% available (in either site) were included. The use of only one species, *S. obtusa*, differed between sexes in site W. Table sorted according to availability of combined sites.

Species	Form	Site E Avail	Male		Female		Site W Avail	Male		Female	
Schmidtia pappophoroides	GS	19.4	29.2	S	38.1	S	9.1	8.9	N	6.0	N
Chrysocoma ciliata	SS	10.7	4.1	A	4.1	A	5.8	4.2	N	3.0	N
Stipagrostis uniplumis	GT	8.4	33.8	S	26.8	S	7.8	15.8	S	21.5	S
Pentzia incana	SS	5.9	7.8	N	7.2	N	9.9	11.3	N	14.5	N
Hermannia tomentosa	Herb	7.3	0.0	A	1.0	A	7.3	0.0	A	0.0	A
Selago paniculata	Herb	9.3	0.0	A	1.0	A	0.6	0.0	N	0.0	N
Eriocephalus ericoides	SS	1.5	0.0	N	0.5	N	8.0	3.3	N	1.5	A
Stipagrostis obtusa	GS	3.3	4.6	N	6.7	N	5.2	5.8	N	20.5	S
Amphiglossa triflora	SS	1.8	7.8	S	2.6	N	6.1	17.9	S	13.0	S
Rosenia humilis	SS	0.6	0.5	N	1.0	N	6.1	5.0	N	3.5	N
Plinthus karooicus	SS	1.9	0.0	A	0.0	A	3.8	0.0	A	0.0	A
Eragrostis lehmanniana	GS	3.6	1.8	N	5.7	N	2.0	0.4	N	0.5	N
Gnidia polycephala	SS	1.2	2.7	N	0.5	N	4.2	4.6	N	6.5	N
Wahlenbergia androsacea	Herb	3.8	0.0	A	0.0	A	0.4	0.0	N	0.0	N
Hermannia comosa	Herb	1.7	0.0	A	0.0	A	1.9	0.0	A	0.0	A
Unknown grass	GU	0.6	3.7	S	0.0	N	2.8	1.3	N	0.0	N
Cymbopogon pospischilii	GT	0.2	0.9	N	0.0	N	2.8	15.4	S	5.5	N
Seedlings	Other	2.0	0.0	A	0.0	A	0.8	0.0	N	0.0	N
Melolobium macrocalyx	SS	0.5	0.0	N	0.0	N	1.8	0.0	A	0.0	A
Eragrostis trichophora	GS	1.6	0.0	N	2.1	N	0.6	0.0	N	1.5	N
Lycium cinereum	SS	0.0	0.0	N	0.0	N	2.2	0.4	N	0.0	N
Senna italica	Herb	1.7	0.0	A	0.0	A	0.5	0.0	N	0.0	N
Acacia erioloba	Tree	1.8	0.0	N	0.5	N	0.0	0.0	N	0.0	N
Deverra denudata	ST	0.7	0.0	N	0.0	N	1.1	0.0	A	0.0	A
Solanum incanum	ST	1.3	0.0	A	0.0	A	0.3	0.0	N	0.0	N
Aristida diffusa	GT	0.3	0.5	N	0.0	N	1.0	5.4	S	2.5	N
Limeum sulcatum	Herb	0.7	0.0	N	0.0	N	0.4	0.0	N	0.0	N
Zaluzianskya violacea	Herb	0.8	0.0	N	0.0	N	0.3	0.0	N	0.0	N
Ifloga sp.	Herb	0.5	0.0	N	0.0	N	0.5	0.0	N	0.0	N
Lycium hirsutum	ST	0.9	0.9	N	0.5	N	0.0	0.0	N	0.0	N

Table 5.6 continued

Species	Form	Site E Avail	Site E Male		Site E Female		Site W Avail	Site W Male		Site W Female	
Aristida adscensionis	GT	0.6	0.0	A	0.0	A	0.3	0.0	N	0.0	N
Nemesia fructicans	Herb	0.6	0.0	N	0.0	N	0.3	0.0	N	0.0	N
Convolvulus ocellatus	SS	0.1	0.0	N	0.0	N	0.6	0.0	N	0.0	N
Themeda triandra	GT	0.6	0.0	N	1.0	N	0.1	0.0	N	0.0	N
Acacia sp	Tree	0.4	0.9	N	0.5	N	0.2	0.0	N	0.0	N
Pentzia calcarea	SS	0.2	0.9	N	0.0	N	0.4	0.4	N	0.0	N
Pogonarthria squarrosa	GT	0.4	0.5	N	0.0	N	0.0	0.0	N	0.0	N

5.3.7.2   Refuge density of plant species and growth forms

Refuge density was recorded for 23 plant species (in combined sites), but nine species had five or fewer records (see Table 5.7). Of these nine species, none occurred more than twice in any one month, and they were thus excluded from analyses, as their use was infrequent. Although refuge densities among species differed significantly (H_{14} = 85.45, $P < 0.0001$), there were few significant differences, only *Aristida diffusa* had a higher density than did *S. obtusa* and *E. trichophora* (Table 5.7). However, when I compared densities of the four growth form subcategories, represented in Table 5.7 (which accounted for over 90% of refuges used), there was a significant difference amongst densities of growth forms (H_2 = 46.029, $P < 0.0001$). Tall grass was denser than short grass and short shrubs, but was not denser than unknown grass.

Table 5.7 Mean densities (±SD) of refuge plant species with more than five records in combined sites. The GF column indicates growth form categories where GS, GT and GU are short, tall and unknown grass respectively, and SS is short shrubs. Unknown grass comprises grazed and dead grasses. Density was ranked 1-5, 1 signifying a tortoise was 25% covered and 5 being 100% covered.

Species	GF	Density	(*n*)
Aristida diffusa	GT	3.8 ± 1.0	(19)
Stipagrostis uniplumis	GT	3.5 ± 1.2	(206)
Amphiglossa triflora	SS	3.4 ± 0.9	(90)
Unknown grass	GU	3.2 ± 1.3	(11)
Cymbopogon pospischilii	GT	3.2 ± 1.3	(50)
Schmidtia pappophoroides	GS	3.0 ± 1.1	(168)

Table 5.7 continued

Species	GF	Density			(*n*)
Gnidia polycephala	SS	2.9	±	1.1	(31)
Eragrostis lehmanniana	GS	2.8	±	1.3	(16)
Pentzia incana	SS	2.7	±	1.1	(87)
Chrysocoma ciliata	SS	2.7	±	1.2	(33)
Rosenia humilis	SS	2.7	±	1.2	(22)
Eriocephalus ericoides	SS	2.4	±	1.0	(12)
Stipagrostis obtusa	GS	2.4	±	1.0	(78)
Eragrostis trichophora	GS	1.9	±	0.9	(7)

5.4 DISCUSSION

5.4.1 *Habitat differences between sexes*

Although this study found differences in habitat use between sexes, these differences were often too isolated (perhaps a function of large sample sizes) or trends were too weak to establish a cause for them. Similarly, other testudinid studies have either found no sex related habitat differences (Wright et al., 1988; Kazmaier et al., 2001c) or when differences in habitat use were found between sexes, they were opaque (Gibson & Hamilton, 1983; Anadón et al., 2006). In any event, differences in habitat use in this study were only explainable in terms of inter-sexual refuge preferences.

Some plant refuges were selected by both sexes while other plant selections were exclusive to a sex. Where plants were selected by one sex, the distribution and abundance of that growth form or species may be contingent on specific environmental factors, e.g., edaphic factors (see Chapter 4) and this may be the case in the tall grass species *Cymbopogon pospischilii*. *Cymbopogon pospischilii* was often found in stonier areas where cover was relatively low (T Keswick, personal observation). *Cymbopogon pospischilii* was also found in rockier areas at Rooiport, a private reserve about 60 km north-west of Benfontein (Bezuidenhout, 2009), and it may be that stony or rocky areas are the plant's preferred habitat in this region. Males used *C. pospischilii* more than it was available in site W and males inhabited more open, stonier habitats than females did here. Thus, males' use of more open, stonier habitats may be partly due to microhabitat choice, their selection of *C. pospischilii*. Equally, in both sites females were found in habitats with more vegetation cover between 10 and 60 cm high than males were. Females used short grass as a refuge more than males did and selected it more than its availability in both sites. As short grass was a large contributor to

vegetation cover between 10 and 60 cm, this may partially explain the abundance of this height category in female habitats.

5.4.2 Burrow use

Seasonal use of mammal burrows suggests that they are a critical resource for *P. oculifer* at Benfontein. Proportional burrow use increased exponentially with mean daily maximum temperature, peaking in February when burrow use (55% of total refuges used) exceeded the use of plant refuges. Limited use of burrows outside the summer 'buffer' months of October and March suggests that tortoises preferred plant to burrow refuges except on hot days. It is likely that the trend in summer burrow use seen at Benfontein occurs throughout the range of *P. oculifer*, as mean maxima temperatures reach 40°C in areas within the Kalahari (Leistner 1967), higher than they are at Benfontein (34.5 °C). Burrowing is a common adaptive trait of vertebrates in arid environments, as it provides relatively stable microclimates when temperatures are extreme (Noy-Meir, 1974; Lovegrove, 1993; Kinlaw, 1999). It is also probable that there is a sufficient supply of burrows available to *P. oculifer* throughout its range due to the omnipresence of burrowing mammals such as *Suricata suricatta* and *Pedetes capensis* that excavate numerous burrows and burrows of sufficient size (Skinner & Chimimba, 2005) for *P. oculifer* to use (but see Chapter 8 concerning regional populations of *P. oculifer*).

Tortoises are known to use burrows for both aestivation (Lagarde et al., 2002) and brumation (Douglass & Layne, 1978; Nagy & Medica, 1986). Interestingly, it appears that burrow use by *P. oculifer*, although similar during summer, differs overall from the burrow use of the widely studied desert species *Gopherus agassizii*. As *P. oculifer* does at Benfontein, *G. agassizii* uses burrows on hot days in summer (Woodbury & Hardy, 1948; Nagy & Medica, 1986). Despite their similar use of burrows in summer, *P. oculifer*, unlike *G. agassizii*, has no burrow 'construction costs'. While it may not incur the cost of burrow excavation, the trade-off for *P. oculifer* is that it relies on burrowing mammals for a vital resource and the decline of these burrowing mammals would affect *P. oculifer* severely.

The major difference in seasonal burrow use between *P. oculifer* and *G. agassizii* is in winter. *Psammobates oculifer* is less active in winter than during the rest of the year (Chapter 6), but its burrow use in winter is low (6.3% of refuges used) and it tends to use low density short grass as refuges, perhaps to maximise basking (see section 5.4.3 below). In contrast, *G. agassizii* constructs substantial, winter burrows (Woodbury

& Hardy, 1948) where they spend approximately four to six months in brumation, depending on year, location and tortoise size (Rautenstrauch et al., 1998; Nussear et al., 2007). Although *G. agassizii* is exposed to low mean minimum temperatures (4.8°C, 1986-95, averaging 25 frost days) for approximately four months of the year in Nevada (Rautenstrauch et al., 1998), *P. oculifer* at Benfontein was also subjected to low night temperatures from May to August. The 46-year average, monthly minima temperature at Benfontein for these four months combined is 3.91±2.16 °C (SAWS). Thus, although both of these species are arid zone tortoises, they have different strategies in seasonal thermoregulation. *Gopherus agassizii* invests in burrow construction to ward off extreme cold, while *P. oculifer* at Benfontein used low density refuges (minimal investment) in winter, thereby maximising basking opportunity. Tortoises basked more in winter months than they did in late spring or summer (Chapter 6). It may be that *P. oculifer* has physiological advantages over *G. agassizii* and *P. oculifer* is the smaller of the two tortoises, a possible advantage for thermoregulation on cooler days. However, tortoise size may not be the primary consideration here as the largest southern African tortoise, *Stigmochelys pardalis* was also found to prefer less dense refuges in winter, when minimum temperatures of -11.7 °C were recorded in the Free State (Douglas & Rall, 2006). Another restraint on thermoregulatory strategies could be seasonal climatic differences between the habitats of *G. agassizii* and *P. oculifer*, e.g., seasonal rainfall and solar radiation patterns. The thermoregulatory behaviour coupled with physiology of *P. oculifer* warrant further investigation.

5.4.3   Selection (avoidance) of refuge plants

A large proportion of the range of *Psammobates oculifer* is arid or semi-arid Savanna (Branch, 1988; Boycott & Bourquin, 2000) where trees and grasses co-exist (Sankaran et al., 2005) and grass was an important refuge for *P. oculifer* at Benfontein. Tortoises in sites E and W used grass as a refuge more often than any other major growth form, despite shrubs being the dominant growth form in site W (Chapter 4). Grass was also the only major growth form, and tall grass the only subcategory, to be selected in excess of its availability in both sites by both sexes. Short grass was also used by females in excess of its availability in both sites and likewise by males in site E. Patterns of short and tall grass refuge use may be a function of density.

The general difference between short and tall grass refuges was structure; tall grass was denser than short grass. Dense, tall grass may be a more suitable microclimate when temperatures are high, but the less dense short grass may be optimal on cooler

days as it facilitates basking in cover (discussed above and see Chapter 6). Tortoises largely conformed to a seasonal pattern of short and tall grass use (though not always significantly so). Use of short grass refuges tended to increase with decreasing temperatures from autumn to winter, and tortoises switched to tall grass refuges in spring and early summer, as temperatures increased. However, use of tall grass declined in the hottest month, February, coinciding with peak burrow use, perhaps because tortoises switched from the use of tall grass to burrows in the hottest part of the day. Use of tall grass increased and reached its peak in March, the hottest month outside summer, as tortoises' burrow use declined.

Amongst the tall grass refuge species used by *P. oculifer* at Benfontein, *S. uniplumis* appeared to be the most important; it was the only species used by both sexes within both sites in excess of its availability. *Stipagrostis uniplumis* is a pan-African, arid zone grass species that occurs throughout the range of *P. oculifer* (van Oudtshoorn, 2004), and thus may be readily available to *P. oculifer*. *Stipagrostis uniplumis* was also abundant at both sites at Benfontein; it had the second highest RCI (abundance) in the study site and was the most abundant tall grass. *Stipagrostis uniplumis* was a high-density grass suggesting it was a suitable refuge for tortoises in warmer months.

Although both sexes selected tall grass and more specifically, *S. uniplumis*, the denseness of tall grass refuges is perhaps of particular advantage to males, which are the smaller sex and thus more vulnerable to extreme heat and predators. Males used tall grass refuges more than females did in both sites (albeit not significantly) and males selected the tall grasses *Aristida diffusa* and *Cymbopogon pospischilii*, both exclusively, in excess of their availability in site W. *Aristida diffusa* was the densest grass recorded, but its availability in site W, 1.0%, was relatively low. *Cymbopogon pospischilii* was the plant with the fifth highest density and was more abundant than *A. diffusa* in site W (2.8%, Table 5.7). *Cymbopogon pospischilii* occurs mainly in the eastern part of the range of *P. oculifer*, and the leaves form an overhanging canopy at the base of the plant (van Oudtshoorn, 2004). This canopy was great enough for males to hide under, but was often too insubstantial to give full cover to females (T Keswick, personal observation).

As tortoises may have preferred tall grass when days were hot, they tended to prefer short grass in cool seasons - it was barely used by tortoises in the hottest month, February. The low density of short grass allowed tortoises to maximise basking when air temperatures were cool, its low density let in diffuse sunlight, while simultaneously

mitigating predation risk as tortoises were partially concealed by cover. Basking is beneficial because it aids feeding in ectotherms (Spencer et al., 1998) and facilitates digestion and activity and this would benefit tortoises, particularly after August when, following a dry winter, the advent of spring rains promotes growth of annual plants (e.g., *Wahlenbergia androsacea*, see Chapter 4) on which tortoises feed.

Schmidtia pappophoroides, a short grass, was the most available plant species in site E, where it was selected in excess of its availability by both sexes. However, in site W tortoises did not select it as a refuge, despite its relative abundance there. It may be that the selection of *S. pappophoroides* in site E is an artefact of different patterns of refuge abundance between sites and the lack of other suitable refuge species. Five refuges plant in site E comprised 80% of plant refuges used and within these five plant species, *S. pappophoroides* and *S. uniplumis* accounted for 65%. In addition, tortoises avoided using the next three most abundant plant species in site E. Thus, in some respects, tortoises' use of *S. pappophoroides* as a refuge in site E was unavoidable as other plants were either used, or unfavourable. In site W, refuge use was more equitable; *S. uniplumis* was the most used refuge plant (18.4%) and the five most frequently used refuges equalled 70% of refuges used and thus tortoises had a greater variety of potential refuge species.

In site W, proportional use of short grass was half (21.1%) of what it was in site E and similarly its availability in site W (17.1%) was slightly more than half of its availability in site E. Whereas short grass in site W remained an important refuge for females, which they selected it in excess of its availability, male use of short grass was relatively low and they used it in accordance with its abundance. This suggests that once short grass abundance dropped in site W (from site E levels) and short shrub availability increased, males were satisfied with using either, as it was available, but they continued to select the denser tall grass. However, females selected short grass and tall grass. Female selection of short grass may suggest it was more suitable for basking in cover than the more available shrubs were. In site W, females selected the short grass *Stipagrostis obtusa* more than males did. Females also used *S. obtusa* more frequently than it was available. Of the abundant species (i.e., those with more than 5 records), *S. obtusa* had the second lowest density and this may have made it suitable for basking in cover. Basking may be less risky for females than it is for males as the female is larger and thus potentially less vulnerable to predators than males are. In addition, reproductive requirements may be an extra incentive for females to bask (Hofmeyr, 2004) when no such incentive may exist for males, and refuge choice by females may optimise

basking in cover (e.g., by using *S. obtusa*). Certainly, in this study, females were found basking more often than males (Chapter 6).

Compared to short grass, short shrub availability was less seasonally variable. With one exception, short shrub species at Benfontein may have provided refuge cover for tortoises under certain seasonal conditions but were used either as they were available, by males in both sites and females in site W, or avoided, as they were by females in site E. Grass was preferred to shrubs when available, but shrubs appeared to be an acceptable surrogate to grass, especially in February, the hottest month. Shrubs were a seasonally more persistent growth form than short grass was and unlike short grass, its abundance did not appear related to short term rainfall (perhaps because of its woody nature, see Chapter 4). Thus, short shrubs were more abundant than grasses in February (mid summer) when it was hot and dry and tortoises may have used them because grass was less available. The seasonal persistence of shrubs, they were usually available as a refuge, may also account for their relatively aseasonal use. *Amphiglossa triflora*, the only shrub refuge selected by tortoises, was selected by both sexes in site W perhaps because of its structure; it was a dense (third most dense) species and spiny shrub and probably provided cover when days were hot, particularly for males. Males, but not females, selected *Amphiglossa triflora* in site E and its dense structure may provide males with protection from predators as well as extreme heat.

The only other growth form selected (in excess of availability), by males in site E, was unknown grasses. Unknown Grass availability was limited to 3.7% and 1.3% in sites E and W respectively, it was used sporadically and 'opportunistically' and usually involved small males sliding under dead or flattened grass, the grass acting as a 'blanket' with perhaps a small portion of the tortoise's rear still visible (T Keswick personal observation). Although this gave adequate covering for small males (it was the fourth densest refuge) it was not a suitable refuge for the larger and more domed females, hence they avoided it.

Of the remaining growth forms recorded at Benfontein, herbs, tall shrubs, trees, geophytes and sedges, all were either avoided or used in accordance with their availability. Herbs were most readily available of the aforementioned growth forms, but they were avoided by both sexes in both sites. Lack of adequate structure was, perhaps, the reason that males and females avoided herbs. Herbs were diverse with a variety of structures and few if any had sufficient basal cover to adequately conceal a

tortoise (T Keswick, personal observation). Tall shrubs were avoided by both sexes in site W and by females in site E, but males neither selected nor avoided them in site E (some tall shrubs, e.g., *Lycium hirsutum*, provided cover but were uncommon). Trees also often lacked enough basal cover to make suitable refuges and were of relatively low availability. Of the remaining growth form categories, geophytes, sedges and 'other' were too small or lacked enough basal foliage to be an effective refuge.

5.4.4   Growth form refuges and burrow dimensions

Other than density, refuge dimension may affect refuge choice between sexes, e.g., through sexual dimorphism precluding refuge access to the larger sex. *Psammobates oculifer* males are significantly smaller than females (Chapter 8) and males used significantly lower and narrower burrows. As males used smaller burrows than females, males may have had a wider choice of burrows across the landscape than females did, advantageous during hot periods when male size may render them more vulnerable to high temperatures than females are. A small burrow also potentially excludes a wider range of predators, another advantage to males, although this is more difficult to substantiate. Burrows were also higher in site W compared with site E. Although I did not expect to find differences in burrow sizes between sites, this may be because site W was stonier than site E (including patches of surface calcrete) and substrate may not only dictate habitat choice of semi-fossorial mammals, but also how they burrow, both of which could affect burrow height. In arid and semi-arid areas of Australia, the southern hairy nosed Wombat, *Lasiorhinus latifrons*, favoured burrowing in areas of calcrete because calcrete was supportive i.e., burrows were less likely to collapse in these areas, particularly when they could access soil between calcrete layers (Walker et al., 2007).

Differences in dimensions of plant refuges may be a function of the type of growth form chosen by a tortoise and thus differences in the dimensions of growth form refuges may be an artefact of refuge choice rather than a cause of it. This may explain why site W refuges were wider than refuges in site E and why males used wider refuges than females in both sites. Inter-site differences in refuge width probably reflect the greater use of shrubs than grasses in site W compared to site E, as shrubs were wider than grass refuges were. Similarly, males tended to use (wide) shrubs more than females did; particularly in site E where males selected the shrub *Amphiglossa triflora* out of proportion to its availability (discussed in section 5.4.3 above).

As well as site and sex differences, changing seasons may affect plant refuge dimensions. These seasonal differences could be due to tortoise choice, e.g., tortoises switching from tall to short grass in autumn and from short to tall grass during spring. Plant refuge dimensions may also change seasonally in response to changes in climate, e.g., grass growth in response to rainfall, with consequent affects on other growth forms because of spatial competition (Vorster & Roux, 1983; O'Connor & Roux, 1995). At Benfontein, most rainfall is in late summer or autumn (179 mm and 72 mm in the February and March prior to the beginning of this study; SAWS) and the corresponding grass growth (see Chapter 4) may account for plant refuge dimensions being at their greatest in April 2006. Equally, in August, plant refuge dimensions were smaller, coinciding with the end of the cold and dry winter, both of which may have arrested plant growth.

5.4.5   Potential bias in refuge records

The vast majority of refuge records (1086 out of 1091) were derived from radio-tracked tortoises. Although a large refuge sample from 'randomly' captured individuals would have eliminated individual bias, in practice this would not have been feasible as *Psammobates oculifer* is a small, cryptic species and was rarely found unless animals were active or in the open (T Keswick, personal observation). Hence, radio-telemetry was an achievable method of gathering adequate data to study effects of sex and season. Leban et al. (2001) suggested a minimum of 20 animals and 50 tracking records per animal per season for resource use analyses based on radio-telemetry data (depending on analyses type). In this study, 15 female and 12 male tortoises were tracked over 12 months averaging 40 records per individual. This sample size is lower than suggested by Leban et al. (2001), however, Leban et al. (2001) used elk as an example and they admit sample size requirements would be reduced for smaller animals with smaller home ranges (e.g., tortoises). In addition, tortoises are ectotherms. Winter, and summer temperatures can severely restrict their movements (see Chapter 7) and this should be considered when evaluating adequate sample sizes for studies of tortoise resource use. Although study duration and techniques used to assess resource availability and resource use may have differed here, sample sizes in this study did not appear low in context of other similar studies (e.g., Bulova, 1994; Riedle et al., 2008). Individual sampling bias could also have affected the number of refuge species/types chosen, but there was a significant correlation between the number of species/types chosen and the number of locations (r_s = 0.681). This suggests that differences amongst individuals in the number of species/refuge types used were, at least in part, a function of sample size.

5.5   CONCLUSIONS
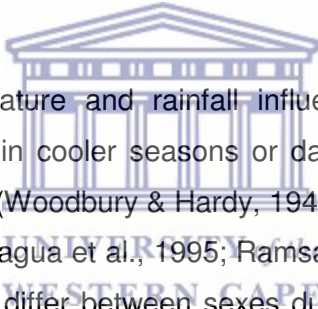
Habitat differences between sexes, e.g. substrate or growth form abundance, may be due, in part, to differences in refuge selection, although inconsistent or weak trends obfuscated interpretation. *Psammobates oculifer* inhabits arid or semi-arid Savanna where grass is the dominant growth form in the herbaceous layer, thus grass is the most available growth form refuge. Despite its high availability, grass and one of its subcategories, tall grass, were the only growth forms that *P. oculifer* selected as refuges in excess of their availability. Both males and females used dense, tall grass (mainly *S. uniplumis*) and burrows during hot months, probably because these refuges offered a benign microclimate. In cooler months, tortoises (particularly females) used less dense, short grass refuges (*S. pappophoroides* for both sexes and *S. obtusa* for females), possibly to maximise basking in cover. Males selected denser refuges than females perhaps because their smaller size makes them more vulnerable to temperature change and predation. Seasonal changes in dimensions of growth form refuges may be due to both seasonal changes in refuge choice and/or climatic effects.

6 ACTIVITY AND BEHAVIOUR

6.1 INTRODUCTION

Ectotherm activity and behaviour is limited by thermoregulatory requirements; daily activity is sporadic and for short periods (Pough, 1980) and this activity pattern is typical of testudinids (Douglass & Layne, 1978; McRae et al., 1981; Nagy & Medica, 1986; Kazmaier et al., 2001a; Lagarde et al., 2002), especially in regions where temperatures are extreme (Nagy & Medica, 1986; Lagarde et al., 2002). Ectotherm activity, particularly a 'specialised' activity such as feeding, may restrict ectotherms to operating within a narrow band of body temperatures, thereby synchronising such activity with internal processes (Pough, 1980). As well as actively basking, a tortoise may increase or decrease the amount of solar radiation it receives, through seasonal choice of refuge orientation, while remaining in the protective cover of its refuge (McMaster & Downs, 2006a).

Seasonal changes in temperature and rainfall influence tortoise activity patterns. Activity tends to be unimodal in cooler seasons or days, switching to bimodal when midday temperatures are high (Woodbury & Hardy, 1948; McRae et al., 1981; Geffen & Mendelssohn, 1989; Diaz-Paniagua et al., 1995; Ramsay et al., 2002). Tortoise activity and behavioural patterns may differ between sexes due to sexual dimorphism and/or physiological idiosyncrasies. After aestivation, small size in male *Testudo horsfieldii* enables them to reach their activity temperature earlier than females do and find females quickly under the duress of a short mating season (Lagarde et al., 2002). As males may reach activity temperature quicker, so the larger females may need to bask for longer and/or more frequently than males. By basking more frequently, female *Chersina angulata* may facilitate reproductive processes, e.g., vitellogenesis (Hofmeyr, 2004). In turn, 'costs' of physiological processes may affect female behaviour via seasonal increases in foraging (Lagarde et al., 2002). Hence, both temporal changes in the external environment and physiological processes may govern tortoise behaviour.

The Kalahari tent tortoise, *Psammobates oculifer*, is a small tortoise that occurs in and around the Kalahari Desert in southern Africa. This little-known species is subjected to large daily and seasonal temperature fluctuations across its range (Lovegrove, 1993). Annual rainfall can be low (100-500 mm) and unpredictable, with coefficients of variation between 20% and 70% (Hofmeyr et al., 2005). This study focuses on determining how a population of *P. oculifer*, by using behaviour, copes with its extreme

and sometimes unpredictable environment. In particular, it explores seasonal activity patterns in context of thermoregulation, namely does this species brumate as do certain other arid zone species? If it does not brumate, how does *P. oculifer* reach activity temperatures in winter? Does this species use refuge orientation to thermoregulate? These questions are asked in context of the different size and physiology of the sexes, which may affect their behaviour within a capricious, semi-arid habitat.

6.2   MATERIALS AND METHODS

From March 2006 to the end of April 2007, I recorded temperature, behaviour and orientation data from 27 (12 males and 15 female) tortoises used in a radio-telemetry study, and 190 tortoises caught opportunistically while radio-tracking. These records covered all hours of the day, and were taken from active and inactive tortoises. Temperature measurements were taken upon first capture and on the first and last day of each field trip, with the exception of winter (see Table 2.1). Because two short field trips were done during February, the tortoises were measured at the start of the first trip and at the end of the second trip. I took air, substrate and body temperatures using an APPA 53 digital thermometer with a K-type thermocouple. Air temperature (T_a) was taken adjacent to the tortoise (within a refuge if the tortoises was within cover), substrate temperature (T_g) was taken on the ground where the tortoise was first located, and body temperature (T_b; all °C) was taken by inserting the thermocouple into the tortoise's inguinal pocket.

When possible, I tracked tortoises more than once a day to obtain a more complete pattern of their activity, movement and behaviour. I also checked five male and five female tortoises with radio-transmitters on five separate nights for night-time activity during the hottest month, February. I located these individuals at dusk and positioned toothpicks marked with high visibility tape at strategic points around the tortoise. Subsequently, I observed the tortoises from a distance in case my activity caused them to move. I then returned to each tortoise at dawn and checked for displaced toothpicks, which would indicate that the tortoise had moved.

Each time I located a tortoise, by telemetry or opportunistically, I noted its behaviour (Table 6.1). I tried to locate tortoises without disturbing them, but *P. oculifer* at Benfontein was nervous and proved difficult to surprise. This may have affected the

number of animals I found feeding. I left a number of hours between daily tracking of individuals, not only to allow animals to settle, but also to give them sufficient time to change their behaviour. After radio-tracked individuals were handled, e.g., to record body temperature, longer periods were left (approximately eight hours or more); particularly if the period after handling (e.g. dusk) meant that the animal was temporally dependent on the environment (e.g. sunrise) to make its next behavioural choice.

Table 6.1 Description of *Psammobates oculifer* behaviours recorded at Benfontein Farm, South Africa, from March 2006 to April 2007. Tortoises were considered inactive when resting or basking and active when walking, feeding or socialising.

Behaviour	Description
Resting (R; inactive)	Under vegetation in shade.
Basking (B; inactive)	Motionless under vegetation or in the open, with part or all of the carapace exposed to the sun.
Walking (W; active)	Any form of locomotion; includes motionless when standing (legs extended).
Feeding (F; active)	Sniffing or biting a food item.
Socialising (S; active)	Includes fighting, i.e., males 'sparring', biting and ramming each other; and mating where a male pursues, cranes neck to smell, or mounts/attempts to mount a female.
Open	In an active behaviour or basking in the open.
Cover	Basking or resting under vegetation.

When I found a tortoise in a refuge, I noted the tortoise's north-south orientation relative to the refuge to assess potential thermoregulatory behaviour. Orientation was limited to categorising animal positions into the eight cardinal positions (e.g., north being at 0° with a range of 45°). Orientation was estimated using a combination of obvious landmarks of known direction (e.g., a telecommunication tower) and the angle of the sun or the compass on a GPS.

From 17 April 2006, rainfall data was collected using an electronic rain gauge erected in the study area. Rainfall prior to 17 April 2006 and hourly air temperatures for the

entire study period were obtained from the South African Weather Service's (SAWS) weather station approximately 5 km from the study area (see Chapter 2 for details).

6.2.1 Data and statistical analyses

The sampling method during March and part of April 2006, when tortoises were collected for the radio-telemetry study, was biased in favour of tortoises out in the open because resting tortoises were hard to locate without the assistance of radio-telemetry (they are small and cryptic). Thus, to analyse inactive behaviour and each of its behavioural categories, e.g., resting (see Table 6.1), and to compare proportions of active versus inactive animals, I used data collected from radio-tracked tortoises only. For analyses of individual categories of active behaviours (walking, feeding and socialising) I used the entire data set.

When analysing refuge data for the orientation analyses, I used data from only the first record when a tortoise was found in the same refuge, consecutively, to avoid pseudoreplication. For all temporal analyses (behaviour and temperature), I divided temporal categories into 1.5 hour intervals, starting with all behavioural records before 7:30 and finishing with all records after 16:30. These categories were chosen as the intervals afforded sufficient sample sizes for analyses and still represented an even diurnal distribution.

Ratio or interval scale data and proportions in behavioural data, were analysed by first testing if the data were parametric, before or after transformation (log_{10}, square, and square root for proportions), in order to use multifactor ANOVAs (*F* statistic), followed by Student-Newman-Keuls (SNK) post hoc tests, to compare monthly, inter-site and inter-sex means. When data did not satisfy the requirements of normality or equal variance, I used Kruskal-Wallis ANOVAs (KW ANOVA; *H* statistic), followed by Dunn's post hoc comparisons, to evaluate differences in sample medians amongst months, and I used Mann-Whitney tests (MW; *T* statistic) or Student's *t* tests (*t* statistic) for inter-site and inter-sex comparisons. This procedure was followed to assess (a) changes in proportional activity and behaviour between sites and sexes, and among months, (b) the effect of sex, site and season on body temperature (T_b), and (c) to evaluate temporal changes in T_b across seasons. Where a multifactor ANOVA would not allow tests of interactions in proportional differences in activity and active behaviours between sexes within months, I used contingency table analyses (χ^2 tests) to assess proportional differences. Contingency table analyses were also used to assess temporal changes in proportional behaviour between and within seasons. The

number of counts of a behaviour within a time-period was considered sufficient when the mean expected values (n/rc, where n = total count, r = the total for each row and c = the total for each column) were more than or equal to six (Zar, 1999). In addition to multi-factor ANOVAs, I used one-way repeated measures ANOVA (RMA) or Friedman's repeated measures ANOVA (FRMA, χ^2 tests) to analyse the proportion of time spent by males, females and all tortoises in each active and inactive behaviour. Paired *t*-tests were used to compare time spent within each sex/the sexes combined for basking in cover or basking in the open. In all instances, I applied a sequential Bonferroni procedure on all families of tests to control for Type I errors (Holm, 1979).

For obtaining mean angles ($\bar{a}$) and lengths of mean vectors (r) for orientation data (circular distributions), I first calculated the rectangular coordinates of the mean angles according to Zar (1999):

$$X = \frac{\Sigma f_i \cos a_i}{n} \quad \text{and}$$

$$Y = \frac{\Sigma f_i \sin a_i}{n}$$

Where a_i is the midpoint of the measurement interval (each cardinal point in degrees), f_i is the frequency of each cardinal point, and $n = \Sigma f_i$. The length of the mean vector, r, was calculated using the equation:

$$r = \sqrt{X^2 + Y^2}$$

The length of the mean vector (r) can vary from 0 to 1.0, representing a measure of data concentration, with 1.0 indicating full orientation in one direction. Because r can be biased for grouped data (Zar, 1999), I used a correction factor (c) for data grouped in intervals of d degrees ($d = 45°$) to calculate an adjusted mean vector (r_c).

$$c = \frac{d\pi / 360°}{\sin(d/2)}$$

$$r_c = Cr$$

The sample mean angle, $\bar{a}$, was then determined as having the following cosine and sine:

$$\cos \bar{a} = \frac{X}{r_c} \quad \text{and}$$

$$\sin \bar{a} = \frac{Y}{r_c}$$

Circular standard deviation (S_0) was calculated according to Zar (1999) by using the equation:

$$S_0 = \frac{180°}{\Pi} * (\sqrt{-2 \ln r})$$

I used Rayleigh's z test to test the null hypothesis that tortoise orientation relative to the refuge did not differ from a uniform, circular distribution, thus that orientation had no mean direction.

$$z = \frac{R^2}{n} \qquad \text{where } R = nr_c.$$

Chi-square tests were used to test for differences in orientation frequencies between sexes and sites, and among seasons (Zar, 1999). I used simple regressions (r^2) to estimate the variance in proportional daily activity that was attributable to minimum, maximum and mean daily temperatures. When data were not normally distributed and/or heteroscedastic (even after transformation), I used Spearman's rank correlation (r_s, e.g. for correlating proportional daily activity with daily rainfall). Only days where there were 10 tortoise locations or more recorded were used in proportional activity regressions or correlations. Spearman' rank correlations were also used to investigate relations between T_b, T_g and T_a when tortoises (male, female and sexes combined) were active and inactive and during specific behaviours where data were heteroscedastic and/or not normally distributed. If data were parametric, I used analysis of covariance (ANCOVA) to evaluate if slopes and elevation of male and female regressions (T_b on T_g) differed, when either resting or basking. When slopes differed, I used Zerbe tests where appropriate, and when elevations differed, I used the adjusted mean Y to compare elevations.

All statistical analyses were performed using SigmaStat 2.03 and SPSS version 17 (SPSS Inc., Chicago, USA) and in the case of ANCOVA and Zerbe tests, Microsoft excel. The programme Oriana, version 3 (Kovach Computing Services, Pentraeth, Wales, UK) was used for all statistics involving circular distributions. For sake of simplicity and ease of comparison, I always reported means (±standard deviations) even when non-parametric tests were used.

6.3 RESULTS

6.3.1 *Activity and behaviour*

6.3.1.1 Effects of site, sex, month, and climate on activity & behaviour

Within each sex and combined, the percentage of tortoises found resting was higher than it was for tortoises found basking or active, but while a higher proportion of tortoises were found basking than active, within each sex the proportion of basking to active animals did not differ ($F_2 \geq 45.16$, df ≥ 42, $P < 0.00001$; Table 6.2). In both sexes and sexes combined, tortoises were more often found basking in cover than they were basking in the open (paired *t*-tests, $t \geq 4.64$, df ≥ 21, $P \leq 0.0001$; Table 6.2).

Table 6.2 Counts and percentages of 12 male and 15 female telemetered *Psammobates oculifer* found active, inactive, in the open and in cover (see Table 6.1 for definitions). Inactive comprised of basking and resting animals, with basking consisting of tortoises in cover (CAB) and or in the open (OAB). An asterisk denotes a significant difference between sexes (three-way ANOVAs, $P \leq 0.037$).

	Females	%	Males	%	Total	%
Inactive	1555	84.5	1611	86.4	3166	85.5
Resting	1045	56.8	1183	63.4*	2228	60.2
Basking	510	27.7*	428	23.0	938	25.3
CAB	357	19.4	322	17.3	679	18.3
OAB	153	8.3*	106	5.7	259	7.0
Active	285	15.5*	254	13.6	539	14.5
Open	438	23.8*	360	19.3	798	21.5
Cover	1402	76.2	1505	80.7	2907	78.5
Totals	1840		1865		3705	

Site did not affect number of tortoises in the open, active, inactive or tortoises in a specific inactive behaviour, e.g., resting (open $\log_{10}$ transformed, three-way ANOVAs, $P > 0.73$), thus results are restricted to sex and month only. Females were more often in the open, 24% of behaviours, and were more often active, 16% of behaviours, than were males, 19% and 14% of behaviours for open and active respectively ($F_{1,10} \geq 7.03$, $P \leq 0.022$; Table 6.2). Tests done for nightly activity indicate that *P. oculifer* is not active after sunset ($n = 10$ tortoises and 5 nights). Sex affected the percentage of tortoises found resting, basking and in the subcategory, basking in the open (OAB; three-way ANOVAs, $F_{1,10} \geq 5.78$, $P \leq 0.037$), but percentage of tortoises basking in cover was similar between sexes ($P = 0.36$). The percentage of males found resting

was higher than it was for females, but females basked and basked in the open more often than males did (Table 6.2).

There was an effect of month on tortoise activity (three-way ANOVA, $F_{10,10}$ = 10.36, P = 0.0005). Activity was lower in May, July and August (winter) than it was in any other month, except September, and activity in April 2006 surpassed that of September (Fig. 6.1). The three-way ANOVA with balanced design does not allow analyses of interactions between factors. However, the graphic representation suggests that female activity was greater than males' was in April 2006 and March 2007, while males were more active than females in October (Fig. 6.1), and these differences between sexes within months were confirmed by χ^2 test results ($\chi^2_1 \geq 5.02$, $P \leq 0.025$).
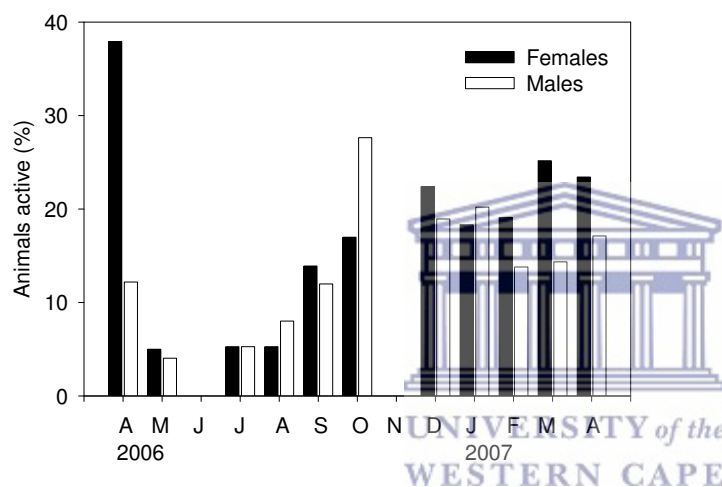
Figure 6.1 Monthly percentages of active *Psammobates oculifer* at Benfontein (sites combined). Data were collected from radio-tracking 12 males and 15 female tortoises.

Daily proportions of tortoises found active (square root transformed, only days with 10 or more records) were significantly affected by changes in both maximum and mean daily temperatures ($r^2_{156} \geq 0.31$, $P < 0.0001$), but the strongest relationship was between activity and minimum daily temperature ($r^2_{150} = 0.32$, $P < 0.0001$; Fig. 6.2). There was also a positive correlation between daily proportional activity and rainfall (r_s = 0.25, n = 156, P = 0.002). There was no correlation between rainfall and mean, maximum or minimum daily temperatures ($P > 0.08$).
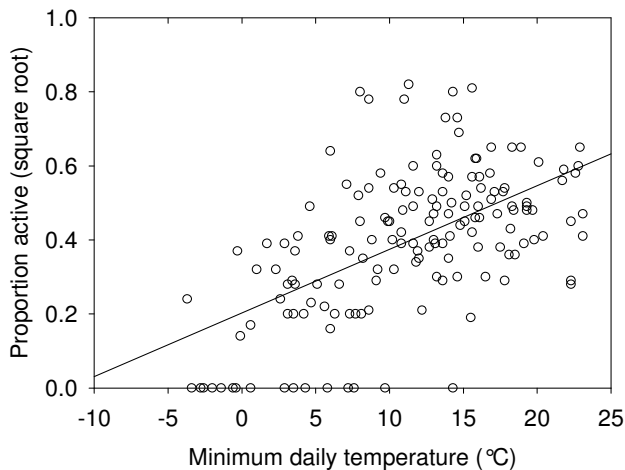
Figure 6.2 Relationship between the proportion of tortoises found active (n = 156) from April 2006 to April 2007 and minimum daily temperature (°C; SAWS; r^2_{156} = 0.32, P < 0.0001). Only days with 10 or more tortoise behavioural records were included.

Both sexes and combined were found walking more often that they were feeding or socialising, but although feeding was more common than socialising in all tortoises and females, within males they did not differ (FRMA, $\chi^2_2 \geq$ 37.0, P < 0.00001; Table 6.3). Feeding frequency was higher in females than it was in males (three-way ANOVA, $F_{1,10}$ = 9.93, P = 0.01), but although the percentage of females found walking tended to be lower than the males found walking, it was not significant (P = 0.055; Table 6.3).

Table 6.3 Counts and percentages of female, male and all tortoises in different active behavioural categories (see Table 6.1 for definitions). Data were collected from radio-tracking 12 males and 15 female tortoises and from opportunistic captures of tortoises while radio-tracking. An asterisk denotes a significant difference between sexes (three-way ANOVA, P = 0.01).

	Females	**%**	**Males**	**%**	**Total**	**%**
Walking	307	83.0	289	84.3	596	83.6
Feeding	49	*13.2	29	8.4	78	10.9
Socialising	14	3.8	25	7.3	39	5.5
Totals	370		343		713	

The frequencies of all inactive behaviours; resting and basking and the subcategories, basking in cover (CAB) and basking in the open (OAB) were affected by month (three-way ANOVAs, $F_{10,10} \geq$ 4.81, P < 0.02). In April and May 2006 and from December to March (summer/early autumn), tortoises were frequently found resting, more so than

they were in August and September 2006 and April 2007. Incidents of resting in April 2007 were also lower than they were in July and October (Fig. 6.3a). Basking and its subcategory, basking in cover, was prevalent in winter and early spring (August to September) when, together with April 2007, the percentage of tortoises basking and basking in cover was higher than it was in October through March (the hotter months) and in April 2006. In addition, in May tortoises basked more than they did in January and together with basking in cover, more in May and October than they did in April 2006 (Fig. 6.3b). Also in August, tortoises were found basking in the open more than they were in April 2006, December and January.
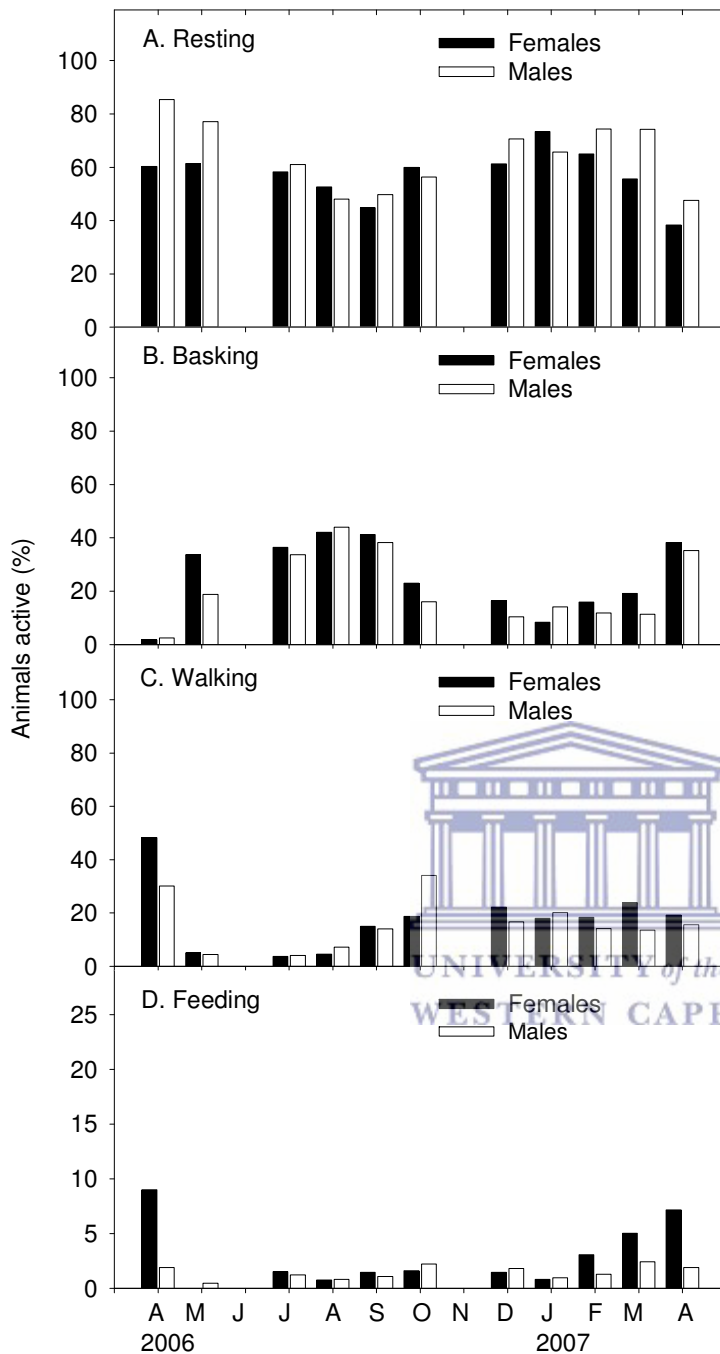
Figure 6.3 Monthly percentages of female and male tortoises found in different behavioural categories (sites combined). Results for resting and basking were derived from 27 telemetered tortoises, whereas results for walking and feeding were based on telemetered tortoises and opportunistic captures. There were no records for June and the few records for the beginning and end of November were included in October and December respectively.

Walking frequency was affected by month (three-way ANOVA, $F_{10,10}$ = 39.06, P < 0.00001; Fig. 6.3c). Incidences of walking were highest in April 2006, next highest in

October and lowest in May to August (winter). Feeding frequency was also affected by month (three-way ANOVA, $F_{10,10} = 4.51$, $P = 0.013$); tortoises in April 2006 were found feeding more often than they were in May, August and January (Fig. 6.3d). The balanced design of the three-way ANOVA did not allow testing for interactions between factors, but the graph suggested that females walked more often than males did in April 2006 and March 2007, the opposite being true in October (Fig. 6.3c). Chi-square tests confirmed graphic trends in October and March 2007 ($\chi^2_1 \geq 5.76$, $P < 0.017$) but in April 2006, the sex difference was not quite significant ($P = 0.052$; Fig. 6.3c). Females were found feeding more often than males were in April 2007 ($\chi^2_1 \geq 5.34$, $P < 0.021$) but not in other months ($P \geq 0.19$; Fig. 6.3d). Socialising was restricted to the period September to January.

The proportion of tortoises found basking, resting and walking within all seasons differed among time-periods ($\chi^2_7 \geq 23.1$, $P \leq 0.0017$; Figs. 6.4 A-E) but after the application of a sequential Bonferroni, feeding was not affected by time-period within any season ($P \geq 0.014 > 0.0125 =$ adjusted α). The lack of temporal difference in feeding was probably due to small sample size (mean frequency per season = 16) and it was excluded from the temporal comparison among seasons. Socialising was also infrequent, and only seen from September to January.

Temporal patterns of resting differed among all seasons ($\chi^2_7 \geq 21.4$, $P \leq 0.003$), but there were some general patterns. During autumn 2006 and winter, tortoises tended to avoid resting during the middle of the day, while in spring and autumn 2007, tortoises largely rested early in the day. In summer, tortoises spent most of the day resting (10:30 to 16:30; see Fig. 6.4 A-E). Basking patterns did not differ in the cooler periods, autumn 2006 and winter, or between autumn 2007 and spring when temperatures were relatively benign ($P \geq 0.14$), but the basking pattern did differ among other seasons ($\chi^2_7 \geq 48.4$, $P < 0.0001$). Tortoises tended to bask more during the middle of the day in autumn 2006 and winter, while in spring and autumn 2007 basking patterns were more uniform throughout the day (Figs. 6.4 A to C and E respectively). In summer, basking was largely confined to the two early time-periods (Fig. 6.4 D).

The temporal pattern of tortoises found walking did not differ in autumn 2006, spring, and autumn 2007 ($P > 0.19$). Walking frequencies within time-periods differed amongst all other seasons ($\chi^2 \geq 26.9$, df ≥ 6, $P < 0.0002$). Walking was most frequent mid-afternoon in winter (unimodal) and early and late in the day in summer (bimodal), but more evenly spread through time-periods (compared to summer or winter) in the two

autumns and spring. However, walking in spring, summer and autumn 2007 was more frequent before 12:00 than it was later in the day (Fig. 6.4 C-D).
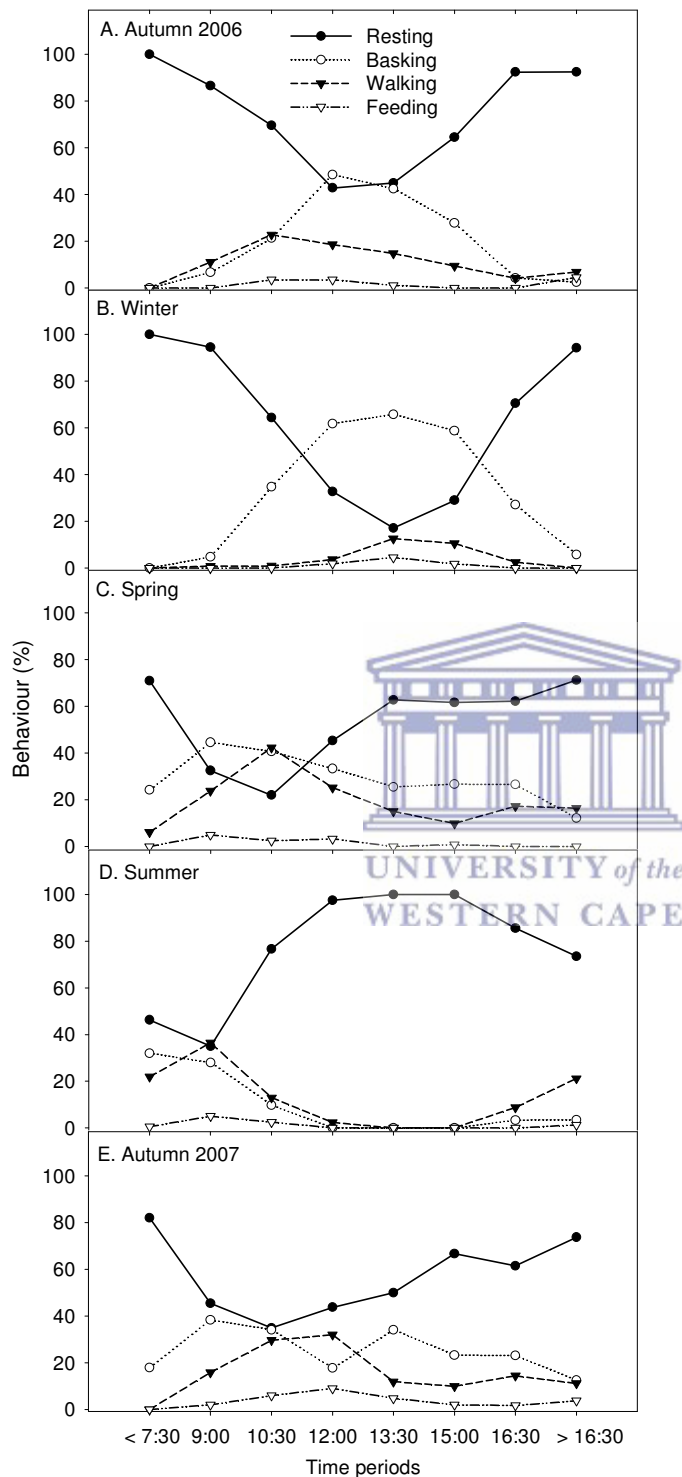
Figure 6.4 Temporal pattern of behaviour in *Psammobates oculifer* during the five seasons of study. Results for resting and basking were derived from 27 telemetered tortoises, whereas walking and feeding results were based on telemetered tortoises and opportunistic captures. Autumn 2006 included April and May (closer to winter) while autumn 2007 was closer to summer (March and April).

6.3.1.2 Orientation

The mean direction (orientation) in which tortoises were found relative to their refuge was east for males (93.9±112.0° circular SD, n = 532) and females (99.6±107.1°, n = 447), and for tortoises in site E (97.0±104.4°, n = 463) and site W (96.4±115.2°, n = 516). The circular distribution of tortoises' orientation was not uniform, neither within sexes nor within sites (Rayleigh's tests, $Z_{0.05}$ ≥ 9.064, n ≥ 447, P < 0.0001) and it did not differ significantly for either sex or site (χ^2 tests, P > 0.49). Within each season, I found no effect of month (χ^2 tests, P ≥ 0.069), thus temporal analyses were restricted to the level of season. The mean orientation in autumn 2006 (April and May) was north-northeast (18.5±76.2°) as it was in winter (July and August; 32.8±65.5°) and there was no difference between the two (χ^2 tests, P > 0.069; Fig. 6.5). Tortoises in summer (December 2006 to February 2007) were orientated east (77.3±107.9°) which was similar to that of autumn 2007 (March and April), east-southeast (116.3±100.3°) and again, mean orientation did not differ (χ^2 tests, P = 0.126; Fig. 6.5). Tortoise orientation in autumn 2006 and winter differed from that of summer and autumn 2007 (χ^2_7 ≥ 23.7, P ≤ 0.001). Spring mean orientation was south-southeast (160.8±96.7°) and it differed significantly from all other seasons (χ^2_7 ≥ 34.4, P ≤ 0.001; Fig. 6.5).
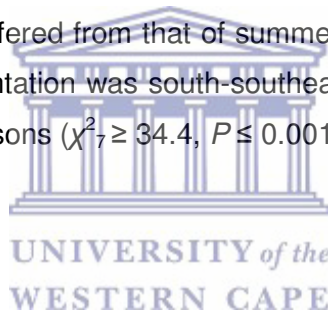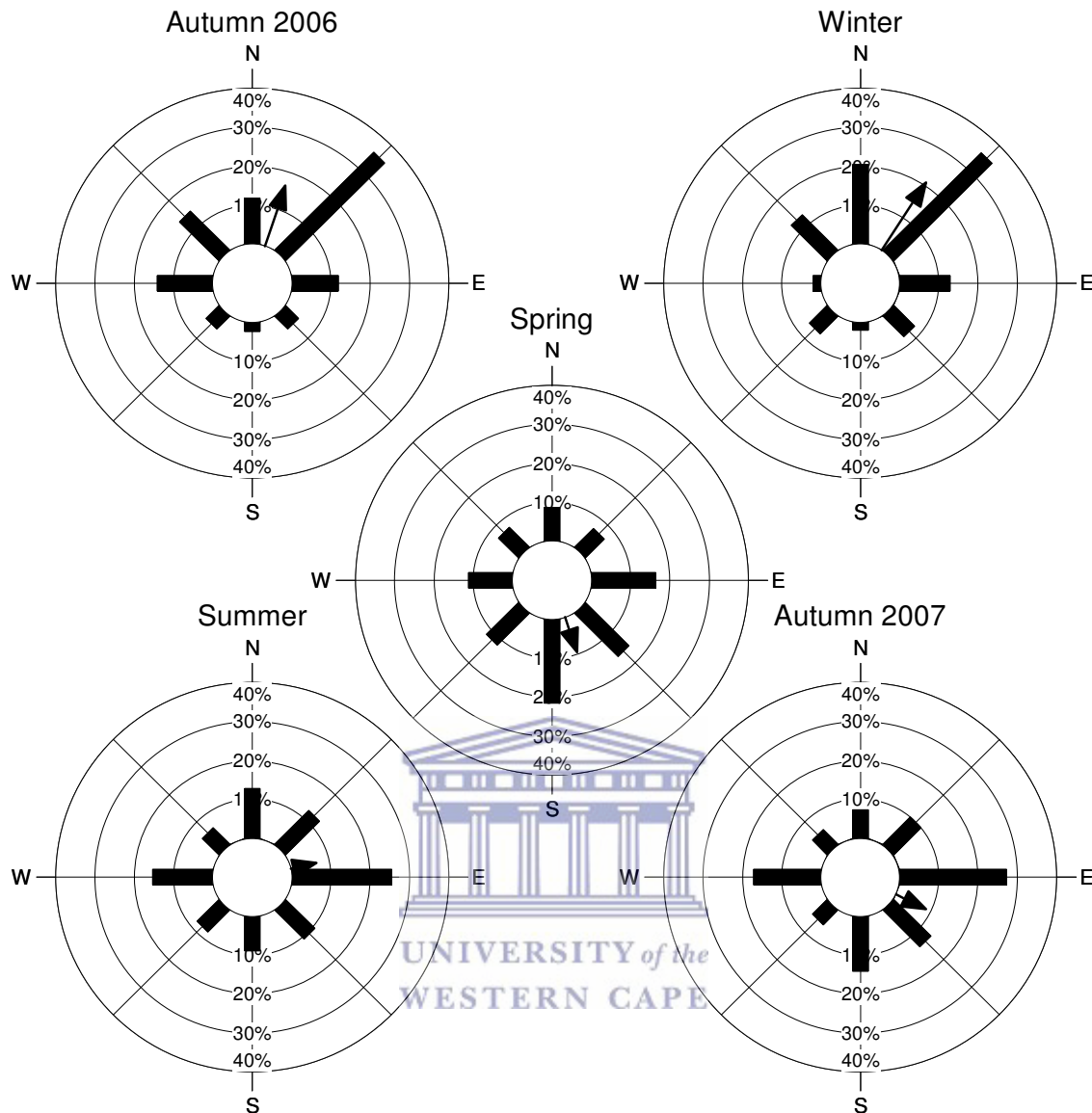
Figure 6.5 Seasonal orientation of tortoises (relative to their refugia). Black bars represent percent (frequencies) of direction (north, northeast, east, southeast, south, and south-west, west and north-west). Mean direction and its magnitude (r) are represented by black arrows. Seasonal *n* = 42, 93, 273, 310 and 261 for autumn 2006, winter, spring, summer and autumn 2007, respectively (total *n* = 979). Autumn 2006 was represented by April and May (nearer to winter - cooler) while autumn 2007 was directly after summer (March and April – warmer). To avoid pseudoreplication, I used data from only the first record when the same tortoise was found in the same refuge consecutively (see Chapter 5).

6.3.2 Temperature

Tortoises' mean body temperature (T_b) during the study was 28.1±7.0 ℃ (n = 589), while mean active T_b was 31.2±4.5 ℃, significantly higher than the inactive T_b of 25.8±8.8 ℃ ($T_{334,255}$ = 90575, P < 0.00001). Of individual behaviours, the mean T_b of the two inactive behaviours, basking and resting, was comparable at 26.0±7.3 ℃ and 25.8±9.4 ℃, respectively. Similarly, there was little difference between the mean body temperatures of tortoises in the three active behaviours, feeding (32.7±2.7 ℃), socialising (33.5±2.3 ℃) and walking (30.8±4.7 ℃). Ground (T_g) and air (T_a) temperatures for the different behaviours followed a broadly similar pattern to that of T_b (Table 6.4). Both T_a and T_b had wider temperature ranges when resting (T_a: 1.5 ℃ to 45.0 ℃ and T_b: 3 ℃ to 40.4 ℃) and basking (T_a: 10.0 ℃ to 36.0 ℃ and T_b: 7.9 ℃ to 36.9 ℃), than they did while walking (T_a: 16.4 ℃ to 36.4 ℃ and T_b: 16.7 ℃ to 39.1 ℃). The range of T_a and T_b was relatively narrow for the more specific active behaviours, feeding and socialising (mating and fighting; Fig. 6.6).
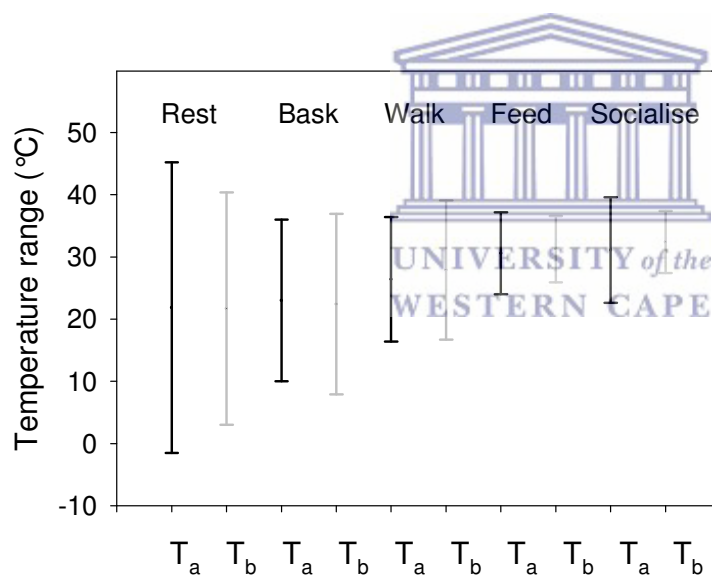
Figure 6.6 The air and body temperature ranges (T_a and T_b, ℃) for tortoises found resting, basking, walking, feeding and socialising (mating and fighting).

Air temperatures during socialising were higher than they were when tortoises basked. Body and ground temperatures of tortoises found in any active behaviour were higher than they were when tortoises were basking or resting (two-way and KW ANOVAs, df = 4, $P ≤$ 0.00001; Table 6.4).

Table 6.4 Mean (±SD): body (T_b) ground (T_g) and air (at ground level; T_a) temperatures (℃) for tortoises when found basking, resting, feeding, socialising (mating and fighting) and walking.

Behaviour	*n*	T_b (℃)	*n*	T_g (℃)	*n*	T_a (℃)
Resting	*227*	25.8 ± 9.4	*227*	24.4 ± 8.7	*227*	26.0 ± 10.3
Basking	*107*	26.0 ± 7.2	*107*	23.4 ± 6.2	*107*	24.8 ± 6.2
Walking	*214*	30.8 ± 4.7	*211*	30.0 ± 5.9	*213*	27.5 ± 4.2
Feeding	*21*	32.7 ± 2.7	*21*	31.2 ± 4.3	*21*	28.7 ± 2.8
Socialising	*20*	33.5 ± 2.3	*20*	31.1 ± 5.0	*20*	30.9 ± 4.7

Although males' mean T_b (28.7±7.7 ℃), behaviours combined, was marginally higher than that of the female T_b (27.6±7.7 ℃), the difference was significant ($T_{292,297}$ = 90765, P = 0.025). As well as testing for the effect of sex, I also tested for effects of site on T_b, T_g and T_a as these temperatures may have been affected by differences in habitat (vegetation cover) between the two sites (see Chapter 4). Tortoises' T_b at site W was higher than it was at site E ($T_{265,324}$ = 71721, P = 0.0017) as were T_g and T_a (two-way ANOVAs, data squared, $F ≥ 4.86$, df1 = 1, df2 ≥ 582, $P ≤ 0.028$).

There was no effect of sex on T_b when tortoises were inactive (P = 0.48), but male T_b, 32.2±4.0 ℃, was higher than female T_b, 30.2±4.8 ℃, when tortoises were active ($T_{133,122}$ = 17651, $P < 0.00001$). Amongst the different behaviours, neither T_g nor T_a differed between sexes, nor did T_b differ between sexes when tortoises were basking, resting or feeding (two-way ANOVAs, MW and *t* tests, df ≥18, $P ≥ 0.07$). However, males' T_b was significantly higher than that of females when they were found socialising (January removed as *n* = 2) and walking (walking T_b squared, two-way ANOVAs, $F ≥ 4.92$, df1 = 1, df2 ≥ 12, $P ≤ 0.047$; Fig. 6.7).

There was little effect of month on tortoise T_b when in active behaviours. It did not differ amongst months when tortoises were found feeding or socialising (socialising without January as *n* = 2, two-way and one-way ANOVAs, $P > 0.07$) and although T_b appeared to differ for tortoises' walking (T_b squared, $F_{8,196}$ = 2.15, P = 0.033) the post hoc test was not significant. Unlike active behaviours, there were monthly differences in T_b for tortoises found in each inactive behaviour (resting, data squared and basking, $F ≥ 8.06$, dfs ≥ 9, 96, $P ≤ 0.00001$; Fig. 6.8). Differences in T_b for basking were restricted to May when it was lower than it was for all other months. Tortoises found resting had higher

body temperatures in summer (December, January and February) than they did in May to August (winter) and April 2007.
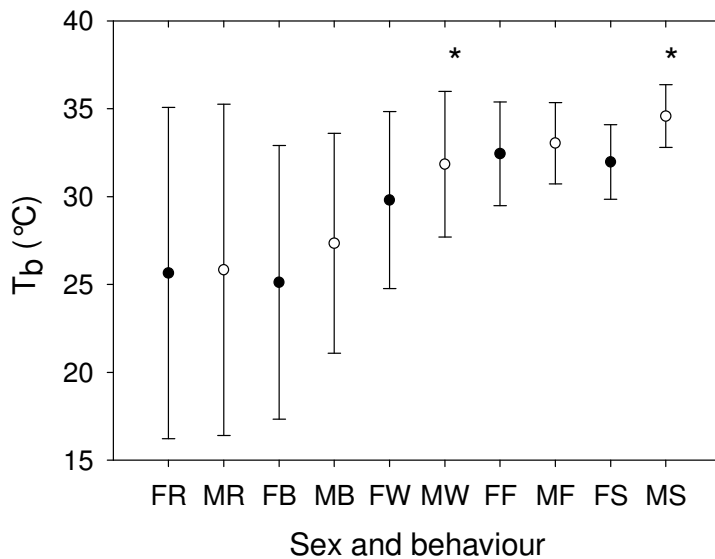
Figure 6.7 Mean body temperatures (T_b, ±SD) of female (F) and male (M) tortoises when found resting (R), basking (B), walking (W), feeding (F) and socialising (S, includes mating and fighting). An asterisk denotes a significant difference in body temperature between sexes (t and MW tests, $P < 0.0084$).
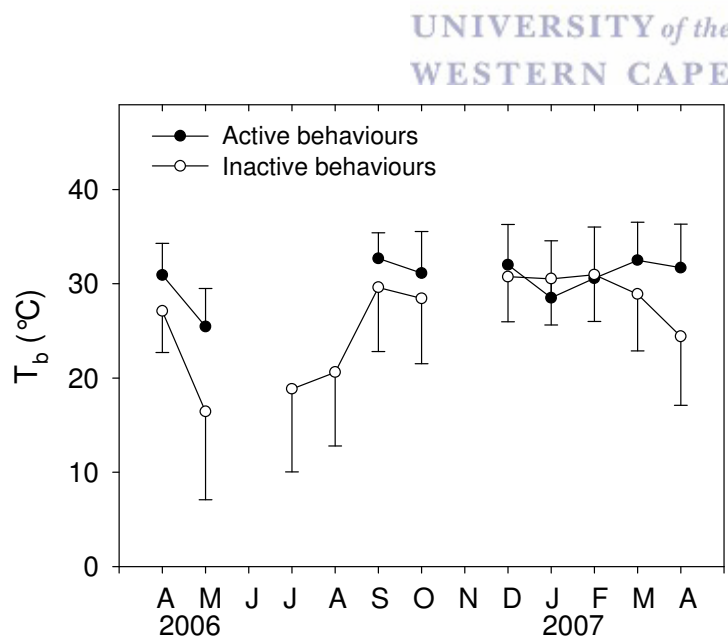
Figure 6.8 Mean monthly body temperatures (T_b in °C, ±SD) for all tortoises found in active (feeding, socialising and walking) and inactive (basking and resting) behaviours.

Tortoise body temperatures differed between time-periods in all seasons (one-way and KW ANOVAs, df 1 ≥ 6, df 2 ≥ 44, $P < 0.0002$) but in autumn 2006, the post hoc was not significant. Tortoise T_b in winter was lowest from 7:30 to 9:00 (the first time-period in winter) and body temperatures between 9:00 and 10:30 were lower than in all remaining periods, while the T_b of tortoises between 13:30 and 15:00 exceeded those measured after 16:30 (Fig. 6.9). In spring, tortoises' T_b was higher between 10:30 and 13:30 than it was before 9:00. In addition, spring body temperatures in the period 10:30 to 12:00 and the periods after 15:00 were higher than they were before 7:30. During summer, T_b in all time-periods was greater than it was before 9:00 and tortoises in the period 7:30 to 9:00 had higher body temperatures than they did before 7:30. Similarly, in autumn 2007 tortoises in all time-periods had a higher T_b than those measured before 9:00 (Fig. 6.9).

Sex did not affect T_b within a time-period (Mann Whitney Rank Sum tests and two-way ANOVAs, $P > 0.05$) but season affected T_b within all time periods (9:00 to 10:30 squared, KW and two-way ANOVAs, df 1 = 1, df 2 ≥ 46, $P < 0.02$) except the period between 13:30 and 15:00 ($P > 0.10$; Fig. 6.9). In the period 9:00 to 10:30 there was also an interaction between season and sex ($F_4 = 4.7$, $P = 0.002$). During the first time-period, summer body temperatures were higher than those taken in both spring and autumn 2007 were. Autumn 2006 only had one record and winter had no records before 7:30 (Fig. 6.9). In the period 7:30 to 9:00, body temperatures in summer were the highest, they were next highest in spring and the T_b in autumn 2007 was greater than it was in autumn 2006 and winter (Fig. 6.9). Body temperatures within males and within the sexes combined were highest in spring and summer in the third time-period (9:00 to 10:30), T_b in autumn 2007 exceeded that of autumn 2006 and the winter T_b was lowest of all. Within females, all body temperatures taken in the third time-period, except winter, were higher than they were in autumn 2006 and again, T_b was lowest in winter. Female T_b was also higher than male T_b in both autumns in the third time-period. During the fourth period, 10:30 to 12:00, T_b was relatively uniform among seasons, summer and spring body temperatures were higher than they were in winter. In the succeeding time-period (12:00 to 13:30), the T_b in spring and summer were higher than they were in autumn 2006 and winter (Fig. 6.9). Body temperatures did not differ among seasons in the sixth time-period (13:30 to 15:00) and in periods' seven and eight (15:00 onwards) results mirrored those for 12:00 to 13:30 (Fig. 6.9).
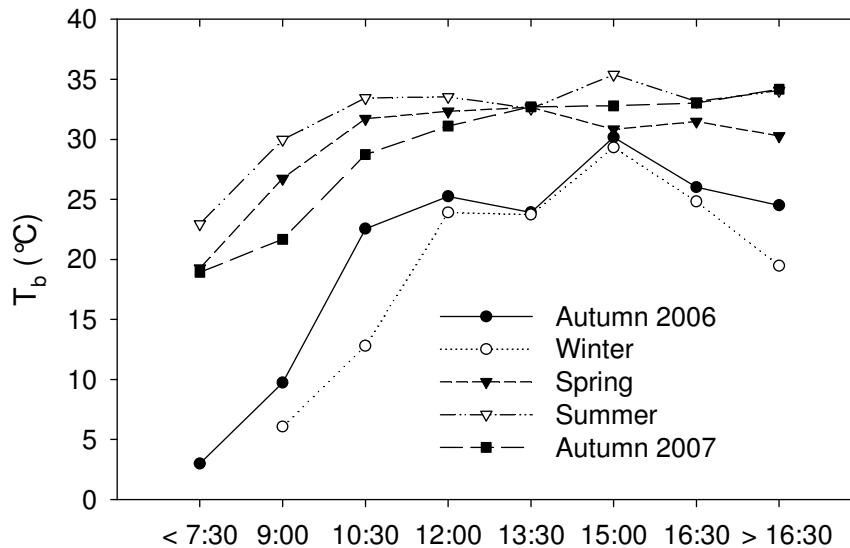
Figure 6.9 Temporal shifts in tortoise body temperature (T_b in °C) among seasons in 1.5 hour intervals. There were no temperatures taken in winter and only one temperature taken in autumn 2006 before 7:30. For clarity, error bars have been omitted.

The T_b of both sexes and for the sexes combined correlated with T_a and T_g (°C) when tortoises were active, inactive or the two combined ($r_s \geq 0.51$, $n \geq 121$, $P < 0.00001$). The correlation of T_b was stronger with T_g than it was with T_a in each category, except when tortoises were inactive, when the correlation was stronger with T_a (Table 6.5).

Table 6.5 Spearman's rank correlations (r_s) between body (T_b) and corresponding ground (T_g) and air (T_a) temperatures (all °C) and sample sizes (n) within each sex and for all tortoises found active, inactive and in the two categories combined. All correlations were significant ($P < 0.00001$).

	All behaviours				**Inactive**				**Active**			
	T_g	n	T_a	n	T_g	n	T_a	n	T_g	n	T_a	n
Females	0.85	*295*	0.81	*296*	0.89	*164*	0.89	*164*	0.77	*131*	0.63	*132*
Males	0.79	*291*	0.71	*292*	0.83	*170*	0.86	*170*	0.67	*121*	0.51	*122*
All	0.82	*586*	0.76	*588*	0.87	*334*	0.88	*334*	0.73	*252*	0.58	*254*

When tortoises (sexes combined) were found basking and resting, T_b was significantly related to T_g, as was T_b to T_a in resting tortoises ($F_{1,105} \geq 198$, $r^2 \geq 0.65$, $P < 0.00001$). In addition, T_b in basking tortoises was correlated to T_a ($r_s = 0.83$, $n = 107$, $P < 0.00001$). When analysed independently, T_b for both males and females was significantly related to T_a and T_g when tortoises were resting or basking ($F \geq 36.9$, dfs $\geq 1, 53$, $r^2 \geq 0.47$, $P <$

0.00001). I compared the regression slopes of T_b on T_g between the two sexes when they were basking and resting, and females' slopes were steeper than male slopes in both cases ($t \geq 2.11$, df ≥ 103, $P \leq 0.038$). However, the Zerbe test for basking and resting showed T_b would not differ between sexes for any given value of T_g.

When found in the most common active behaviour, walking, the body temperature of males, females and the two sexes combined correlated with T_g and T_a ($r_s \geq 0.51$, $P <$ 0.0001, Table 6.6). The body temperature of all feeding tortoises, sexes combined, and socialising tortoises was also correlated to T_g and T_a as was the T_b of feeding males to T_g ($r_s \geq 0.47$, $n \geq 8$, $P < 0.038$; Table 6.6). There was no significant relationship between T_b and T_g in feeding females, nor were the regressions between T_b and T_a significant for feeding tortoises in either sex ($P > 0.06$).

Table 6.6 The correlation coefficients between body temperature (T_b) and corresponding ground (T_g) and air (T_a) temperatures (all °C) together with sample sizes (*n*) when tortoises were found walking, feeding or socialising (mating and fighting). Spearman's rank correlations (r_s) were used for all analyses ($P < 0.05$ for all significant correlations). No remaining T_a and T_g categories were significant (ns; $P > 0.06$). "NA" means not applicable.

	Walking				Feeding				Socialising			
	T_g	*n*	T_a	*n*	T_g	*n*	T_a	*n*	T_g	*n*	T_a	*n*
Females	0.81	*110*	0.63	*111*	ns	*13*	ns	*13*	NA	NA	NA	NA
Males	0.66	*101*	0.51	*102*	0.71	8	ns	8	NA	NA	NA	NA
All	0.75	*211*	0.58	*213*	0.47	*21*	0.48	*21*	0.73	*20*	ns	*20*

6.4 DISCUSSION

As is generally true of ectotherms, daily activity of *Psammobates oculifer* at Benfontein was low. Tortoises' activity level at 15% is broadly similar to those of other testudinids that have an approximate daily activity range of 10% to 20% depending on season and study design (Nagy & Medica, 1986; Moskovits & Kiester, 1987; Hailey & Coulson, 1999; Kazmaier et al., 2001a; Keswick et al., 2006). When active, the mean body temperature (T_b) of *Psammobates oculifer* (31.2±4.5, range 16.7 to 39.1 °C) was comparable to that of other arid zone tortoises. The desert tortoise, *Gopherus agassizii*, has a mean active T_b of 30.6 °C and a range of 19.0 to 37.8 °C (Brattstrom, 1965) and the Egyptian tortoise, *Testudo kleinmanni* (similar in size to *P. oculifer*), was recorded as having a mean active T_b of 29.7±4.5 °C and a range of 18 to 36 °C (Geffen &

Mendelssohn, 1989). Within the boundaries of thermoregulation, sexual dimorphism and physiological differences between sexes also influence an ectotherm's activity and behaviour (Dunham et al., 1989).

Psammobates oculifer is sexually dimorphic; males are smaller than females (Chapter 8), thus, males are potentially more vulnerable to predation and extreme temperature than females are. Males spent more time in cover than females did, which may be a consequence of either of these threats, or a combination of the two. At Benfontein, black-backed jackals (*Canis mesomelas*) preyed upon tortoises (Klare et al., 2010) and although the authors did not specify which tortoise species, one of the scutes found in a jackal scat looked to belong to *P. oculifer* (T Keswick, personal observation). Exposure to high temperatures also appeared to influence the amount of time males spent in cover. Despite spending more time in cover and choosing denser refuges than females did (Chapter 5), mean male T_b was higher than that of females.

At Benfontein, temperature was an important driver of seasonal activity in *P. oculifer*. The cool winter months (July and August) heralded a low point in tortoise activity, but unlike some testudinids in arid or semi-arid environments (Rautenstrauch et al., 1998; Lagarde et al., 2002; and see Diaz-Paniagua et al., 1995), activity did not cease entirely. Winter activity may be linked to the favourable winter environment at Benfontein. Despite mean winter night-time temperatures of between 2 and 5 °C, diurnal conditions, which were clear and dry with mean afternoon temperatures of 18 to 20 °C, allowed *P. oculifer* relatively uninterrupted basking so they could attain a sufficient T_b for activity. Even in winter in this study, tortoises managed to reach a T_b of approximately 27 °C in the period between 13:30 and 15:00 – not significantly different from the T_b from any other season at these times. An incentive for tortoise activity in winter is food; winter annuals such as *Ifloga* sp., and the abundance of the small, perennial shrub *Plinthus karooicus* (see Chapter 4), were both consumed by tortoises during winter (T Keswick, unpublished data). In this respect, *P. oculifer* may be similar to another relatively small tortoise, *Testudo kleinmanni*, which also feeds on annuals during winter in the Negev desert (Geffen & Mendelssohn, 1988).

Gender was not a recognised factor affecting tortoise activity in winter, but seasonal trends in activity suggested there were monthly differences between sexes, perhaps due to differing physiological requirements. Males were more active than females during October, the middle of the mating season. Male testudinids are known be more active than females in the spring (when mating) both to find females and to patrol

territories (Douglass & Layne, 1978; McRae et al., 1981; Lagarde et al., 2002; Keswick et al., 2006), and this seems to be case with *P. oculifer* at Benfontein. The roles reversed in April 2006 and March 2007, when females tended to be more active than males, and in April 2007, when females were found feeding more often than males. A gravid female was found in early April 2006 (MD Hofmeyr, unpublished data) and it is possible that females were more active in autumnal periods because of foraging related to high seasonal reproductive output.

Although females were more active than males, partly due to higher levels of foraging, all tortoise activity had a positive relationship with air temperature. An interesting pattern emerged between body (T_b) and air temperatures (T_a) as tortoises moved from passive to active behaviours. The range of T_b narrowed with air temperature as tortoises went from passive to active, and narrowed further as activity became more specific (feeding and socialising). Air temperature and T_b ranges were wide in resting tortoises, probably reflecting both the pre-resting behaviour (e.g. evading heat after walking) and the amount of time passed since exhibiting such behaviour. Basking T_b and T_a was also wide-ranging but less so than resting as tortoises moved from a low to 'operational' T_b. From walking, where the minimum activity T_b was 16.7 °C, T_b and T_a narrowed through feeding and socialising. Narrowing of T_b for specific behaviours is important in ectotherms as it simplifies the integration of a specific activity with its internal processes (Pough, 1980). Performance in ectotherms has been shown to improve at certain temperatures, but 'optimal' T_b may vary depending on the type of behaviour being performed (Stevenson et al., 1985). Walking is the most general of active behaviours and it would be expected that walking may take place at a relatively wide range of temperatures, as walking may have many outcomes (e.g. walking to find cover, forage or to mate).

Despite there being no effect of sex on T_b when tortoises were in passive behaviours, or while they were feeding, male T_b was higher than female T_b when tortoises were found walking or socialising. High temperatures in walking males may be a function of them being smaller than females and thus more susceptible to having an elevated T_b while in the open. Males having a higher T_b than females when socialising is probably linked to males being more active than females during the mating season, and thus were more exposed than females were.

Although T_b did not differ between sexes when they were basking, females were found basking more often than males were. Females probably bask for longer than males

because they are larger and thus need more exposure to reach similar temperatures. Females may also need to bask more frequently than males to meet specific reproductive requirements (Hofmeyr, 2004). When basking, male and female T_b were similar overall, but female T_b was higher than male T_b in both autumn 2006 and 2007 during the early 'basking' period from 9:00 to 10:30. Unfortunately, autumn 2006 was the beginning of the study and sample sizes of behavioural frequencies were small, so comparisons are difficult. Despite small sample size, 8 out of 10 feeding records in autumn 2006 were females, of which 80% took place between 9:30 and 12:10. Equally, in autumn 2007, out of 30 feeding records, 17 took place between 9:00 and 12:00 and 71% were females (females were also found feeding more often than males were in April 2007). In order to feed, females would have had to reach a specific temperature range to do so and this may account for their elevated T_b in these periods. Although sex may affect the amount of basking and basking periods, all tortoises exhibited a distinct seasonal refuge orientation pattern, which may assist in thermoregulation.

During the cold period of late autumn (April and May 2006) and winter (July and August), tortoises predominately positioned themselves north-northeast of their refuges. By doing so, they received the first rays of sun and remained well positioned to receive solar radiation from sunrise while remaining in protective cover (which tended to be less dense in autumn and winter, see Chapter 5). At midday, between 55 and 60% of tortoises were actively basking in autumn 2006 and winter. Equally, tortoise T_b in winter increased from just over 5 °C before 9:00 to nearly 25 °C at midday. Although frequencies were low, tortoises were most active during the period from 13:30 to 15:00 in winter (10:30 to 15:00 in autumn 2006), and T_b was highest at 15:00 in both seasons. Thus during colder seasons, tortoises effectively 'tracked the sun' from the beginning to the end of the day which allowed them to reach a T_b high enough to be active and feed.

From winter to summer (December to February), tortoises went from tracking to avoiding the sun, as they spent a large proportion of the middle of the day during summer in animal burrows. Even after discounting refuges used by tortoises on consecutive days, 67% of refuges ($n = 131$) used between 10:30 and 15:00 were burrows (see Chapter 5). However, their orientation in summer suggests that they still used the sun judiciously. Tortoises were orientated in an easterly direction, where they would receive early morning sun. Basking, though generally low in summer, tended to be higher in the early morning (before 7:30), by which time tortoises' T_b had already reached a similar level to that of midday in winter. Thus, the predominant active T_b was

similar in winter and summer, but the amount of 'thermoregulating' time (basking and through refuge orientation) needed to reach this T_b was much greater in winter than it was in summer. In turn, the attainment of an 'active T_b' was reflected by proportional tortoise activity, which was highest at midday in winter and between 7:30 and 9:00 in summer. Hence, despite generally avoiding the summer sun, refuge orientation in summer still assisted tortoises to reach 'activity T_b'. As burrow use was predominant in the middle part of the day in summer, the opposite was true in the mornings prior to 9:00 (the end of the peak tortoise activity period) when 88% of tortoise refuges (*n* = 88) were plants. Plant refuges allowed tortoises to bask while in cover in the early summer mornings. Tortoises were also active, albeit less so than in the morning, in the late afternoon and unlike the other seasons, summer activity was bimodal. Bimodal activity has been recorded for other species of testudinids when midday temperatures are high (McRae et al., 1981; Geffen & Mendelssohn, 1989; Diaz-Paniagua et al., 1995; Lagarde et al., 2002).

Autumn 2007 (March and April) and spring (September and October) were both periods where temperatures were relatively benign – less extreme than winter or summer. Temporal basking patterns were generally uniform and did not differ between autumn 2007 and spring. Although mean orientation differed between the two, spring was south-southeast and autumn 2007 east-southeast, orientation was towards the morning sun in both cases. Both seasons had unimodal activity patterns (temporal walking patterns did not differ between autumn 2007 and spring), probably reflecting moderate air temperatures compared with summer or winter. However, tortoise T_b increased quicker in spring than it did in autumn 2007 and T_b was higher in the periods 7:30 to 10:30 in spring than it was in autumn 2007. Proportional activity reflects this; a higher proportion of tortoises were active earlier (9:00 to 10:30) in spring than they were in autumn 2007. Earlier tortoise activity in spring compared with autumn 2007 may reflect earlier sunrises in the spring compared with autumn; receipt of early sun by tortoises would hasten activity time. Male tortoises have been shown to heat up quicker than females (males are smaller) and thus be active earlier for mate searching (Lagarde et al., 2002). The male *P. oculifer* is also smaller than the female and more males (57%, *n* = 88) were active than females (44%, *n* = 45) at Benfontein between 9:00 and 10:30 during spring but the difference in activity frequency between sexes was not significant.

In summary, tortoises' use of orientation appeared to utilise the sun in all seasons, although winter was when it was most pronounced. Orientation towards the sun early in

the day, while remaining in protective cover, would be an advantage to tortoises in any season as it would hasten the arrival of the 'T_b threshold' for activity. Further indication of a 'T_b threshold' for activity was that mean active T_b did not differ among seasons. An 'optimum' T_b for converting food into energy has been determined for insectivorous lizards (Beaupre et al., 1993) and although the effect of T_b on digestion may differ between insectivorous and herbivorous lizards, T_b can still influence gut transit times in herbivorous lizards (Zimmerman & Tracy, 1989). Zimmerman & Tracy (1989) discuss gut transit times in context of large, herbivorous lizards that can maintain a stable T_b easier than can smaller animals. Thus, the ability of *P. oculifer* to keep a stable 'operating' temperature may be advantageous for efficiently processing food as well as for general activity.

Studies of refuge orientation in South African testudinids are rare, but *Stigmochelys pardalis* in the Northern Cape were found to be orientated south or south-west during winter (McMaster & Downs, 2006a). Winter orientation of *S. pardalis* is opposite to that found for *P. oculifer* in this study. Differences in results between the two studies may be due to *Stigmochelys pardalis* being a much larger tortoise than *P. oculifer* (Branch, 1988; Boycott & Bourquin, 2000) and size affects heating and cooling rates in ectotherms (Stevenson, 1985). This study determined refuge orientation using a random selection of refuges in each season when tortoises were not actively basking, while in the study by McMaster & Downs (2006a), tortoises were divided into forms (overnight) and shelters (diurnal), in which tortoises showed or did not show thermoregulatory behaviour. It may be that differences in winter orientation between these studies are a function of differences in design and interpretation. Of other studies of thermoregulation, the small arid zone tortoise, *Testudo kleinmanni*, was recorded most often (77% of the time) on the east and south side of bushes during winter and spring in the Negev desert (Geffen & Mendelssohn, 1989). These appear similar for the equivalent seasons at Benfontein considering that *T. kleinmanni* occurs in the Northern Hemisphere. However, the sampling method for refuge orientation in the study of Geffen & Mendelssohn (1989) was not clear and it only involved two (lumped) seasons.

During this study, both air (T_a) and ground (T_g) temperatures were taken in tandem with T_b and generally, there was a stronger relationship between T_b and T_g than there was between T_b and T_a and this was true when tortoises were found in active behaviours. A possible reason for this is that ground temperatures taken near active tortoises may include the effect of irradiance in a similar way to a tortoise's carapace, the same not being true of T_a. Active T_b had a greater correlation to T_g than T_a for two other studies

of testudinid species *T. kleinmanni* (Geffen & Mendelssohn, 1989) and *Gopherus polyphemus* (Douglass & Layne, 1978), both of which inhabit arid or semi-arid areas and habitats with sandy substrates. Interestingly, habitat appeared to affect the thermal environment at Benfontein, as it did tortoise body temperatures. Site W had significantly less vegetation cover than site E did (Chapter 4) and T_a, T_g and T_b were all higher in site W. Active tortoises would be more exposed to the sun in site W, which may account for higher temperatures in all cases (the chances of encountering a tortoise in the open were higher in site W).

Apart from thermoregulation, rainfall can also affect tortoises' activity and behaviour, and daily proportions of tortoises active correlated with rainfall in this study. With rainfall comes lower diurnal temperatures and this may give tortoises more opportunities to be active, particularly in summer in the Northern Cape. However, there was no correlation between rainfall and minimum, maximum or mean temperature in this study and in any event, cloud cover may also reduce diurnal air temperatures but again, I did not record it. Tortoises, particularly in arid areas where rainfall timings and quantity are unpredictable, are known to emerge during/after rain to drink and forage (Nagy & Medica, 1986) and this may be an influencing factor here.

6.5 CONCLUSION

Male tortoises spent more time in cover than females, perhaps due to their small size making them more vulnerable to predators and extreme temperatures. Females basked more than males, possibly because they were larger and to facilitate female reproductive processes. As expected, tortoises spent little time active, with activity being lowest during the colder months, May to August. Unlike some arid zone tortoises, *P. oculifer* did not brumate. This was partly due to warm midday temperatures in winter and tortoises using refuge orientation and basking to reach 'active' body temperatures by midday, enabling tortoises to feed. Tortoises' body temperature during activity did not differ among seasons but ranges of body temperature narrowed as an activity became more specialised. The ability to keep a constant 'operating' temperature may facilitate food processing as well as general activity. Although females were more active than males, male tortoises were more active in spring, probably because of mating related behaviour, while females were more active in autumn when they tended to forage more than males, possibly related to a seasonal increase in female reproductive costs.

7   SPACE REQUIREMENTS AND MOVEMENT PATTERNS

7.1   INTRODUCTION

The concept of a home range appears relatively simple; an area within which an animal can fulfil most of its basic life history requirements, i.e., sheltering, foraging and procreation (Burt, 1943). As part of their paper on home range and body weight in mammals, Harestad & Bunnell (1979) outline a fundamental relationship between an animal and its home range; energy requirements relate to habitat productivity. In areas of high productivity, it is not necessary for an animal to forage as far and home ranges are smaller. Habitat productivity links in to rainfall and escalating aridity requires an increase in home range size in order for an animal to satisfy energy requirements. However, climatic affects on home range may be more easily identifiable with season than they are with a surrogate variable such as rainfall. For example in the northern hemisphere, home ranges in winter decline with a declining availability of quality forage (Harestad & Bunnell, 1979).
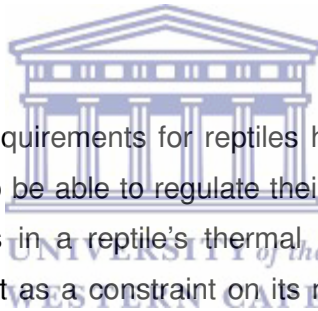
The fulfilment of life history requirements for reptiles has an additional component to that of mammals; they need to be able to regulate their body temperature (Dunham et al., 1989). Temporal changes in a reptile's thermal environment and availability of suitable microclimates may act as a constraint on its movement and, hence its home range (Grant & Dunham, 1988). In addition, many reptiles have lower aerobic energy production than endotherms, which restricts sustained movement (Pough, 1980) and consequently, may impact on their home range size. Other aspects of reptile physiology, such as a low resting metabolic rate and the ability to go into 'torpor' allow them to tolerate periods of low resources where the more 'expensive' physiology of endotherms can not (Pough, 1980), and this may reduce the requirement of a reptile having to move (e.g. to forage) during such periods.

Peculiar among reptiles is the tortoises' shell. The degree of protection afforded by the shell make it less vulnerable to predators than other reptiles and thus their movements are less restrained by the need to be close to protective cover (Hailey, 1989). Despite this, arid zone tortoises are vulnerable to heat and drought in summer, and cold in winter, and may need to centralise their home range around burrows or shelters during such periods, thereby restricting space use (Geffen & Mendelssohn, 1988; Rautenstrauch et al., 1998; Duda et al., 1999; Freilich et al., 2000). Gender can affect tortoise movements due to intraspecific differences in life histories, e.g., males covering

large areas in mating related behaviour (Diemer, 1992; Lagarde et al., 2003) or females looking for nesting sites (Bulova, 1994). Males of the desert tortoise, *Gopherus agassizii*, were recorded as having larger home ranges than females in some studies (Duda et al., 1999; Freilich et al., 2000; Harless et al., 2009) but other studies found no differences between sexes (Barret, 1990; O'Connor et al., 1994; Riedle et al., 2008). As it may be in mammals (see Harestad & Bunnell, 1979), sexual dimorphism is a possible reason for gender related home range differences in tortoises. Larger (longer) specimens of the Texas tortoise, *Gopherus berlandieri*, were found to travel further than shorter specimens did (Auffenberg & Weaver Jr, 1969) but neither O'Connor et al. (1994) nor Harless et al. (2009) found a relationship with body size and home range size in *G. agassizii*. Hailey & Coulson (1996b) compared area used among tortoise species and the largest species, *Stigmochelys pardalis*, used a significantly bigger area than the two smaller species. However, this may not have been entirely due to size, but possibly a quest for mineral nutrients.

Calculation of an animal's home range is subject to differing opinions and can prove problematic (Kernohan et al., 2001; Horne & Garton, 2006; Row & Blouin-Demers, 2006; Laver & Kelly, 2009). Theoretically, an animal should show site fidelity (Spencer et al., 1990) before it can have a home range. However, site fidelity can be defined, subjectively, based on knowledge gained by observation of a species (Powell, 2000). Home range analyses are affected by sampling regime, specifically when testing for time to statistical independence between location points (see Swihart & Slade, 1985a; Swihart & Slade, 1985b; Swihart & Slade, 1997). Statistical independence of location points is not easily attained with tortoises, which move small distances punctuated by occasional longer forays (Rose & Judd, 1975; O'Connor et al., 1994). In achieving statistical independence of location points in a tortoise study, one would likely lose other important biological information such as understanding an animal's use of space (de Solla et al., 1999; Otis & White, 1999). The sampling regime and number of location points are critical elements of home range analyses as both minimum convex polygons and kernel analyses are sensitive to sample size (Powell, 2000; Kernohan et al., 2001). Without being able to compare sampling regimes and location data, it is difficult to make comparison with other studies and this information is often not reported in tortoise studies (Harless et al., 2010).

The main objective of this study was to quantify, for the first time, space use in a wild population of the Kalahari Tent Tortoise, *Psammobates oculifer*. I used radio-tracking to document the effect of changing seasons on its movements and home range and

compared sexes, sizes and animals in different habitats to see whether this influenced space use. Finally, I attempted to evaluate how the space use of *P. oculifer* compared with other arid zone tortoises where available sampling information between studies allowed.

7.2   MATERIALS AND METHODS

7.2.1   *Radio-telemetry and location points*

The study took place at Benfontein farm (28°53' S; 24°51' E), Kimberley, South Africa, at two study sites (E and W) with different vegetation characteristics (Chapter 4). Both sites were located within a fenced-off cattle area of approximately 2,700 ha (see Chapter 2 for further details on the study area). The boundaries and farm tracks of the entire farm, as well as the boundaries of the study sites were mapped using a hand-held GPS unit (eTrex GPS, Garmin Corp, Olathe, KS, USA).

The study duration was mid March 2006 to end April 2007, slightly over one year, but for sake of ease of comprehension all measurements made from animals over the entire study period is referred to hereinafter as 'annual'. During March and early April 2006, I captured 12 male and 13 female tortoises which were fitted with carapace-mounted radio-transmitters (mass <12% of body mass, AVM Instrument Company Limited, Colfax, USA) to study, inter alia, their movement patterns and spatial requirements. Males were distinguished from females because they were flatter than females and had a longer tail (Boycott & Bourquin, 2000; Branch, 1988). In order to investigate if differences in vegetation and gender affected animal space use, I divided sexes more or less equally between the two sites to allow statistical comparisons. After they had been fitted with transmitters, tortoises were returned to their point of original capture (marked with a flagged cane and GPS located). On locating a telemetered tortoise, I recorded, inter alia, its behaviour (Chapter 6), the date, time, and GPS coordinates (±3-5 m). I weighed tortoises on first capture and approximately twice per field excursion (see Chapter 3 for weighing schedules and methods), allowing me to investigate the effect of body mass on tortoise home range and movement, both seasonally and over a tortoise's entire tracking period. I collected rainfall data on the study site and rainfall and temperature data was available from the South African Weather Service (SAWS) weather station 5 km from the study area (Chapter 2). Climate results are discussed in Chapter 4.

Radio-tracking was carried out using an R-1000 hand-held telemetry receiver (Communications Specialist Inc, Orange, CA, USA) and a three-element, hand-held, Yagi antenna. Relocations were low in autumn 2006, when I started radio-tracking tortoises, and in winter, when animal movements were limited, but I tracked each tortoise once per day on a minimum of 20 separate days in each of spring, summer and autumn 2007 (see Chapter 2, Table 2.1 for a monthly breakdown of seasons and field excursion days). The number of location points per tortoise differed (Table 7.1), as tortoises were sometimes temporarily lost because they made a large displacement or a transmitter signal became weak, or a combination of the two. At the end of spring (beginning of November 2006), I lost one female tortoise (#102) possibly due to transmitter failure. During summer, two females, #707 and #726, died at beginning December and another female (#101) died at the end of January. Male #743 also died in summer (end January) and male #721 had a low body mass and its condition may have compromised its movements, thus it was excluded from analyses starting beginning February (marked 'LBM' – low body mass). Tortoise 721 died beginning autumn 2007 along with females #725 and #737 (Table 7.1). One male (#743), found turned over in deep sand, probably died from heat exposure but the cause of death was unknown for the remainder. I captured two additional females (one in site E and one in the site W) in January 2007 and fitted them with transmitters to supplement the lost or dead tortoises (Table 7.1). Ten male and seven female tortoises were radio-tracked throughout the study period.

Table 7.1 Number or relocation points for each Kalahari tent tortoise in the five seasons covered by the study and the entire study period from April 2006 to April 2007. Data collected from tortoises 743, 101, and 721 were excluded from seasonal analyses in the season that they died, or the season before they died (#721), hence *N*-Total does not equal the sum of seasonal *n* for these tortoises. Similarly, tortoises 7016 and 7017 were tracked from the middle summer, but due to the small summer sample size were only included in autumn 2007 seasonal analyses.

ID	Site	Sex	*n*-total	*n*-au06	*n*-wi	*n*-sp	*n*-su	*n*-au07
15	E	F	103	14	14	23	38	14
703	E	F	113	17	14	24	38	20
717	E	F	103	12	12	24	37	18
726	E	F	51	13	12	26	Died	Dead
737	E	F	88	12	13	24	39	Died
738	E	F	103	12	13	23	38	17

Table 7.1 continued

ID	Site	Sex	*n*-total	*n*-au06	*n*-wi	*n*-sp	*n*-su	*n*-au07
7017	E	F	35	n/a	n/a	n/a	n/a	20
18	E	M	116	15	13	24	38	26
23	E	M	116	18	13	24	40	21
715	E	M	116	16	13	27	38	22
716	E	M	104	15	13	25	29	22
739	E	M	111	13	13	24	39	22
743	E	M	69	13	13	27	Died	Dead
101	W	F	75	13	12	25	Died	Dead
102	W	F	53	19	12	22	Lost	Lost
706	W	F	111	19	12	22	38	20
707	W	F	55	18	12	25	Died	Dead
708	W	F	113	19	12	24	37	21
710	W	F	110	18	10	25	37	20
725	W	F	91	14	13	24	40	Died
7016	W	F	33	n/a	n/a	n/a	n/a	21
704	W	M	129	20	13	29	40	27
709	W	M	125	19	13	25	41	27
714	W	M	122	16	13	27	39	27
721	W	M	85	17	13	27	LBM	Died
733	W	M	121	15	13	25	41	27
747	W	M	121	14	12	28	40	27

7.2.2 Data and statistical analyses

The minimum period between relocations was one day (ca. 24 hours). In certain seasons, particularly winter, activity was minimal and the nature of tortoise movements (sporadic and often over relatively small distances with occasional long displacements) meant data were bound to be autocorrelated (see O'Connor et al., 1994). Reducing relocations would have been punitive to seasonal sample sizes and would have impacted on other information collected such as behaviour. I therefore ignored breaches of statistical independence (Swihart & Slade, 1985a; Swihart & Slade, 1985b; Swihart & Slade, 1997) in the data (see de Solla et al., 1999; Otis & White, 1999). I removed all displacements less than 5 m as GPS locations were accurate to 3-5 m. Because tortoises sometimes moved exaggerated distances after being handled ($T_{184,1734} = 231237$, $P < 0.00001$), I removed all displacement records of the day subsequent to an animal being weighed. Records for the first and last few days in

November 2006 were combined with October and December data, respectively, as sample sizes from these November periods were small.

I used ArcView GIS 3.1.1 (Environmental Services Research Institute, Redland, CA, USA) and the extension: Animal Movement, 2.04 beta SA version (AME, Hooge & Eichenlaub, 1997) to calculate consecutive displacements, annual and seasonal home range areas, and site fidelity of Kalahari tent tortoises. Rayleigh's Z test scores (see methods in Chapter 6 for formulae used) were generated as part of the AME home range statistics and allowed me to test if an animal's movements were non-directional over a specified period.

Site fidelity was assessed in accordance with Hooge & Eichenlaub (1997) based on the Monte Carlo random walk test developed by Spencer et al. (1990); 100 simulated walks per animal were used to test, using 95% confidence intervals, if space use was random, indicated dispersion or was constrained, i.e., showed fidelity (as discussed by Hooge et al., 2000). In cases where animals were close to exhibiting site fidelity after 100 walks, I ran 1000 simulated walks, which increased accuracy (Hooge & Eichenlaub, 1997; Hooge et al., 2000). I started the random walk simulation at the first location point for the entire tracking period of each tortoise and within seasons.

To analyse space use and utilisation distributions (UD), I used 95% and 50% probability, volume contoured, fixed kernel estimates (FK-95 and FK-50) and 100% minimum convex polygons (MCP). For FK-50 and FK-95, I calculated the smoothing factor or bandwidth (*h*) using the least square cross validation (LSCV) method (Seaman & Powell, 1996; Seaman et al., 1999) and grid extents were automatically calculated by the AME. Whenever seasonal home ranges of an animal either exceeded its annual home range or appeared over-smoothed due to a combination of low seasonal sample sizes and the distribution pattern of location points, I used the annual smoothing factor value (*h*) to constrain the seasonal home range (Seaman & Powell, 1996; van Bloemestein, 2005). For male #709, the LSCV method clearly under-smoothed its annual home ranges, therefore I used the *h* ref method (Silverman, 1986; Worton, 1989; Worton, 1995) rather than the LSCV method with un-standardised data to calculate the bandwidth (*h*) for both its FK-95 and FK-50 annual home ranges using the Home Range Extension version 3.2a for ArcView (Rodgers & Carr, 1998). I also counted how many MCP home ranges overlapped between males, females, males & females and all animals combined within each season.

All displacements were reported in meters (m) and home ranges were reported in hectares (ha). I recorded locations in GPS coordinates and converted these to decimal degrees by dividing minutes by 60. Consecutive displacements were measured using data in decimal degrees, but I calculated FK-95, FK-50 and MCP by first converting each ArcView shape file containing an animal's location points from decimal degrees to UTM 1983, WGS 84 (zone 35 south for Kimberley, South Africa). Fixed kernel and polygon UTM conversions were necessary for the calculation of area in ArcView. Animals' displacements were represented as daily displacements (relocations with one-day intervals) or as accumulated displacements for the study period and within seasons. Long movements were then defined as movements exceeding the 75th percentile for all one-day movements.

Tortoises that died were only included in daily displacement analyses up to the end of a month (field excursion, see Table 2.1) where their sample sizes and movements were comparable to all other tortoises within such month. Seasonal analyses were restricted to tortoises that were active for full seasons only (see Table 7.1 above for details). Annual MCP and FK estimates included animals that were not tracked for the entire period (see Table 7.1) but results excluding animals without a full data set were also given. A male (#739) made a 'sallie' (Burt, 1943) in spring and female #738 made three consecutive movements in autumn 2007 that appeared to be migratory. In the case of male #739, the sallie consisted of one large movement, the tortoise then stayed there for a day (i.e., two location points) before returning to its previous position prior to making the sallie. The tortoise did not return to the 'sallie' area again. Female #738 displaced 1.2 km over four days including travelling up and down a game fence until she found a hole and was still moving across the neighbouring farm when I captured her at the end of the study and removed her transmitter. As is suggested by Kernohan et al. (2001), these location points were omitted, subjectively, from each animal's respective home range analyses, including directional movement and site fidelity.

Simple regressions (r^2) were used to evaluate the effect of body mass (g) on displacement and home range. All regression analyses were done using the mean body mass for the relevant period. I also used a regression analysis to see if MCP sizes for each tortoise were dependent on the number of location points. When analysing ratio or interval scale data, I first tested if the data were parametric, before or after $\log_{10}$ transformation, in order to use multifactor ANOVAs (F statistic), followed by Student-Newman-Keuls (SNK) post hoc tests. When data did not satisfy the requirements of normality or equal variance after $\log_{10}$ transformation, I used Kruskal-

Wallis ANOVAs (KW ANOVA; *H* statistic), followed by Dunn's post hoc comparisons, to evaluate differences in sample medians amongst seasons and Mann-Whitney tests (MW; *T* statistic) or Student's *t* tests (*t* statistic) for inter-site and inter-sex comparisons. This procedure was followed to: (a) assess if male and female seasonal and seasonal-accumulated displacements at the two sites differed and (b) to evaluate the effects of site, sex and season on FK-95, FK-50 and MCP sizes. I also assessed the effect of sex and season (there was no effect of site) on daily distance by using two-way repeated measures ANOVA (RMA) on the mean of the $\log_{10}$ transformed daily distance moved for each individual tortoise. In addition, when site and/or sex did not affect annual data, a one-way RMA was used to assess effects of season on accumulated displacements, MCP and FKs using the individual tortoises as the subject. I used one-way or Friedman's RMAs to compare the effect of different home range analyses among MCP, FK-95 and FK-50, on area calculated, both annually and within each season.

Analyses of the effect of site, sex and season on proportion of 'long' to 'normal' tortoise displacements and overlapping MCPs were done using chi-square tests (χ^2) with a Yates correction for continuity where the degrees of freedom equalled one, or alternatively I used Fisher's exact tests where sample sizes were low. In all instances where chi-square analyses were used, mean expected frequencies were more than or equal to six in each case (Zar, 1999). Where contingency tables were 2 x 3 and frequencies were low (as was the case in counts of site fidelity versus random movement and dispersion), I used the Freeman-Halton extension to the Fisher's exact test. For all analyses, I applied a sequential Bonferroni procedure on all families of tests to control for Type I errors (Holm, 1979). All statistical analyses were performed using SigmaStat 2.03 and PASW version 18 (SPSS Inc., Chicago, USA), except VassarStats was used to calculate the Freeman-Halton (1951) extension to Fisher's exact test. Where data met assumptions of normality and equal variance, I reported means (±standard deviations), but for non-parametric data (the majority of results), I provided medians with 25th-75th percentiles.

7.3 RESULTS

7.3.1 *Displacements*

7.3.1.1 *Directional movement and site fidelity*

One tortoise, male 747 in site W, showed annual movements (mean bearing 240±98°, south-westerly) over its respective tracking periods that differed from random direction (Rayleigh's tests, $Z_{0.05} \geq 4.5$, $n = 121$, $P = 0.02$). Half the males showed site fidelity, a

male was close to showing fidelity ($P = 0.06$) and one male's movement pattern was indicative of dispersion, but the remaining males' movements did not differ from random (95% CI). The movements of five females indicated site fidelity while three indicated dispersion (another was close to dispersion) and all other female movements were 'random' (95% CI, Appendix A). Deaths and losses (and a short tracking period in the case of two females; Table 7.1) may have affected site fidelity results. Neither site nor sex affected the proportion of animals showing random, dispersed or constrained movements (χ^2 tests, $P \geq 0.60$, Appendix A). Among seasons, the proportion of animals showing site fidelity, dispersion or random movements differed between autumn 2006 and summer (Fisher's exact test, $P = 0.001$) but not among other seasons ($P \geq 0.008 >$ adjusted $\alpha = 0.005$; Table 7.2)

Table 7.2 Seasonal results of site fidelity tests (see Appendix A for annual details) from movements of male and female tortoises at Benfontein with mean number of location points per animal (±SD). Abbreviations Au-06, Wi, Sp, Su, Au-07 stand for autumn 2006, winter, spring, summer and autumn 2007 respectively. Low mean location points in autumn 2006 reflect that animals were still being captured for radio-tracking in this period and I reduced the number of relocations in winter, as tortoise activity was low. Tortoises that died or were lost have been removed from the relevant season and although tracking of females 7016 and 7017 started in the middle of January they have only been added to autumn 2007.

Season	Locations	Random	%	Fidelity	%	Dispersion	%	*n*
Au-06	16 ± 3	18	72	1	4	6	24	25
Wi	13 ± 1	15	60	4	16	6	24	25
Sp	25 ± 2	19	76	5	20	1	4	25
Su	38 ± 3	11	58	8	42	0	0	19
Au-07	22 ± 4	9	47	8	42	2	11	19

7.3.1.2 Effects of site, sex and season on daily displacements

Median (25th-75th percentiles) daily displacements for females and males respectively were 24.2 m (12.4-46.2 m) and 30.3 m (16.2-53.1 m) in site E, and 23.2 m (12.7-47.1 m) and 31.4 m (14.1-57.0 m) in site W. Site did not affect daily displacements (data $\log_{10}$ transformed, two-way ANOVA, $P = 0.99$) nor was there an interaction between site and sex ($P = 0.25$), but males made greater daily displacements than females did ($F_{1,807} = 7.8$, $P = 0.0052$). Similarly, males displaced further than females when I considered only tortoises with data for the whole study period ($F_{1,633} = 6.87$, $P = 0.009$).

As there was no effect of site on daily displacements, I combined sites for seasonal analyses of males and females separately. Seasonal means of $\log_{10}$ daily displacement for each animal did not differ between sexes (two-way RMA, $P = 0.26$) but there were differences among seasons ($F_{4,71} = 7.8$, $P = 0.00003$). Displacements in spring and autumn 2007 were greater than they were in summer and winter and in autumn 2006, they were greater than they were in winter (Fig. 7.1).
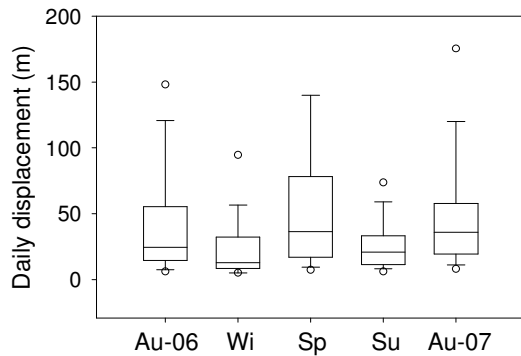
Figure 7.1 Seasonal median daily displacements (m; black centre line) with 25th-75th percentiles (bottom-top of box), 10th and 90th percentiles (error bars) and 95th percentiles (circles). Maximum distances (not shown) moved in a day were 293, 106, 519, 478, 622 m, respectively, in autumn 2006, winter, spring, summer and autumn 2007.

The median (25%-75%) of daily displacements was 27 m (13-51 m), and I thus considered long displacements as those that exceeded 50 m per day. Tortoises in site E (25%, $n = 364$) and W (27%, $n = 447$) completed similar numbers of long displacements, as did females (24%, $n = 380$) and males (27%, $n = 431$; all χ^2 tests, $P \geq 0.13$). Seasons affected proportion of long displacements made ($\chi^2_4 = 52.2$, $P < 0.00001$; Fig. 7.2). Tortoises in spring and autumn 2007 made a higher proportion of long distance displacements than they did in summer and frequencies of long distance movements in spring were higher than they were in winter ($\chi^2_1 \geq 10.4$, $P \leq 0.001$; Fig. 7.2). In addition, tortoises in autumn 2007 appeared to make a greater proportion of long distance displacements than they did in winter, but it did not differ after application of a sequential Bonferroni ($P = 0.02 > 0.007 = $ adjusted α).
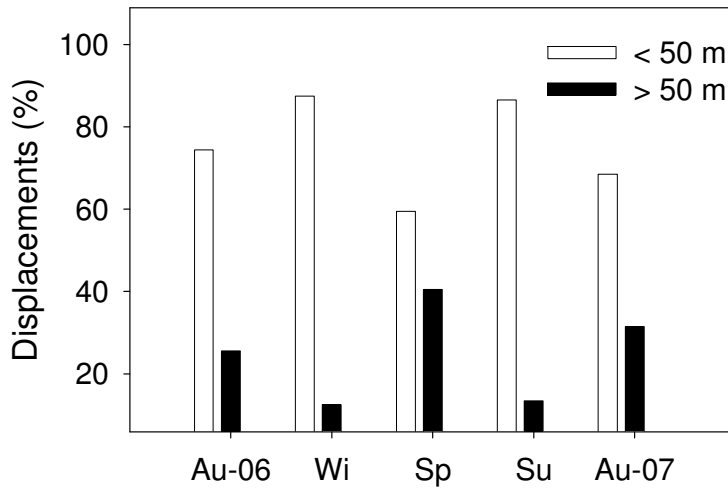
Figure 7.2 Seasonal percentage of short (< 50 m) and long (> 50 m) displacements by *Psammobates oculifer* at Benfontein. The proportion of long, daily displacements was higher in spring and autumn 2007 than it was in summer, and in spring, it was higher than it was in winter (χ^2 tests, $P \leq 0.001$).

7.3.1.3 Accumulated displacements

Annual accumulated displacements were not influenced by site or sex, nor was there an interaction between the factors (either with or without animals with an incomplete annual data set, two-way ANOVAs, $P > 0.21$; Table 7.3).

Table 7.3 Mean annual accumulated displacements (m; ±SD) of female (F) and male (M) *P. oculifer* in sites E and W. There was no effect of site or sex or an interaction between the two ($P > 0.21$).

Sex	Site	*n*	Mean			Minimum	Maximum
F	E	6	2657.9	±	1638.9	1235.3	5679.0
M	E	6	2449.5	±	1071.5	718.4	3430.4
F	W	7	2090.7	±	1242.7	717.5	3695.1
M	W	6	3569.6	±	2854.4	801.0	7508.3

Accumulated displacements differed among seasons (data $\log_{10}$ transformed, one-way RMA, $F_{4,82} = 93.6$, $P < 0.00001$); they were higher in spring, summer and autumn 2007 than in autumn 2006, and winter had the lowest accumulated displacement (Table 7.4). Within each season, there was no effect of sex or site or an interaction between the two (two-way ANOVAs, $P > 0.08$).

Table 7.4 Median (25th-75th percentiles) seasonal accumulated displacements (m) of *Psammobates oculifer* at Benfontein.

Season	*n*	Median	25th		75th	Minimum	Maximum
Au-06	25	206.8	134.7	-	269.3	25.8	384.3
Wi	25	81.5	36.7	-	133.8	20.2	236.4
Sp	25	890.9	485.9	-	1374.2	211.6	3924.2
Su	19	710.5	534.7	-	974.2	259.5	1892.8
Au-07	19	639.9	495.6	-	1085.6	140.8	2346.6

7.3.2 Home ranges

7.3.2.1 Annual

After excluding females #7016 and #7017 with short tracking durations from annual home range calculations, females had 94±23 location points in site E and 87±26 in site W. Males had 105±18 and 117±16 (min = 69) location points in sites E and W respectively (Table 7.5). Tortoises tracked over the whole study duration (*n* = 17) had 114±8 (min-max = 103-129) location points. Home range estimations of individuals varied substantially (Table 7.5) but did not differ for MCP and FK-95 estimates, which were both larger than FK-50 estimates (data $\log_{10}$ transformed, one-way RMA, $F_{2,48}$ = 225.1, $P < 0.00001$).

Total MCP size was not dependent on the number of location points (MCPs $\log_{10}$ transformed, *n* = 25, r^2 = 0.005, P = 0.74). Annual MCPs of six females and six males in site E were 8.0 (4.4-30.2) ha [individuals tracked of full study period: 8.0 (3.3-23.6), *n* = 4] and 2.9 (1.5-16.7) ha [3.6 (1.9-16.8), *n* = 5], respectively. Although mean annual MCPs in site W, 30.7 (1.3-72.5) ha for seven females [30.7 (8.7-39.8), *n* = 3] and 4.0 (2.0-241.0) for six males [4.7 (2.8-262.6), *n* = 5], appeared larger than they were in site E, there was much individual variation and neither sex nor site influenced mean annual MCP size (MCPs $\log_{10}$ transformed, two-way ANOVA, $P > 0.30$; Table 7.5). The result was similar when restricted to animals tracked for the entire study period (*n* = 17, $P > 0.30$).

Table 7.5 Annual MCP, FK-95 and FK-50 areas with smoothing factor (*h*) and number of location points for female (F) and male (M) tortoises at sites E and W (East and West). Date indicates the end of the tracking period, or the tracking duration for #7016 and #7017. The asterisk indicates that *h* was calculated by *h* ref instead of LSCV.

Sex	Site	ID	Points	MCP	FK-95	FK-50	*h*	Date
F	E	15	103	2.1	9.0	2.3	48	Apr-07
F	E	703	113	7.0	6.7	1.2	30	Apr-07
F	E	717	103	8.9	8.0	1.6	35	Apr-07
F	E	726	51	35.2	38.5	6.7	93	Oct-06
F	E	737	88	5.2	8.2	1.3	43	Feb-07
F	E	738	103	28.5	13.1	2.2	53	Apr-07
F	E	7017	35	2.4	3.6	1.0	34	Jan-Apr-07
F	W	101	75	11.3	14.7	2.2	58	Jan-07
F	W	102	53	96.1	163.6	20.2	232	Oct-06
F	W	706	111	42.8	56.4	7.5	141	Apr-07
F	W	707	55	0.7	0.7	0.1	12	Oct-06
F	W	708	113	30.7	10.3	0.8	44	Apr-07
F	W	710	110	1.3	1.2	0.1	16	Apr-07
F	W	725	91	72.5	79.2	20.5	170	Feb-07
F	W	7016	33	1.1	1.3	0.2	16	Jan-Apr-07
M	E	18	116	17.1	15.4	3.2	62	Apr-07
M	E	23	116	16.6	10.6	1.1	38	Apr-07
M	E	715	116	1.7	1.3	0.3	13	Apr-07
M	E	716	104	3.6	3.1	0.3	22	Apr-07
M	E	739	111	2.1	1.7	0.2	15	Apr-07
M	E	743	69	1.0	1.1	0.2	15	Dec-06
M	W	704	129	3.4	2.4	0.4	19	Apr-07
M	W	709	125	2.3	2.1	0.3	15*	Apr-07
M	W	714	122	4.7	3.6	0.6	19	Apr-07
M	W	721	85	1.1	0.7	0.1	10	Jan-07
M	W	733	121	219.3	105.9	12.0	161	Apr-07
M	W	747	121	306.0	181.3	39.7	243	Apr-07

Similar to annual MCPs, there was a great deal of variance in annual FK-50 and FK-95 areas and neither were affected by sex or site, either with all 25 tortoises included or when analyses were restricted to the 17 tortoises tracked over the duration of the study period (data $\log_{10}$ transformed, 2-Way ANOVAs, $P > 0.20$; Table 7.6).

Table 7.6 Median area (ha; 25th-75th percentiles) and minimum and maximum of both 50% and 95% volume contoured fixed kernels for 13 male and 12 male tortoises radio-tracked in at the West (W) and East (E) sites (see Table 7.5 for details of individual tortoises).

Sex	Site	FK	n	Median	25th		75th	Minimum	Maximum
F	E	50	6	1.87	1.20	-	1.20	1.20	6.72
		95		8.58	6.65	-	6.65	6.65	38.50
	W	50	7	2.18	0.11	-	0.11	0.11	20.47
		95		14.70	0.69	-	0.69	0.69	163.65
M	E	50	6	0.33	0.22	-	0.22	0.22	3.22
		95		2.40	1.14	-	1.14	1.14	15.36
	W	50	6	0.50	0.04	-	0.04	0.04	39.72
		95		3.01	0.60	-	0.60	0.60	181.27

7.3.2.2 Seasonal

MCPs differed among seasons (RMA, $F_{4,82}$ = 49.2, P < 0.00001). Spring MCPs were the largest and winter MCPs were the smallest (Table 7.7, Fig. 7.3). Within winter, there was a significant interaction between sex and site (data $\log_{10}$ transformed, 2-Way ANOVA, $F_{1,21}$ = 10.1, P = 0.005); tortoises in site E had larger MCPs than those in site W and within site E females had larger MCPs than males had, the opposite being true in site W. There were no other significant effects of sex or site within the remaining seasons (P > 0.11).

Both FK categories differed among seasons (RMAs, $F_{4,82}$ ≥ 27.4, P < 0.00001). The results for FK-95 areas were the same as those for MCPs; FK-95 areas were greatest in spring and smallest in winter (Table 7.7). Seasonal post hoc results for FK-50 areas were similar to those of FK-95 areas, but areas in spring and autumn 2007 did not differ and FK-50 areas in autumn 2007 were larger than they were in summer (Table 7.7). When I tested for sex and site differences within each season, there were none after I applied a sequential Bonferroni (two-way ANOVAs, P ≥ 0.02 > 0.01 = adjusted α). Concerning seasonal home range estimates, FK-95 areas were largest except in summer when MCP and FK-95 areas were the same; FK-50 areas were the smallest in all seasons (one-way RMA and FRMA tests, n ≥ 19, P ≤ 0.00001, Table 7.7).

Table 7.7 Median (25th-75th percentiles) seasonal MCP, FK-95 and FK-50 home ranges for 15 female and 12 male tortoises with minimum and maximum areas and the number of location points (mean ± SD). Animal were captured over the course of autumn 2006 and they were relatively sedentary in winter (and thus were located less frequently) hence the smaller sample sizes in these months. Annual *h* (Appendix A) was used as the smoothing factor for males 18 (Sp), 23 (Au-07), 714 (Au-06), 715 (Au-06 and Sp) and 716 (Sp and Su); and for females 703 (Sp), 710 (Su) and 7017 (Au-07) as the derived seasonal *h* overestimated the size of the seasonal home range in each case.

Season	*n*	Type	Median	25th		75th	Minimum	Maximum	Location Points
Au-06	25	MCP	0.74	0.36	-	1.99	0.10	6.44	16 ± 3
		FK-95	1.49	0.61	-	4.25	0.08	11.75	
		FK-50	0.17	0.09	-	0.75	0.01	1.68	
Wi	25	MCP	0.06	0.02	-	0.13	0.00	0.61	13 ± 1
		95	0.14	0.06	-	0.41	0.01	1.39	
		50	0.02	0.01	-	0.07	0.00	0.21	
Sp	25	MCP	2.47	0.90	-	10.95	0.39	73.46	25 ± 2
		FK-95	3.63	1.30	-	14.86	0.46	105.36	
		FK-50	0.42	0.18	-	2.01	0.05	31.11	
Su	19	MCP	0.87	0.43	-	1.17	0.05	4.13	38 ± 3
		FK-95	0.81	0.33	-	2.19	0.07	6.09	
		FK-50	0.11	0.04	-	0.38	0.02	1.47	
Au-07	19	MCP	0.89	0.29	-	6.10	0.06	52.80	22 ± 4
		FK-95	1.40	0.50	-	7.58	0.08	157.06	
		FK-50	0.21	0.11	-	1.15	0.01	24.18	

Site did not affect the number of MCP home ranges of telemetered tortoises that overlapped within a season (Fisher's exact tests, $P \geq 0.03 > 0.01$ = adjusted α) so I combined sites for all MCP overlap analyses. Frequencies of tortoises with MCP overlap differed among seasons ($\chi^2_4 = 35.2$, $P < 0.00001$, Table 7.8, Fig. 7.3), with more home ranges overlapping in spring than in winter, summer and autumn 07 ($\chi^2 \geq 11.5$, $P < 0.0007$; Table 7.8). The number of males with an MCP that overlapped with female MCPs also differed among seasons ($\chi^2_4 = 20.3$, $P = 0.004$). There were higher frequencies of male MCPs that overlapped with female MCPs during spring than there were in winter or autumn 2007 ($\chi^2 \geq 20.3$, $P \leq 0.006$) but not in autumn 2006 or

summer ($P \geq 0.027 > 0.0063$ = adjusted α). Season did not affect occurrence of same sex overlap of MCPs ($P > 0.05$, Table 7.8, Fig. 7.3).

Table 7.8 The number of minimum convex polygons overlapping between males (M-M), between females (F-F), between males and females (M-F), all tortoises ('All'), and the number of tortoises without overlaps ('None'). An asterisk denotes a significant difference among seasons (χ^2 tests, P ≤ 0.006).

Season	M-M	%	F-F	%	M-F	%	All	%	None	%	Total
Au-06	0	0.0	4	16.0	4	16.0	8	32.0	17	68.0	25
Wi	2	8.0	0	0.0	*0	0.0	*2	8.0	23	92.0	25
Sp	4	16.0	5	20.0	*9	36.0	*18	72.0	7	28.0	25
Su	2	10.5	0	0.0	1	5.3	*3	15.8	16	84.2	19
Au-07	1	5.3	0	0.0	*0	0.0	*1	5.3	18	94.7	19
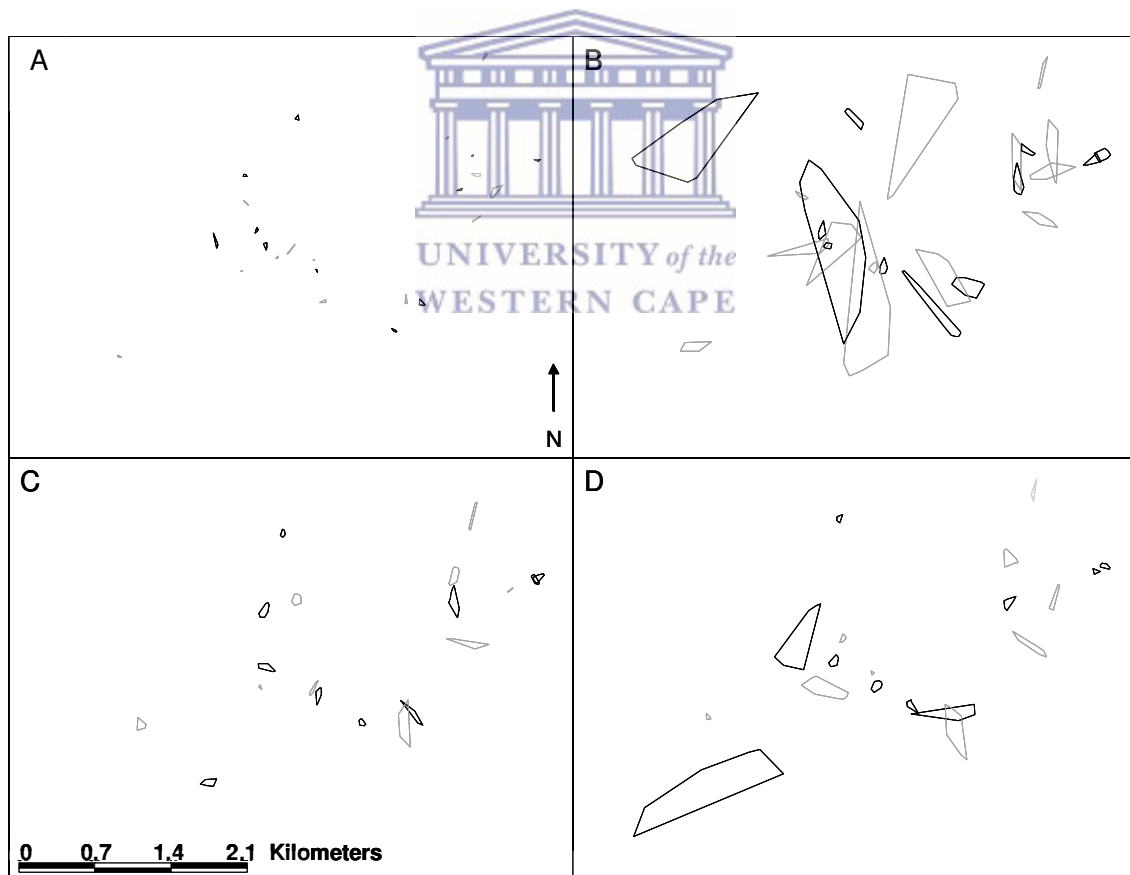
Figure 7.3 Winter (A), spring (B), summer (C) and autumn 2007 (D) minimum convex polygons (ha) for male (black outlines) and female (grey outlines) tortoises at Benfontein. Autumn 2006 was omitted to illustrate the change across four seasons. Panels are to scale in kilometres.

7.3.3   The effects of body mass on movement and space use

The effect of body size on home range size was limited to a few tenuous relationships within particular seasons. The significant regression between female body mass (g) and accumulated displacements in autumn 2007 ($F_{1,7} = 5.6$, $r^2 = 0.45$, $P = 0.049$) disappeared when one outlier was removed. In summer, MCP size increased with an increase in male body mass ($F_{1,8} = 14.8$, $P = 0.005$, $r^2 = 0.65$; Fig. 7.4). The regression FK-95 area on male body mass was also significant ($F_{1,8} = 13.0$, $P = 0.007$, $r^2 = 0.62$) but the regression graph suggested that the trend was spurious. The FK-50 area was not significant after removal of an outlier ($P > 0.09$). No other regression between body mass and annual or seasonal MCP, FK-95 or FK-50 areas were significant ($P > 0.06$).
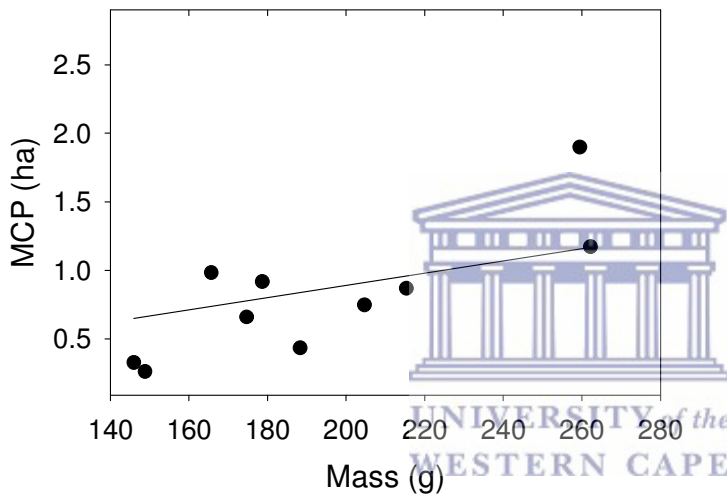
Figure 7.4 Regression of summer minimum convex polygons (ha) on body mass (g) for males at Benfontein. The regression was significant ($F_{1,8} = 14.8$, $P = 0.005$, $r^2 = 0.65$).

7.4   DISCUSSION

According to the site fidelity test devised by Spencer et al. (1990), half the males and nearly half the females in this study showed annual site fidelity, with a small number that were 'dispersing'. Powell (2000) stated that while a (statistical) test for site fidelity is good practice, it might ultimately be left to the researcher to decide if an individual shows site fidelity. Female #15 is one such example in this study. The fidelity test deemed her movements random, when actually she spent a large part of the study shuttling up and down 300 m of a farm track, often returning to the same refuges (T Keswick, unpublished data) and thus clearly showing site fidelity. During winter and summer when activity was limited by temperature (Chapter 6), tortoises either used few refuges or returned to the same mammal burrows (Chapter 5 and discussed below);

this site fidelity was not reflected by the tests. However, male #747 had a tendency to move south-westerly over its tracking period and could have been described as dispersing, in accordance with the fidelity test. Tortoises' activity areas were greatest in spring and autumn 2007, i.e., tortoises were more 'nomadic' in these seasons, but the number of tortoises calculated as having site fidelity over these periods did not differ from other seasons. Thus, in this study I assumed tortoises had both seasonal and annual home ranges despite them not always exhibiting site fidelity (Spencer et al., 1990) as site fidelity tests did not appear accurate.

I used FK-95 and FK-50 as well as 100% MCPs to evaluate space use and found no difference between annual MCP and FK-95 estimates. Although Powell (2000) suggested that MCPs should be restricted to summarising the boundaries of a home range, Row & Blouin-Demers (2006) argued that in studies of herpetofauna, an MCP is a better indicator of space use than a kernel as kernels perform badly when data are autocorrelated, as herpetology data generally are. With the exception of one male (for which I used *h* ref), I used LSCV to calculate the smoothing factor (*h*) for all FK-95 (and 50) estimates, which closely fitted the distribution of annual location points for most tortoises. On this basis, the similarity between FK-95 areas and MCP areas indicates that within the boundary of tortoises' annual activity areas (defined by MCPs), tortoises had a high degree of space 'utilisation' (defined by FK-95s). This study suggests that it is worth using both methods, as one may help you understand the other (i.e., space is intensely utilised).

With the exception of summer, the similarity between FK-95 and MCP estimates was not evident at a seasonal level, where FK-95 areas were larger. The reduction in locations per season, compared with annual sampling, may have affected FK-95 estimates. Kernel estimation was thought to overestimate areas when sample sizes are low, less than 30-50 locations (Seaman et al., 1999). In this study, mean locations were fewer than 30 in all seasons except summer, the one season in which MCP and FK-95 areas did not differ. Börger et al. (2006) used cervid and avian data to show that with a consistent sampling regime, 10 location points a month were sufficient to get accurate 90% FK areas. In this study, the sampling regime was relatively consistent (this chapter and see Chapter 2). However, temporary tortoise losses and thus a degree of uneven sampling were inevitable. Tortoises could move long distances (this study) depending on season and ranges of transmitter signals varied, both contributing to temporary losses. I also attempted to locate, visually, each individual daily to collect other ecological data and given that individuals were spread over a wide area, compromises

had to be made. Despite occasional temporary losses, only one tortoise was permanently lost during the study and the majority of tortoises were tracked consistently. Differences between FK-95 and MCP sizes within the confines of this study mattered little on the basis that the effects of the changing season were the same for both types of measurement.

As may be evident thus far from this discussion, to enable valid comparisons of MCP and kernel sizes with other studies, it is important to report the sampling regime, the number of location points for individuals per period and the analytical methods used, as they all affect home range size. Harless et al. (2010) cited ten studies involving MCPs of radio-tracked desert tortoises, *Gopherus agassizii*, of which seven did not provide the mean number of location points by gender for the year or months of their study. It is thus difficult to make direct comparisons with genders separately in these studies. This study is broadly similar to the original ('SRO') sampling regime of Harless et al. (2010) who in their 2005 year of study recorded 105±2 location points compare with 114±8 for tortoises tracked over 13 months here.

Unlike Harless et al. (2009; 2010), I found no differences between male and female annual home range sizes (MCP, FK-95 or FK-50). Lack of gender differences in home ranges in this study is largely due to individual variation. Individual variation has been shown to be a large component of the total variance in home range analyses, 40-95% (only 25% in MCPs) in case of a roe deer study (Börger et al., 2006). In the same study, 31-44% of the variance in Kestrel home ranges were attributed to individual variation and site differences, i.e., individual variance does not appear to be taxa dependent. Large inter-individual variation is common in testudinid home range studies (Rose & Judd, 1975; Geffen & Mendelssohn, 1988; Diemer, 1992; O'Connor et al., 1994; Nieuwolt, 1996; Arvisais et al., 2002; McMaster & Downs, 2009) and potentially masks patterns in gender space use, particularly when sample sizes are small. Sample sizes were relatively high in this study; 13 females and 12 males were tracked for over half the study period and no fewer than 10 males and 9 females were tracked within each season, yet the variance was still too great to detect sex or site effects. However, both sexes had the capacity to wander over large areas, despite their diminutive size.

Male #747 with a 100 mm SCL and an average mass of 240 grams had annual MCP and FK-95 home ranges of 300 and 180 ha, respectively. One female that was lost half way through the study had an MCP of 96 ha and an FK-95 home range of 164 ha. Thus, what may be most important to *P. oculifer* is applicable to both sexes: the

species is able to traverse large areas. The ability to cover such expanses is advantageous to *P. oculifer* in a habitat where resources are potentially patchy and temporarily limited due to seasonal rainfall (see Chapter 4), or where low tortoise density makes finding mates difficult (discussed in Chapter 3). Home ranges of mammals are often large in areas of low productivity, e.g. arid areas, because resources are sparse (Harestad & Bunnell, 1979; Powell, 2000). Similarly, home ranges of testudinid populations in arid or harsh environments tend to be large (Geffen & Mendelssohn, 1988; Barret, 1990; O'Connor et al., 1994; Freilich et al., 2000; Lagarde et al., 2003; McMaster & Downs, 2009), as does *P. oculifer* in this study.

Harless et al. (2009; 2010) reported mean annual MCPs and FK-95s, respectively, as 48 and 36 ha for male and 16 and 11 ha for female *Gopherus agassizii* compared to 48 and 32 ha for male, and 26 and 27 ha for female *P. oculifer* in this study (although sample sizes were lower and variance higher here). *Gopherus agassizii* males at 256 mm and females at 235 mm are considerable larger than their *P. oculifer* counterparts (99 and 113 mm, Chapter 8), which puts the large areas *P. oculifer* can cover into context. Certainly, they have managed to disperse throughout the range of the greater Kalahari area (see Chapter 8), which has reduced their vulnerability to localised environmental change. A sympatric species, *Geochelone pardalis*, with recorded mean SCL of over 400 mm and mass of 10 kg had mean annual MCPs of approximately 200 ha (McMaster & Downs, 2009), i.e., similar to male #747 in this study despite *G. pardalis* being 40 times heavier. However, when comparing the two species it must be born in mind that the annual sampling regime in McMaster & Downs (2009) was based on two locations per day (one per day in this study), and this may have affected MCP estimates of *G. pardalis*.

Unlike Harless et al. (2009; 2010), whose study spanned two years and could consider changing environments between years, this study was limited to 13 months. The short study period is partially compensated for by analysing home range and space use among seasons (i.e., periods of environmental change), and differences were found. Temperature and rainfall were most likely the main drivers of change in seasonal tortoise activity in this study (Chapter 6 and see Chapter 4 for climate results). After heavy rainfall, before and during autumn 2006, grass cover and water were abundant (Chapter 4) and tortoises, particularly females, were found walking and feeding. Activity was curtailed in May with the onset of cool temperatures and in winter, tortoise activity consisted of short, midday forays (Chapter 6). This was evident in home range sizes, which were smallest in winter.

Seasons with the most benign climates, spring and autumn 2007 (Chapter 4), also heralded the greatest movements (spring in particular). Diurnal temperatures and temporal activity patterns were similar in these two seasons and tortoises were active throughout the day (Chapter 6). This suggests that, unlike winter or summer, temperature did not restrict their daily movements and they could move further afield. Annual plant abundance in spring and increases in grass as well as geophytes in autumn 2007 (Chapter 4) gave incentive to animals to move and forage in these seasons. In autumn 2007, females were found feeding more often than males were, perhaps due to seasonal reproductive requirements (see Chapter 6). Equally, males were more active than females during October, the middle of the breeding season (Chapter 6) which falls within spring. Certain individuals of both sexes had large spring home ranges, suggesting the incentive to move in spring was not restricted to males mate searching. Lagarde et al. (2003) found *Testudo horsfieldii* females to have larger home ranges than males and suggested 'gene shopping' as a possible reason. By overlaying their home ranges over a number of male home ranges, Lagarde et al. (2003) suggested that female could mate with more than one male and that sperm competition would decide ultimately, which male was fittest. Gene shopping may be equally plausible for *P. oculifer* females, although further research on their reproductive biology is necessary to confirm this. Another possibility for a female having a large spring home range would be to look for specific nutrients related to female reproduction (Marlow & Tollestrup, 1982; and see Hailey & Coulson, 1996b) although it is unlikely to have been calcium as this was plentiful in the study site (Chapter 4).

High summer diurnal temperatures (Chapter 4) restricted the activity of tortoises to early morning and evening (Chapter 6). During the middle of summer days, tortoises spent much of their time sheltering in mammal burrows (Chapter 5) and movement was limited. Hence, movements and home ranges were contained around this pattern of activity, any long movements being restricted to periods of cooler weather (five out of six daily movements of over 100 m were before 10th December, at the beginning of summer). This was also reflected by FK-50 sizes in summer, which, unlike MCPs and FK-95 areas, were more constrained than they were in autumn 2007 as well as spring. It was during summer that MCP area increased with males of larger body mass although with the small sample size this relationship was somewhat tenuous. Mating behaviour may explain this trend. The last mating incident I recorded was in January 2007 (Chapter 6). It could be that the heavier males, which usually coincided with them

having a greater SCL, were better equipped for mate searching when summer temperatures began to rise compared to smaller and lighter tortoises.

Trends in both daily and accumulated displacements were similar to home ranges, but over the course of the study, male daily displacements were greater than those of females were. As there was no effect of sex on spring displacements, mating related behaviour does not explain difference between sexes, nor did genders differ in the number of long displacements made. It could be that longer displacement in males is an artefact of analyses. Analyses were done on log_{10} means of all displacements made, and some tortoises had more records than others did, thus not all individuals contributed equally to analyses. When the mean of log_{10} displacements for each individual tortoise were compared, i.e., each tortoise contributed equally to analyses, there was no sex effect.

7.5   CONCLUSIONS

Tortoise behaviour indicated that statistical tests underestimated the number of tortoises exhibiting site fidelity. Although the use of MCP and FK-95 home range estimation have both been criticised, in this study the annual estimates were generally complementary; they implied that animal activity areas were well utilised. Seasonal FK-95 areas were larger than MCP areas, possibly because of a reduction in location points per individual compared with annual estimates. Not all tortoise home range studies are comparable due to differing sampling regimes and lack of detail in methods, but a comparable study involving a larger tortoise than *P. oculifer*, *Gopherus agassizii*, showed that *P. oculifer* is capable of utilising very large areas relative to its size. However, individual variance was high in this study and I found no intraspecific differences in activity areas, but I did find differences among seasons. Large movements were limited to spring and autumn, when daily temperatures were benign and/or primary productivity is higher after seasonal rainfall. Hence, spring and autumn 2007 had the largest home ranges. There may be various incentives for tortoises to have large home ranges in these seasons including mate searching for males in spring and foraging by females in autumn. However, these activities are not mutually exclusive.

8   MORPHOLOGY

8.1   INTRODUCTION

The morphology of an individual may define its gender and, ultimately, its reproductive fitness (Darwin, 1871). Sexual dimorphism embodies phenotypic traits of a species, which reflect the different selective pressures acting on genders. Sexual dimorphism may convey an advantage within a sex by enhancing an individual's reproductive success, e.g., larger body sizes in males conferring sexual dominance over conspecifics, and/or size increasing their attractiveness to females (Darwin, 1871; Andersson, 1994).

Sexual dimorphism is common in chelonians. There have been numerous studies undertaken on chelonian populations that specifically address and interpret sexual dimorphism (Berry & Shine, 1980; Mushinsky et al., 1994; Dodd, 1997; St. Clair, 1998; Bonnet et al., 2001; Lagarde et al., 2001). Berry & Shine (1980) reviewed sexual dimorphism in testudinids and suggested that in species where males engage in agonistic displays and combat to secure mates, males tend to be larger (SCL) than females are. Dodd (1997) disagreed with Berry & Shine (1980) and suggested that males were larger than females in a population of *Terrapene carolina bauri* because large size facilitates the mounting of females during copulation. The reason given for large size in females is less tenuous than in males, it is often attributed to fecundity; large size optimising egg size or number of eggs produced (Berry & Shine, 1980; Wilbur & Morin, 1988; Iverson, 1992).

In harsh or arid regions, female testudinids, particularly the small South African endemics, tend to have smaller clutches but produce larger eggs (Loehr et al., 2004; Hofmeyr et al., 2005). Large eggs are less prone to desiccation and large hatchlings (from large eggs) are more likely to survive in an arid and unpredictable environment (Hofmeyr et al., 2005). Thus, small arid zone testudinid females are often larger than males, although this may not apply to (relatively) large-bodied species such as the North American, arid zone genus *Gopherus* (Germano, 1993). The central Asiatic *Testudo horsfieldii* inhabits the harsh environment of the Russian Steppe where the extreme climate only allows it to be active between three to four months a year (Lagarde et al., 2002). Bonnet et al. (2001) evaluated sexual dimorphism in *T. horsfieldii* and found that males are smaller, have longer legs, bigger shell openings, a more domed shell, and longer tails than females have. The authors hypothesized that

the long legs and large openings probably enhance male mobility and consequently their efficacy to search for mates and patrol territories. The domed shells of males would assist righting when turned over in combat and the long tail probably facilitates copulation. The wider, barrel-shaped bodies of female *T. horsfieldii* could infer selection for fecundity, allowing more space for egg production (Lagarde et al., 2002).

The potential confounding effects of sexual dimorphism make juvenile chelonians an interesting comparison to adults as juvenile morphology reflects the process of natural selection alone (Gibbons & Lovich, 1990). Environment is an important factor in defining the evolution of tortoise morphology, e.g., the development of carpus and cranium for burrowing (in friable substrates) in the genus *Gopherus* (Bramble, 1982). Although burrowing behaviour could be a consequence of predator avoidance, Morafka & Berry (2002) surmised that burrowing in *Gopherus* spp. was at least partly due to environmental change. They suggested that increasing aridity may have caused a reduction in vegetation cover, and consequently, burrowing behaviour in tortoises was a means of avoiding high surface temperatures.

Psammobates ('sand loving') is a testudinid genus endemic to southern Africa. With the exception of *P. geometricus*, *Psammobates* taxa inhabit arid or semi-arid regions (< 500 mm rainfall, Hofmeyr et al., 2005). *Psammobates oculifer*, the Kalahari tent tortoise, occurs in semi-arid and arid Savanna in and adjacent to the Kalahari Desert (Branch, 1988; Boycott & Bourquin, 2000). However, within South Africa, *P. oculifer* occurs in at least two relatively distinct habitats, the Eastern-Kalahari Bushveld and the Central Bushveld Bioregions. Although both are areas of arid or semi-arid Savanna, the substrate and vegetation differ considerably between the two bioregions (see Rutherford et al., 2006a for bioregion descriptions). *Psammobates oculifer* is sexually dimorphic, with females being larger and heavier than males. Additional features that distinguish males from females include a plastral concavity, a long tail, and an incurved and rounded supracaudal shield (Branch, 1988; Boycott & Bourquin, 2000). Apart from general descriptions of the species' morphology in field guides (Branch, 1988; Boycott & Bourquin, 2000), *P. oculifer* lacks detailed information concerning morphological variation attributable to sexual dimorphism or biogeography.

The sister taxon to *P. oculifer*, *Psammobates geometricus*, inhabits cooler areas with higher rainfall than does *P. oculifer*; the mean annual rainfall in the range of *P. geometricus* is 500 – 750 mm (Hofmeyr et al., 2005). *Psammobates geometricus* is a Western Cape endemic and has a small and fragmented habitat; it frequents Shale

Renosterveld and Alluvium Fynbos vegetation in low-lying areas surrounding the Cape Fold Mountains (Baard, 1993; Cunningham et al., 2002). Soils in Alluvium Fynbos are a mixture of gravel and cobbles, while renosterveld soils are shale based (clay and loam), and the landscape in both vegetation types is dominated by evergreen shrubs (Rebelo et al., 2006). Thus, despite being sister taxa, stark differences in the climate and habitat of *P. geometricus* and *P. oculifer* may have imposed differences on the morphology of the two species. Similar to *P. oculifer*, morphological descriptions of *P. geometricus* are restricted to field guides (Branch, 1988; Boycott & Bourquin, 2000) and a more detailed morphological description is required to enable comparisons between these species.

I had four main objectives in this chapter: (1) to provide the first full morphological description, with statistical support, for cohorts of *P. oculifer* and *P. geometricus*, (2) to evaluate sexual dimorphism in both species, (3) to assess the morphology of each species in context of its environment, and (4) to contrast the morphology of these sister taxa to illustrate environmental effect.

8.2   MATERIALS AND METHODS

8.2.1   *Morphological assessments*

8.2.1.1   *Study animals*

During March and April 2006, searches were made to find male and female *Psammobates oculifer* for a radio-telemetry study. Searches involved one to five people and were done either on foot, particularly in site W where vegetation was less dense, or by driving on farm tracks, particularly in site E where vegetation was denser. Driving was a more effective search method in areas of dense cover because *P. oculifer* is a cryptic species and animals were easier to detect when active and in the open (i.e., on farm tracks). Incidental captures of *P. oculifer* for this morphological study were made during the course of radio-tracking from April 2006 to April 2007. The capture of live *Psammobates geometricus* was carried out on foot over three days between 22 and 29 October 2008 and four days between 26 May and 1 July 2009. Captures formed part of a population census of *P. geometricus* organised by CapeNature, a public entity responsible for biodiversity conservation in the Western Cape Province, South Africa. Searches were made in the Ceres and Worcester valleys at farms and reserves determined by CapeNature (see Baard, 1993 for distributions) and at Elandsberg nature reserve near Wellington.

Upon capture, I classified each tortoise (*P. geometricus* or *P. oculifer*) as male, female or juvenile. Males were distinguished from females by their smaller size, flatter shell, longer tail, large, incurved supracaudal scute and, in the case of *P. geometricus*, an obvious plastral concavity (Branch, 1988; Boycott & Bourquin, 2000). Small animals with no clear sexual dimorphic characteristics were classified as juveniles. I determined body mass (BM) of tortoises with a digital balance (±0.1 g), and took a suite of morphometric measurements for each tortoise with vernier callipers (±0.01 mm), except for domed measurements, which I took with a flexible tape measure (±1 mm). Shell volume (SV) was estimated using a modified formula for an ellipsoid: $\pi*SCL*SHM*SWM/6000$ as cm^3 (Loehr et al., 2004).

As well as evaluating live *P. oculifer* and *P. geometricus*, I studied both dry preserved ("dry") and alcohol preserved ("wet") specimens of both species from collections at the Iziko South African Museum ("Iziko"), and for *P. oculifer* only, at the Transvaal Museum. For museum specimens and live *P. geometricus*, I included measurements not taken for live *P. oculifer* at Benfontein (Table 8.1). Methods of gender classification and measurement techniques of museum specimens followed that of live tortoises.

8.2.1.2 Morphometric measurements

A basic outline of the carapace and plastron of tortoises is given in Fig. 8.1 to assist with understanding morphological structures described in Table 8.1 as well as the scute types referred to in Section 8.2.1.3 and 8.3.3.2. Morphological measurements were chosen to allow detailed descriptions of *P. oculifer* and *P. geometricus,* to evaluate sexual dimorphism and possible adaptations to the species' respective habitats, and to compare *P. oculifer* from different geographic regions (Table 8.1). Measurements relating to sexual dimorphism corresponded with those taken in similar studies (Bonnet et al., 2001; Hofmeyr et al., 2005; Loehr et al., 2006; Mann et al., 2006), but incorporate novel measurements, e.g., plastral width (PW; Table 8.1). Subsequent to measuring live *P. oculifer* at Benfontein, I added new measurements for live *P. geometricus* and museum specimens of both species to help assess morphological differences between *P. oculifer* and *P. geometricus*, e.g., differences possibly related to habitat (Table 8.1).
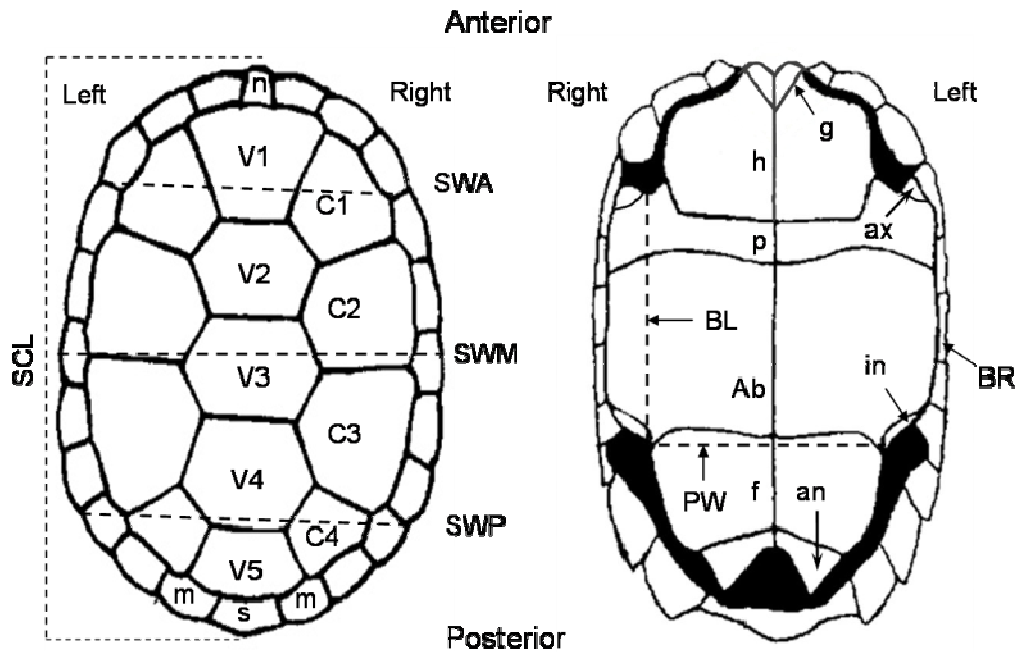
Figure 8.1   A dorsal (carapace, left) and ventral (plastron, right) view showing morphological details applicable to *P. oculifer* and *P. geometricus*. Carapacial measurements listed are straight carapace length (SCL) and shell width at the anterior (SWA, across $3^{rd}/4^{th}$ marginal scutes), middle (SWM, across 6th marginal scutes) and posterior (SWP, across $8^{th}/9^{th}$ marginal scute). Costal (C) and vertebral (V) scutes are numbered but not marginal (m) scutes (11 on both sides in this example). The single nuchal and supracaudal scutes are marked "n" and "s" respectively. Plastral measurements shown are the bridge length (BL) and plastral width (PW), with the bridge ridge indicated on the side (BR). Plastral length is the length of the midline seam running along the centre of the plastron. The plastral scutes divided by the midline seam are the gulars (g), humerals (h), pectorals (p) abdominals (Ab), femorals (f) and the anals (an). Also marked are the axillary (ax) and inguinal (in) scutes. Diagrams were modified from Boycott & Bourquin (2000).

Table 8.1 Description of measurements taken from *Psammobates oculifer* and *P. geometricus*. Measurements of *P. oculifer* were of live animals at Benfontein farm, South Africa, and from wet and dry specimens at the Iziko and Transvaal museums. Measurements of *P. geometricus* were taken from live animals in the south-western Cape and from wet and dry specimens at the Iziko museum. The comments column includes the motive(s) for a measurement (e.g., sexual dimorphism) and indicates measurements unique to a particular group or groups.

Measurement	Abbreviation	Description	Comments
Straight carapace length	SCL	Midline distance between tips of nuchal and supracaudal scutes	
Shell width, anterior	SWA	Width at seam of 3rd and 4th marginal scutes	Museums only
Shell width, middle	SWM	Width at 6th marginal scutes	
Shell width, posterior	SWP	Width at seam of 8th and 9th marginal scutes	Museums only. Sexual dimorphism
Shell height, middle	SHM	Height at the apex of the highest vertebral scute	
Plastron length	PL	Midline distance between the notch of the gular and the notch of the anal scutes	
Plastron width	PW	Width at inguinals	Sexual dimorphism and habitat
Domed carapace length	DCL	Curved midline distance between tips of nuchal and supracaudal scutes	
Domed carapace width	DCW	Curved width at 6th marginal scutes between bridge ridges	
Nuchal width	NW	Where nuchal meets 1st vertebral scute	
Nuchal length	NL	Base to tip	
Costal right scute 1, length	CR1L	Length across costal at contact points with 1st vertebral, 2nd costal and adjacent marginals	Museums only
Costal right scutes 2-5, length	CR2-5L	Length across costal at contact points with adjacent costals and marginals	Museums only. Usually 2-4

Table 8.1 continued

Measurement	Abbreviation	Description	Comments
Costal right scute 3, width	CR3W	Dorso-ventral width between two furthest points	Museums only
Vertebral scutes 1-7, length	V1-7L	At middle of scute	Museums only. Usually 1-5
Vertebral scute 3, width	V3W	Width between two furthest points in contact with costals	Museums only
Marginal scute right 6, length	MR6L	Anterior-posterior length at middle of scute	Museums only
Marginal scute right 6, width	MR6W	Dorso-ventral width between two furthest points	Museums only
Gular scute width	GW	At widest point between seams with humeral scutes	Museums only
Gular scute length	G	At midline seam	
Humeral scute length	H	At midline seam	
Pectoral scute length	P	At midline seam	
Abdominal scute length	Ab	At midline seam	
Femoral scute length	F	At midline seam	
Anal scute length	An	At midline seam	
Supracaudal scute width (Proximal)	S(P)	Across the seam of the supracaudal and last vertebral scute	Museums only
Supracaudal scute width (Distal)	S(D)	At shell rim between seams with last marginal scutes	Sexual dimorphism
Bridge length	BL	Shell length between axillary and inguinal scutes	Museums only. Sexual dimorphism and habitat
Cranial Space	CS	Dorso-ventral space between tip of nuchal and gular seam	Museums only. Sexual dimorphism and habitat
Head width	HW	Behind eyes	Museums only.
Front foot right width	FFRW	At base of claws	Museums only. Habitat

Table 8.1 continued

Measurement	Abbreviation	Description	Comments
Forearm right length	FARL	From the elbow to the base of foot	Museums only. Habitat
Hind foot right width	HFRW	At base of claws	Museums only. Sexual dimorphism & habitat
Hind leg right length	HLRL	From the knee to the base of foot	Museums only. Sexual dimorphism & habitat
Anal width	AW	Distance between tips of anal scutes	Sexual dimorphism.
Anal gap	AG	Dorso-ventral space between anal scute notch and tip of the supracaudal scute	Sexual dimorphism

8.2.1.3 Meristic counts, shell colour, and other characteristics

I first counted the number of carapacial and plastral scutes, and the number and location of axillary and inguinal scutes (Fig. 8.1). Subsequently, I recorded which marginal scutes showed serrations, and noted the strength of the serrations (none, weak, medium or strong). For live *P. geometricus* and all museum tortoises, I noted the presence and intensity (weak, moderate or strong) of a marginal groove (indentation between costal and marginal scutes) and bridge ridge (edge along side of shell) and the associated marginal scute numbers (Fig. 8.1). Furthermore, I recorded the curvature (up- or incurved or straight) and its intensity of anterior and posterior marginal scutes, and the presence or absence of a plastral concavity. Plastral concavities were rated weak or strong and I reported the position relative to abdominal scutes along the midline seam (Fig. 8.1).

I made notes of tortoises with shell damage, deformed scutes or other abnormalities and divided these malformations into four categories: (1) shell damage by cattle, game or dogs, (2) scute abnormalities, (3) nuchal scute abnormalities, and (4) other abnormalities. Shell damage refers to tortoises found with scutes staved in, cracked or chewed (Fig. 8.2 A). Scute abnormalities refer to tortoises that had twisted, warped or merged scutes (Fig. 8.2 B) and also peeling or shedding scutes. Nuchal scute abnormalities refer to instances when the nuchal scute was fused to a marginal scute, or when a tortoise was missing or had an extra nuchal scute. 'Other' abnormalities refer to rare morphological anomalies (e.g., a throat growth).

I took dorsal and ventral photographs of each tortoise using a Panasonic DMC-FZ30 digital camera to do a qualitative evaluation of the dark and light colours on the carapace and plastron. I recorded dark pigment in ten percent increments but for comparisons, I grouped individuals into four categories. The first category (0%, 10% & 20%) included three increments (Fig. 8.2 C) because only one animal had no dark pigment. All remaining categories comprised of two increments each: 30% & 40%, 50& & 60%, and 70% & 80% (Fig 8.2 D-F).
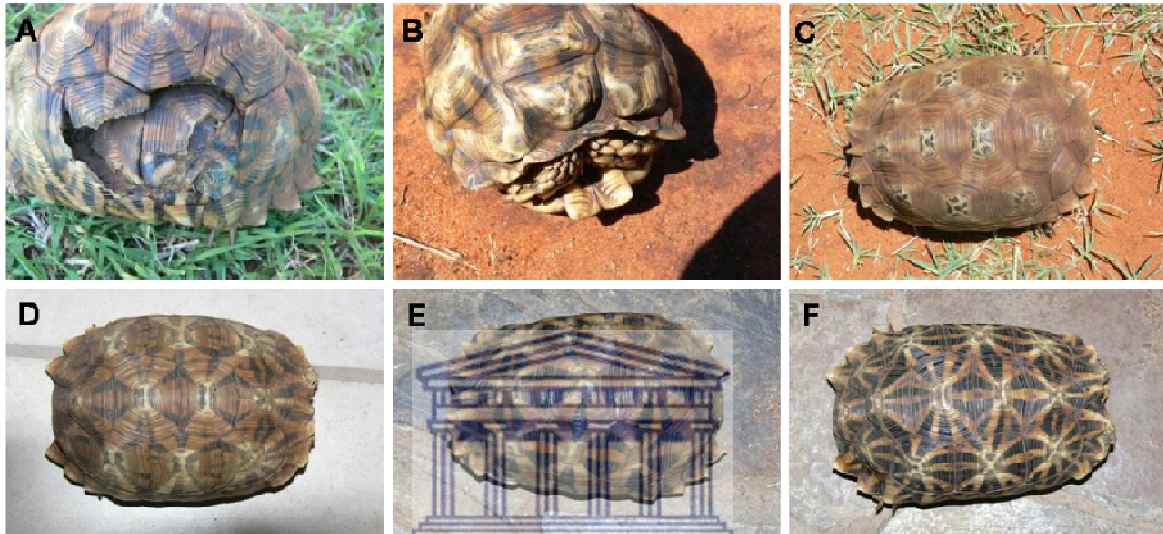
Figure 8.2 Shell damage or deformities and dark pigment categories. (A) Cattle or game damage to shell, (B) deformed vertebral and costal scutes, (C) pigment category 1 (0, 10 & 20%), (D) category 2 (30 & 40%), (E) category 3 (50 & 60%) and (F) category 4 (70 & 80%).

For live *P. geometricus* and museum specimens of *P. oculifer* and *P. geometricus*, I photographed the front of each specimen to assess the proportion of small, medium and large scales (armour) on the forearms. Forearm scales were graded in four categories: (1) having small scales with less than 50% medium scales (Fig. 8.3 A), (2) having small scales with more than 50% medium scales (Fig. 8.3 B), (3) having medium scales and less than 50% large scales (Fig. 8.3 C) and (4) having medium scales and > 50% large scales (Fig. 8.3 D). Other characteristics recorded include the number of claws on the front and hind feet, the number and size of buttock tubercles, the presence/absence of tail tubercles, the position of the nostrils relative to the eyes, as well as the shape (uni-, bi, or tricuspid) and serration of the beak.
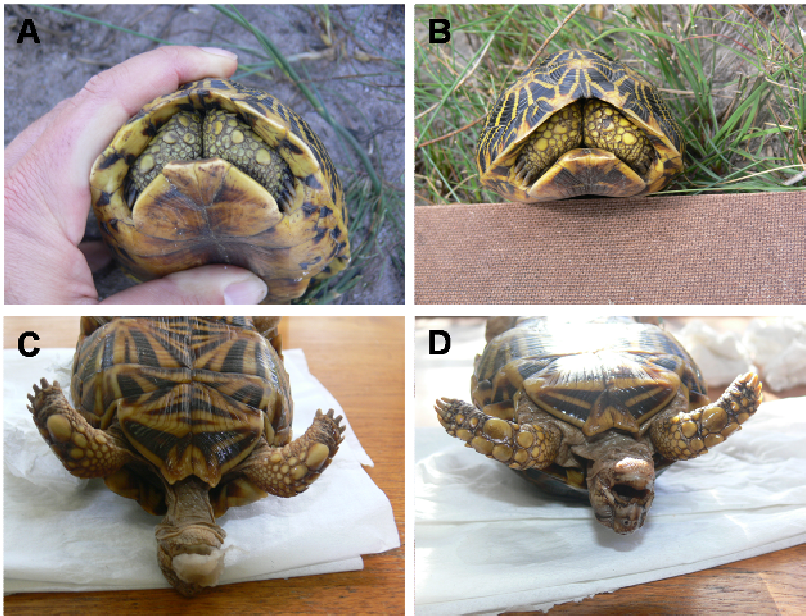
Figure 8.3 Degrees of forearm armour for *P. oculifer* and *P. geometricus*. (A) Small scales with < 50% medium scales, (B) small scales with > 50% medium scales, (C) medium scales with < 50% large scales and (D) medium scales with > 50% large scales.

During spring at Benfontein, tortoises' peak activity period, there was not always enough time to take detailed measurements for new tortoises, thus some *P. oculifer* individuals do not have complete records. Equally, time constraints imposed by the CapeNature census meant that I did not always complete measurements for individual *P. geometricus*. Some museum specimens were damaged, thus full sets of measurements were not possible in all instances.

8.2.2 Geographical regions of the Kalahari tent tortoise

Psammobates oculifer is reported as being a semi-arid, Savanna species, which occurs in northern South Africa, eastern Namibia and large parts of Botswana (Boycott & Bourquin, 2000; Branch, 1988). Within the Savanna Biome in South Africa, museum records (this study) and records from the South African Reptile Conservation Assessment (SARCA; unpublished data) suggest there are two major areas of *P. oculifer* occurrence, the Eastern-Kalahari Bushveld and Central Bushveld Bioregions (see Rutherford et al., 2006b for descriptions of these bioregions). Tortoises from these two bioregions in South Africa were thus classified into two separate geographic regions.

Eastern-Kalahari Bushveld covers parts of the Northern Cape, Free State and North-west provinces, whereas Central Bushveld is found mainly in the Limpopo and North-west provinces, but also occurs in Gauteng and Mpumalanga provinces. The Dry Highveld Grassland Bioregion separates the Eastern-Kalahari Bushveld and Central Bushveld Bioregions, and may act as a dispersal barrier to the species. Some specimens were collected from the Serowe/Palapye region of south-eastern Botswana, near to the Limpopo border. Vegetation in this region of the Limpopo is classified as 'Limpopo Sweet Bushveld' and this vegetation category is found in adjacent Botswana (Rutherford et al., 2006a). Thus, specimens from Serowe/Palapye were included with animals from the Central Bushveld Bioregion, as habitats between the two appeared broadly similar.

The remaining animals were collected over a wide area from the Kgalagadi National Park, north and west to Ghanzi and Ngamiland in Botswana and up to the north of Namibia near the Angolan border. It was difficult to classify this group by habitat as samples were dilute, but some vegetation appears similar to the Eastern-Kalahari Bushveld vegetation although the north has areas of both Zambesian vegetation and Mopane woodland. Thus for regional analyses, specimens were divided into three 'regions' according to habitat: (1) the 'Central' region covering the Eastern-Kalahari Bushveld Bioregion, (2) the 'Eastern' region covering the Central Bushveld Bioregion and south-eastern Botswana, and (3) the 'North-west' region covering remaining specimens from Botswana (Ghanzi and Ngamiland) and Namibia.

8.2.3   Data and statistical analyses

Before analysing the morphological measurements, I first compared the treatments (dry, wet and live) of specimens within cohorts (female, male, juvenile) for both species to see if I could combine treatments for analyses. Initially I chose SWM and SHM measurements to test for the effect of treatment, because these measurements best represented tortoise shape. I regressed SWM (width) and SHM (height) on SCL (length), using ANCOVA to control for individual size (SCL) within a cohort. Where small sample sizes ($n \leq 4$) of a treatment within a cohort did not allow ANCOVA (through failure of equal variance), I visually inspected regression lines to see if there were differences in slopes or elevations. Treatment did not affect SWM in any group, but treatment did affect SHM in *P. oculifer* (but not in *P. geometricus*). Measurements of SHM for live adult *P. oculifer* at Benfontein were higher than they were for their wet and dry counterparts (the latter two treatments did not differ from one another, nor did juvenile *P. oculifer* differ among treatments). The vernier callipers used to measure

SHM of live *P. oculifer* had shorter jaws than the vernier callipers used to measure SHM in live *P. geometricus* and all museum specimens. The short-jawed callipers did not fully span the plastron width, which may have affected the accuracy of SHM measurements in live, adult *P. oculifer*. To test this, I did further ANCOVA comparisons by regressing DCL (domed length) and DCW (domed width) on SCL. Both these measures are good indicators of body shape and the same instrument was used for all specimens. I found no difference in DCL and DCW among treatments within groups of *P. oculifer* and *P. geometricus*, and I thus combined treatments (live, wet, and dry) for all morphological analyses. However, I excluded SHM and shell volume data for live specimens of *P. oculifer* from analyses.

I used multivariate analyses of covariance (MANCOVA) and univariate analysis of covariance (ANCOVA) with SCL as the covariate to compare measurements of cohorts within and between species. In tortoises, SCL is a more consistent measure of body size than mass, because mass can fluctuate with climatic variations such as rainfall. I regressed all morphometric measurement on SCL and I did not use the data in a MANCOVA or an ANCOVA if the regression was not significant. If the data were not parametric, I used $\log_{10}$ transformations. When doing MANCOVA or ANCOVA, I first tested for differences in slopes, and if the slopes did not differ, I tested for differences in elevations (Quinn & Keough, 2002). In the case of ANCOVA, when slopes differed, I used Zerbe tests (Zerbe et al., 1982) to calculate the regions of SCL where the dependent variable differed between regressions lines. In the case of MANCOVA, I removed the dependent variables for which slopes were heterogeneous and repeated the model without these dependent variables. In all instances where I used MANCOVA, four test statistics were generated: Pillai's Trace, Wilks' Λ, Hotelling's Trace and Roy's Largest Root, and unless stated otherwise, results (converted *F* and corresponding *P* values) were similar for each test. If there were no differences between the four test statistics, I only reported Wilks' Λ as this is the most widely used and thus most comparable statistic (Zar, 1999; Tabachnick & Fidell, 2007). Where a measurement for a group (cohort or species) had the same or a lower sample size (*n*) than the number of dependent variables being tested, I did not include that measurement in the MANCOVA model. Before running a MANCOVA, I first checked for: a) multivariate outliers by calculating Mahalanobis distance (chi-square statistic), where degrees of freedom equalled the number of variables in the test, and b) I inspected the variance of each variable being tested. If measurements with a larger *n* produced large variances and those with a smaller *n* smaller variances, I assumed the level of α was conservative (Tabachnick & Fidell, 2007). Another criterion of MANCOVA is absence of

multicollinearity. I based multicollinearity in MANCOVA on whether the condition index for a given dimension (root) was higher than 30 and that the same dimension (root) contributed more than 0.50 of the variance proportion to ≥ 2 dependent variables (Belsley et al., 1980). When multicollinearity was detected, I omitted the dependent variable with the highest variance proportion from the MANCOVA analyses (Tabachnick & Fidell, 2007). Sidak tests were used for all multivariate post hoc analyses. In all instances where I carried out multiple tests of univariate ANCOVA, I applied a sequential Bonferroni to control for the Type I error.

I divided the tortoises into four size categories based on SCL: < 90 mm, 90-109 mm, 110-119 mm and ≥ 120 mm. Comparisons of scute counts, scute serrations, shell colouration and pigmentation patterns were done amongst cohorts and different size classes within each species, amongst cohorts between species and, in the case of *P. oculifer* only, amongst cohorts and regions. There was individual variation in the number and symmetry of marginal scutes, thus I summarised the frequencies as number occurring per individual on each side. I divided marginal scute serration patterns into anterior (1-5) and posterior (6-12) and summarised frequencies for each side.
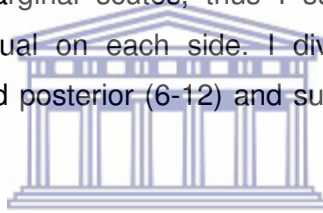
To test for differences in frequencies of marginal scute numbers, serration and colour patterns, I used χ^2 tests or Fisher's exact tests (2 x 2) where frequencies were low, with a Yates' correction if degrees of freedom equalled one and with mean expected frequencies always equalling six or more (Zar, 1999). Where contingency tables were 2 x 3, 2 x 4 or 3 x 3 and frequencies were low, I used the Freeman-Halton extension to the Fisher's exact test (Freeman & Halton, 1951). Chi-square and Fisher's exact test procedures were carried out among cohorts and size classes within each species, among cohorts between species, and among regions in *P. oculifer*. I used repeated measures ANOVA (RMA, *F* statistic) or Friedman's repeated measures ANOVA (FRMA, χ^2 tests) where data were non-parametric, followed by SNK post hoc tests to rank the plastral, costal, and vertebral scutes formulae for males, females and juveniles in a species or regional morph. I used paired *t* tests or, when data was non-parametric, Wilcoxon Signed Rank tests, to evaluate differences between carapacial and plastral dark pigmentation within each cohort, size class, and for all tortoises combined. All remaining morphological characteristics (nostril placement, front and back claw counts, beak type, axillary and inguinal scutes and adjoining scutes, tail and buttock tubercles, plastral concavity occurrences and bridge characteristics) were summarised as percentages among groups and size classes. PASW 18 (SPSS Inc., Chicago. U.S) and

Microsoft Excel were used for the ANCOVA analyses and PASW 18 for MANCOVA analyses. VassarStats were used to calculate the Freeman-Halton (1951) extension to Fisher's exact test. I used SigmaStat 2.03 (SPSS Inc., Chicago. U.S) and Microsoft Excel for all other statistical analyses. All statistical tests were considered significant if $P \leq 0.05$.

8.3 RESULTS

8.3.1 The Kalahari tent tortoise

8.3.1.1 Measurements and cohort comparisons

Descriptive statistics for all shell and body measurements are given in Appendix B. Absolute values of measurements were greatest in females and lowest in juveniles ($F_2 \geq 24.66$, residual df ≥ 105, $P < 0.0001$). The exceptions were femoral scute length, anal gap and hind right foot width, which did not differ between males and females ($P > 0.05$), and anal width, which was greater in males than it was in females ($F_{2,284} \geq 137.03$, $P < 0.00001$). Costal, vertebral, and plastral scute lengths were compared using formulae based on proportional length, and were not included in regression analyses. All measurements, except hind foot width in juveniles, had a positive relationship with body size (SCL, before or after $\log_{10}$ transformation) in males ($F \geq 4.22$, $P \leq 0.04$, residual df ≥ 54, $r^2 \geq 0.05$), females ($F \geq 6.47$, $P \leq 0.01$, residual df ≥ 37, $r^2 \geq 0.12$) and juveniles ($F \geq 20.41$, $P \leq 0.0007$, residual df ≥ 8, $r^2 \geq 0.42$).

After correcting for body size, there were significant differences among cohorts in the regression slopes of SWM, SHM, PL, V3W, MR6L, AW, AG, DCW, BL and BM on SCL ($F_2 \geq 6.1$, error df ≥ 134, $P \leq 0.003$; Fig. 8.4 and Table 8.2). The SCL at which females diverged from males was relatively small for shell height middle (Fig. 8.4A), shell width middle, plastral length, domed carapace width, and bridge length (Fig. 8.4B and Table 8.2), whereas the divergence was at a larger SCL for 3rd vertebral width, 6th marginal length, AW and BM (Table 8.2). Female and juvenile slopes were often similar, indicating that females continue the growth pattern of juveniles for the particular parameter. For SHM (Fig. 8.4A), female and juvenile slopes were steeper than the male slope, whereas only the female slope for BL was steeper than the male slope (Fig. 8.4B). The slope for adult anal gap size diverged from that of juveniles at a small size (22 mm). Males only had a steeper regression slope than females did for AW (> 95 mm; Table 8.2).
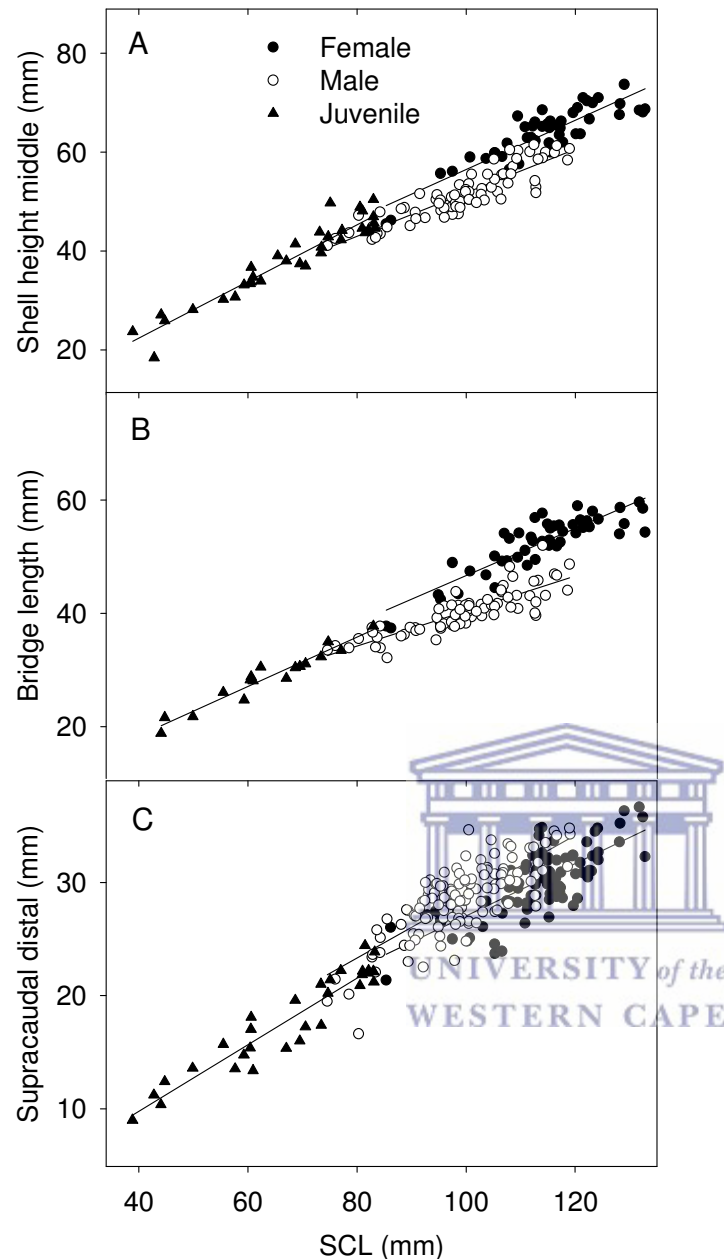
Figure 8.4 Regressions of (A) shell height middle, (B) bridge length, and (C) distal supracaudal scute width on SCL for *Psammobates oculifer* cohorts. Slopes differed for SHW (f=j>m) and BL (f>m; f=j; m=j), whereas elevations differed for the supracaudal scute (m>f=j).

Regression elevations among cohorts differed for many measurements ($F_2 \geq 5.6$; error df $\geq$ 93, $P \leq$ 0.004; Table 8.2). Regression elevations of SWA, SWP, PW, CR3W, MR6W, S(P) and DCL length were all greater in females than they were in males. The male regression elevation was higher than it was in females for S(D) (Fig. 8.4C), GW, AG, HFRW and CS. There were no differences among cohorts for NW, NL, HW, FFRW, FARL and HLRL.

Table 8.2 Homogeneity of slopes and ANCOVA tests for regression lines of morphometric parameters on SCL of *Psammobates oculifer* cohorts. Where a slope test was not significant (e.g., f=j), I tested for differences among regression elevations. The Zerbe test indicates at what SCL the slope differed. If differences are reported for both slopes and elevations, the lowest *F* and *P* value of the two tests is given, but I report the error df for slope only. See Table 8.1 for abbreviations.

Measure	*F*	*P*	Error df	Slope	Zerbe	Elevation
SWA	4.8	0.009	136			f > m; j = f; j = m
SWM	7.4	0.0007	308	f = j > m	> 83	f > j
SWP	7.6	0.0007	138			f > m; j = f; j = m
SHM	30.7	0.009	150	f = j > m	> 79	f = j
SV *	64.6	0.0001	152			f = j > m
PL	7.7	0.001	301	f = j > m	> 72	f > j
PW	86.8	0.0001	258			f > m = j
V3W	7.1	0.001	135	f > m; f = j; j = m	> 92	f > j; j = m
CR3W	12.9	0.0001	137			f > m; j = f; j = m
MR6W	15.4	0.0001	136			f > m; j = f; j = m
MR6L	6.1	0.003	134	f > m; f = j; j = m	> 94	f > j; j = m
S(P)	7.2	0.03	136			f > m; j = f; j = m
S(D)	37.1	0.0001	242			m > f = j
GW	3.4	0.037	130			m > f; j = f; j = m
AW *	20.9	0.0001	281	m > f; j = f; j = m	> 95	m > j; j = f
AG	26.0	0.0001	275	m = f > j	> 22	m > f
HFRW [1]	18.9	0.0001	93			m > f
CS *	9.3	0.002	126			m > f; j = f; j = m
DCL	5.6	0.004	287			f > m; j = f; j = m
DCW	6.9	0.001	285	f = j > m	> 83	f > j
BL	5.33	0.006	134	f > m; j = f; j = m	> 74	f > j; j = m
BM	14.2	0.0001	183	f > j = m	> 91	j > m

* Data $\log_{10}$ transformed

[1] juvenile regression not significant

A comparison of morphometric measurements among cohorts using multivariate slope tests and MANCOVA (SCL as covariate) had similar results to those of multiple univariate tests. Certain measurements were not included in multivariate tests; BM (because it was subject to seasonal variation), head width and rear hind leg length (due to the small sample sizes) and shell volume (due to constraints of multicollinearity). Differences among regression slopes and/or elevations for remaining measurements

(Wilks' Λ, exact $F \geq 1.8$, $df_h \geq 38$, $df_e \geq 126$, $P \leq 0.004$, partial eta-squared ≥ 0.40) were similar to univariate results except SWA, S(P), and DCL did not differ among cohorts in multivariate tests ($P > 0.05$). In addition, multivariate differences for SWM, SHM and PL were in elevations rather than slopes (as the univariate results were) and post hoc results were f > m, j = m & f (SWM); and f > m = j (SHM and PL).

8.3.1.2 Scute counts and scute length formulae

All animals had one supracaudal scute and a single nuchal scute with the exception of one female with no nuchal scute and one male with two nuchal scutes (Appendix C). There was little variation in the number of vertebral scutes with 119 females (97%), 144 males (94%) and 34 juveniles (97%) having five vertebral scutes (Appendix C). The highest point of the shell for most tortoises ($n = 162$) was at the apex of the third vertebral scute; the shell of four males and four females was highest at the apex of the second vertebral scute. Costal scute numbers differed little with only four tortoises having asymmetrical costal scutes and 96% males ($n = 149$), 94% females ($n = 118$) and 94% juveniles ($n = 33$) having four costal scutes on both sides (Appendix C).

Psammobates oculifer usually had either 10 or 11 marginal scutes on a side (Table 8.3), and the pattern was usually symmetrical (89%, $n = 279$; Table 8.3). There was no difference amongst cohorts in the number of individuals with 10 or 11 marginal scutes on each side, or those with asymmetrical versus symmetrical marginals (χ^2 tests, $P \geq 0.61$; Table 8.3).

Table 8.3 Frequencies and percentages of the number of left and right marginal scutes per tortoise amongst males, females, juveniles and all *Psammobates oculifer* from live specimens (Benfontein) and wet and dry specimens (Iziko and Transvaal museums).

	12:12	%	11:11	%	11:10	%	10:11	%	10:10	%	9:10	%	12:10	%
Males	3	1.9	83	53.5	12	7.7	6	3.9	50	32.3	0	0.0	1	0.6
Females	2	1.6	74	59.2	8	6.4	5	4.0	35	28.0	1	0.8	0	0.0
Juveniles	0	0.0	22	62.9	2	5.7	0	0.0	10	28.6	1	2.9	0	0.0
Totals	5	1.6	179	56.8	22	7.0	11	3.5	95	30.2	2	0.6	1	0.3

All males ($n = 148$) and juveniles ($n = 34$), and all except one (that had no axillary scutes) females ($n = 126$) had one axillary scute on each side of the plastron. The axillary scutes of all *P. oculifer* were in contact with the humeral and pectoral scutes, and were most often in contact with marginals three and four in females (98%, $n = 48$),

males (93%, *n* = 67) and juveniles (100%, *n* = 17; Appendix D). All tortoises (*n* = 125, 150 and 34 for females, males and juveniles respectively) had one inguinal scute on each side of the plastron, which was always in contact with the abdominal and femoral scutes. Contact of inguinal with marginal scutes was more variable than seen for axillary scutes, but 65% of females (*n* = 32), 68% males (*n* = 50) and all juveniles (*n* = 17) had inguinals in contact with the 7th and 8th marginal scutes (Appendix D). Variation in the positioning of the inguinal scutes did not differ between males and females (*P* = 0.95), but inguinal positioning was more variable in adults than it was in juveniles (Fisher's exact tests, *P* < 0.006; Appendix D).

Scute lengths differed significantly within cohorts for vertebrals (χ^2_4 > 26.5, *P* < 0.0001), costals (χ^2_3 > 30.9, *P* < 0.0001), and the plastron (χ^2_5 > 160.2, *P* < 0.0001). Vertebral scute formulae differed among the three cohorts: it was V5=V1=V4=V3>V2 for females, V5>V1>V4>V3>V2 for males, and V1>V5>V4=V3>V2 for juveniles (Appendix B). The costal scute formula for males (C1>C3>C2>C4) was different from those of females and juveniles (C1>C3=C2>C4). The plastral arrangement for females and juveniles was Ab>H>G>An>F>P, whereas it was Ab>H>G>F>An>P for males.

8.3.1.3 *Marginal scute serrations, marginal curvature and bridges*

All tortoises had between zero and five anterior, and two to six posterior, marginal scutes serrations on each side. The majority of females (92%, *n* = 108), males (91%, *n* = 135) and juveniles (76%, *n* = 25) had three anterior serrations on each side with only five females and two males having less than three (Appendix E). Juveniles had more than three anterior serrations on each side more often than females did (χ^2_1 = 8.61, *P* < 0.003) and tended to have more than males did but it was not significant (χ^2_1 = 3.78, *P* = 0.052; Appendix E). Males (72%, *n* = 109) and females (74%, *n* = 90) usually had three posterior serrations on each side, but this was not so in juveniles, where more than half (52%, *n* = 17) had four or more posterior serrations on each side. Juveniles had greater posterior serration than males or females (χ^2_1 ≥ 5.4, *P* ≤ 0.02) but serration in males and females did not differ (*P* = 0.29; Appendix E). Five tortoises, all females (4%, marked as 'others' in Appendix E), had only two sets of posterior serrations. Serrations in all *Psammobates oculifer* were strong except for three females and one male where serrations were of 'medium' strength.

There was a significant effect of body size on marginal scute serrations. The occurrence of individuals with more than three anterior serrations on each side was higher in the SCL < 90 mm category than it was in any other size category (Fisher's exact tests, *P* ≤ 0.0015 < than sequential Bonferroni, α = 0.008; Fig. 8.5). Anterior

marginal serration patterns among other size groups did not differ ($P \geq 0.16$). Similarly, tortoises < 90 mm SCL had a higher incidence of individuals with more than three posterior serrations on each side than did any other SCL category ($\chi^2_1 \geq 6.81$, $P \leq 0.0091$ < than sequential Bonferroni, $\alpha = 0.0125$). Posterior marginal scute serration patterns did not differ among the other size classes ($P > 0.81$; Fig. 8.5).
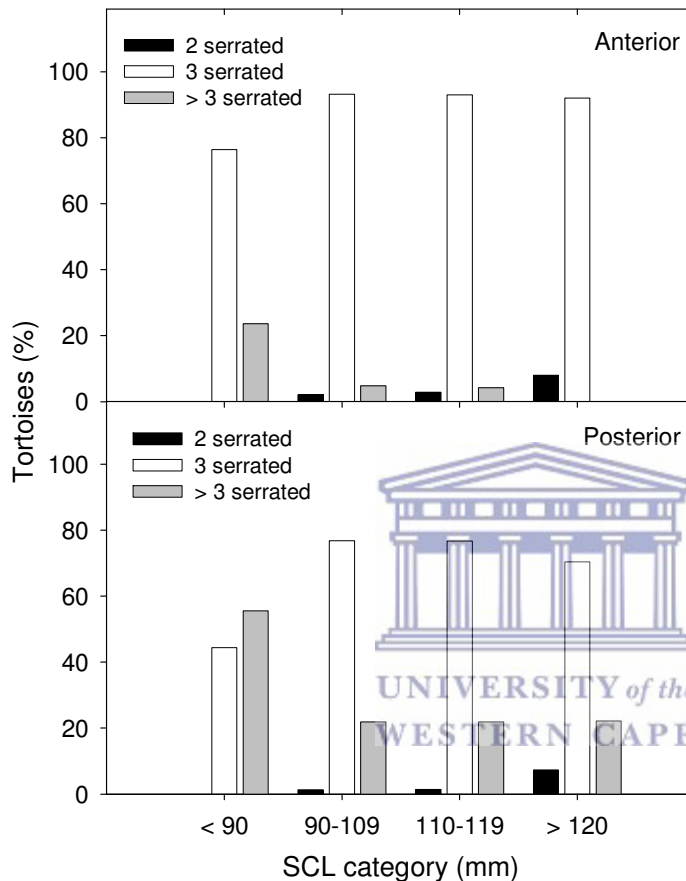
Figure 8.5 Anterior and posterior marginal scute serration of live (Benfontein) and museum (Iziko and Transvaal museums) *Psammobates oculifer*. Sizes were divided into four groups: < 90 mm ($n = 55$ and 53 for anterior and posterior respectively), 90-109 mm ($n = 147$ and 143 for anterior and posterior respectively), 110-119 ($n = 71$ and 67 for anterior and posterior respectively) and > 120 mm ($n = 25$).

All animals had a weak upward posterior marginal curve ($n = 140$) and no anterior marginal curve ($n = 139$). A weak bridge ridge was present in all specimens ($n = 139$), but a marginal groove was absent ($n = 138$). Bridge ridges comprised of marginal scutes three to seven or three to eight in all juveniles ($n = 17$), most males (84%, $n = 61$) and females (81%, $n = 39$; Appendix F).

8.3.1.4   Shell colouration

The majority of tortoises (75%, n = 212) had a carapacial background colour (i.e., other than dark pigmentation) of either orange/brown or orange/yellow. The frequencies of occurrence of individuals within different carapace colouration categories differed between males and females, males and juveniles and females and juveniles (χ^2_3 ≥ 11.1, P ≤ 0.011). Generally, the juveniles' carapace had the palest colouration (yellow and orange/yellow) with males also tending to have a paler background than females (orange/yellow and orange/brown; Appendix G). Size affected the proportions of individuals within each colour category; small tortoises (< 90 mm) differed from all other size classes and tortoises between 90-109 mm differed from tortoises > 120 mm SCL (χ^2_3 ≥ 14.41, P ≤ 0.0024). Although tortoises 90-109 mm tended to differ in colour from tortoises 110-119 mm, it was not significant after a sequential Bonferroni (P = 0.029 > 0.025 = adjusted α). Small tortoises tended to be paler than larger tortoises. There was no difference among remaining size categories (P ≥ 0.056; Appendix H).

With the exception of one female, all tortoises had a degree of dark pigment on the carapace (n = 282; Appendix I). Juveniles had high proportions of dark pigment on the carapace with 94% (n = 30) falling into pigment category 4 (Appendix I). The proportion of juveniles with a high degree of dark carapacial pigment exceeded that of adults, as it did for males over females (χ^2_3 ≥ 12.31, P ≤ 0.0064). The plastrons of all tortoises had dark pigment (n = 283) with 87% of tortoises (n = 247) falling in categories 2 and 3 (Appendix I). There was no difference in the colour patterns of the plastrons among males, females and juveniles (P = 0.28). Comparisons of dark pigment on the carapace and plastron revealed that the proportion of dark pigment on the carapace was marginally, but significantly greater than that on the plastron for females (T_{117} = 1135, P = 0.04), whereas the carapaces of males and juveniles were substantially darker than their plastrons (T ≥ 528, n ≥ 32, P < 0.00001).

Similar to cohort differences, there were differences in the dark colouration of the carapace and plastron of different size classes. Percentage of dark pigment on the carapace was greatest in small tortoises (< 90 mm SCL) and was greater in the next smallest category (90-109 mm SCL) than it was in the two remaining size classes (χ^2_3 ≥ 13.18, P ≤ 0.0043; Fig. 8.6). There was no difference in the pattern of carapacial dark pigment between the other two size classes (P = 0.15). Size did not affect the percentage of dark pigment on the plastron (P = 0.59; Fig. 8.6). The percentage of dark pigmentation on the carapace was greater than it was on the plastron for the smallest

size classes (SCL < 109 mm; Wilcoxon SRT, $T \geq 884$, $n \geq 52$, $P < 0.00001$), but not the larger ones (SCL > 109 mm, $P > 0.18$).
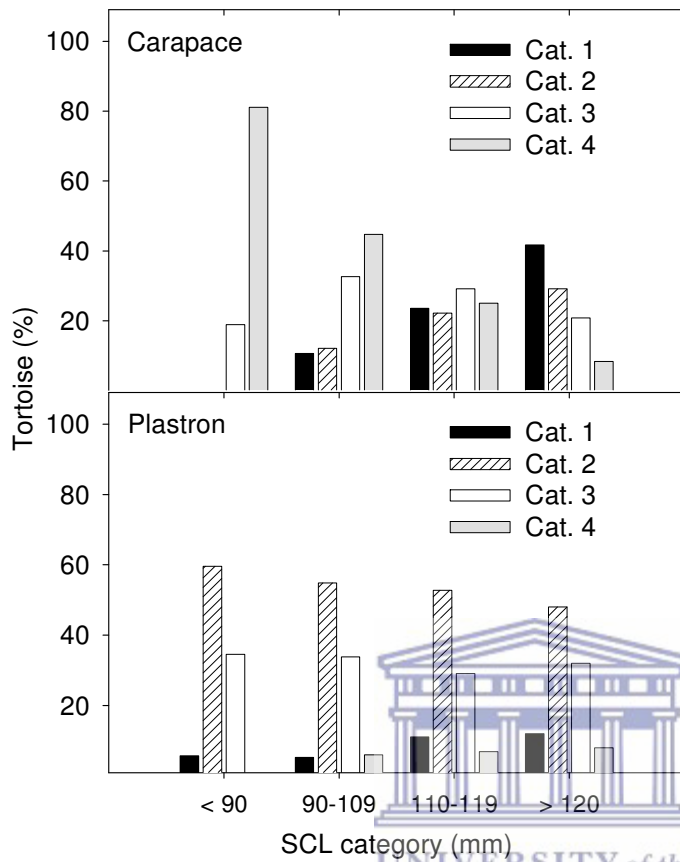
Figure 8.6 Percentages plastral and carapacial dark pigment by category for different size groups of live (Benfontein) and museum (Iziko and Transvaal museums) *Psammobates oculifer*. Sizes were divided into four groups: < 90 mm ($n = 53$ and 52 for carapace and plastron respectively), 90-109 mm ($n = 132$ and 133 for carapace and plastron respectively), 110-119 ($n = 72$) and > 120 mm ($n = 24$ and 25 for carapace and plastron respectively). Dark pigment Category (Cat.) 1 represents 0, 10 & 20% black pigment, whereas categories 2, 3 and 4 each represents two pigments increments, 30 & 40%, 50 & 60%, and 70 & 80%, respectively.

8.3.1.5 *Occurrence of shell damage and deformities*

Some type of abnormality occurred in 19% ($n = 57$) of tortoises sampled (Table 8.4). This included two males and two females that had two types of abnormality, while juveniles had no abnormalities (Table 8.4). The most frequently occurring abnormalities were scute abnormalities (see Fig. 8.2 B for illustration) which occurred in 12% ($n = 37$) of all animals assessed. In addition, eight females and ten males had the nuchal scutes fused to an adjacent marginal scute. Cattle and game damage was found in 4% ($n = 11$) of tortoises (Table 8.4) although 10 out of 123 (8%) animals at Benfontein were

damaged by cattle or game. Percentage of scute abnormalities and cattle and game damage did not differ significantly between genders (χ^2 tests, $P \geq 0.32$, Table 8.4).

Table 8.4 Occurrences (number and percentage) of shell abnormalities in male, female and juvenile *Psammobates oculifer* from live specimens (Benfontein) and wet and dry specimens (Iziko and Transvaal museums). 'Other' refers to scute damage of unknown origin but also included one animal that had a pronounced marginal groove, one with an unusually large cranial space and one with a large growth on the throat.

	Scutes		**Cattle & Game**		**Other**		**None**	
	Count	%	Count	%	Count	%	Count	%
Females	20	*16.8*	7	*5.9*	6	*5.0*	86	*72.3*
Males	17	*11.7*	4	*2.8*	3	*2.1*	121	*83.4*
Juveniles	0	*0.0*	0	*0.0*	0	*0.0*	34	*100*
Total abnormalities	**37**	*12.4*	**11**	*3.7*	**9**	*3.0*	**241**	*80.9*

8.3.1.6 Other morphological characteristics

Typically, *P. oculifer* had five claws on both anterior feet and four claws on both posterior feet. All females ($n = 113$), 99% males ($n = 137$) and 93% juveniles ($n = 30$) had five claws on the anterior feet, with no tortoises having less than four claws on an anterior foot. All juveniles ($n = 31$) and almost all males (99%, $n = 143$) and females (98%, $n = 117$) had four claws on the posterior feet. One male had a claw missing and one had an additional claw, both on the right posterior feet, while two females had three claws on each posterior foot. Where tortoises had less than five anterior claws or four posterior claws, there was no obvious, visual indicator (e.g. a broken claw) for reduced numbers of claws on an individual. Although not measured, all tortoises' hind claws appeared longer and thinner than front claws, and front claws appeared closer together and more evenly spaced.

Nostrils were located below the eye line in all juveniles ($n = 12$) and in the majority of males (88%, $n = 57$) and females (88%, $n = 38$). In all other animals, nostrils were at eye level. Most females (94%, $n = 100$), males (88%, $n = 96$) and juveniles (95%, $n = 19$) had tricuspid beaks. Twelve males, two females and one juvenile appeared to have worn beaks, one female and one male had serrated beaks, and three females had broken beaks.

Females did not have a plastral concavity ($n = 48$) and out of 17 juveniles, one had a small concavity on the midline where the abdominals met the femoral scutes. The majority of males (71%, $n = 51$) had a small plastral concavity, while 10 males (14%) had a large concavity, and 11 (15%) had no concavity. Male concavities occurred either where the abdominals met the femoral scutes (44%, $n = 27$) or were longer and stretched the length of the abdominal up to the femoral scute (56%, $n = 34$; on midline seam in both cases).

Most tortoises had either one (41%, $n = 115$) or two (57%, $n = 160$) large buttock tubercles on either side of the tail. The percentage occurrence of individuals with one or two large buttock tubercles was similar within each cohort: males, 46% ($n = 63$) and 51% ($n = 70$); females, 35% ($n = 40$) and 65% ($n = 75$); and juveniles, 43% ($n = 12$) and 54% ($n = 15$). One juvenile and four males had no large buttock tubercles and one male had three large buttock tubercles on each side. Out of 273 tortoises, 62 (23.3%) had one or more small buttock tubercles additional to the larger ones. Females had small tubercles ($n = 36$, 34%) more often than males had ($n = 22$, 16%; $\chi^2_1 = 8.6$, $P = 0.003$), but frequencies of small buttock tubercles in juveniles ($n = 4$, 14%) did not differ from males or females ($P > 0.08$). Although not counted, most animals had a number of small to large scales around the tubercles on the buttocks. Scaling on the forearms was heavy with all juveniles ($n = 17$), 92% of males ($n = 61$) and 95% of females ($n = 39$) having more than 50% medium and large scales on their forearms.

8.3.2 Regional differences in the morphology of the Kalahari tent tortoise

Regional analyses were difficult because samples sizes for females and juveniles within regions were relatively low, compared with the Central region. The North-west region comprised 11 females, 16 males and 6 juveniles. The collection from the Eastern region was largely males, 17 in total, but also included seven juveniles and two females. The bulk of samples were from the 'Central' region, which contributed 111 females, 121 males and 20 juveniles. Three females, two males and two juveniles were from unknown locations except for one of the three females that was found in KwaZulu Natal and had probably been released there (W.D. Haacke, pers. comm.). All tortoises of unknown or dubious locations were excluded from regional analyses. I limited analyses to aspects that showed degrees of individual variation (e.g., more than 95% of specimens had an axillary scale on each side in the same position thus axillary scute comparisons were omitted from the regional analyses). In addition, I combined cohorts for regional analyses when there was little variation among groups. Morphological comparisons among regions focussed mainly on measurements that may best reflect

habitat effect; general shell shape differences (height and width), limb size, and plastral width, which reflects the space for hind limb movement. I also analysed plastral, costal and vertebral scute formulae as they can be a diagnostic feature of a species' morphology and may reflect shell shape differences.

8.3.2.1   Morphometric measurements and scute formulae

Male and female SCL was not affected by region (ANOVA, $P > 0.09$) and although juvenile SCL appeared to be affected by region ($F_{2,33} = 3.5$, $P = 0.042$) it was not significant at a post hoc level. Regressions of several parameters on SCL were not significant; consequently, I could only compare SWM, SHM and PW among regions in females and juveniles, and hind leg length in females only. There were no regional effects on morphometric measurements of juvenile (all regions) or females (Central vs. North-west only, Eastern females not tested as $n = 2$) either using multiple ANCOVA tests ($P \geq 0.14$) or MANCOVA ($P > 0.08$).

Psammobates oculifer males differed in SWM, SHM, PW, FFRW and HLRL, after accounting for body size differences (Table 8.5). The regression slope for shell width middle (SWM) on SCL was steeper in males of the Central region than in the East region; the slopes diverged at 98.6 mm ($F_{2,147} = 4.6$, $P = 0.01$; Table 8.5). Males from the Central region also had a higher regression elevation for plastron width, front foot width and hind leg length than males from the Eastern region and shells of Central region males were higher than shells of males in the East and North-west regions ($F_2 = 3.6$, error df ≥ 55, $P \leq 0.034$). Region did not affect forearm length and hind foot width ($P > 0.13$).

Results of a multivariate homogeneity of slope test and MANCOVA were similar to multiple univariate tests. There was a significant difference of regression slopes among regions, but only for the Hotellings Trace statistic ($F_{7,76} = 1.85$, $P = 0.047$, partial eta-squared = 0.25, power = 0.89) and Roy's Largest Root statistic (upper bound $F_{7,40} = 3.6$, lower bound $P = 0.004$, partial eta-squared = 0.25, power = 0.94). As per the univariate tests, male SWM slope differed (Central = North-west > East) but so did male plastron width (Central > East). MANCOVA also showed significant differences in elevations among regions (Wilks' Λ exact $F_{10,86} = 2.2$, $P = 0.027$, partial eta-squared = 0.20, power = 0.88). Male regression elevations for SHM did not quite differ at a post hoc level ($P = 0.053$), but elevation differed for front foot width and hind leg length as per univariate results (Table 8.5).

Table 8.5 ANCOVA and homogeneity of slopes tests for regression lines (morphometric measures scaled on SCL) of male *Psammobates oculifer* from the central ("c"), east ("e") and north-west ("nw") regions. Where a slope test was not significant, I tested for differences among regression elevations. When results were significant, I used Sidak tests for pairwise post hoc analyses. See Table 8.1 for abbreviations.

Measure	*F*	*P*	Error df	Slope	Zerbe	Elevation
SWM	4.6	0.01	147	c > e; c=nw; e=nw	> 98.6	c=nw; e=nw
SHM	7.4	0.001	68			c > e = nw
PW	5.3	0.006	129			c > e; c=nw; e=nw
FFRW	3.6	0.034	55			c > e; c=nw; e=nw
HLRL	3.7	0.031	55			c > e; c=nw; e=nw

The length of individual vertebral scutes differed within each cohort of the three regions (Friedman's RM and RM ANOVA: $\chi^2_4 > 10.4$, $P < 0.034$; $F_{4,35} = 3.23$, $P = 0.023$), except for Eastern females and Central juveniles that had sample sizes of two. Vertebral formulae of females were identical for the Central and North-west regions, but differed among regions for males and juveniles. The pattern also differed among cohorts (Table 8.6). The length of individual costal scutes differed within each cohort of the three regions (FRMA: $\chi^2_3 > 10.7$, $P < 0.013$), except for Eastern females and Central juveniles with sample sizes of two. Costal formulae of Central and North-west females were identical, as were the formulae for Central and North-west males. For males from the East, costal scutes 2 and 3 did not differ in length, which was similar to the female pattern in the Central and North-west regions. There was no difference in the costal scute pattern of juveniles from the East and North-west, but the juvenile pattern differed from the adult pattern (Table 8.6). The length of individual plastral scutes differed within each cohort of the three regions (RM ANOVA: $\chi^2_5 > 23.5$, $P < 0.0003$), except for Eastern females that had a sample size of two. The plastral pattern differed among regions for females, males and juveniles, and corresponded only between males from the Eastern and North-west regions (Table 8.6).

Table 8.6 Vertebral, costal and plastral formulae for cohorts of *Psammobates oculifer* in three regions of their distribution.

	Females	Males	Juveniles
Vertebrals			
Central	V3=V5=V1=V4>V2	V5=V1>V3=V4>V2	No difference, n=2
East	No difference, n=2	V5>V1>V4>V3>V2	V1=V5>V4=V3=V2
North-west	V4=V5=V1=V3>V2	V5=V1>V4>V3>V2	V1=V5>V2
Costals			
Central	C1>C2=C3>C4	C1>C3>C2>C4	No difference, n=2
East	No difference, n=2	C1>C3=C2>C4	C1>C2=C3=C4
North-west	C1>C2=C3>C4	C1>C3>C2>C4	C1>C2=C3=C4
Plastral scutes			
Central	Ab>H>G>An>F>P	Ab>H>G>An>F>P	Ab>H>G>An>F>P
East	No difference, n=2	Ab>H>G>An=F>P	Ab>H>G>An=F>P
North-west	Ab>H>G>An=F>P	Ab>H>G>An=F>P	Ab>H>G=An=F>P

8.3.2.2 Shell colour and other characteristics

Marginal scute numbers did not differ between cohorts on the left or right sides and the number of scutes on the right side did not differ among regions ($P \geq 0.02 >$ adjusted α = 0.017) so I limited my regional analyses to marginal scute numbers on the left side only, cohorts combined. The number of marginal scutes on the left side differed between tortoises of Central and Eastern regions. Of Eastern tortoises, 88% ($n = 23$) had 11 or more marginals whereas in the central region, 39% ($n = 97$) of animals had less than 11 marginals and the difference was significant (Fisher's exact test, $P = 0.008$; Appendix J). The number of marginals from animals in the North-west region did not differ from those in the East or Central regions ($P > 0.11$, Appendix J).

The strength of plastral concavity (weak) did not differ for males among regions ($P > 0.72$), but the position did (χ^2 and Fisher's exact tests, $P < 0.004$). The proportion of animals with short plastral concavities, localised on the midline at the seam of the abdominal and femoral scutes (see Fig. 8.1 for plastral diagram), was greater in the Central region (71%, $n = 24$) than in the East (18.2% $n = 11$) and North-west (0%, $n = 14$; Appendix K).

Frequencies of tortoises with more than one large buttock tubercle were greater in tortoises from the Central region than they were for any other region (Fisher's exact tests, *P* ≤ 0.00001; Appendix L). Tortoises sometimes had small buttock tubercles in addition to the large buttock tubercles. Occurrence of small buttock tubercles on tortoises did not differ among regions (Fisher's exact tests. *P* ≥ 0.032 > 0.017 = adjusted α).

The bridge of Central regions tortoises consisted of a greater range of marginal scutes than in the Eastern and the North-west regions, where the bridge usually consisted of marginals 3-7 or 3-8 (all, and 93 % for East and North-west respectively; Appendix M). Patterns of bridge scutes in the Central region differed significantly from other regions (Fisher's exact tests, *P* ≤ 0.0004) but it did not between East and North-west (*P* = 0.34; Appendix M).

Not only did region affect marginal scute numbers, but also it affected marginal scute serration patterns. Anterior serrations of males in Central and Eastern regions were similar (*P* = 0.56) but both differed from males of the North-west region (Fisher's exact tests, *P* ≥ 0.017; Appendix N). All males in the Eastern region (*n* = 15) and most males in the Central region (92%, *n* = 109) had three serrated, symmetrical anterior marginal scutes, while North-west males sometimes had three (60%, *n* = 9) and sometimes more than three (40%, *n* = 6) anterior serrations on both sides (Appendix N). Anterior serration patterns did not differ for females and juveniles among regions (χ^2 and Fisher's exact tests, *P* = 0.32; Appendix N). No tortoise had less than three posterior marginal scutes serrated on both sides and I split categories into animals with three and animals with more than three posterior serrations. Prevalence of animals with more than three serrations was high in North-west males (71%, *n* = 10), where it occurred more often than it did in Central region males (19%, *n* = 22; Fisher's exact test, *P* = 0.00006; Appendix N). All Eastern juveniles (*n* = 6) had more than three, serrated posterior marginal scutes, different from juveniles in the Central region who usually had three only (74%, *n* = 14; Fisher's exact test, *P* = 0.0026; Appendix N). Juveniles in the North-west also had high frequencies of specimens with more than three posterior marginal serrations (80%, *n* = 4) more than juveniles in the Central region but not significantly so after application of a sequential Bonferroni (*P* = 0.047 > 0.025 = adjusted α). Females in both North-west and Eastern regions appeared to have a greater number of serrated posterior marginal scutes than did females in the Central region but again, it was not significant after application of a sequential Bonferroni (*P* = 0.036 > 0.025 = adjusted α; Appendix N).

The only significant difference in dark plastral pigmentation was between North-west and Eastern males: North-west males had darker plastrons (60%, *n* = 9, in category 3) than Eastern males had (81%, *n* = 13, in category 2; Fisher's exact test, *P* = 0.0073). There was regional variation for cohorts in carapacial background colouring. Females in the Central region had different carapacial colouring than females in the North-west and Eastern regions (Fisher's exact tests, *P* ≤ 0.002). Central region females were distinguished from females of other regions by the relatively high frequency of tortoises with brown pigmentation on the carapace (30%, *n* = 31); North-west females had no brown specimens, nor did the two females from the Eastern region (Appendix O).

8.3.3 *The geometric tortoise*

8.3.3.1 *Measurements and cohort comparisons*

Mean straight carapace length (SCL) and most other measurements in Appendix P (without accounting for SCL) were greatest in females and lowest in juveniles (SCL; $F \geq$ 27.95, residual df ≥ 29, *P* ≤ 0.00001). The exceptions were nuchal length, supracaudal (distal) scute width, anal width and anal gap, which did not differ between males and females, and nuchal width, which was greater in females than it was in juveniles only ($F \geq 5.06$, residual df ≥ 61, *P* < 0.009). Most morphometric measurements listed in Appendix P (before or after $\log_{10}$ transformation) had a positive relationship with body size in males (SCL; $F \geq 8.16$, *P* ≤ 0.009, residual df ≥ 16, $r^2 \geq 0.27$), females ($F \geq 11.16$, *P* ≤ 0.003, residual df ≥ 10, $r^2 \geq 0.35$) and juveniles ($F \geq 19.56$, *P* ≤ 0.0003, residual df ≥ 12, $r^2 \geq 0.52$). Measurements that did not show a relationship with body size were the nuchal length and width in females (*P* > 0.49). Juvenile sample size for mass (*n* = 4) was too small to compare with other groups. As with *P. oculifer*, costal (CR), vertebral (V) and plastral scute lengths were compared using formulae and were not included in regression analyses.

Generally, regression slopes were homogeneous, but *P. geometricus* females had steeper slopes than males for four measurements; shell width middle (SWM), shell width posterior (SWP), bridge length (BL) and mass (BM; Table 8.7). In the case of SWP and BL, the juvenile regression slope was also steeper than the male slope was. Female regression elevations were higher than male regression elevations for SWA, SHM, SV ($\log_{10}$), PL, PW, V3W, CR3W, MR6W ($\log_{10}$), MR6L, DCL and DCW. Juvenile regression elevations were higher than they were in males for SWA, SWM, SHM, SV, NW, and MR6L (Table 8.7). Male regression elevations for AW, AG ($\log_{10}$) and S(D) were greater than in females, and male AW and FARL were greater than in juveniles

(Table 8.7). There were no differences among cohorts for NL, S(P), GW, FFRW, HFRW, HLRL and CS. The slopes for HW differed among cohorts ($F_{2,39}$ = 3.7, *P* = 0.035), but post hoc tests showed no differences (see Appendix P).

Table 8.7 Homogeneity of slopes and ANCOVA tests for regression lines of morphometric parameters on SCL of *Psammobates geometricus* cohorts. Where a slope test was not significant, I tested for differences among regression elevations. The Zerbe test indicates at what SCL the slope differed. If differences are reported for both slopes and elevations, the lowest *F* and *P* value of the two tests is given, but I report the error df for slope only. See Table 8.1 for abbreviations.

Measure	*F*	*P*	Error df	Slope	Zerbe	Elevation
SWA	13.1	0.0001	62			f = j > m
SWM	6.8	0.002	64	f > m; j = f; j = m	> 95.5	j > m; j = f
SWP	4.9	0.01	60	f = j > m		f = j
SHM	92.3	0.0001	66			f > m, j; j > m
SV*	91.4	0.0001	64			f > m, j; j > m
PL	40.4	0.0001	59			f > m; j = f; j = m
PW	27.4	0.0001	61			f > m; j = f; j = m
NW[1]	13	0.0008	44			j > m
V3W	23.6	0.0001	65			f > m; j = f; j = m
CR3W	29	0.0001	64			f > m; j = f; j = m
MR6W*	17.7	0.0001	63			f > m; j = f; j = m
MR6L	23.1	0.0001	64			f = j > m
S(D)	20.1	0.0001	64			m > f; j = f; j = m
AW	30.1	0.0001	62			m > f = j
AG*	12.6	0.0001	60			m > f; j = f; j = m
FARL	4.3	0.02	48			m > j; f = j; f = m
DCL	7.3	0.001	64			f > m; j = f; j = m
DCW*	40.3	0.0001	62			f > m; j = f; j = m
BL	20.1	0.0001	62	f = j > m	> 96.2	f = j
BM[2]	33.6	0.0001	26	f > m	> 90.7	

*Data log10 transformed

[1]M vs. J only as female regression not significant

[2]Sample size (*n*=4) for juveniles too small for comparisons

Sample sizes within cohorts of *Psammobates geometricus* were small relative to the number of dependent variables being tested (see Appendix P) hence I did not use multivariate statistics to evaluate measurements among cohorts of *P. geometricus*.

8.3.3.2 Scute counts and scute length formulae

All animals (n = 73) had one supracaudal scute and with one exception a single nuchal scute; the exception, a female, had two nuchal scutes (Appendix Q). There was little variation in the number of vertebral scutes, with all females (n = 23), 27 males (96.4%) and 21 juveniles (95.5%) having five vertebral scutes (Appendix Q). Similarly, there was little variation in costal scute numbers with 96% males (n = 26), 88% females (n = 21) and 96% juveniles (n = 21) having four costal scutes on both sides. Costal scute abnormalities include one male with three scutes on one side, a male and a female with asymmetrical (five and four) scutes and a female and a juvenile with five scutes on both sides (Appendix Q).

Scute lengths differed within cohorts for the vertebrals (χ^2_4 > 27.3, P < 0.0001), costals (χ^2_3 > 42.4, P < 0.0001), and the plastron (χ^2_5 ≥ 78, P < 0.0001). The vertebral scute formula differed among males (V5>V1>V4>V3>V2), females (V5=V1=V4>V3>V2) and juveniles (V1>V5=V4=V3=V2; Appendix P). The pattern for costal scutes also differed among cohorts: females (C1>C3>C4>C2), males (C1>C4>C3>C2), and juveniles (C1>C3=C2>C4). The plastral arrangement for females, males and juveniles respectively, was Ab>H=G>F>An>P, Ab>H=G>F>An>P and Ab>H>G>F>An=P (Appendix P).

As seen for other carapacial scutes, frequencies of marginal scutes in *P. geometricus* varied little; 79% females (n = 19), 96% males (n = 26) and 90% juveniles (n = 18) had 11 marginals on each side and marginal scute frequencies did not differ among cohorts (Fisher's exact tests, P ≥ 0.14; Appendix R). Furthermore, size did not affect marginal scute counts, 90% of tortoises (n = 64) had 11 marginals on both sides. All *P. geometricus* had one axillary and one inguinal scute on each side of the body, which respectively bordered the humeral and pectoral scutes, and the abdominal and femoral scutes. The axillary scute of all females (n = 25) and juveniles (n = 19) and 96% males (n = 25) was in contact with the third and fourth marginal scutes with the axillary scute of one male being in contact with the third marginal only. The inguinal scute of all tortoises (n = 68) was in contact with marginal scutes seven and eight.

8.3.3.3 Marginal scute serrations, marginal curvature and bridges

All juvenile *P. geometricus* (n = 18) had serration of anterior marginals but serration was absent in 58% of males (n = 14) and 59% of females (n = 13, Appendix S). Where serration in adults did occur, males tended to have a higher proportion of individuals

with two serrated scutes on each side (29%, $n = 7$) while females had a higher proportion with three serrated marginal scutes on each side (27%, $n = 6$) but the difference was not significant ($P = 0.18$). I compared individuals with less than three, three and more than three serrated anterior marginal scutes among cohorts and juveniles were more often found with three or more serrated anterior scutes than males were (Fisher's exact test, $P = 0.007$) but not females ($P = 0.18$). As with anterior marginal scutes, all juveniles had serration in posterior marginal scutes ($n = 20$), but 48% of males ($n = 12$) and 55% of females ($n = 11$) lacked serration in this area (Appendix S). Females and juveniles had a higher proportion of individuals with more than three serrated posterior marginal scutes than males had (Fisher's exact tests, $P \leq 0.023$), but posterior marginal serration patterns between juveniles and females did not differ ($P = 0.39$, Appendix S). All females with serrations ($n = 10$) and 88% of males ($n = 15$) had weak serrations, but 60% of juveniles ($n = 12$) had 'medium' strength serrations and juveniles had stronger serration than males or females did (Fisher's exact tests, $P \leq 0.005$).

There was little effect of body size on anterior and posterior marginal scute serration in *P. geometricus*. Tortoises less than 90 mm in length tended to have more serrated anterior marginal scutes than those between 90 and 119 mm SCL, but it was not significant after applying a sequential Bonferroni (Fisher's exact tests, $P \geq 0.0123 > 0.008 = $ adjusted α). Anterior serration patterns in large tortoises (> 120 mm SCL) did not differ from that of small ones (< 90 mm, $P = 0.37$). Patterns in posterior marginal scute serration suggested that animals with three serrated posterior marginal scutes on each side were more common in tortoises less than 90 mm than they were in animals from 90 to 109 mm SCL, but it was not significant after applying a sequential Bonferroni (Fisher's exact tests, $P \geq 0.012 > 0.008 = $ adjusted α). There were no differences in posterior marginal scute serration among other size categories ($P \geq 0.13$).

All females, 96% of males ($n = 26$) and 94% juveniles ($n = 16$) lacked anterior marginal curves; one male and one juvenile had a weak upcurve. A weak upcurve of the posterior marginals was found in 50% females ($n = 11$), 67% males ($n = 18$) and 88% juveniles ($n = 15$), with three males having 'intermediate' posterior marginal curves and remaining animals ($n = 10$) having none. Out of 71 animals sampled, only one female lacked a bridge ridge (Appendix T). Bridge ridges tended to be more substantial in adults than they were in juveniles; 39% of males ($n = 11$) and 16.7% of females ($n = 4$) had 'medium' strength ridges, compared to one 'medium' and one 'strong' ridge (5% each) in juveniles (Appendix T). Frequencies of different ridge strengths differed among

groups ($\chi^2_2 = 5.98$, $P = 0.05$), with males having a higher proportion of medium strength ridges than females or juveniles. The bridges were often comprised of marginal scutes three to eight; this was true for 70% of females and males ($n = 16$ and 19 for females and males respectively) and 78% of juveniles ($n = 14$, Appendix T).

8.3.3.4 Shell colouration

There was minimal variation in shell colouration of *P. geometricus*; the light colour was yellow for all individuals assessed ($n = 65$) except for one female (orange) and one juvenile (orange/yellow). All tortoises ($n = 66$) had Cat. 4 (70-80%) dark pigmentation on their carapaces. Plastral pigmentation was more variable than carapacial pigment but it did not differ significantly among cohorts ($P > 0.09$, Appendix U). Females had a high proportion of individuals in Cat. 3 and Cat. 4 of plastral dark pigmentation (83%, $n = 19$) while for juveniles (78%, $n = 14$) and males (83% $n = 19$), Cat. 2 and Cat. 3 plastral dark pigmentation was prevalent (Appendix U). Size did not have an effect on the proportion of dark pigment on the plastron (Fisher's exact tests, $P \geq 0.098$). Dark pigment on the carapace was significantly greater than it was on the plastron in all cohorts and within size classes (Paired *t* tests, $t \geq 4.97$, df ≥ 13, $P < 0.00012$).

8.3.3.5 Occurrence of shell damage and deformities

Incidences of abnormalities in *Psammobates geometricus* were relatively low, only 10% ($n = 8$) were recorded as having an abnormality, of which no juveniles ($n = 25$) had an abnormality and one male had two abnormalities, a scute abnormality and cattle or game damage. Of the remainder, shells of three females were damaged by animals, of which one appeared to have dog bites; two males had scute abnormalities and one (live) female had broken tips on the right three posterior marginal scutes (cause unknown).

8.3.3.6 Other morphological characteristics

Typically, *P. geometricus* has five claws on both anterior feet and four claws on both posterior feet. All males ($n = 19$ for left and 17 for right), females ($n = 19$) and juveniles ($n = 14$ for left and 12 for right) had five claws on the anterior feet. All females ($n = 22$), juveniles ($n = 11$ right, 12 left) and males ($n = 18$) had four claws on each posterior foot, with an additional male specimen with only one leg having three claws. The latter specimen may have had claws damaged by a predator.

Of females, 61% ($n = 11$) had nostrils below eye level, and it was the same for 73% males and juveniles ($n = 8$). All remaining animals had nostrils at eye level and

differences in nostril position among cohorts was not significant (P = 0.9). *Psammobates geometricus* usually had a tricuspid beak; beaks were tricuspid in 88% of females (n = 15) and 83% of males and juveniles (n = 10 in both cases). Two males, a female and juvenile had serrated beaks and the beaks of a female and a juvenile were worn. Females (n = 24) did not have a plastral concavity and one juvenile (n = 20) had a weak concavity and all except one male (n = 26) had a plastral concavity. Of male concavities, 20% were 'weak' and '80%' were strong and all stretched along the midline seam of the plastron. Male concavities either ran from the seam of the pectoral and abdominal scute to the seam of the abdominal and the femoral scute (44%, n = 11) or from the seam of the gular and humeral scutes through to seam of the abdominal and the femoral scute (52%, n = 13; see Fig. 8.1). One concavity was localised around the seam of the abdominal and femoral scutes. All tortoises (n = 47) lacked large or small, buttock tubercles except for two juveniles that had small, buttock tubercles. As sample sizes were low, I consolidated forearm armour from four to two categories, those with predominantly medium sized scales (categories one and two) and those with predominantly larger sized scales (categories three and four). Females and juveniles were similar; 76% (n = 13) and 71% (n = 5), respectively, had predominantly medium scales while a greater proportion of males had predominantly large scales (63%, n = 10), but difference in forearm armour among cohorts was not significant (Fisher's exact test, P = 0.075).

8.3.4 Comparison of *Kalahari tent* and *geometric tortoises*

Similar to regional comparisons of *P. oculifer*, I chose specific morphological measurements and characteristics to best illustrate the effect of habitat and climate on the two sister taxa. I analysed shape (SHM and SWM), and legs and feet dimensions (as done for *P. oculifer* regional analyses). I also included head width (*P. oculifer* and *P. geometricus* may have differences in diet which may affect head dimensions) as well as all measurements that may influence the size of shell openings (cranial space, plastron width, anal gap and bridge length). Shell openings may be affected by differences in predation pressure, behaviour (e.g. fighting may require extra mobility) and the environment (different substrates and habitat affecting animal movement). I limited qualitative characters to forearm armour (which may mitigate vulnerability to predation for a larger cranial opening), shell colouration (it may be affected by climate) and plastral concavities that may be influenced by (climate-induced) changes in body shape.

8.3.4.1 Morphological measurements

Regression slopes of the two species differed only for female hind limb length (HLRL) and bridge length (BL); slopes were steeper for *Psammobates geometricus* females in each case (Table 8.8). Regression elevations differed for many morphological parameters of females, males and juveniles. Elevations for shell width (SWM) did not differ for females, but SWM of male and juvenile *P. oculifer* was wider than in *P. geometricus* after accounting for body size (SCL) differences. Shell height (SHM) differences between the two species were limited to females; *P. geometricus* females had higher shells than *P. oculifer* females had. For both plastral width (PW) and bridge length (BL), male and juvenile *P. geometricus* had wider PWs and longer BLs than corresponding cohorts of *P. oculifer* did. The anal gap (AG) was bigger for females and males of *P. oculifer* than *P. geometricus*, but did not differ between the juveniles of the two species (Table 8.8). All three cohorts of *P. oculifer* had wider front feet (FFRW), cranial spaces (CS) and head widths (HW) than corresponding cohorts of *P. geometricus* had. Hind feet width (HFRW) was wider only for male *P. oculifer* than for male *P. geometricus*, whereas the length of the forearm (FARL) in *P. oculifer* exceeded that of *P. geometricus* only for juveniles (Table 8.8).

Multivariate test results for females were generally similar to univariate results; there was a significant difference in slopes of females between the two species (Wilks' Λ exact $F_{11,33}$ = 2.33, *P* = 0.030, Partial eta squared = 0.44, power = 0.87). Only the slope for hind leg length and bridge length differed (PG females steeper than PO females in both cases). Regression elevations for measurements between the females of each species also differed (Wilks' Λ exact $F_{10,35}$ = 10.3, *P* = 0.0001, Partial eta squared = 0.75, power = 1), they were the same as univariate results except SWM was wider in *P. geometricus*. Concerning multivariate analyses between males, I could not compare hind leg and foot measurements because of small sample sizes for *P. geometricus* (Appendix P). Otherwise, morphometric difference were as per univariate analyses (multivariate slopes did not differ, *P* = 0.13; elevations differed, Wilks' Λ exact $F_{9,51}$ = 15.9, *P* = 0.0001, Partial eta squared = 0.74, power = 1). Similar to univariate tests of juveniles, multivariate slopes were homogeneous (*P* = 0.13) and regression elevations differed between juveniles of the two species (Wilks' Λ exact $F_{8,13}$ = 9.6, *P* = 0.0001, Partial eta squared = 0.86, power = 1). Only bridge length, it was longer in *P. geometricus* juveniles, differed on the carapace. Differences in appendages and cranial space was the same as for univariate tests, but head width and right hind leg length were not included in the multivariate model because sample sizes were too small (Appendix B and Appendix P).

Table 8.8 Comparison between cohorts of *Psammobates oculifer* (PO) and *P. geometricus* (PG) for regression lines of morphometric measures scaled on SCL. Where a slope test was not significant, I tested for differences among regression elevations. See Table 8.1 for abbreviations.

Measure	Cohort	*F*	*P*	Error df	Slope	Zerbe	Elevation
SWM	F	ns					
SWM	M	10.2	0.002	178			PO > PG
SWM	J	5.8	0.02	50			PO > PG
SHM	F	49.1	0.0001	70			PG > PO
SHM	M	ns					
SHM	J	ns					
PW	F	ns					
PW	M	14.2	0.0001	157			PG > PO
PW	J	4.8	0.034	45			PG > PO
AG	F	15.3	0.0001	133			PO > PG
AG	M	4.6	0.034	156			PO > PG
AG	J	ns					
FFRW	F	35	0.0001	57			PO > PG
FFRW	M	37.2	0.0001	74			PO > PG
FFRW	J	14.5	0.001	27			PO > PG
FARL	F	ns					
FARL	M	ns					
FARL	J	17	0.0001	29			PO > PG
HFRW	F	ns					
HFRW	M	33.5	0.0001	65			PO > PG
HFRW[1]	J	na					
HLRL	F	4.8	0.033	54	PG > PO	> 117	
HLRL	M	ns					
HLRL	J	ns					
BL	F	6.3	0.014	69	PG > PO	> 107	
BL	M	49.6	0.0001	99			PG > PO
BL	J	52.1	0.0001	30			PG > PO
CS	F	15.2	0.0001	66			PO > PG
CS	M	53.3	0.0001	89			PO > PG
CS[*]	J	4.2	0.05	27			PO > PG
HW	F	12.7	0.001	54			PO > PG
HW	M	22.5	0.0001	71			PO > PG
HW	J	25.9	0.0001	19			PO > PG

[*] $\log_{10}$ transformed
[1] Regresssion with SCL failed

8.3.4.2 Meristic counts and carapacial colour differences

Female and male *P. oculifer* had three or more serrated anterior and posterior marginal scutes more frequently than did female and male *P. geometricus* ($\chi^2 \geq 75.09$, df ≥ 2, *P* < 0.00001). Neither anterior nor posterior marginal scute serration patterns differed between juveniles of the two species (Fisher's exact tests, *P* ≥ 0.145, Appendix V). All *P. oculifer* except for three females and one male had 'strongly' serrated marginal scutes. In contrast, only juveniles had 'medium' strength serrations in *P. geometricus* (adults had weak or no serration).

Shell colouration was dissimilar between the two species. All *P. geometricus* had 70-80% dark pigment. Despite all but two juvenile *P. oculifer* (*n* = 32) having 70-80% dark pigment, pigment in *P. geometricus* was a dense, matt black, while it was more opaque in *P. oculifer*. Although some specimens of *P. oculifer* had partially yellow carapaces, the yellow was a pale straw colour and not comparable with the gold on the carapace of *P. geometricus*. The texture of the carapaces of the two species also appeared to differ (which may also have affected the colour). The carapace of *P. geometricus* has a smooth texture, and the seams between scutes were very fine, while *P. oculifer* had a grainier carapace with coarser divisions between scutes.

The presence and strength of the plastral concavity differed between males of the two species ($\chi^2_1 = 35.73$, *P* = 0.00001; females did not have concavities and juveniles rarely so). A plastral concavity was absent in 15% (*n* = 11) of *P. oculifer* and when present, the majority of concavities (71%, *n* = 51) were weak. Only one *P. geometricus* (4%) lacked a plastral concavity, and of males with a concavity, 80% (*n* = 20) were strong. Not only was the plastral concavity more substantial in *P. geometricus* than it was in *P. oculifer*, but it was also longer. Concavities either ran from the seam of the pectoral and abdominal scute to the seam of the abdominal and the femoral scute (44%, *n* = 11) or from the seam of the gular and humeral scutes through to seam of the abdominal and the femoral scute (52%, *n* = 13). The concavity in *P. oculifer* was more localised; 56% (*n* = 34) ran the length of the abdominal to touch the femoral scute seam and the remainder had small concavities at the seam of the femoral and abdominal scute (all concavities ran along the plastral midline seam - see Fig. 8.1). The placement of the concavity differed between species (Fisher's exact test, *P* < 0.00001).

8.4 DISCUSSION

8.4.1 *Morphological descriptions*

8.4.1.1 *Psammobates oculifer*

Psammobates oculifer is a relatively small testudinid (see Ernst et al., 2000 for testudinid size ranges). Females averaged 113 mm SCL and 319 g, and males 99 mm SCL and 196 g although BM varied seasonally. Mean width and height in the middle was 86 and 64 mm for females and 72 and 51 mm for males. Width (at the sixth marginal scute) was marginally wider than it was at the posterior (8th/9th marginal scute seam) but they narrowed towards the anterior carapace (3rd/4th marginal scutes' seam).

A relatively broad nuchal scute was present, longer than it was wide, with five vertebral scutes and a single supracaudal scute. The shell was usually highest at the apex of the third vertebral scute. There were four costal scutes on both sides, and the costal scute formula of males differed from that of females and juveniles; the first costal was always the widest and the fourth costal was the narrowest. Vertebral scute formulae were subject to regional variation and differed among cohorts, but V2 was always the shortest vertebral scute. Marginal scutes were largely symmetrical; tortoises had either 11 or 10 (and rarely 12) marginal scutes on each side. Most animals had strong serrations on the first and last three sets of marginal scutes, but juveniles and small adults sometimes had additional marginal scute serrations. Posterior (but not anterior) marginal scutes had a weak upward curve. The carapace lacked a marginal groove but had a weak bridge ridge encompassing marginal scutes three to seven or three to eight.

An axillary scute was located on both sides of the plastron in contact with the humeral and pectoral scutes and the seam of the third and fourth marginal scutes. The axillaries appeared to be fused to the humerals. One inguinal scute was also present on both sides of the plastron, touching the abdominal and femoral scutes, and the seams of marginal scutes seven and eight (always in juveniles and frequently in adults). The plastral arrangement of males differed from that of females and juveniles only in that femoral scutes were longer than anal scutes in males. The plastral arrangement was subject to regional variation. Males most often had a small plastral depression along the midline seam of the plastron, either localised around the seam of the abdominal and femoral scutes or reaching from the top of the abdominal (at the pectoral seam) to the femoral scute. Females had no plastral depression.

Carapacial background colour was yellow (lighter), orange/yellow, orange/brown and brown (darker); orange/brown or orange/yellow forms were most common and became darker in adults, particularly females. Dark pigmentation, rays, between the light colouration was also present on the carapace. Small tortoises (juveniles and males) tended to have a higher percentage of dark pigment on their carapace than larger individuals. All cohorts had a higher proportion of dark pigment on the carapace than they did on the plastron.

Tortoises had five anterior, broad and evenly spaced claws and four, longer and thinner, posterior claws. Heads were broad and nostrils were usually located below the eye line. Beaks were tricuspid and, very occasionally, serrated. One or two large buttock tubercles were found either side of the tail, and smaller buttock tubercles were sometimes present although less so in males than it was in females. Occurrence of buttock tubercles was subject to regional variation. Scaling was often present around the tubercles. Forearms were heavily armoured with large scales.

8.4.1.2   *Psammobates geometricus*

Psammobates geometricus is a slightly larger tortoise than *P. oculifer*, females averaged 122 mm SCL and 467 g, and males 108 mm SCL and 248 g but BM may vary seasonally. Mean shell width and height in the middle were 92, 73 mm and 75, 56 mm for females and males respectively. Middle width (at the sixth marginal scute) was similar to posterior width (8th/9th marginal scute seam) but the carapace width tapered markedly at the anterior (3rd/4th marginal scutes' seam) creating a 'tear drop' shell shape.

A relatively thin nuchal scute was present, longer than it was wide, with five vertebral scutes and a single supracaudal scute. There were four costal scutes on both sides, and the costal scute formulae differed among cohorts, with C1 always being the longest and C2 the shortest in adults. The vertebral scute pattern also differed among cohorts; V2 was always the shortest vertebral scute. Marginal scutes were largely symmetrical with 11 marginal scutes on each side. Weak marginal anterior (1-2 or 3, 40% of adults) and posterior (8-11 or 9-11, 50% of adults) marginal scute serrations were present, but anterior and posterior serration was omnipresent in juveniles (and smaller tortoises) and juveniles had more and stronger serrations than adults did. Anterior marginal scute curves were rare but weak posterior upcurves occurred in females (occasionally), often in males and frequently in juveniles. The carapace lacked a marginal groove but tortoises have a bridge ridge and the ridge was stronger in

males than it was in females or juveniles. Bridges usually comprised marginal scutes three to eight.

One axillary scute was located on both sides of the plastron in contact with the pectoral and humeral scutes and the seam of the third and fourth marginal scutes. A single inguinal scute was also present on both sides of the plastron, in touch with abdominal and femoral scutes and with seams of marginal scutes seven and eight. The longest plastral scute was always the abdominal scute with the shortest being the pectoral scute. Males usually had a strong plastral depression along the midline seam of the plastron, stretching either from the seam of the abdominal and pectoral scutes to the seam of the abdominal and femoral scute, or from the gular and humeral seam to the seam of the abdominal and femoral scute. Female plastral depressions were not obviously visible.

Carapacial colouration was ubiquitous among individuals; pigmentation was dark with narrow and golden rays that emanate symmetrically from scute bosses. Plastral colouration was more variable. The females tended to have a plastron of which 50 to 80% consists of dark pigmentation, while males and juveniles sometimes had a lighter plastron than females did, dark pigmentation being restricted to 30 to 60% of their plastrons. The carapace had more dark pigment than the plastron, regardless of cohort or size class. The carapace had a smooth, almost paper-like quality.

Tortoises had five anterior and four posterior claws and claws were thick. Heads were narrow and nostrils were usually located below the eye line, although juveniles tended to have nostrils level with the eyes. Beaks were tricuspid and, very occasionally, serrated. Tortoises lacked buttock tubercles. Medium and small size scales were present on the forearms.

8.4.2 Sexual dimorphism

Female *P. oculifer* were larger (have a greater SCL), higher and wider than males were relative to their body size. Darwin (1871) attributed large female size in iteroparous species to selection for fecundity; greater size facilitating increased egg production. In southern African testudinids, it may be important to consider fecundity in terms of habitat.

Psammobates oculifer inhabits an arid and 'harsh' environment through much of its range (Chapter 4). Rall (1990) x-rayed 18 females over a two-year period between

September and April (approximately) in each year, of which seven were gravid, with all gravid females being found between the last day of December and mid-March. Only single eggs were found and they were large eggs (mean 36 x 29 mm). The only gravid females found at Benfontein were also found from January to March (M.D. Hofmeyr, unpublished data). Larger body size in female *P. oculifer* would facilitate the production of a large egg (which may be less prone to desiccation than a small egg) and a large hatchling, and these two factors increase the likelihood of offspring survival in an unpredictable (arid) environment (Hofmeyr et al., 2005).

Berry & Shine (1980) found that in testudinid species featuring male-male combat, males tended to be bigger than females (simply, larger males win more fights and get more mates). This is true of *Chersina angulata*, another southern African testudinid (Mann et al., 2006), but not of *P. oculifer*, where males fight (Chapter 6) but are considerably smaller than females. Large female size in *P. oculifer* could be an effect of habitat. *Chersina angulata* is a larger tortoise than *P. oculifer* (e.g., see Hofmeyr et al., 2005), it occurs in a diversity of habitats (Van Den Berg & Baard, 1994), body size does not affect egg size, females can be gravid for a large proportion of the year (long egg retention time) and they can have multiple one-egg clutches (Hofmeyr, 2004). Aseasonal reproduction implies that sufficient resources for reproduction and nourishment for a hatchling could become available at any given time. Such reproductive flexibility suggests that the relationship between egg size and body size in *C. angulata* is less important than its ability to retain an egg over a long period and have numerous clutches (see Hofmeyr, 2004). Conversely, in female *P. oculifer*, seasonal climate extremes (Chapter 4) limit the viable egg-laying period and a large egg and resulting large offspring may increase fecundity in a semi-arid environment (see Hofmeyr et al., 2005). Thus, seasonal constraints may force *P. oculifer* to put 'all its egg(s) in one basket' to maximise reproductive success (i.e., selection for increased female body size), while *C. angulata* spreads its bets (eggs) over a longer period (and therefore large body size is less crucial).

Although *P. oculifer* males are small, adaptations for combat success is not limited to size, manoeuvrability may also be important. *Psammobates oculifer* males were smaller and lighter than females and had shorter and narrower plastrons and shorter bridge lengths than females, all of which would assist mobility through extra leg space. In addition, male *P. oculifer* also have a higher cranial space than females do, which assists in anterior mobility. All these morphological attributes may assist males not only in fighting, but also in patrolling territories and finding mates. Male *P. oculifer* were

more active than females in October (the middle of the mating season) and they fight in the mating season (see Chapter 6). Bonnet et al. (2001) had similar findings to this study for *Testudo horsfieldii*, another small testudinid inhabiting a harsh environment. Male *T. horsfieldii* were smaller, lighter, had more domed shells, longer limbs, a longer tail, and more space (less shell) around limbs than females did. Although I did not measure tail length, visual comparisons of male tails showed them to be of undoubted greater size than female tails and longer tails assist males when copulating (T Keswick, personal observation). Unlike *T horsfieldii*, *P. oculifer* females were more domed than males, which may aid egg production in females. Greater 'domedness' in male (than female) *T. horsfieldii* was attributed to ease of self-righting when flipped in combat. In the case of *P. oculifer* males, it may be that natural selection has constrained male carapace morphology more than sexual selection has. For instance, male *P. oculifer* used lower burrows than female did in summer to escape the midday heat and a less domed shell may allow access to a smaller burrow, thereby increasing the number of burrows available as microclimates. Studies of male combat in southern African testudinids is limited to *Chersina angulata* (Mann et al., 2006), and more studies are needed to assess the role of combat in sexual selection within this group.

Measurements also attributable to sexual selection in *P. oculifer* were their anal width (AW), anal gap (AG), supracaudal width (distal) and hind-right foot width (HRFW). Anal width is highly dimorphic in some European *Testudo* spp. (Willemsen & Hailey, 2003) as well as in *T. horsfieldii* (Bonnet et al., 2001), and together with AG, provide male *P. oculifer* with more space for the large tail to move during copulation. In the case of AW, males had a steeper slope than females, i.e., AW becomes more dimorphic as males get bigger. Greater distal width of the supracaudal scute in males most probably serves to protect the large male tail. The rear feet of *P. oculifer* males were wider than in females, perhaps due to a combination of habitat and sexual selection pressure. Loose sand is the prevailing substrate over the range of *P. oculifer* (see Chapter 4). There are at least two incidences where wide hind foot width would be of extra benefit to males; fighting and mating. During combat, males circled, rammed and bit each other (T Keswick, personal observation) and a wider hind foot gives better purchase (larger surface area) on the loose substrate when circling and launching attacks (T Keswick, personal observation). During copulation, males needed to be able to mount females and hold their position, difficult when the substrate is loose (sandy), and a wider foot would assist in this regard.

Female *P. geometricus* shared sexually dimorphic characteristics with female *P. oculifer*. Body size and shape (SHM, SWM, SWP, DSW and DCL) were all greater in females than they were in males suggesting selection for fecundity. *Psammobates geometricus* follows the Berry & Shine (1980) hypothesis as females are larger and males are not known to fight (Baard, 1995b). *Psammobates geometricus* shared certain sexually dimorphic traits with *P. oculifer*, which suggests greater mobility is also an advantage in *P. geometricus* males, possibly for mate searching. Van Bloemestein (2005) found males displaced greater distances from refuge to refuge and although mate searching could be a reason for this, empirical data for mating behaviour of *P. geometricus* in the wild is lacking. Certainly, males had a shorter and narrower plastron than females did and a shorter bridge length, increasing male mobility. Hind foot width was not sexually dimorphic in *P. geometricus*. As with *P. oculifer*, I did not measure *P. geometricus* tail lengths, but again inspection showed them to be obviously larger in males than they were in females and correspondingly, AG, AW and supracaudal (distal) scute width were all greater (as per *P. oculifer*). An additional, easily discernible, sexually dimorphic feature of *P. geometricus* was a substantial plastral concavity in males (usually absent or very shallow in *P. oculifer*, but see section 8.4.4). This was noted by Baard (1995b), but he also recorded (much less distinct) concavities in females, although they were not discernible in the female specimens I assessed. Plastral concavities are associated with mating success (Willemsen & Hailey, 2003; Pritchard, 2008) possibly because they help prevent males from sliding off the female's shell during copulation (Moskovits, 1988).

Sexual dimorphism can be contrasted by comparing adults with juveniles, juvenile morphology being largely free of the compounding effects of sexual selection (Gibbons & Lovich, 1990). The shape of juvenile *P. geometricus* and *P. oculifer* resembled female more than male shape (although univariate and multivariate results for *P. oculifer* differed here) but the juvenile regression slope for SWM was steeper and the SHM elevation higher than it was in males. This means that the male, and not the female, growth pattern deviates from the juvenile pattern. The flatter shape of the males may assist in thermoregulation that is important in small-bodied tortoises (Reiber et al., 1999). Marginal scute serration was also greater in juveniles of both species and width combined with serration probably reduces palatability to a potential predator.

8.4.3 Regional differences in the morphology of the Kalahari tent tortoise

Small sample sizes for females and juveniles effectively restricted regional analyses to males only and the most discernible differences were between the East and Central

region males. The East and Central regions are separate bioregions and relatively (geographically) isolated from each other after accounting for 'buffer zones' of unsuitable habitat separating them (section 8.2.2). Tortoises from the North-west region were spread over a wider area than the other two regions, and the resulting increase in habitat heterogeneity in the North-west region made comparisons between it and the other two regions difficult.

East region males tended to be smaller bodied (SWM and SHM), relative to SCL than those of the Central region and had a narrower front foot and shorter back leg. Many Central region animals were collected from Kimberley Thornveld (SVk4) areas where the soil was predominantly sand (see Chapter 4 for a full habitat description). Most East region specimens were collected from Limpopo Sweet (SVcb19) and Makhado Sweet (SVcb 20) Bushveld vegetation units (Rutherford et al., 2006a). Although the climate in these two vegetation units appears broadly similar to Kimberley's climate (see Chapter 4 for a description of Kimberley's climate), soil and vegetation differ. Vegetation is described as open woodland in SVcb19 and shrubby bushveld in SVcb20 and although there are localised areas of Kalahari sand in the former vegetation unit, geology and soils in both vegetation units are more heterogeneous than they are at Kimberley (Rutherford et al., 2006a).

While differences in geology and soil may directly affect habitat by influencing plant community ecology, it may also have an indirect effect on the habitat of *P. oculifer*, by changing microhabitat availability (burrows). In summer at Benfontein, *P. oculifer* frequently used mammal burrows for shelter during the heat of the day (Chapter 5). Burrows of the size used by tortoises (Chapter 5) were most likely made (or modified) by *Pedetes capensis* (springhare), *Cynictis pencillata* (yellow mongoose), *Suricata suricatta* (suricate) and *Xerus inauris* (South African ground squirrel), all common on the study site (see Skinner & Chimimba, 2005 for details of mammal burrows). In the East region, *S. suricatta* and *X. inauris* do not occur there, *C. pencillata* occurs in part and *P. capensis* is found throughout. Friable soil (sand) and calcrete layers, which occur in Kimberley and through much of the range of *P. oculifer*, are important for burrow architecture (Walker et al., 2007). Lack or limited quantities of sand and calcrete in the East region may explain why certain semi-fossorial mammals, abundant over the rest of the range of *P. oculifer*, do not occur there. A reduction in semi-fossorial mammal species could affect *P. oculifer* by reducing the number of suitable microhabitats (burrows) available on hot days. Thus, in the East region small body size

in *P. oculifer* may be advantageous, as it would potentially increase the number of microhabitats other than burrows (e.g. rock crevices) available in summer.

The shorter hind limbs and narrower feet of East region males could also be habitat-related. Long hind limbs in the Central region could be a result of habitats being more open there than they are in the East region. Long hind limbs in desert lizards were associated with more open habitats and visa versa for short hind limbs (Pianka, 1969). Narrow front feet in East region males may also be a result of natural selection. The advantages afforded by wide feet on the sandy substrates of the Central region (moving and digging in sand) may not increase mobility on the heterogeneous substrates in the East region (see also section 8.4.4). Although a more thorough investigation is warranted, both to assess the habitat and to collect a larger sample of tortoise morphometrics there, this preliminary investigation of males suggest that a different ecomorph of *P. oculifer* may occur in the East region.

8.4.4 Environmental adaptations

Unfortunately, there has been insufficient molecular data published to establish the divergence time of *P. oculifer* and *P. geometricus* and hence to identify the manner of such change, climatic or otherwise, that may have caused such divergence. However, Baard & Mouton (1993) hypothesised that the two sister species, *P. geometricus* and *P. oculifer*, may have once been an entire, 'warm adapted', tortoise species with a large range extending to the south-west Cape. A western population of this 'warm adapted' species subsequently became isolated by glacial events and range contraction. Due to their isolation in the environs of the Cape Fold Mountains, a temperate climate, the western population may have become 'cool adapted' and diverged. Baard & Mouton's (1993) hypothesis was based on a hypothesis by Mouton & Oelofsen (1988) explaining divergence in melanistic species of Cordylid lizards in the south-western Cape during the Pleistocene. However, subsequent molecular evidence showed the timing of divergence of these Cordylid species and hence the possible climatic event responsible, cooling due to upwelling events, were earlier than previously hypothesised (Miocene Epoch, Daniels et al., 2004). Similarly, divergence of Western and Southern clades of *Chersina angulata* also coincided with climatic change in the Miocene (Daniels et al., 2007). Aridification and faunal speciation in south-west Africa during the Miocene epoch is reviewed by Pickford (2004). Pickford (2004) surmises that the presence of the Miocene fossil *Namibchersus* in the region, as well as extant genera including *Chersina*, *Psammobates* and *Homopus*, all of which are small, southern African testudinid endemics, may also be linked to climatic events in

the Miocene. Ultimately, with the lack of molecular data, one is first left to establish morphological differences between these two sister taxa and interpret these morphological differences in context of the different habitats of *P. geometricus* and *P. oculifer*.

Psammobates geometricus inhabits a mesic habitat, mean annual precipitation (MAP) is between 500 and 750 mm (Hofmeyr et al., 2005). Its habitat covers a small area; it is endemic to Shale Renosterveld and Alluvium Fynbos vegetation in low-lying areas surrounding the Cape Fold Mountains (Baard, 1993; Cunningham et al., 2002). Asteraceous shrubs are common to both habitats and soils often consist of gravel interspersed with cobbles in Alluvium Fynbos, while renosterveld soils tend to be shale based (clay and loam; Rebelo et al., 2006). Renosterveld soils are relatively productive, hence the rarity of this vegetation type; much of it has been claimed for agricultural use. Another important aspect of this habitat is that it is fire adapted, but renosterveld ecology remains poorly known (see Rebelo et al., 2006 for overview of Renosterveld and Alluvial Fynbos). *Psammobates oculifer* lives in arid and semi-arid areas (< 500 mm MAP) of the Savanna biome. Temperature extremes are prevalent in the environment of *P. oculifer*, but are less so in areas frequented by *P. geometricus*. Substrate in the range of *P. oculifer* is relatively homogenous (except see the East region description, section 8.2.2) - it is largely Kalahari sand. Although fires occur, fire is not an integral part of semi-arid or arid savanna ecology compared with more mesic ecosystems (Sankaran et al., 2005). The habitat of *P. oculifer* is the subject of Chapter 4. *Psammobates oculifer* inhabits a theoretically 'harsher' environment than *P. geometricus*. Thus, extreme temperatures may impose constraints on the morphology of *P. oculifer* that are not evident in the morphology of *P. geometricus* that inhabit a milder climate. Differences between morphological traits of the two sister species may also be a function of substrate in their respective habitats, specifically in appendages and the amount of shell space for limbs (mobility).

Morphological adaptations can be the product of more than one selective pressure, e.g. niche divergence and sexual selection (Shine, 1988; Shine, 1989). One example is large female size, which, as well as benefiting fecundity, may also lower predation risk. Comparisons are simplified between juveniles, as the confounding effect of sexual selection is removed (Gibbons & Lovich, 1990). In this study, four morphological characters differed between both juveniles and adults of *P. oculifer* and *P. geometricus*; front foot width, head width, bridge length and cranial space. Wider front foot width (in *P. oculifer*) is likely to be an adaptation for manoeuvring on sandy substrates. A

revision of the genus *Gopherus* identified a modified (wider) manus in those species found in sandy habitats (Bramble, 1982). Although *P. oculifer* does not dig burrows as do *Gopherus spp.*, they do dig to modify the entrance of small mammal burrows (T Keswick, personal observation). Interestingly *P. oculifer* males from the East region, where soils are heterogeneous - less sandy, had narrower front feet (i.e., similar to *P. geometricus*).

Psammobates oculifer had a higher cranial space and shorter bridge length (female BL diverged at 107 mm SCL) than *P. geometricus* did. Extra cranial space allows *P. oculifer* more lateral limb movement when traversing sand. *Psammobates oculifer* is known to cover much larger areas (Chapter 7) than *P. geometricus* (van Bloemestein, 2005) and extra space for limb movement, also provided by a reduction in bridge length, facilitate this. This is important in an arid area where resources may be temporally patchy (Chapter 4) and animals may have to travel far to procure them. A larger head would also influence cranial space size, but I did not measure head depth. A disadvantage of having larger cranial space is an increase in vulnerability to predators. *Psammobates oculifer* compensates for their enlarged cranial space by having heavily armoured (scaled) forearms, more armoured than *P. geometricus* has. Armoured forearms help protect the cranial space when forearms are retracted. The wider head of *P. oculifer* perhaps reflects a difference in trophic morphology. Different head widths have been associated with diet in the turtle species *Graptemys*; turtles with wider heads have a higher proportion of molluscs in their diet (Lindeman, 2000). The evolution of the skull in aquatic and terrestrial turtles and the influence of ecology on head shape were studied by Claude et al. (2004) and habitat and diet effects were both prominent factors determining skull morphology.

Three morphological features differed in juveniles of the two species, two of which also differed between male *P. geometricus* and *P. oculifer*. The shell of both male and juvenile *P. oculifer* was wider than their *P. geometricus* counterparts were, but shell height did not differ. Both male and juvenile *P. oculifer* are small and extra width may increase the surface area to volume ratio, thereby assisting in thermoregulation in a semi-arid environment (see Cloudsley-Thompson, 1999; Reiber et al., 1999). *Psammobates oculifer* males and juveniles also had a narrower plastron than did males and juveniles of *P. geometricus*. Narrower plastral width gives more space for hind limbs, which may increase manoeuvrability. This is an advantage when you are small and on a sandy substrate as it may assist in predator evasion or in dispersal; *P. geometricus* males have smaller home ranges than *P. oculifer* males (van Bloemestein,

2005 and see Chapter 7). Shell width and a narrow plastron in males may also be influenced by sexual selection (see below). A difference found between juveniles only was forearm length – it was longer in *P. oculifer*. I do not know the reason for this, but it is possible that longer forearms produce more thrust, akin to flippers on a marine turtle (Llorente et al., 2008), that would assist a small and flat juvenile in moving quicker across sand lessening exposure to predators.

Adult *P. oculifer* had a larger anal gap than *P. geometricus*, possibly because they had a shorter plastron, but I did not compare interspecific plastron lengths. Concerning sexual dimorphism, the additional shell width and narrower plastron of male *P. oculifer* compared with male *P. geometricus* may also assist male *P. oculifer* in fighting. A narrow plastron promotes mobility which is beneficial for combat (section 8.4.2), but shell width may also assist in combat by increasing stability. Greater posterior width was attributed to combat success in *Chersina angulata* (Mann et al., 2006). Male *P. oculifer* also have wider hind feet than their *P. geometric* counterparts, which assists in fighting or mating on a sandy substrate (section 8.4.2). Such morphological features may be relatively redundant in male *P. geometricus* that are not known to fight (Baard, 1995b).
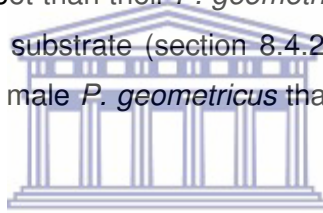
Among female differences, *P. geometricus* were significantly higher than *P. oculifer*, perhaps due to selection for fecundity. Number of eggs per clutch can differ between the two species. *Psammobates geometricus* have clutches of between one and five eggs while *P. oculifer* lays one large egg. Single-egg clutches of large eggs in *P. oculifer* may reflect a restriction imposed by an arid and unpredictable environment; multi-egg clutches with smaller eggs being more viable in a less extreme environment (Hofmeyr et al., 2005). In addition, renosterveld is possibly a more productive ecosystem than semi-arid Savanna is. Although I found no confirmation of this in the relevant literature, I thought it possible based on the higher rainfall, lower summer temperatures and relatively fertile soil in Renosterveld. A more productive ecosystem would suggest that *P. geometricus* females could access more energy for reproduction than *P. oculifer* females can. Natural selection may also limit shell dimension in *P. oculifer*. As discussed above in context of males and juveniles, a flatter (greater surface area to volume) carapace aids thermoregulation (Reiber et al., 1999) assisting *P. oculifer* females in their extreme environment. In addition, *P. oculifer* uses mammal burrows during hot days in summer (Chapter 5) and a high shell like that of *P. geometricus* would restrict the number of available microclimates. A high shell in female *P. geometricus* may have had a correlative effect on males of this species;

males have a pronounced plastral concavity. A pronounced plastral concavity probably assists males during copulation given the relatively high carapace of *P. geometricus*. In contrast, *P. oculifer* females are relatively flat, and *P. oculifer* males has either no or a shallow plastral concavity. The only remaining difference between females was greater hind leg length in *P. geometricus*. *Psammobates geometricus* lays between one and five eggs in a clutch in areas where soil may be hard e.g., clay (MD Hofmeyr, personal communication). Longer legs thus may assist *P. geometricus* when digging nests that need to be deep given the large clutch size, and are harder to dig in compact soil. In contrast, *P. oculifer* lays one egg in sandy soil.

There are two additional, diagnostic, aspects of morphology that differ considerably between these two species in all cohorts, colour and marginal scute serration. The carapace of *Psammobates geometricus* has a higher proportion of dark pigment than does *P. oculifer*. A darker carapace in *P. geometricus* may be climate related. For example, the divergence of melanistic types of Cordylid lizard in the south-western Cape coincided with upwelling events that cooled the tip of the south-western cape (Daniels et al., 2004) i.e., they are 'cool adapted'; melanism assisting in thermoregulation. Also, Ernst (1982) hypothesised that a possible cause of melanism in tropical emydids was that it would be advantageous on cooler, spring mornings for reducing basking time. Basking and consequent activity is particularly important for *P. geometricus* in winter, when food is seasonally abundant (MD Hofmeyr, personal communication).

The other diagnostic feature, marginal scute serration in *P. oculifer*, is more difficult to interpret. As discussed, smaller tortoises in both species are more serrated, which suggests it is a defensive rather than, say, a sexually dimorphic feature. No other small, southern African, endemic testudinid shares this feature to the same degree (Boycott & Bourquin, 2000), and to analyse habitat effects (e.g. amount of ground cover as a function of 'vulnerability') and/or predator densities across taxa would be a major task.

8.4.5 Conclusion

This chapter represents the first morphological description of *P. oculifer* and *P. geometricus* with statistics, and thus contributes to a better understanding of both testudinid, and more specifically *Psammobates* spp., morphometrics. *Psammobates oculifer* males from the Eastern region differ morphologically from males in the Central region; habitat differences between the two regions being a possible cause. Both *P.*

oculifer and *P. geometricus* are sexually dimorphic; females are larger than males perhaps due to selection for fecundity. Dimorphic features exclusive to male *P. oculifer* such as a narrow plastron, which aids hind limb movement, are possibly combat related; *P. geometricus* males do not fight. However, *P. geometricus* males may also benefit from extra shell space; they have a shorter bridge length than females, which may increase male mobility for mate searching. Possible environmental effects manifested in the morphology of *P. oculifer*, which differ from *P. geometricus*, include an enlarged cranial space and wide front feet, both would assist manoeuvring on sandy substrates. Morphology in an arid environment could be a trade off between natural and sexual selection. A flatter female shell in a small testudinid may reduce fecundity, but promote survival in an arid environment; it may facilitate thermoregulation and/or thermoregulatory behaviour (burrow use). Molecular analyses of these sister species may give more insight into their divergence and, hence, their evolutionary pathways.

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9 GENERAL CONCLUSIONS AND CONSERVATION IMPLICATIONS

9.1 GENERAL CONCLUSIONS

The climate at Benfontein was typical of a semi-arid environment. Annual rainfall was 320 mm, it mainly fell in late summer or autumn, and temperatures were extreme ranging from -4 °C on winter nights and attaining 40 °C during hot summer days. Rainfall patterns influenced vegetation abundance, in particular grass positively correlated with rainfall and annual plants appeared with late winter/early spring rains (Chapter 4). However, vegetation at the study sites was not typical of Kimberley Thornveld (SVk4), the dominant vegetation type in the area (Mucina et al., 2006a). Site E was reminiscent of a Savanna community, *Schmidtia pappophoroides – Acacia erioloba*, described by Bezuidenhout (1994; 2009) for nearby reserves, whereas vegetation in site W was closer in composition to the shrubby Northern Upper Karoo vegetation (Nku3, Mucina et al., 2006b).

In both sites, but particularly in site W, livestock grazing had made a visible impact on vegetation; it looked to have created a piosphere (see Jeltsch et al., 1997; Todd, 2006) and the abundance of invasive shrubs such as *Chrysocoma ciliata* may be related to overgrazing (e.g., see Roux & Vorster, 1983). Vegetation cover was lower at site W than at site E and combined with differences in vegetation structure, could have negatively affected tortoises. Tortoises in site W had lower mean seasonal body condition than those in site E (Chapter 3), which is possibly linked to a greater abundance of preferred food plants and/or adequate shelter in site W. I did not study the feeding ecology of *P. oculifer* at Benfontein, but I occasionally observed tortoises eating. Tortoises fed on annuals, and in particular on the spring annual *Wahlenbergia androsacea* (T Keswick, unpublished data and see Rall and Fairall 1993), both more abundant is site E than in site W. I also observed tortoises feeding on the grasses *Schmidtia pappophoroides* and *Eragrostis lehmanniana* and, again, they were more abundant in site E than they were in site W. Thus, a greater abundance of preferred food plants in site E may be responsible for the superior tortoise body condition there. Vegetation cover and structure in site W may also have affected tortoises' thermal ecology to the detriment of their body condition. Tortoises selected grass as refuges in both sites, but not shrubs in site W, where they were the dominant plant form (Chapters 4 and 5). Lower vegetation cover and fewer 'suitable' refuges appeared to affect the tortoises' thermal environment; air, ground and tortoise body temperatures were all higher in site W than they were in site E (Chapter 6). Possible consequences of having

a higher body temperature include increased metabolic rate and water loss, both of which would negatively affect tortoise body mass and hence body condition (e.g., see Cloudsley-Thompson, 1999). *Psammobates oculifer* is primarily a Savanna species (Branch 1988) and in this respect, it is not surprising that body condition of tortoises in site E, where vegetation is closer to Savanna vegetation, i.e. mainly grass, was higher than it was in site W, where shrubs were prevalent. A future study of tortoises in the two sites would need to first establish that shrub abundance in site W was a result of overgrazing (data on stocking units for the two sites was not available) and/or carry out a full study of the feeding ecology of *Psammobates oculifer*. In the latter case, this may have to be from a study of tortoise scats, as *Psammobates oculifer* in this study was easily disturbed and thus difficult to observe while feeding (T Keswick, personal observation).

Vegetation cover also indirectly influenced the demographics at Benfontein. Reduced cover made it easier to locate tortoises in site W; hence, tortoise captures were biased in favour of this site (Chapter 3). Sex did not affect the number of animals captured, but finding juveniles was harder than finding adults. Although I did not estimate density of *P. oculifer* at Benfontein, the hours per unit capture suggested Kalahari tent tortoise density was relatively low. This is in keeping with other studies of testudinid populations in arid and semi-arid areas (Freilich et al., 2000; Berry et al., 2006; McMaster & Downs, 2006b).

This study highlights several mechanisms that *Psammobates oculifer* uses to persist in a semi-arid environment. These mechanisms are a combination of physical and behavioural traits, such as the advantage small size confers upon a species in an arid or semi-arid environment (Shmida et al., 1986; Cloudsley-Thompson, 1999; Yom-Tov & Geffen, 2006), and the ability to roam over wide areas (Chapter 7) when resources, e.g., food or mates, are patchily distributed (see Chapters 3 and 4). *Psammobates oculifer* in this study showed that while it may have preferences, e.g., in its choice of refuge plants, it was generally opportunistic as emphasised by its behaviour.

Through a combination of judicious use of microhabitats and changes in temporal activity, this species was able exploit seasonal, diurnal temperatures to remain active throughout the year and take advantage of ephemeral or sporadic resources (Chapters 5 & 6). In winter, the tortoises' refuge orientation maximised early sun exposure (Chapter 6). Tortoises selected refuges of short sparse grass (Chapter 5), further increasing sun exposure while they remained in protective cover, and combined with

basking, they reached an operative body temperature to take advantage of pulses of late winter annual plants on which they fed (Chapter 6). The advent of benign spring temperatures increased time available for activity, and although males were more active than females in October, the middle of the mating season, individuals of both sexes had large activity areas (Chapter 7). Even in summer when shackled by high midday temperatures (Chapter 4), *P. oculifer* harnessed the early morning sun through refuge orientation and basking before becoming active and feeding (Chapter 6), and then retreating to mammal burrows during the middle of the day (Chapter 5). With the onset of late rain in autumn 2007, females foraged more than males, perhaps linked to differences in seasonal female reproductive requirements (Chapters 6). As seen in spring, both sexes benefited from ameliorated diurnal temperatures in autumn 2007, and activity areas increased accordingly (Chapter 7).

Thermoregulation by oscillating temporal activity patterns, and by choice of seasonal microhabitats, both seen here in *P. oculifer*, are common behaviours among arid and semi-arid ectotherms (Stevenson, 1985; Grant & Dunham, 1988; Cloudsley-Thompson, 1999). Tortoises are known to switch to bimodal activity on hot days (McRae et al., 1981; Diaz-Paniagua et al., 1995; Lagarde et al., 2002) and may aestivate or brumate during seasons with an adverse climate (Rautenstrauch et al., 1998; Lagarde et al., 2002). *Psammobates oculifer* did not aestivate at Benfontein and although winter activity was low, it did not brumate (Chapter 6). The relatively small size of *P. oculifer* may assist in the latter case; it hastens the arrival of the body temperature required for activity (Chapter 6). In addition, the seasonal climates for *P. oculifer* at Benfontein may be less extreme than they are for other harsh or arid zone testudinids; such species may be obligated to aestivate due to seasonal climate severity (e.g., see Lagarde et al., 2002).

Testudo kleinmanni, which is similar in size to *P. oculifer* (see Geffen & Mendelssohn, 1988 for SCL ranges), has a comparable thermal ecology. The minimum and maximum air temperatures recorded during a study of *T. kleinmanni* in the Negev Desert (Geffen & Mendelssohn, 1989) were comparable to those recorded for *P. oculifer* in this study (Chapter 4). *Testudo kleinmanni* has a mean activity temperature (T_b) and range of body temperatures akin to *P. oculifer*, it was most active during winter (unimodal) and spring (bimodal when temperatures were high) and similar to *P. oculifer*, they orientated themselves in shrub refuges to receive early morning sun and fed on annual plants. Unlike *P. oculifer*, in summer they were either relatively inactive or they aestivated in rodent burrows (Geffen & Mendelssohn, 1989). Thus although similar in

many respects, *P. oculifer* appears to be a greater opportunist than other arid and semi-arid zone testudinids, partly because it is small and partly because its less harsh climate allows it to be so.

Some individuals of *Psammobates oculifer* ranged over large areas (Chapter 7). Mammals of arid and semi-arid areas, areas of low productivity, have large home ranges, as they need to roam further to find resources (Harestad & Bunnell, 1979). This trend is also true of some tortoise species; *Testudo horsfieldii*, *Gopherus agassizii* and *Geochelone pardalis* all inhabit arid and semi-arid environments and have large home ranges (Lagarde et al., 2003; McMaster & Downs, 2009; Harless et al., 2010). However, these three tortoises are larger than is *P. oculifer*. Only *T. kleinmanni* from the Negev Desert is of a similar size to *P. oculifer* and has large home ranges (Geffen & Mendelssohn, 1988). Thus, space use of *P. oculifer* is typical of an arid zone testudinid, but it may have the added advantage of being small, with the benefits that this may convey in a low-productive habitat, e.g., a reduction in energy requirement related to small size (see Yom-Tov & Geffen, 2006).

Although the ecology and behaviour of *P. oculifer* highlight its competitiveness in a semi-arid environment, manifestations of potential arid or semi-arid adaptations should be evident in its morphology. Ideally, morphology should be interpreted in context of the palaeoecology and phylogenetics of *P. oculifer*, information that is currently unavailable. Thus, morphology provides the only evidence of potential arid or semi-arid 'adaptations' in this species even if the 'when' and 'how' remain elusive. These 'adaptations' may be emphasised by comparing *P. oculifer* with *Psammobates geometricus*, its sister taxon that inhabits a cooler climate.

Interspecific comparisons between juveniles minimise the confounding effects of sexual dimorphism. Morphological differences between the two species, common to juveniles and adults, were bridge length, cranial space, front foot width and head width (Chapter 8). Reduced bridge length and increased cranial space in *P. oculifer* no doubt assist in overall limb mobility, aiding travel over large distances (Chapter 7) on sandy terrain (Chapter 4). *Psammobates geometricus* probably does not need such large shell openings, because the species inhabits areas of mixed soil types, including gravel and cobbles (Rebelo et al., 2006), and has smaller home ranges than *P. oculifer* (see van Bloemestein, 2005). When not a functional necessity, large shell openings may be maladaptive because it would leave the body more exposed to predators. Although an enlarged cranial space may increase vulnerability to predators in *P. oculifer*, their

armoured forearms mitigate it; such armour is not present to the same degree in *P. geometricus*. The wider front feet of *P. oculifer* are also likely to be a trait that is substrate related as wider feet would assist in both movement on sand and accessing or modifying sandy burrows (Bramble, 1982). Interestingly, *P. oculifer* specimens from the region with more diverse substrates had narrower front feet than those from the sandier region. *Psammobates oculifer* has the greater head width of the two species, which is perhaps a function of interspecific differences in diet (for example see Lindeman, 2000), but research on their respective feeding ecologies warrants further investigation. I did not measure head depth, but a larger head would also help explain the wider cranial space in *P. oculifer*. Juveniles and male *P. oculifer* were wider but not higher than their *P. geometricus* counterparts, which may have thermoregulatory advantages in small-bodied tortoises in a semi-arid environment as it increases surface area to volume ratio (see Reiber et al., 1999).

Differences between male and female *P. oculifer* and *P. geometricus* may reflect a combination of environmental and sexual selective pressures. Female *P. oculifer* have a lower carapace, which possibly reflects a trade-off between selection for fecundity and natural selection. A low carapace may reduce fecundity but, as already discussed for *P. oculifer* males and juveniles, it may benefit females' thermoregulation by increasing relative shell surface area, as well as facilitating access to benign microclimates (burrows; Chapter 5) both of which are advantageous in a semi-arid environment. Male *P. oculifer* were wider, had narrower plastrons (see above) and wider back feet than *P. geometricus* males. *Psammobates oculifer* fought with male conspecifics in the mating season (Chapter 6) while male *P. geometricus* are not known to fight (Baard, 1995b). Additional shell width in *P. oculifer* may add stability, a morphological feature that has been related to combat success (see Mann et al., 2006), and a narrower plastron aids mobility when fighting (see Bonnet et al., 2001), particularly on sand, and wider back feet afford better purchase on sand (this study). The wide back feet of *P. oculifer* may also assist males' stability when mounting females on sandy substrates.

A question asked by Morafka & Berry (2002) of *Gopherus agassizii* was whether it is a 'Desert-adapted tortoise or an Exaptive opportunist?'. Currently information gaps in the biology of *P. oculifer*, e.g., concerning its phylogenetics, physiology and palaeoecology, make this question difficult to answer here. What we can say of *P. oculifer* is that it is opportunistic. It can take advantage of resources in almost all seasons, in part because its small size helps it thermoregulate. Small size may also reduce its resource

requirement in an area where resources can be scarce. Combined with its ability to roam areas as wide as much larger tortoise species, *P. oculifer* is well placed to cope with its semi-arid habitat.

9.2 CONSERVATION IMPLICATIONS

Psammobates oculifer is listed as CITES appendix II, i.e., although not necessarily threatened, its trade is monitored. Among criteria that make a species vulnerable to extinction and climate change in particular are a specialised habitat, susceptibility to changes in the environment, dependence on climate-sensitive exogenous cues, reliance on symbiotic relationships, and having limited dispersal mechanisms (Foden et al., 2008). *Psammobates oculifer* has a wide distribution and although the environment may be similar in parts of its range, it can inhabit different vegetation types (Chapter 4). Therefore, vulnerability of habitat does not seem to be of particular concern. Generally, the inhospitable nature of arid and semi-arid regions benefits *P. oculifer* because people do not covet these areas. The opposite is true of *P. geometricus*; its habitat is sought after as farmland (Baard, 1993).

Despite there being no immediate concern over its habitat, the demographics and ecology of *P. oculifer* at Benfontein suggest they may be more vulnerable to habitat change than they first appear. If they occur in low densities, as the hours per unit capture indicates here, then a large distribution range does not imply that they occur in large numbers. Certain plant species such as *Stipagrostis uniplumis*, a grass with a very similar distribution to *P. oculifer*, was favoured as refuges, particularly in warmer months (the grass was dense). Refuge selection by *P. oculifer* implies it may be sensitive to habitat changes. It actively prefers certain plant species to others as refuges and disappearance of these species may affect tortoises' ability to thermoregulate. Higher body temperatures and (perhaps consequently) lower body condition in the less 'typical' habitat, site W, illustrate such habitat sensitivity. As already alluded to, the occurrence of certain 'invasive' plants in the study area may be indicative of over-grazing. Other than a cause of altering habitat, livestock can be a direct threat to tortoises via trampling. Eight percent of tortoises found at Benfontein had damage indicative of trampling by cattle or game (Chapter 8); thus, high stocking rates would be of concern when considering conservation of this species. As well as choosing specific plant species as refuges, *P. oculifer* has commensalistic relationships with mammals that provide essential microhabitats (Chapter 5). Burrows comprised 55% of refuges used by tortoises in February, the hottest month at Benfontein,

indicating they were an important resource there. Thus, disappearance of fossorial mammal species within its range may impact heavily on this species' survival.

Climate change in South Africa may detrimentally affect or at least change the distribution of many South African species (see Erasmus et al., 2002), including *P. oculifer*. In this study, there were a number of tortoise fatalities in summer and although I do not know the reason for most of these fatalities, a delay in summer rainfall, coinciding with high temperatures at that time, would have caused the animals stress. Rainfall usually occurs in January and February; the months with the highest temperatures (see Chapter 4). A shift in the rainfall pattern, as occurred during this study, may make tortoises physiologically more vulnerable to high temperatures (see Chapter 3 and also Chapter 7), and drought coupled with high temperatures has ancillary negative effects, e.g., on plant growth and, hence, on food availability.

When contemplating adequate conservation areas for this species, it is important to consider the ability of some individuals to move large distances (Chapter 7). The relatively small size of this tortoise could indicate, erroneously, that it needs limited space. I followed one 'migrating' female at the end of my study that displaced 1.4 kilometres in four days and this included over a day travelling up and down a game fence, looking for an opening (which it found). Thus, periodic small holes in farm fencing would facilitate this species' movements. It should be remembered that this study occurred at the far south of the animals' range. Conservation of *P. oculifer* would have to be re-assessed in the event that isolated populations, such as those in the eastern part of its range, proved to be genetically distinct (see Chapter 8).

10   REFERENCE LIST

Acocks, J. P. H. 1988. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa*, **57,** 1-146.

Altmann, S. A. & Altmann, J. 2003. The transformation of behaviour field studies. *Animal Behaviour*, **65,** 413–423.

Anadón, J. D., Giménez, A., Pérez, I., Martinez, M. & Esteve, M. A. 2006. Habitat selection by the spur-thighed tortoise *Testudo graeca* in a multisuccessional landscape: implications for habitat management. *Biodiversity and Conservation* **15,** 2287-2299.

Andersson, M. 1994. *Sexual selection.* Princeton, New Jersey: Princeton University Press.

Aranibar, J., Otter, L., Macko, S. A., Feral, C. J. W., Epstein, H. E., Dowty, P. R., Eckardt, F., Shugart, H. H. & Swap, R. J. 2004. Nitrogen cycling in the soil-plant system along a precipitation gradient in the Kalahari sands. *Global Change Biology*, **10,** 359-373.

Arvisais, M., Bourgeois, J. C., Lévesque, E., Daigle, C., Masse, D. & Jutras, J. 2002. Home range and movements of a wood turtle (*Clemmys insculpta*) population at the northern limit of its range. *Canadian Journal of Zoology*, **80,** 391-398.

Auffenberg, W. & Weaver Jr, W. G. 1969. *Gopherus berlandieri* in southeastern Texas. *Bulletin of the Florida State Museum*, **13,** 141-203.

Baard, E. H. W. (1990). Biological aspects and conservation status of the geometric tortoise, *Psammobates geometricus* (Linnaeus, 1758) (Cryptodira: Testudinidae). Ph.D. thesis, University of Stellenbosch, Stellenbosch.

Baard, E. H. W. 1993. Distribution and status of the geometric tortoise, *Psammobates geometricus*, in South Africa. *Biological Conservation*, **63,** 235-239.

Baard, E. H. W. 1995a. A preliminary analysis of the habitat of the geometric tortoise, *Psammobates geometricus*. *South African Journal of Wildlife Research*, **25,** 8-13.

Baard, E. H. W. 1995b. Growth, age at sexual maturity and sexual dimorphism in the geometric tortoise, *Psammobates geometricus*. *Journal of Herpetological Association of Africa*, **44,** 10-15.

Baard, E. H. W. & Hofmeyr, M. D. in press. *Psammobates geometricus* (Linnaeus, 1758). In: *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland* (Ed. by Bates, M. F., Branch, W. R., Bauer, A. M., Burger, M.,

Marais, J., Alexander, G. J. & de Villiers, M. S.). Pretoria: South African Biodiversity Institute.

Baard, E. H. W. & Mouton, L. P. N. 1993. A hypothesis explaining the enigmatic distribution of the geometric tortoise, *Psammobates geometricus*, in South Africa. *Herpetological Journal*, **3,** 65-67.

Bailey, B. J. R. 1980. Large Sample Simultaneous Confidence-Intervals for the Multinomial Probabilities Based on Transformations of the Cell Frequencies. *Technometrics*, **22,** 583-589.

Bailey, S. J., Schwalbe, C. R. & Lowe, C. H. 1995. Hibernaculum used by a population of desert tortoise (*Gopherus agassizii*) in the Sonoran desert. *Journal of Herpetology*, **29,** 361-369.

Bancroft, C. M., Bezuidenhout, H. & Nel, J. G. 1998. Use of veld condition assessment to set objectives and targets for an ISO 14001 environmental management system for Vaalbos National Park. *Koedoe*, **41,** 1-12.

Barret, S. L. 1990. Home Range and Habitat of the Desert Tortoise (*Xerobates agassizi*) in the Picacho Mountains of Arizona. *Herpetologica*, **46,** 202-206.

Beaupre, S. J., Dunham, A. E. & Overall, K. L. 1993. The Effects of Consumption Rate and Temperature on Apparent Digestibility Coefficient, Urate Production, Metabolizable Energy Coefficient and Passage Time in Canyon Lizards (*Sceloporus merriami*) From Two Populations. *Functional Ecology*, **7,** 273-280.

Begon, M., Harper, J. L. & Townsend, C. R. 1996. *Ecology.* Oxford: Blackwell Science Ltd.

Belsley, D. A., Kuh, E. & Welsch, R. E. 1980. Detecting and Assessing Collinearity. In: *Regression Diagnostics*, pp. 85-191: John Wiley & Sons, Inc.

Berry, J. F. & Shine, R. 1980. Sexual Size Dimorphism and Sexual Selection in Turtles (Order Testudines). *Oecologia*, **44,** 185-191.

Berry, K. H. 1986. Desert Tortoise (*Gopherus agassizii*) Research in California, 1976-1985. *Herpetologica*, **42,** 62-67.

Berry, K. H., Bailey, T. Y. & Anderson, K. M. 2006. Attributes of desert tortoise populations at the National Training Center, Central Mojave Desert, California, USA. *Journal of Arid Environments*, **67,** 165-191.

Bezuidenhout, H. 1994. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 1. The Than-Droogeveld section. *Koedoe*, **37,** 19-42.

Bezuidenhout, H. 2009. The classification, mapping and description of the vegetation of the Rooipoort Nature Reserve, Northern Cape, South Africa. *Koedoe*, **51,** 1-11.

Bogert, C. M. 1949. Thermoregulation in Reptiles, A Factor in Evolution. *Evolution*, **3,** 195-211.

Bonnet, X., Lagarde, F., Henen, B. T., Corbin, J., Nagy, K. A., Naulleau, G., Balhoul, K., Chastel, O., Legrand, A. & Cambag, R. 2001. Sexual dimorphism in steppe tortoises (*Testudo horsfieldii*): influence of the environment and sexual selection on body shape and mobility. *Biological Journal of the Linnean Society*, **72,** 357-372.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75,** 1393-1405.

Bothma, J., du P. 2002. *Game Ranch Management*. Pretoria: Van Schaik.

Bourn, D. & Coe, M. 1978. The Size, Structure and Distribution of the Giant Tortoise Population of Aldabra. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **282,** 139-175.

Boycott, R. C. & Bourquin, O. 2000. *The Southern African Tortoise Book*. South Africa: Hilton

Bramble, D. M. 1982. *Scaptochelys*: Generic Revision and Evolution of Gopher Tortoises. *Copeia*, **4,** 852-867.

Branch, W. R. 1984. Preliminary observations on the ecology of the angulate tortoise (*Chersina angulata*) in the Eastern Cape Province, South Africa. *Amphibia-Reptilia*, **5**, 43-55.

Branch, W. R. 1988. *Field guide to snakes and other reptiles in southern Africa*. Cape Town: Struik.

Brattstrom, B. H. 1965. Body temperatures of reptiles. *American Midland Naturalist*, **73,** 376-422.

Bridges, E. M. 1997. *World Soils*. Cambridge: Cambridge University Press.

Broadley, D. G., Hunt, J. & Cantle, G. 2010. Geographical distributions. *Psammobates oculifer*. *African Herp News*, **51,** 24-25.

Brower, J. E., Zar, J. H. & von Ende, C. N. 1998. *Field Laboratory Methods for General Ecology*. Boston: WCB McGraw-Hill.

Bull, J. J. & Charnov, E. L. 1989. Enigmatic Reptilian Sex Ratios. *Evolution*, **43,** 1561-1566.

Bulova, S. J. 1994. Patterns of Burrow Use by Desert Tortoises: Gender Differences and Seasonal Trends. *Herpetological Monographs*, **8,** 133-143.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammology*, **24,** 346-352.

Byers, R. C., Steinhorst, R. K. & Krausman, P. R. 1984. Clarification of a Technique for Analysis of Utilisation-Availability Data. *The Journal of Wildlife Management*, **48,** 1050-1053.

Cao, M., Prince, S. D., Small, J. & Goetz, S. J. 2004. Remotely Sensed Interannual Variations and Trends in Terrestrial Net Primary Productivity 1981–2000. *Ecosystems*, **7,** 233–242.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. *Journal of Wildlife Management*, **60,** 653-658.

Clarke, K. R. & Warwick, R. M. 2001. *Change in marine communities: An approach to statistical analysis and interpretation*. Plymouth: PRIMER-E Ltd.

Claude, J., Pritchard, P. C. H., Tong, H., Paradis, E. & Auffray, J-C. 2004. Ecological Correlates and Evolutionary Divergence in the Skull of Turtles: A Geometric Morphometric Assessment. *Systematic Biology*, **53,** 933-948.

Cloudsley-Thompson, J. L. 1999. *The diversity of amphibians and reptiles: an introduction*. Berlin: Springer-Verlag.

Coe, M. J., Bourn, D. & Swingland, I. R. 1979. The Biomass, Production and Carrying Capacity of Giant Tortoises on Aldabra. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **286,** 163-176.

Cunningham, J., Baard, E. H. W., Harley, E. H. & O'Ryan, C. 2002. Investigation of genetic diversity in fragmented geometric tortoise (*Psammobates geometricus*) populations. *Conservation Genetics*, **3,** 215-223.

Cunningham, P. L. & Simang, A. 2009. Ecology of the Bushmanland Tent Tortoise (*Psammobates tentorius verroxii*) in Southern Namibia. *Chelonian Conservation and Biology*, **7,** 119-124.

Daniels, S. R., Mouton, P. l. F. N. & Du Toit, D. A. 2004. Molecular data suggest that melanistic ectotherms at the south-western tip of Africa are the products of Miocene climatic events: evidence from cordylid lizards. *Journal of Zoology*, **263,** 373-383.

Daniels, S. R., Hofmeyr, M. D., Henen, B. T. & Crandall, K. A. 2007. Living with the genetic signature of Miocene induced change: Evidence from the phylogeographic structure of the endemic angulate tortoise *Chersina angulata*. *Molecular Phylogenetics and Evolution*, **45,** 915-926.

Darwin, C. 1871. *The descent of man and selection in relation to sex*. London: Murray.

Day, P. R. 1956. Report of the committee on physocal analyses. *Proceedings - Soil Science Society of America*, **20,** 267-269.

de Solla, S. R., Bonduriansky, R. & Brooks, R. J. 1999. Eliminating Autocorrelation Reduces Biological Relevance of Home Range Estimates. *Journal of Animal Ecology*, **68,** 221-234.

Diaz-Paniagua, C., Keller, C. & Andreu, A. C. 1995. Annual variation of the activity and daily distances moved in adult spur-thighed tortoises, *Testudo graeca*, in southwestern Spain. *Herpetologica*, **51,** 225-233.

Diemer, J. F. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. *Journal of Herpetology*, **26,** 158-165.

Dodd, C. K., Jr. 1997. Population structure and the evolution of sexual dimorphism and sex ratios in an insular population of Florida box turtles (*Terrapene carolina bauri*). *Canadian Journal of Zoology*, **75,** 1495-1507.

Douglas, R. M. & Rall, M. 2006. Seasonal Shelter Selection by Leopard Tortoises (*Geochelone pardalis*) in the Franklin Nature Reserve, Free State, South Africa *Chelonian Conservation and Biology*, **5,** 121-129.

Douglass, J. F. & Layne, J. N. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. *Herpetologica*, **34,** 359–374.

Downes, S. & Shine, R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Animal Behaviour*, **55**, 1387-1396.

Duda, J. J., Krzysik, A. J. & Freilich, J. E. 1999. Effects of Drought on Desert Tortoise Movement and Activity. *The Journal of Wildlife Management*, **63,** 1181-1192.

Dunham, A. E., Grant, B. W. & Overall, K. L. 1989. Interfaces between Biophysical and Physiological Ecology and the Population Ecology of Terrestrial Vertebrate Ectotherms. *Physiological Zoology*, **62,** 335-355.

Eksteen, L. L. 1969. The determination of the lime requirement of soils for various crops in the Winter Rainfall Region. *Fertiliser Society of South Africa*, **2,** 13-14.

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

Ernst, C. H. 1982. Why are More Tropical Emydid Turtles Black? *Biotropica*, **14,** 68.

Ernst, C. H., Altenberg, R. G. M. & Barbour, R. W. 2000. Turtles of the World. In: *World Biodiversity Database CD-ROM series*: Springer Verlag, UNESCO, Heidelberg.

Ewert, M. A. & Nelson, C. E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. *Copeia*, **1,** 50-69.

Foden, W., Mace, G., Vié, J-C., Angulo, A., Butchart, S., DeVantier, L., Dublin, H., Gutsche, A., Stuart, S. N. & Turak, E. 2008. Species susceptibility to climate change impacts In: *The 2008 Review of The IUCN Red List of Threatened*

Species (Ed. by Vié, J-C., Hilton-Taylor, C. & Stuart, S. N.). Gland, Switzerland: IUCN.

Fourie, J. & Roberts, B. 1977. Seasonal dry matter production and digestibility of *Themeda triandra* and *Eragrostis lehmanianna*. *Agroplantae*, **9,** 129-133.

Freeman, G. H. & Halton, J. H. 1951. Note on an Exact Treatment of Contingency, Goodness of Fit and Other Problems of Significance. *Biometrika*, **38,** 141-149.

Freilich, J. E., Burnham, K. P., Collins, C. M. & Garry, C. A. 2000. Factors Affecting Population Assessments of Desert Tortoises. *Conservation Biology*, **14,** 1479-1489.

Geffen, E. & Mendelssohn, H. 1988. Home range use and seasonal movements of the Egyptian tortoise (*Testudo kleinmanni*) in the northwestern Negev, Israel. *Herpetologica*, **44,** 354-359.

Geffen, E. & Mendelssohn, H. 1989. Activity Patterns and Thermoregulatory Behavior of the Egyptian Tortoise, *Testudo kleinmanni*, in Israel. *Journal of Herpetology*, **23,** 404-409.

Germano, D. J. 1992. Longevity and Age-Size Relationships of Populations of Desert Tortoises. *Copeia*, **2,** 367-374.

Germano, D. J. 1993. Shell Morphology of North American Tortoises. *American Midland Naturalist*, **129,** 319-335.

Germano, D. J. 1994. Growth and age at maturity of North American tortoises in relation to regional climates. *Canadian Journal of Zoology*, **72,** 918-931.

Germishuizen, G. & Meyer, N. L. 2003. Plants of Southern Africa: an annotated checklist. Pretoria: Strelitzia 14, National Botanical Institute.

Gibbons, J. W. & Lovich, J. E. 1990. Sexual Dimorphism in Turtles with Emphasis on the Slider Turtle (*Trachemys scripta*). *Herpetological Monographs*, **4,** 1-29.

Gibson, C. W. D. & Hamilton, J. 1983. Feeding Ecology and Seasonal Movements of Giant Tortoises on Aldabra Atoll. *Oecologia*, **56,** 84-92.

Grant, B. W. & Dunham, A. E. 1988. Thermally Imposed Time Constraints on the Activity of the Desert Lizard *Sceloporus Merriami*. *Ecology*, **69,** 167-176.

Hailey, A. 1988. Population ecology and conservation of tortoises: the estimation of density, and dynamics of a small population. *Herpetological Journal*, **1,** 263-271.

Hailey, A. 1989. How far do animals move? Routine movements in a tortoise. *Canadian Journal of Zoology*, **67,** 208-215.

Hailey, A. 1995. Diets and food preferences of two South African tortoises: implications for niche separations. *South African Journal of Wildlife Research*, **25,** 65.

Hailey, A. & Coulson, I. M. 1996a. Temperature and the tropical tortoise *Kinixys spekii*: tests of thermoregulation. *Journal of Zoology*, **240,** 537-549.

Hailey, A. & Coulson, I. M. 1996b. Differential scaling of home-range area to daily movement distance in two African tortoises. *Canadian Journal of Zoology*, **74,** 97-102.

Hailey, A. & Coulson, I. M. 1999. Measurement of time budgets from continuous observation of thread-trailed tortoises (*Kinixys spekii*) *Herpetological Journal*, **9,** 15-20.

Harestad, A. S. & Bunnell, F. L. 1979. Home range and body weight - a reevaluation. *Ecology*, **60,** 389-402.

Harless, M. L., Walde, A. D., Delaney, D. K., Pater, L. L. & Hayes, W. K. 2009. Home Range, Spatial Overlap, and Burrow Use of the Desert Tortoise in the West Mojave Desert. *Copeia*, **2009,** 378-389.

Harless, M. L., Walde, A. D., Delaney, D. K., Pater, L. L. & Hayes, W. K. 2010. Sampling Considerations for Improving Home Range Estimates of Desert Tortoises: Effects of Estimator, Sampling Regime and Sex. *Herpetological Conservation and Biology*, **5,** 374-387.

Hartemink, A. 2006. Assessing soil fertility decline in the tropics using soil chemical data. In: *Advances in Agronomy* (Ed. by Sparks, D. L.). San Diego: Academic Press.

Hartemink, A. E. & Huting, J. 2008. Land cover, Extent, and Properties of Arenosols in Southern Africa. *Arid Land Research and Management*, **22,** 134-147.

Hellgren, E. C., Kazmaier, R. T., Ruthven, D. C., III & Synatzske, D. R. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. *Ecology*, **81,** 1297-1310.

Henen, B. T. 1997. Seasonal and Annual Energy Budgets of Female Desert Tortoises (*Gopherus agassizii*). *Ecology*, **78,** 283-296.

Henen, B. T. 2002a. Reproductive Effort and Reproductive Nutrition of Female Desert Tortoises: Essential Field Methods. *Integrative and Comparative Biology*, **42,** 43-50.

Henen, B. T. 2002b. Energy and water balance, diet, and reproduction of female Desert Tortoises (*Gopherus agassizii*). *Chelonian Conservation and Biology*, **4,** 319-329.

Hill, R. A. 1999. Size-dependent tortoise predation by baboons at De Hoop Nature Reserve, South Africa. *South African Journal of Science*, **95,** 123.

Hoffman, M. T., Barr, G. D. & Cowling, R. M. 1990. Vegetation dynamics in the semi-arid eastern Karoo, South Africa: the effect of seasonal rainfall and competition on grass and shrub basal cover. *South African Journal of Science*, **86,** 462-463.

Hofmeyr, M. D. 2004. Egg Production in *Chersina angulata*: An Unusual Pattern in a Mediterranean Climate. *Journal of Herpetology*, **38,** 172-179.

Hofmeyr, M. D., Henen, B. T. & Loehr, V. J. T. 2005. Overcoming environmental and morphological constraints: egg size and pelvic kinesis in the smallest tortoise, *Homopus signatus. Canadian Journal of Zoology*, **83,** 1343-1352.

Holm, S. 1979. A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics*, **6,** 65-70.

Honegger, R. E. 1979. Marking amphibians and reptiles for future identification. In: *International Zoo Yearbook 19*, pp. 14-22.

Hooge, P. N. & Eichenlaub, W. M. 1997. Animal Movement Extension to ArcView. Alaska Biological Science Centre, Anchorage: U.S. Geological Survey.

Hooge, P. N., Eichenlaub, W. M. & Solomon, E. K. 2000. Using GIS to Analyze Animals in the Marine Environment. Alaska Biological Science Centre, Gustavus, AK: U.S. Geological Survey.

Horne, J. S. & Garton, E. O. 2006. Selecting The Best Home Range Model: An Information-Theoretic Approach. *Ecology,* **87,** 1146-1152.

Hornek, D. A. & Miller, R. O. 1998. Determination of Total Nitrogen in Plant Tissue. In: *Handbook of reference methods for plant analysis* (Ed. by Kalra, Y. P.), pp. 81-83. Boca Raton: CRC Press.

Huey, R. B. 1991. Physiological Consequences of Habitat Selection. *The American Naturalist*, **137,** S91-S115.

Iverson, J. B. 1992. Correlates of Reproductive Output in Turtles (Order Testudines). *Herpetological Monographs*, **6,** 25-42.

Janzen, F. J. & Paukstis, G. L. 1991. Environmental Sex Determination in Reptiles: Ecology, Evolution, and Experimental Design. *The Quarterly Review of Biology*, **66,** 149-179.

Jeltsch, F., Milton, S. J., Dean, W. R. J. & van Rooyen, N. 1997. Simulated Pattern Formation around Artificial Waterholes in the Semi-Arid Kalahari. *Journal of Vegetation Science*, **8,** 177-188.

Joshua, Q. I., Hofmeyr, M. D., Henen, B. T. & Weitz, F. M. 2005. Seasonal changes in the vegetation of island and mainland habitats of angulate tortoises in the Western Cape, South Africa. *South African Journal of Science*, **101,** 439-445.

Jost, L. 2006. Entropy and diversity. *Oikos*, **113,** 363-375.

Judd, F. W. & Rose, F. L. 1977. Aspects of the Thermal Biology of the Texas Tortoise, *Gopherus berlandieri* (Reptilia, Testudines, Testudinidae). *Journal of Herpetology*, **11,** 147-153.

Kassas, M. 1953. Habitat and Plant Communities in the Egyptian Desert: II. The Features of a Desert Community. *The Journal of Ecology*, **41,** 248-256.

Kazmaier, R. T., Hellgren, E. C. & Synatzske, D. R. 2001a. Patterns of behavior in the Texas tortoise, *Gopherus berlandieri*: a multivariate ordination approach. *Canadian Journal of Zoology*, **79,** 1363–1371.

Kazmaier, R. T., Hellgren, E. C., Synatzske, D. R. & Rutledge, J. C. 2001b. Mark-recapture analysis of population parameters in a Texas tortoise (*Gopherus berlandieri*) population in southern Texas. *Journal of Herpetology*, **35,** 410-417.

Kazmaier, R. T., Hellgren, E. C. & Ruthven, D. C., III. 2001c. Habitat Selection by the Texas Tortoise in a Managed Thornscrub Ecosystem. *The Journal of Wildlife Management*, **65,** 653-660.

Kernohan, B. J., Gitzen, R. A. & Millspaugh, J. J. 2001. Analysis of Animal Space Use and Movements. In: *Radio Tracking and Animal Populations* (Ed. by Millspaugh, J. J. & Marzluff, J. M.), pp. 1-467. San Diego, California, USA: Academic Press.

Keswick, T., Henen, B. T. & Hofmeyr, M. D. 2006. Sexual disparity in activity patterns and time budgets of angulate tortoises (*Chersina angulata*) on Dassen Island, South Africa. *African Zoology*, **41,** 224-233.

Kinlaw, A. l. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments*, **41,** 127-145.

Klare, U., Kamler, J. F., Stenkewitz, U. & MacDonald, D. W. 2010. Diet, Prey Selection, and Predation Impact of Black-Backed Jackals in South Africa. *Journal of Wildlife Management*, **74,** 1030–1042.

Lagarde, F., Bonnet, X., Henen, B. T., Corbin, J., Nagy, K. A. & Naulleau, G. 2001. Sexual size dimorphism in steppe tortoises (*Testudo horsfieldii*): growth, maturity and reproduction. *Canadian Journal of Zoology*, **79,** 1433-1441.

Lagarde, F., Bonnet, X., Nagy, K. A., Henen, B. T., Corbin, J. & Naulleau, G. 2002. A short spring before a long jump: the ecological challenge to the steppe tortoise (*Testudo horsfieldii*). *Canadian Journal of Zoology* **80,** 493–502.

Lagarde, F., Bonnet, X., Henen, B. T., Corbin, J., Nagy, K. A. & Naulleau, G. 2003. Sex divergence in space utilisation in the steppe tortoise (*Testudo horsfieldii*). *Canadian Journal of Zoology*, **81,** 380-387.

Laver, P. N. & Kelly, M. J. 2009. A Critical Review of Home Range Studies. *Journal of Wildlife Management*, **72,** 290-298.

Leban, F. A., Wisdom, M. J., Garton, E. O., Johnson, B. K. & Kie, J. G. 2001. Effect of sample size on the performance of resource selection analyses. In: *Radio tracking and animal populations* (Ed. by Millspaugh, J. J. & Marzluff, J. M.). San Diego: Academic press.

Leistner, O. A. 1967. The plant ecology of the southern Kalahari. *Memoirs of the Botanical Survey of South Africa*, **38,** 1-140.

Leistner, O. A. & Werger, M. J. A. 1973. Southern Kalahari Phytosociology. *Vegetatio*, **28,** 353-399.

Leuteritz, T. E. J. & Hofmeyr, M. D. 2007. The extended reproductive season of tent tortoises (*Psammobates tentorius tentorius*): A response to an arid and unpredictable environment. *Journal of Arid Environments* **68,** 546-563.

Lindeman, P. V. 2000. Evolution of the relative width of the head and alveolar surfaces in map turtles (Testudines: Emydidae: *Graptemys*). *Biological Journal of the Linnean Society*, **69,** 549-576.

Llorente, G. A., Ruiz, X., Casinos, A., Barandalla, I. & Viladiu, C. 2008. Long Bone Allometry in Tortoises and Turtles. In: *Biology of Turtles* (Ed. by Wyneken, J., Godfrey, M. H. & Bels, V.), pp. 45-83. Boca Raton: CRC Press.

Loehr, V. J. T. 2002. Population Characteristics and Activity Patterns of the Namaqualand Speckled Padloper (*Homopus signatus signatus*) in the Early Spring. *Journal of Herpetology*, **36,** 378-389.

Loehr, V. J. T. (2008). The ecology of the world's smallest tortoise, *Homopus signatus signatus*: effects of rainfall. Ph.D. thesis, University of the Western Cape, Belville.

Loehr, V. J. T., Henen, B. T. & Hofmeyr, M. D. 2004. Reproduction of the smallest tortoise, the Namaqualand speckled padloper, *Homopus signatus signatus*. *Herpetologica*, **60,** 444-454.

Loehr, V. J. T., Henen, B. T. & Hofmeyr, M. D. 2006. Shell Characteristics & Sexual Dimorphism in the Namaqualand Speckled Padloper, *Homopus signatus signatus*. *African Journal of Herpetology*, **55,** 1-11.

Loehr, V. J. T., Hofmeyr, M. D. & Henen, B. T. 2007. Annual variation in the body condition of a small, arid-zone tortoise, *Homopus signatus signatus*. *Journal of Arid Environments*, **71,** 337-349.

Longepierre, S., Hailey, A. & Grenot, C. 2001. Home range area in the tortoise *Testudo hermanni* in relation to habitat complexity: implications for conservation of biodiversity. *Biodiversity and Conservation*, **10,** 1131-1140.

Longshore, K. M., Jaeger, J. R. & Sappington, J. M. 2003. Desert Tortoise (*Gopherus agassizii*) Survival at Two Eastern Mojave Desert Sites: Death by Short-Term Drought? *Journal of Herpetology*, **37,** 169-177.

Lovegrove, B. 1993. *The living deserts of southern Africa*. Vlaeberg, South Africa: Fernwood Press.

Low, A. B. & Rebelo, A. G. 1996. Vegetation of South Africa, Lesotho and Swaziland. A companion to the vegetation map of South Africa, Lesotho and Swaziland. Pretoria: Department of Environmental Affairs and Tourism.

Luiselli, L. 2005. Aspects of comparative thermal ecology of sympatric hinge-back tortoises (*Kinixys homeana* and *Kinixys erosa*) in the Niger Delta, southern Nigeria. *African Journal of Ecology*, **43,** 64-69.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. & Erickson, W. P. 2002. *Resource Selection by Animals, Statistical Design and Analysis for Field Studies*. Dordrecht: Kluwer Academic Publishers.

Mann, G. K. H., O'Riain, M. J. & Hofmeyr, M. D. 2006. Shaping up to fight: sexual selection influences body shape and morphology in the fighting tortoise, *Chersina angulata*. *Journal of Zoology*, **269,** 373-379.

Marlow, R. W. & Tollestrup, K. 1982. Mining and exploitation of natural mineral deposits by the desert tortoise, *Gopherus agassizii*. *Animal Behaviour*, **30,** 475-478.

Marquardt, D. W. 1963. An Algorithm for Least Squares Estimation of Parameters. *Journal of the Society of Industrial and Applied Mathematics*, **11,** 431-441.

Mason, M. C., Kerley, G. I. H., Weatherby, C. A. & Branch, W. R. 2000. Angulate and leopard tortoises in the Thicket Biome, Eastern Cape, South Africa: populations and biomass estimates. *African Journal of Ecology*, **38,** 147-153.

McCoy, E. D., Mushinsky, H. R. & Lindzey, J. 2006. Declines of the gopher tortoise on protected lands. *Biological Conservation*, **128,** 120-127.

McMaster, M. K. & Downs, C. T. 2006a. Do seasonal and behavioral differences in the use of refuges by the Leopard Tortoise (*Geochelone pardalis*) favor passive thermoregulation? *Herpetologica*, **62,** 37-46.

McMaster, M. K. & Downs, C. T. 2006b. Population Structure and Density of Leopard Tortoises (*Geochelone pardalis*) on Farmland in the Nama-Karoo. *Journal of Herpetology*, **40,** 495-502.

McMaster, M. K. & Downs, C. T. 2009. Home Range and Daily Movement of Leopard Tortoises (*Stigmochelys pardalis*) in the Nama-Karoo, South Africa. *Journal of Herpetology*, **43,** 561-569.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem. *Ecological Monographs*, **55,** 259-294.

McNay, R. S., Morgan, J. A. & Bunnell, F. L. 1994. Characterizing independence of observations in movements of Columbian black-tailed deer. *Journal of Wildlife Management*, **58,** 422-429.

McRae, W. A., Landers, J. L. & Garner, J. A. 1981. Movement patterns and home range of the gopher tortoise. *American Midland Naturalist* **106,** 165–179.

Milstein, P. l. S. 1968. Hibernation of the Kalahari Geometrid Tortoise and other species in the Transvaal. In: *Fauna and Flora*, pp. 42-44.

Morafka, D. J. & Berry, K. H. 2002. Is *Gopherus agassizii* a Desert-Adapted Tortoise, or an Exaptive Opportunist? Implications for Tortoise Conservation. *Chelonian Conservation and Biology*, **4,** 263-287.

Moskovits, D. K. & Kiester, A. R. 1987. Activity levels and ranging behaviour of the two Amazonian tortoises, *Geochelone carbonaria* and *Geochelone denticulata*, in north-western Brazil. *Functional Ecology* **1,** 203–214.

Moskovits, D. K. 1988. Sexual Dimorphism and Population Estimates of the Two Amazonian Tortoises (*Geochelone carbonaria* and *G. denticulata*) in Northwestern Brazil. *Herpetologica*, **44,** 209-217.

Mouton, L. P. N. & Oelofsen, B. W. 1988. A model explaining patterns of geographic variation in *Cordylus cordylus* (Reptilia: Cordylidae) in south-western Cape, South Africa. *South African Journal of Zoology*, **23,** 20-31.

Mucina, L., Rutherford, M. C. & Powrie, L. W. 2006a. The Logic of the Map: Approaches and Procedures. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.), pp. 12-29. Pretoria: South African Biodiversity Institute.

Mucina, L., Rutherford, M. C., Palmer, A. R., Milton, S. J., Scott, L., Lloyd, W., van der Merwe, B., Hoare, D. B., Bezuidenhout, H., Vlok, J. H. J., Euston-Brown, D. I. W., Powrie, L. W. & Dold, A. P. 2006b. Nama-Karoo Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.), pp. 324-347. Pretoria: South African Biodiversity Institute.

Mucina, L., Rutherford, M. C. & Powrie, L. W. 2006c. Inland Azonal Vegetation. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.), pp. 616-657. Pretoria: South African Biodiversity Institute.

Mushinsky, H. R., Wilson, D. S. & McCoy, E. D. 1994. Growth and sexual dimorphism of *Gopherus Polyphemus* in central Florida. *Herpetologica*, **50,** 119-128.

Nagy, K. A. & Medica, P. A. 1986. Physiological ecology of desert tortoises in southern Nevada. *Herpetologica*, **42,** 73-92.

Nash, J. C. 1979. *Compact Numerical Methods for Computers: Linear Algebra and Function Minimization*. New York: John Wiley & Sons, Inc.

Neu, C. W., Byers, R. C. & Peek, J. M. 1974. A Technique for analyzing Utilization-Availability data. *The Journal of Wildlife Management*, **38,** 541-545.

Nieuwolt, P. M. 1996. Movement, activity, and microhabitat selection in the western box turtle, *Terrapene ornata luteola*, in New Mexico. *Herpetologica*, **52,** 487-495.

Noy-Meir, I. 1973. Desert Ecosystems: Environment and Producers. *Annual Review of Ecology and Systematics*, **4,** 25-51.

Noy-Meir, I. 1974. Desert Ecosystems: Higher Trophic Levels. *Annual Review of Ecology and Systematics*, **5,** 195-214.

Nussear, K. E., Esque, T. C., Haines, D. F. & Richard Tracy, C. 2007. Desert Tortoise Hibernation: Temperatures, Timing, and Environment. *Copeia*, **2,** 378-386.

O'Connor, M. P., Zimmerman, L. C., Ruby, D. E., Bulova, S. J. & Spotila, J. R. 1994. Home range size and movements by desert tortoises, *Gopherus agassizii*, in the eastern Mojave Desert. *Herpetological Monographs*, **8,** 60-71.

O'Connor, T. G. & Roux, P. W. 1995. Vegetation changes (1949-1971) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: Influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology*, **32,** 612-626.

Otis, D. L. & White, G. C. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management*, **63,** 1039-1044.

Peterson, C. C. 1996. Ecological Energetics of the Desert Tortoise (*Gopherus agassizii*): Effects of Rainfall and Drought. *Ecology*, **77,** 1831-1844.

Pianka, E. R. 1969. Sympatry of Desert Lizards (*Ctenotus*) in Western Australia. *Ecology*, **50,** 1012-1030.

Pianka, E. R. 1989. Desert Lizard Diversity: Additional Comments and Some Data. *The American Naturalist*, **134,** 344-364.

Pickford, M. 2004. Southern Africa: a cradle of evolution. *South African Journal of Science*, **100,** 205-214.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *The American Naturalist*, **115,** 92–112.

Powell, R. A. 2000. Animal Home Ranges and Territories and Home Range Estimators. In: *Research and Techniques in Animal Ecology: Controversies and Consequences* (Ed. by Boitani, L. & Fuller, T. K.), pp. 64-110. New York: Colombia University Press.

Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. 1986. *Numerical Recipes*. Cambridge: Cambridge University Press.

Pritchard, C. H. 2008. Evolution and Structure of the Turtle Shell. In: *Biology of Turtles*

(Ed. by Wyneken, J., Godfrey, M. H. & Bels, V.), pp. 45-83. Boca Raton: CRC Press.

Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.

Rall, M. 1990. *Psammobates oculifer*, serrated tortoise: egg production. *The Journal of the Herpetological Association of Africa*, **37,** 45-52.

Rall, M. & Fairall, N. 1993. Diets and food preferences for two South African tortoises *Geochelone pardalis* and *Psammobates oculifer*. *South African Journal of Wildlife Research*, **23,** 63-70.

Ramsay, S. L., Hofmeyr, M. D. & Joshua, Q. I. 2002. Activity patterns of the angulate tortoise (*Chersina angulata*) on Dassen Island, South Africa. *Journal of Herpetology*, **36,** 161-169.

Rautenstrauch, K. R., Rager, A. L. H. & Rakestraw, D. L. 1998. Winter Behavior of Desert Tortoises in Southcentral Nevada. *The Journal of Wildlife Management*, **62,** 98-104.

Rebelo, A. G., Boucher, C., Mucina, L. & Rutherford, M. C. 2006. Fynbos Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.), pp. 52-219. Pretoria: South African Biodiversity Institute.

Reiber, C. L., Malekpour, S. & McDaniel, M. 1999. Effects of Post-Hatching Maintenance Temperature on Desert Tortoise (*Gopherus agassizii*) Shell Morphology and Thermoregulatory Behavior. *Journal of Herpetology*, **33,** 234-240.

Riedle, J. D., Averill-Murray, R. C., Lutz, C. L. & Bolen, D. K. 2008. Habitat Use by Desert Tortoises (*Gopherus agassizii*) on Alluvial Fans in the Sonoran Desert, South-Central Arizona. *Copeia*, **2,** 414-420.

Ringrose, S., Matheson, W. & Vanderpost, C. 1998. Analysis of soil organic carbon and vegetation cover trends along the Botswana Kalahari Transect. *Journal of Arid Environments*, **38,** 379-396.

Ringrose, S., Matheson, W., Wolski, P. & Huntsman-Mapila, P. 2003. Vegetation cover trends along the Botswana Kalahari transect. *Journal of Arid Environments*, **54,** 297-317.

Rodgers, A. R. & Carr, A. P. 1998. User's Manual for Home Range Extension to ArcView. Center for Northern Forest Ecosystem Research.

Rose, F. L. & Judd, F. W. 1975. Activity and Home Range Size of the Texas Tortoise, *Gopherus berlandieri*, in South Texas. *Herpetologica*, **31,** 448-456.

Roux, P. W. & Vorster, M. 1983. Vegetation change in the Karoo. *Proceedings of the Grassland Society of South Africa*, **18,** 25-29.

Row, J. R. & Blouin-Demers, G. 2006. Kernels Are Not Accurate Estimators of Home-Range Size for Herpetofauna. *Copeia*, **2006,** 797-802.

Rutherford, M. & Westfall, R. 1986. Biomes of southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa*, **54,** 1-98.

Rutherford, M. C. 1997. Biomes. In: *The vegetation of southern Africa* (Ed. by Cowling, R. M., Richardson, D. M. & Pierce, S. M.). Cambridge: Cambridge University Press.

Rutherford, M. C., Mucina, L., Lotter, M. C., Bredenkamp, G. J., Smit, J. H. L., Scott-Shaw, C. R., Hoare, D. B., Goodman, P. S., Bezuidenhout, H., Scott, L., Ellis, F., Powrie, L. W., Siebert, F., Mostert, T. H., Henning, B. J., Ventner, C. E., Camp, K. G. T., Siebert, S. J., Matthews, W. S., Burrows, J. E., Dobson, L., van Rooyen, N., Schmidt, E., Winter, P. J. D., du Preez, P. J., Ward, R. A., Williamson, S. & Hurter, P. J. H. 2006a. Savanna Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.), pp. 440-529. Pretoria: South African National Biodiversity Institute.

Rutherford, M. C., Mucina, L. & Powrie, L. W. 2006b. Biomes and Bioregions of Southern Africa. In: *The Vegetation of South Africa, Lesotho and Swaziland* (Ed. by Mucina, L. & Rutherford, M. C.). Pretoria: South African Biodiversity Institute.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Jonas, A., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Wellington, E., Feral, C. J. W., February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H. T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature*, **438,** 846-849.

Scholes, R. J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography*, **17,** 415-419.

Scholes, R. J. 1997. Savanna. In: *Vegetation of southern Africa* (Ed. by Cowling, R. M., Richardson, D. M. & Pierce, S. M.). Cambridge: Cambridge University Press.

Scholes, R. J., Dowty, P. R., Caylor, K. K., Parsons, D. A. B., Frost, P. G. H. & Shugart, H. H. 2002. Trends in Savanna Structure and Composition along an Aridity Gradient in the Kalahari. *Journal of Vegetation Science*, **13,** 419-428.

Seaman, D. E. & Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77,** 2075-2085.

Seaman, E. D., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of sample size on kernel home ranges estimates. *Journal of Wildlife Management*, **63,** 739-747.

Seymour, C. L. 2008. Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology*, **197,** 131-138.

Shearing, D. & van Heerden, K. 1997. *Karoo*. Kirstenbosch: Botanical Society of S.A.

Shine, R. 1988. The Evolution of Large Body Size in Females: A Critique of Darwin's "Fecundity Advantage" Model. *The American Naturalist*, **131,** 124-131.

Shine, R. 1989. Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. *The Quarterly Review of Biology*, **64,** 419-461.

Shmida, A., Evenari, M. & Noy-Meir, I. 1986. HOT DESERT ECOSYSTEM: AN INTEGRATED VIEW. In: *Hot Deserts and Arid Shrublands, B* (Ed. by Evenari, M., Noy-Meir, I. & Goodall, D. W.). Amsterdam: Elsevier Science Publishers B. V.

Shrager, R. I. 1970. Regression with Linear Constraints: An Extension of the Magnified Diagonal Method. *Journal of the Association for Computing Machinery*, **17,** 446-452.

Shrager, R. I. 1972. Quadratic Programming for N. *Communications of the ACM*, **15,** 41-45.

Silverman, B. W. 1986. *Density Estimation for Statistics and Data Analysis*. London: Chapman and Hall.

Singh, S., Smyth, A. K. & Blomberg, S. P. 2002. Thermal ecology and structural habitat use of two sympatric lizards (*Carlia vivax* and *Lygisaurus foliorum*) in subtropical Australia. *Austral Ecology*, **27,** 616-623.

Skarpe, C. 1986. Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Plant Ecology*, **68,** 3-18.

Skinner, J. D. & Chimimba, C. T. 2005. *The mammals of the southern African subregion*. Cambridge: Cambridge University Press.

Soil and plant analysis Council. 1999a. Conductance, soluble salts, and sodicity. In: *Soil analysis handbook of reference methods* (Ed. by Benton Jones Jr., J.), pp. 5-67. Boca Raton, FL, USA: CRC Press LLC.

Soil and plant analysis Council. 1999b. Soil pH, and exchangeable acidity and aluminium. In: *Soil analysis handbook of reference methods* (Ed. by Benton Jones. Jr., J.), pp. 27-39. Boca Raton, FL, USA: CRC Press LLC.

Soil and plant analysis Council. 1999c. Major cations (Potassium, Calcium, Magnesium and Sodium). In: *Soil analysis handbook of reference methods* (Ed. by Benton Jones. Jr., J.), pp. 93-115. Boca Raton, FL, USA: CRC Press LLC.

Soil and plant analysis Council. 1999d. Phosphorus. In: *Soil analysis handbook of reference methods* (Ed. by Benton Jones. Jr., J.), pp. 69-91. Boca Raton, FL, USA: CRC Press LLC.

Soil and plant analysis Council. 1999e. Organic and humic matter. In: *Soil analysis handbook of reference methods* (Ed. by Benton Jones. Jr., J.), pp. 27-39. Boca Raton, FL, USA: CRC Press LLC.

Spencer, A. R. G., Cameron, G. N. & Swihart, R. K. 1990. Operationally defining a home range: Temporal independence exhibited by hispid cotton rats. *Ecology*, **71,** 1817-1822.

Spencer, R-J., Thompson, M. B. & Hume, I. D. 1998. The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*, **121,** 341-349.

St. Clair, R. C. 1998. Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. *Oecologia*, **115,** 501-507.

Stevenson, P. R., Borda, C. A., Rojas, A. M. & Álvarez, M. 2007. Population size, habitat choice and sexual dimorphism of the Amazonian tortoise (*Geochelone denticulata*) in Tinigua National Park, Colombia. *Amphibia-Reptilia*, **28,** 217-226.

Stevenson, R. D. 1985. Body size and Limits to the Daily Range of Body Temperature in Terrestrial Ectotherms. *The American Naturalist*, **125,** 102-117.

Stevenson, R. D., Peterson, C. R. & Tsuji, J. S. 1985. The Thermal Dependence of Locomotion, Tongue Flicking, Digestion, and Oxygen Consumption in the Wandering Garter Snake. *Physiological Zoology*, **58,** 46-57.

Stubbs, D., Hailey, A., Pulford, E. & Tyler, W. 1984. Population ecology of European tortoises: review of field techniques. *Amphibia-Reptilia*, **5,** 57-68.

Swihart, R. K. & Slade, N. A. 1985a. Influence of Sampling Interval on Estimates of Home-Range Size. *The Journal of Wildlife Management*, **49,** 1019-1025.

Swihart, R. K. & Slade, N. A. 1985b. Testing for independence of observations in animal movements. *Ecology*, **66,** 1176-1184.

Swihart, R. K. & Slade, N. A. 1997. On Testing for Independence of Animal Movements. *Journal of Agricultural, Biological, and Environmental Statistics*, **2,** 48-63.

Swingland, I. R., North, P. M., Dennis, A. & Parker, M. J. 1989. Movement patterns and morphometrics in giant tortoises. *Journal of Animal Ecology*, **58,** 971-985.

Tabachnick, B. G. & Fidell, L. S. 2007. *Using Multivariate Statistics*. Boston: Pearson Education, Inc. / Allyn and Bacon.

The Non Affiliated Soil Analysis Work Committee. 1990a. Extractable cations: Ammonium acetate. In: *Handbook of standard soil testing methods for advisory purposes*, pp. 8/1-8/3. Pretoria: Soil Science Society of South Africa.

The Non Affiliated Soil Analysis Work Committee. 1990b. Extractable phosphorus: Bray-2. In: *Handbook of standard soil testing methods for advisory purposes*, pp. 21/1-21/4. Pretoria: Soil Science Society of South Africa.

Thomas, A. D. & Dougill, A. J. 2006. Distribution and characteristics of cyanobacterial soils in the Molopo Basin, South Africa. *Journal of Arid Environments*, **64,** 270-283.

Todd, S. W. 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. *Journal of Applied Ecology*, **43,** 293-304.

Todd, S. W. & Hoffman, M. T. 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, **142,** 169-178.

van Bloemestein, U. P. (2005). Seasonal movement and activity patterns of the endangered geometric tortoise, *Psammobates geometricus*. M.Sc. thesis, University of the Western Cape, Belville.

Van Den Berg, P. & Baard, E. H. W. 1994. Regional variation in morphometric characters in the angulate tortoise, *Chersina angulata*, from South Africa. *The Journal of the Herpetological Association of Africa*, **43,** 28-32.

van der Watt, H. V. H. 1966. Improved tables and a simplified procedure for soil particle size analyses by the hydrometer method. *African Journal of Agricultural Science*, 911-916.

Van Heezik, Y. M., Cooper, J. & Seddon, P. J. 1994. Population characteristics and morphometrics of angulate tortoises on Dassen Island, South Africa. *Journal of Herpetology*, **28,** 447-453.

van Oudtshoorn, F. 2004. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

van Rooyen, H. 1984. The soils of the Kalahari Gemsbok National Park. *Koedoe*, **Supplement,** 45-61.

van Rooyen, N. 2001. *Flowering plants of the Kalahari dunes*. Ekotrust cc.

van Rooyen, N. & van Rooyen, M. W. 1998. Vegetation of the south-western arid Kalahari: an overview. *Transactions of the Royal Society of South Africa*, **53,** 113-140.

Veenendaal, E. M., Ernst, W. H. O. & Modise, G. S. 1996. Effect of seasonal rainfall pattern on seedling emergence and establishment of grasses in a savanna in south-eastern Botswana. *Journal of Arid Environments*, **32,** 305-317.

Vorster, M. & Roux, P. W. 1983. Veld of the Karoo areas. *Proceedings of the Grassland Society of South Africa*, **18,** 18-24.

Walker, F. M., Taylor, A. C. & Sunnucks, P. 2007. Does soil type drive social organization in southern hairy-nosed wombats? *Molecular Ecology*, **16,** 199-208.

Wang, L., D'Odorico, P., Ringrose, S., Coetzee, S. & Macko, S. A. 2007. Biogeochemistry of Kalahari sands. *Journal of Arid Environments*, **71,** 259-279.

Wilbur, H. M. & Morin, P. J. 1988. Life history evolution in turtles. In: *Biology of the reptilia. Ecology B.* (Ed. by Gans, D., Huey, B. & Riss, A.), pp. 387-437. New York: Avademin Press.

Willemsen, R. E. & Hailey, A. 2002. Body Mass Condition in Greek Tortoises: Regional and Interspecific variation. *Herpetological Journal*, **12,** 105-114.

Willemsen, R. E. & Hailey, A. 2003. Sexual dimorphism in European tortoises. *Journal of Zoology*, **260,** 353-365.

Wilson, D. S., Tracy, C. R. & Richard Tracy, C. 2003. Estimating Age of Turtles from Growth Rings: A Critical Evaluation of the Technique. *Herpetologica*, **59,** 178-194.

Woodbury, A. M. & Hardy, R. 1948. Studies of the Desert Tortoise, *Gopherus Agassizii*. *Ecological Monographs*, **18,** 145-200.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70,** 164-168.

Worton, B. J. 1995. Using Monte Carlo Simulation to Evaluate Kernel-Based Home Range Estimators. *The Journal of Wildlife Management*, **59,** 794-800.

Wright, J., Steer, E. & Hailey, A. 1988. Habitat separation in tortoises and the consequences for activity and thermoregulation. *Canadian Journal of Zoology*, **66,** 1537-1544.

Yom-Tov, Y. & Geffen, E. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia*, **148,** 213-218.

Zar, J. H. 1999. *Biostatistical analysis*. Upper Saddle River, New Jersey: Prentice Hall.

Zerbe, G. O., Archer, P. G., Banchero, N. & Lechner, A. J. 1982. On comparing regression lines in unequal slopes. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, **242,** 178-180.

Zimmerman, L. C. & Tracy, C. R. 1989. Interactions between the Environment and Ectothermy and Herbivory in Reptiles. *Physiological Zoology*, **62,** 374-409.

Zug, G. R. 1991. Age determination in turtles. In: *Herpetology Circular Number 20*, pp. 5-19: Society for the Study of Amphibians and Reptiles.

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11 APPENDICES

Appendix A Monte Carlo random walk tests using 100 simulated paths for 15 female and 12 male tortoises radio-tracked at Benfontein. Fidelity tests reflect relocation points removed from #101, #707, #721, #725, #737 due to poor condition; #743 died between December and January; #102 was lost at the end of October; and #7016 and 7017 were only tracked from the middle of January. #739 had two 'outlier' location points removed and #738 had three 'outlier' points removed prior to calculating fidelity. For #704, #714 and #738, I used 1000 simulated walks as they were close to having a lower mean square distance (MSD) than 95% of the 100 simulated walks. Site fidelity was ascertained using 95% confidence intervals, with actual tortoises that were in the top 5% exhibiting dispersion and those in the bottom 5% showing fidelity. An asterisk denotes a tortoise being close to fidelity or dispersion.

Sex	Site	ID	Locations	% higher MSD	% lower MSD	Dispersion	Random	Fidelity
F	E	15	103	48			Y	
F	E	703	113	97				Y
F	E	717	103	96				Y
F	E	726	51		99	Y		
F	E	737	88	36			Y	
F	E	738	103	95				Y
F	E	7017	35	59			Y	
F	W	101	75		99	Y		
F	W	102	53		96	Y		
F	W	706	111	27			Y	
F	W	707	55	95				Y
F	W	708	113	79			Y	
F	W	710	110	97				Y
F	W	725	91		93		Y	
F	W	7016	33	89			Y	
M	E	18	116	52			Y	
M	E	23	116	86			Y	
M	E	715	116	99				Y
M	E	716	104	99				Y
M	E	739	111	99				Y
M	E	743	70	79			Y	
M	W	704	129	96			Y	Y
M	W	709	125	99				Y
M	W	714	122	94			Y	*
M	W	721	85	99				Y
M	W	733	121	81			Y	
M	W	747	121		97	Y		

Appendix B Mean (±SD) measurements for *Psammobates oculifer*. Measurements were taken from live animals (Benfontein), and wet and dry museum specimens (Iziko and Transvaal museums). The measurements for SHM and SV are from museum specimens only. Morphometric measurements are in bold (see Table 8.1 for measurement descriptions) while the minimum and maximum measurements (Min-Max) and number of animals measured (*n*) appear underneath and adjacent to means respectively. Mass is in g, shell volume in cm^3, with all other measurements in mm. Measurements marked with an asterisk indicate deformity or small sample size

Measurement	Female		Male		Juvenile	
SCL	**113.05 ± 8.89**	(126)	**99.16 ± 8.79**	(156)	**68.10 ± 13.13**	(35)
Min-Max (n)	85.36 132.80		74.58 119.07		38.86 83.25	
SWA	**69.53 ± 5.64**	(50)	**60.91 ± 5.62**	(75)	**44.20 ± 7.37**	(17)
Min-Max (n)	55.74 79.78		44.40 72.23		32.06 58.51	
SWM	**85.85 ± 6.34**	(126)	**72.34 ± 4.90**	(155)	**56.92 ± 8.14**	(35)
Min-Max (n)	63.97 97.59		59.87 84.97		38.31 66.00	
SWP	**79.67 ± 7.32**	(49)	**68.78 ± 6.21**	(76)	**48.95 ± 8.66**	(17)
Min-Max (n)	60.82 90.55		53.90 83.11		35.77 64.17	
SHM	**63.56 ± 6.05**	(48)	**51.49 ± 5.18**	(74)	**38.48 ± 7.92**	(35)
Min-Max (n)	45.48 73.70		41.10 61.50		18.39 50.40	
SV	**330.96 ± 81.65**	(47)	**197.89 ± 53.72**	(74)	**84.79 ± 38.01**	(35)
Min-Max (n)	130.58 460.96		96.09 315.11		17.64 144.56	
PL	**94.95 ± 7.13**	(125)	**79.15 ± 6.22**	(148)	**57.80 ± 10.33**	(34)
Min-Max (n)	72.52 109.70		63.51 95.82		35.07 71.60	
PW	**55.46 ± 5.07**	(96)	**45.04 ± 3.85**	(135)	**33.50 ± 5.95**	(31)
Min-Max (n)	38.47 65.92		35.59 53.95		21.79 41.49	
NL	**9.81 ± 1.89**	(50)	**8.72 ± 1.39**	(70)	**5.45 ± 1.36**	(17)
Min-Max (n)	6.13 15.64		5.50 11.53		3.56 8.79	
NW	**6.39 ± 1.43**	(50)	**5.61 ± 1.22**	(76)	**3.94 ± 1.02**	(18)
Min-Max (n)	3.27 10.23		2.46 8.63		2.42 6.23	
V1L	**24.43 ± 2.69**	(50)	**21.08 ± 2.10**	(72)	**14.27 ± 2.66**	(18)
Min-Max (n)	17.95 31.11		15.96 24.56		9.47 17.63	
V2L	**22.43 ± 2.95**	(50)	**17.62 ± 2.20**	(71)	**11.96 ± 2.31**	(18)
Min-Max (n)	16.64 28.37		12.30 21.82		8.35 15.34	
V3L	**24.55 ± 2.98**	(50)	**19.22 ± 2.37**	(72)	**12.61 ± 2.34**	(18)
Min-Max (n)	17.54 30.12		14.45 24.58		9.40 16.96	
V4L	**24.33 ± 3.18**	(49)	**20.12 ± 2.61**	(70)	**12.91 ± 3.13**	(17)
Min-Max (n)	16.92 31.47		14.62 25.84		7.91 19.39	
V5L	**24.81 ± 3.38**	(49)	**22.22 ± 3.73**	(72)	**13.64 ± 3.99**	(16)
Min-Max (n)	17.19 31.30		15.26 33.27		6.11 21.15	

Appendix B continued

Measurement	Female		Male		Juvenile	
V6L*	18.45 ± 8.42	(2)	17.18 ± 6.75	(3)	14.18 ±	(1)
Min-Max (n)	12.49　24.40		9.44　21.84		14.18　14.18	
V7L*		(0)	24.65	(1)		0
Min-Max (n)						
CR1L	35.59 ± 3.60	(51)	29.73 ± 2.89	(75)	20.51 ± 3.62	(17)
Min-Max (n)	26.87　43.27		22.75　35.41		15.06　25.43	
CR2L	25.51 ± 2.63	(115)	19.89 ± 2.01	(136)	15.21 ± 2.93	(34)
Min-Max (n)	18.57　32.35		15.42　24.80		8.81　18.60	
CR3L	25.75 ± 2.94	(46)	20.96 ± 2.32	(72)	13.38 ± 2.54	(16)
Min-Max (n)	18.43　30.71		16.55　26.81		9.54　17.56	
CR4L	22.42 ± 2.77	(48)	19.14 ± 2.61	(72)	12.62 ± 2.41	(15)
Min-Max (n)	16.85　27.39		13.55　25.44		7.58　16.76	
CR5L*	21.19 ± 2.74	(2)	13.95 ± 0.82	(2)	±	(0)
Min-Max (n)	19.25　23.13		13.37　14.53			
V3W	39.68 ± 4.68	(50)	31.40 ± 3.00	(75)	21.89 ± 3.23	(18)
Min-Max (n)	24.89　46.64		24.82　38.40		16.40　27.61	
CR3W	34.86 ± 3.36	(49)	29.27 ± 2.95	(75)	20.63 ± 3.83	(18)
Min-Max (n)	26.11　40.29		23.39　36.02		14.12　26.08	
MR6W	21.62 ± 2.20	(48)	17.92 ± 1.94	(75)	12.51 ± 2.46	(17)
Min-Max (n)	15.58　25.48		14.12　22.07		7.44　15.85	
MR6L	15.76 ± 1.92	(48)	12.60 ± 1.20	(75)	8.88 ± 1.59	(17)
Min-Max (n)	10.46　20.00		9.68　15.19		5.37　10.94	
S(P)	23.20 ± 2.78	(49)	19.53 ± 2.86	(74)	12.17 ± 2.67	(17)
Min-Max (n)	17.79　30.33		13.47　26.03		9.14　17.36	
S(D)	30.00 ± 2.98	(89)	28.53 ± 3.19	(126)	18.00 ± 4.29	(31)
Min-Max (n)	21.37　36.66		16.63　34.81		9.00　24.43	
GW	20.70 ± 2.29	(48)	19.35 ± 2.12	(70)	14.55 ± 2.04	(17)
Min-Max (n)	14.27　25.18		13.02　24.58		11.07　18.84	
G	13.16 ± 1.79	(120)	11.84 ± 1.72	(133)	8.32 ± 1.82	(34)
Min-Max (n)	9.17　17.97		7.64　16.79		5.03　12.27	
H	23.33 ± 2.60	(121)	19.51 ± 2.70	(135)	14.35 ± 3.52	(34)
Min-Max (n)	16.02　28.72		11.26　28.31		7.81　23.00	
P	5.78 ± 1.69	(117)	4.61 ± 1.51	(127)	3.72 ± 1.31	(34)
Min-Max (n)	2.10　9.53		1.04　8.19		1.19　6.63	
Ab	33.21 ± 3.55	(119)	24.96 ± 3.06	(137)	18.73 ± 3.29	(34)
Min-Max (n)	20.94　39.88		17.75　33.18		11.95　25.00	
F	9.21 ± 1.94	(120)	9.22 ± 1.99	(136)	5.62 ± 1.35	(34)

Appendix B continued

Measurement	Female		Male		Juvenile	
Min-Max (n)	4.72 13.59		5.08 14.64		2.76 8.87	
An	**11.00 ± 1.83**	(120)	**8.85 ± 1.34**	(137)	**6.75 ± 1.72**	(34)
Min-Max (n)	6.13 15.29		5.00 12.79		3.78 10.60	
AW	**25.29 ± 2.81**	(119)	**26.17 ± 3.78**	(136)	**14.99 ± 4.40**	(32)
Min-Max (n)	19.57 33.44		15.07 35.51		5.90 23.80	
AG	**14.66 ± 2.86**	(113)	**14.46 ± 2.43**	(133)	**8.75 ± 2.06**	(33)
Min-Max (n)	8.91 21.54		9.20 21.86		5.01 13.38	
FFRW	**12.54 ± 1.49**	(41)	**11.09 ± 1.51**	(60)	**7.02 ± 0.84**	(13)
Min-Max (n)	8.44 14.74		8.28 14.19		5.36 8.07	
FARL	**26.63 ± 2.79**	(41)	**24.40 ± 2.80**	(63)	**16.48 ± 2.61**	(15)
Min-Max (n)	19.54 33.42		17.31 31.02		12.59 20.85	
HFRW	**10.90 ± 1.60**	(40)	**10.38 ± 1.35**	(56)	**6.35 ± 0.84**	(12)
Min-Max (n)	6.06 13.51		7.46 13.09		4.98 7.30	
HLRL	**29.89 ± 2.56**	(40)	**26.75 ± 3.21**	(60)	**15.94 ± 2.73**	(12)
Min-Max (n)	21.69 35.24		18.70 32.84		11.87 19.21	
CS	**20.47 ± 2.08**	(49)	**19.74 ± 2.11**	(68)	**13.87 ± 1.98**	(14)
Min-Max (n)	15.84 23.73		14.37 23.67		10.83 17.80	
HW	**18.80 1.50**	(39)	**17.12 1.52**	(59)	**12.23 1.09**	(10)
Min-Max (n)	14.37 21.71		14.08 19.92		10.60 13.61	
DCL	**155.25 ± 12.95**	(119)	**134.15 ± 12.58**	(137)	**91.16 ± 19.00**	(35)
Min-Max (n)	114.00 189.00		101.50 163.00		47.00 121.00	
DCW	**140.50 ± 11.52**	(120)	**116.21 ± 9.15**	(137)	**87.53 ± 15.30**	(35)
Min-Max (n)	103.00 164.00		93.00 139.50		53.00 107.00	
BL	**52.26 ± 5.18**	(49)	**40.25 ± 3.83**	(74)	**28.72 ± 4.95**	(17)
Min-Max (n)	37.40 59.63		32.16 52.00		18.83 37.77	
BM	**318.83 ± 57.97**	(84)	**195.84 ± 35.49**	(88)	**105.68 ± 35.71**	(17)
Min-Max (n)	197.50 463.20		113.00 288.00		24.50 156.00	

Appendix C Summary of the carapacial scute counts of *Psammobates oculifer* from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums) showing the number of each scute type with its occurrence (counts and percentages) amongst males, females, juveniles, and all cohorts combined.

Scute type	Number	Females Count	%	Males Count	%	Juveniles Count	%	Total Count	%
Nuchal	0	1	*0.8*	0	*0.0*	0	*0.0*	1	*0.3*
	1	123	*99.2*	153	*99.4*	35	*100.0*	311	*99.4*
	2	0	*0.0*	1	*0.6*	0	*0.0*	1	*0.3*
Vertebrals	4	2	*1.6*	3	*1.9*	0	*0.0*	5	*1.6*
	5	119	*96.7*	144	*93.5*	34	*97.1*	297	*95.2*
	6	2	*1.6*	6	*3.9*	1	*2.9*	9	*2.9*
	7	0	*0.0*	1	*0.6*	0	*0.0*	1	*0.3*
Costals-left	3	0	*0.0*	1	*0.6*	1	*2.9*	2	*0.6*
	4	118	*94.4*	149	*96.1*	33	*94.3*	300	*95.2*
	5	7	*5.6*	5	*3.2*	1	*2.9*	13	*4.1*
	6	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
Costals-right	3	0	*0.0*	1	*0.6*	1	*2.9*	2	*0.6*
	4	120	*96.0*	149	*96.1*	34	*97.1*	303	*96.2*
	5	5	*4.0*	4	*2.6*	0	*0.0*	9	*2.9*
	6	0	*0.0*	1	*0.6*	0	*0.0*	1	*0.3*
Marginals-left	9	1	*0.8*	0	*0.0*	1	*2.9*	2	*0.6*
	10	40	*32.0*	56	*36.1*	10	*28.6*	106	*33.7*
	11	82	*65.6*	95	*61.3*	24	*68.6*	201	*63.8*
	12	2	*1.6*	4	*2.6*	0	*0.0*	6	*1.9*
Marginals-right	9	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	10	44	*35.2*	63	*40.6*	13	*37.1*	120	*38.1*
	11	79	*63.2*	89	*57.4*	22	*62.9*	190	*60.3*
	12	2	*1.6*	3	*1.9*	0	*0.0*	5	*1.6*
Supracaudal	1	122	*100.0*	154	*100.0*	35	*100*	311	*100.0*

Appendix D   Contact zone of inguinal and axillary scutes with marginal scutes for female, male and juvenile *Psammobates oculifer*, both live (Benfontein) and wet and dry museum (Iziko and Transvaal museums) specimens.

Scute type	Marginals	Females Count	%	Males Count	%	Juveniles Count	%	Total Count	%
Axillary	3, 4	48	*98.0*	67	*93.1*	17	*100.0*	132	*95.7*
	2, 3	0	*0.0*	3	*4.2*	0	*0.0*	3	*2.2*
	3	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	4	1	*2.0*	2	*2.8*	0	*0.0*	3	*2.2*
Inguinal	6, 7	13	*26.5*	22	*29.7*	0	*0.0*	35	*25.0*
	7, 8	32	*65.3*	50	*67.6*	17	*100.0*	99	*70.7*
	7	2	*4.1*	2	*2.7*	0	*0.0*	4	*2.9*
	8, 9	2	*4.1*	0	*0.0*	0	*0.0*	2	*1.4*

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Appendix E Frequencies and percentages of the number of anterior and posterior marginal scutes serrated per tortoise amongst males, females, juveniles and all *Psammobates oculifer* from live specimens (Benfontein) and wet and dry specimens (Iziko and Transvaal museums). Of the female 'others', five had two, five had three and a female had five posterior marginal scutes serrated on both sides. Of the male 'others' two had three, two had four and one had 5 posterior marginal scutes serrated on both sides. A juvenile had three posterior marginal scutes serrated on both sides.

Serrated	Males		Females		Juveniles		Total	
Marginals	Count	%	Count	%	Count	%	Count	%
1-2	0	0.0	4	3.4	0	0.0	4	1.3
1-3	135	90.6	108	92.3	25	75.8	268	89.6
1-4	2	1.3	1	0.9	3	9.1	6	2.0
1-5	10	6.7	2	1.7	5	15.2	17	5.7
2-3	0	0.0	1	0.9	0	0.0	1	0.3
None	2	1.3	1	0.9	0	0.0	3	1.0
Total	149		117		33		299	
6-11	3	2.0	0	0.0	5	15.2	8	2.6
7-10	2	1.3	4	3.3	1	3.0	7	2.3
7-11	7	4.6	3	2.5	6	18.2	16	5.2
8-10	44	29.1	27	22.3	7	21.2	78	25.6
8-11	27	17.9	18	14.9	5	15.2	50	16.4
9-11	53	35.1	51	42.1	6	18.2	110	36.1
8-10L, 9-11R	7	4.6	3	2.5	0	0.0	10	3.3
8-10R, 9-11L	3	2.0	4	3.3	2	6.1	9	3.0
None	0	0.0	0	0.0	0	0.0	0	0.0
Other	5	3.3	11	9.1	1	3.0	17	5.6
Total	151		121		33		305	

Appendix F The frequencies and percentages of marginal scutes contributing to the bridge ridge in male (M), female (F) and juvenile (J) *Psammobates oculifer*. Counts are from live specimens (Benfontein), and wet and dry museum specimens (Iziko and Transvaal museums).

Marginals	Females		Males		Juveniles		Total	
	Count	%	Count	%	Count	%	Count	%
3-6	2	*4.2*	5	*6.8*	0	*0.0*	7	*5.1*
3-7	26	*54.2*	37	*50.7*	7	*41.2*	70	*50.7*
3-8	13	*27.1*	24	*32.9*	10	*58.8*	47	*34.1*
4-7	6	*12.5*	5	*6.8*	0	*0.0*	11	*8.0*
4-8	1	*2.1*	2	*2.7*	0	*0.0*	3	*2.2*
Totals	**48**		**73**		**17**		**138**	

Appendix G The frequencies and percentages of carapace colouration in male (M), female (F) and juvenile (J) *Psammobates oculifer*. Data are from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums). Colour is ordered from light to dark as yellow, orange yellow, orange/brown and brown.

Carapace colour	F	%	M	%	J	%	Total	%
Yellow	6	*5.1*	9	*6.8*	6	*18.8*	21	*7.4*
Orange/yellow	27	*22.9*	53	*39.9*	21	*65.6*	101	*35.7*
Orange/brown	54	*45.8*	52	*39.1*	5	*15.6*	111	*39.2*
Brown	31	*26.3*	19	*14.3*	0	*0.0*	50	*17.7*
Total	**118**		**133**		**32**		**283**	

Appendix H The frequencies and percentages of carapacial colour in different body size ranges (mm) of *Psammobates oculifer*. Data are from live specimens (Benfontein), and wet and dry museum specimens (Iziko and Transvaal museums). Colour is ordered from light to dark as yellow, orange yellow, orange/brown and brown.

Carapace	< 90	%	90-109	%	110-119	%	> 120	%	Total	%
Yellow	7	*13.2*	12	*9.1*	2	*2.7*	0.0	*0.0*	21	*7.4*
Orange/yellow	32	*60.4*	50	*37.9*	18	*24.7*	1	*4.2*	101	*35.8*
Orange/brown	14	*26.4*	50	*37.9*	34	*46.6*	12	*50.0*	110	*39.0*
Brown	0.0	*0.0*	20	*15.2*	19	*26.0*	11	*45.8*	50	*17.7*
Total	**53**		**132**		**73**		**24**		**282**	

Appendix I The frequencies and percentages of male, female and juvenile *Psammobates oculifer* in each dark pigment category for the carapace and plastron. Category (Cat.) 1 represents 0, 10 & 20% black pigment, whereas categories 2, 3 and 4 each represents two pigments increments, 30 & 40%, 50 & 60%, and 70 & 80%, respectively. Assessments were made from live specimens (Benfontein), and wet and dry museum specimens (Iziko and Transvaal museums).

	Cat. 1	%	Cat. 2	%	Cat. 3	%	Cat. 4	%	Totals
Male carapace	17	*12.8*	14	*10.5*	42	*31.6*	60	*45.1*	133
Female carapace	24	*20.5*	25	*21.4*	36	*30.8*	32	*27.4*	117
Juvenile carapace	0	*0.0*	0	*0.0*	2	*6.3*	30	*93.8*	32
Total carapace	**41**	***14.5***	**39**	***13.8***	**80**	***28.4***	**122**	***43.3***	**282**
Male plastron	7	*5.2*	76	*56.7*	46	*34.3*	5	*3.7*	134
Female plastron	11	*9.4*	59	*50.4*	37	*31.6*	10	*8.5*	117
Juvenile plastron	3	*9.4*	20	*62.5*	9	*28.1*	0	*0.0*	32
Total plastron	**21**	*7.4*	**155**	*54.8*	**92**	***32.5***	**15**	***5.3***	**283**

Appendix J Left side marginal scute counts and percentages taken from *Psammobates oculifer*. Specimens are divided by region and were taken from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums).

Region	< 11	%	11	%	> 11	%
Central	97	*38.8*	150	*60.0*	3	*1.2*
East	3	*11.5*	22	*84.6*	1	*3.8*
North-west	7	*21.9*	24	*75.0*	1	*3.1*

Appendix K The position of the plastral concavity in male *Psammobates oculifer* by region. Data is from wet and dry museum specimens (Iziko and Transvaal museums). Plastral concavities either were localised around the seam of the abdominal and femoral scutes (short concavity) or stretched the length of the abdominal to the femoral scute (long concavity).

Region	Long	%	Short	%
Central	10	*29.4*	24	*70.6*
East	9	*81.8*	2	*18.2*
North-west	14	*100.0*	0	*0.0*

Appendix L Number of large buttock tubercles on individuals of *Psammobates oculifer* by region. Data is from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums).

Region	0	%	1	%	> 1	%
Central	4	*1.7*	69	*29.5*	161	*68.8*
East	1	*5.6*	17	*94.4*	0	*0.0*
North-west	0	*0.0*	25	*100.0*	0	*0.0*

Appendix M Combinations of marginal scutes comprising the bridge ridge in specimens of *Psammobates oculifer* by region. Data is from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums). 'Other' refers to six females and five males from the Central region where the bridge ridge consisted of marginals 4-7, one female and one male from the Central region where it consisted of marginals 4-8 and a North-western female where it consisted of marginals 4-8.

Region	3-7	%	3-8	%	Other	%
Central	43	*56.6*	14	*18.4*	19	*25.0*
East	12	*48.0*	13	*52.0*	0	*0.0*
North-west	10	*33.3*	18	*60.0*	2	*6.7*

Appendix N Frequencies and percentage of anterior (A) and posterior (P) marginal scute serrations in *Psammobates oculifer* by region and cohort. Data are from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums). 'Other' refers to two males and one female in the Central region without anterior serration, two males and two females in the Central region where serrations were worn and one Eastern male with broken anterior marginal scutes. No tortoise had less than three posterior marginal scutes serrated or was categorised as 'Other' (hence 'na').

Region	Sex	A/P	< 3	%	3	%	> 3	%	Other	%
Central	F	A	5	*4.8*	93	*89.4*	3	*2.9*	3	*2.9*
East	F	A	0	*0.0*	2	*100.0*	0	*0.0*	0	*0.0*
North-west	F	A	0	*0.0*	10	*100.0*	0	*0.0*	0	*0.0*
Central	J	A	0	*0.0*	17	*85.0*	3	*15.0*	0	*0.0*
East	J	A	0	*0.0*	4	*66.7*	2	*33.3*	0	*0.0*
North-west	J	A	0	*0.0*	3	*60.0*	2	*40.0*	0	*0.0*
Central	M	A	0	*0.0*	109	*91.6*	6	*5.0*	4	*3.4*
East	M	A	0	*0.0*	15	*93.8*	0	*0.0*	1	*6.3*
North-west	M	A	0	*0.0*	9	*60.0*	6	*40.0*	0	*0.0*
Central	F	P	na	*na*	79	*82.3*	17	*17.7*	na	*na*
East	F	P	na	*na*	0	*0.0*	2	*100.0*	na	*na*
North-west	F	P	na	*na*	5	*50.0*	5	*50.0*	na	*na*
Central	J	P	na	*na*	14	*73.7*	5	*26.3*	na	*na*
East	J	P	na	*na*	0	*0.0*	6	*100.0*	na	*na*
North-west	J	P	na	*na*	1	*20.0*	4	*80.0*	na	*na*
Central	M	P	na	*na*	95	*81.2*	22	*18.8*	na	*na*
East	M	P	na	*na*	8	*61.5*	5	*38.5*	na	*na*
North-west	M	P	na	*na*	4	*28.6*	10	*71.4*	na	*na*

Appendix O Regional comparisons of counts and percentages of the proportion of light carapacial colouration among cohorts of *Psammobates oculifer*. Colouration was divided into four categories (beginning with palest) namely yellow (Y), orange/yellow (O/Y), orange/brown (O/B) and brown (B). Data were from live specimens (Benfontein) and wet and dry museum specimens (Iziko and Transvaal museums).

Region	Sex	Y	%	O/Y	%	O/B	%	B	%
Central	F	2	*1.9*	24	*23.3*	46	*44.7*	31	*30.1*
East	F	2	*100*	0	*0*	0	*0*	0	*0*
North-west	F	1	*10*	3	*30*	6	*60*	0	*0*
Central	J	2	*11.1*	13	*72.2*	3	*16.7*	0	*0*
East	J	1	*14.3*	6	*85.7*	0	*0*	0	*0*
North-west	J	3	*60*	2	*40*	0	*0*	0	*0*
Central	M	4	*4*	40	*39.6*	39	*38.6*	18	*17.8*
East	M	2	*13.3*	5	*33.3*	8	*53.3*	0	*0*
North-west	M	3	*20*	7	*46.7*	4	*26.7*	1	*6.7*

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Appendix P Mean (±SD) measurements for *Psammobates geometricus*. Measurements were taken from live specimens (South-western Cape) and wet and dry museum specimens (Iziko Museum). Morphometric measurements are in bold (see Table 8.1 for measurement descriptions) while the minimum and maximum measurements (Min-Max) and number of animals measured (*n*) appear underneath and adjacent to means respectively. Mass is in g, shell volume in cm^3, with all other measurements in mm. Measurements marked with an asterisk indicate deformity or small sample size.

	Females		Males		Juveniles	
SCL	**121.85 ± 14.67**	(26)	**107.60 ± 9.28**	(28)	**62.35 ± 15.05**	(23)
Min-Max (n)	91.80 146.08		80.31 120.50		35.27 84.78	
SWA	**71.55 ± 7.73**	(25)	**61.23 ± 4.62**	(27)	**43.17 ± 7.25**	(16)
Min-Max (n)	55.83 83.00		48.05 67.27		24.44 53.81	
SWM	**92.46 ± 11.33**	(27)	**74.90 ± 5.34**	(26)	**52.96 ± 9.53**	(19)
Min-Max (n)	71.34 112.00		60.66 83.20		30.60 66.37	
SWP	**87.88 ± 10.05**	(25)	**73.18 ± 5.41**	(26)	**49.33 ± 9.66**	(16)
Min-Max (n)	66.02 102.71		57.32 80.29		26.68 63.96	
SHM	**72.73 ± 8.55**	(27)	**56.03 ± 4.69**	(26)	**35.13 ± 9.27**	(19)
Min-Max (n)	54.70 86.00		42.19 62.80		17.65 48.79	
SV	**443.77 ± 145.98**	(26)	**240.90 ± 52.20**	(25)	**70.88 ± 40.63**	(17)
Min-Max (n)	187.57 711.73		107.62 305.75		9.97 143.75	
PL	**105.89 ± 10.50**	(23)	**84.86 ± 7.63**	(24)	**51.92 ± 13.37**	(19)
Min-Max (n)	82.99 126.60		64.09 97.64		25.67 72.74	
PW	**60.59 ± 6.98**	(24)	**49.66 ± 3.98**	(25)	**31.89 ± 6.71**	(18)
Min-Max (n)	45.32 73.12		38.37 55.87		17.69 45.07	
NL	**7.40 ± 1.20**	(23)	**7.17 ± 1.47**	(27)	**3.65 ± 1.26**	(21)
Min-Max (n)	5.41 9.78		3.43 9.38		0.89 5.47	
NW	**3.28 ± 1.06**	(24)	**2.79 ± 1.09**	(27)	**2.28 ± 0.97**	(21)
Min-Max (n)	1.50 5.52		0.79 4.76		0.41 3.68	
V1L	**28.78 ± 3.93**	(22)	**24.31 ± 1.97**	(26)	**14.98 ± 2.72**	(20)
Min-Max (n)	19.60 37.46		19.11 27.14		8.47 18.67	
V2L	**25.06 ± 4.47**	(24)	**19.71 ± 2.07**	(25)	**12.40 ± 2.25**	(20)
Min-Max (n)	15.16 31.46		14.03 23.45		6.77 15.81	
V3L	**26.21 ± 4.12**	(24)	**20.10 ± 1.82**	(26)	**12.71 ± 2.39**	(19)
Min-Max (n)	16.70 33.14		14.79 23.96		7.04 17.20	
V4L	**27.42 ± 3.93**	(25)	**22.40 ± 2.50**	(26)	**12.90 ± 2.56**	(20)
Min-Max (n)	20.41 34.62		16.57 26.19		7.20 16.58	
V5L	**28.60 ± 2.76**	(23)	**25.95 ± 3.14**	(26)	**13.31 ± 3.31**	(19)
Min-Max (n)	22.93 33.89		17.89 30.08		8.07 19.54	

Appendix P continued

	Females		Males		Juveniles	
CR1L	**39.59 ± 4.53**	(24)	**32.73 ± 3.16**	(26)	**20.66 ± 4.06**	(21)
Min-Max (n)	31.87 48.43		25.43 38.03		11.67 26.66	
CR2L	**25.57 ± 3.44**	(24)	**19.61 ± 2.01**	(26)	**13.37 ± 2.19**	(21)
Min-Max (n)	17.94 31.13		15.39 24.05		8.40 16.46	
CR3L	**27.42 ± 4.18**	(22)	**21.00 ± 1.88**	(27)	**13.43 ± 2.44**	(21)
Min-Max (n)	19.26 36.63		16.67 24.35		8.09 17.09	
CR4L	**26.71 ± 4.32**	(22)	**22.39 ± 2.60**	(26)	**12.28 ± 2.61**	(21)
Min-Max (n)	19.33 36.14		15.96 25.58		7.10 16.72	
CR5L*	**25.90 ±**	(1)	**±**	0	**12.79 ±**	(1)
Min-Max (n)					12.79 12.79	
V3W	**39.85 ± 6.23**	(24)	**30.50 ± 3.42**	(26)	**19.02 ± 3.58**	(21)
Min-Max (n)	26.54 50.05		20.78 36.02		10.76 24.28	
CR3W	**39.82 ± 4.53**	(24)	**31.95 ± 2.69**	(25)	**20.62 ± 4.33**	(21)
Min-Max (n)	32.05 47.99		24.83 36.19		11.45 26.77	
MR6W	**29.94 ± 4.38**	(24)	**22.72 ± 2.39**	(26)	**13.69 ± 3.53**	(19)
Min-Max (n)	20.72 38.74		16.49 27.60		6.93 19.96	
MR6L	**16.80 ± 2.60**	(24)	**12.82 ± 1.39**	(27)	**9.13 ± 1.89**	(19)
Min-Max (n)	11.47 21.81		10.28 15.49		5.65 12.38	
S(P)	**20.96 ± 3.05**	(23)	**17.34 ± 2.19**	(28)	**9.96 ± 3.03**	(19)
Min-Max (n)	13.45 25.86		12.48 22.29		5.70 14.38	
S(D)	**36.03 ± 4.37**	(23)	**34.44 ± 3.86**	(27)	**17.95 ± 5.00**	(18)
Min-Max (n)	26.34 42.90		23.39 39.87		9.45 27.16	
GW	**21.31 ± 1.80**	(23)	**19.53 ± 1.92**	(25)	**13.40 ± 2.38**	(19)
Min-Max (n)	17.54 24.17		15.87 22.36		8.29 16.62	
G	**16.85 ± 1.65**	(22)	**13.34 ± 2.18**	(25)	**7.90 ± 2.34**	(20)
Min-Max (n)	13.12 20.17		9.47 16.87		3.33 12.48	
H	**18.03 ± 2.55**	(23)	**14.79 ± 2.12**	(24)	**8.85 ± 2.31**	(20)
Min-Max (n)	13.09 23.32		10.50 18.93		4.77 13.30	
P	**8.58 ± 1.96**	(25)	**6.29 ± 1.46**	(24)	**5.12 ± 1.29**	(21)
Min-Max (n)	2.84 11.27		3.32 9.87		2.11 7.10	
Ab	**39.75 ± 5.34**	(24)	**31.12 ± 3.40**	(25)	**19.10 ± 5.08**	(19)
Min-Max (n)	29.88 53.11		23.74 36.79		9.15 26.44	
F	**12.62 ± 2.03**	(23)	**11.19 ± 1.68**	(27)	**6.95 ± 1.69**	(20)
Min-Max (n)	7.57 16.17		8.36 14.33		3.68 9.04	
An	**11.13 ± 2.22**	(23)	**8.79 ± 1.19**	(26)	**5.31 ± 1.72**	(19)
Min-Max (n)	6.27 15.78		6.19 11.13		2.19 8.91	
AW	**26.62 ± 3.25**	(24)	**27.68 ± 3.67**	(26)	**13.54 ± 3.50**	(19)
Min-Max (n)	17.20 33.13		17.65 33.36		7.79 19.99	

Appendix P continued

	Females		Males		Juveniles	
AG	**14.46 ± 3.40**	(23)	**14.97 ± 2.23**	(26)	**7.29 ± 2.19**	(15)
Min-Max (n)	8.96 23.57		9.82 19.65		4.60 11.40	
FFRW	**11.84 ± 1.57**	(20)	**10.25 ± 1.03**	(17)	**6.04 ± 1.52**	(18)
Min-Max (n)	7.60 13.93		8.07 11.82		3.58 9.34	
FARL	**28.58 ± 3.39**	(20)	**25.80 ± 2.62**	(16)	**13.28 ± 4.07**	(18)
Min-Max (n)	21.55 35.88		19.62 29.05		6.95 23.20	
HFRW	**11.62 ± 1.96**	(18)	**9.51 ± 1.11**	(12)	**5.11 ± 1.37**	(12)
Min-Max (n)	7.43 14.70		7.27 11.07		3.07 8.00	
HLRL	**34.19 ± 5.17**	(18)	**27.64 ± 2.74**	(13)	**14.69 ± 4.62**	(11)
Min-Max (n)	23.04 43.09		22.43 32.14		7.45 22.90	
CS	**20.34 ± 2.17**	(22)	**17.99 ± 1.98**	(24)	**12.33 ± 2.64**	(17)
Min-Max (n)	17.27 24.29		14.93 22.09		8.00 16.74	
HW	**18.99 1.40**	(19)	**16.60 1.15**	(15)	**10.95 2.54**	(12)
Min-Max (n)	16.16 21.35		14.00 18.09		7.10 15.44	
DCL	**177.43 ± 21.09**	(23)	**149.92 ± 14.11**	(28)	**84.79 ± 18.59**	(17)
Min-Max (n)	132.00 213.00		107.50 172.00		45.00 114.00	
DCW	**165.91 ± 20.22**	(23)	**131.06 ± 10.62**	(27)	**85.06 ± 17.12**	(17)
Min-Max (n)	121.00 200.00		101.00 152.00		45.00 108.00	
BL	**60.11 ± 7.97**	(25)	**45.98 ± 3.03**	(28)	**32.23 ± 6.53**	(17)
Min-Max (n)	45.22 77.56		38.87 50.59		16.82 40.79	
BM	**467.18 ± 141.98**	(11)	**247.94 ± 41.36**	(17)	**54.45 ± 37.84**	(4)
Min-Max (n)	225.00 679.50		168.50 323.00		12.50 91.00	

Appendix Q A summary of the carapacial scute counts of live (South-western Cape) and wet and dry Iziko Museum specimens of *Psammobates geometricus* showing the number of each scute type with its occurrence (counts and percentages) amongst males, females, juveniles, and all cohorts combined.

Scute type	Number	Females Count	%	Males Count	%	Juveniles Count	%	Total Count	%
Nuchal	0	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	1	23	*95.8*	28	*100.0*	22	*100.0*	73	*98.6*
	2	1	*4.2*	0	*0.0*	0	*0.0*	1	*1.4*
Vertebrals	4	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	5	23	*100.0*	27	*96.4*	21	*95.5*	71	*97.3*
	6	0	*0.0*	1	*3.6*	1	*4.5*	2	*2.7*
	7	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
Costals-left	3	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	4	22	*91.7*	26	*96.3*	21	*95.5*	69	*94.5*
	5	2	*8.3*	1	*3.7*	1	*4.5*	4	*5.5*
	6	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
Costals-right	3	0	*0.0*	1	*3.6*	0	*0.0*	1	*1.4*
	4	21	*87.5*	27	*96.4*	21	*95.5*	69	*93.2*
	5	3	*12.5*	0	*0.0*	1	*4.5*	4	*5.4*
	6	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
Marginals-left	9	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	10	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	11	21	*87.5*	27	*100.0*	20	*95.2*	68	*94.4*
	12	3	*12.5*	0	*0.0*	1	*4.8*	4	*5.6*
Marginals-right	9	0	*0.0*	0	*0.0*	0	*0.0*	0	*0.0*
	10	1	*4.2*	1	*3.6*	1	*5.0*	3	*4.2*
	11	19	*79.2*	27	*96.4*	18	*90.0*	64	*88.9*
	12	4	*16.7*	0	*0.0*	1	*5.0*	5	*6.9*
Supracaudal	1	24	*100*	28	*100*	21	*100*	73	*100*

Appendix R Frequencies and percentages of the number of left and right marginal scutes per tortoise amongst males, females, juveniles and all *Psammobates geometricus* from live (South-western Cape) and wet and dry Iziko Museum specimens.

	12:12	%	11:11	%	11:10	%	11:12	%
Males	0	*0.0*	26	*96.3*	1	*3.7*	0	*0.0*
Females	3	*12.5*	19	*79.2*	1	*4.2*	1	*4.2*
Juveniles	1	*5.0*	18	*90.0*	1	*5.0*	0	*0.0*
Totals	**4**	*5.6*	**63**	*88.7*	**3**	*4.2*	**1**	*1.4*

Appendix S Frequencies and percentages of serrations on anterior (1-5) and posterior (6-11) marginal scutes per tortoise (both sides) for males, females, juveniles and all *Psammobates geometricus* from live (South-western Cape) wet and dry Iziko Museum specimens. 'Other' refers to two females, one with marginals 9-12 and one with marginals 10-12 serrated on both sides.

Serrated Marginals	Males Count	%	Females Count	%	Juveniles Count	%	Total Count	%
1-2	7	*29.2*	3	*13.6*	2	*11.1*	12	*18.8*
1-3	3	*12.5*	6	*27.3*	11	*61.1*	20	*31.3*
1-4	0	*0.0*	0	*0.0*	1	*5.6*	1	*1.6*
1-5	0	*0.0*	0	*0.0*	4	*22.2*	4	*6.3*
None	14	*58.3*	13	*59.1*	0	*0.0*	27	*42.2*
Total	**24**		**22**		**18**		**64**	
6-11	0	*0.0*	0	*0.0*	4	*20.0*	4	*6.2*
8-11	1	*4.0*	4	*20.0*	10	*50.0*	15	*23.1*
9-11	12	*48.0*	3	*15.0*	5	*25.0*	20	*30.8*
None	12	*48.0*	11	*55.0*	0	*0.0*	23	*35.4*
Other	0	*0.0*	2	*10.0*	1	*5.0*	3	*4.6*
Total	**25**		**20**		**20**		**65**	

Appendix T Frequencies and percentages of bridge ridge strength and the marginal scutes (M) contributing to the bridge ridge for male, female, juvenile and all *Psammobates geometricus* from live (South-western Cape) wet and dry Iziko Museum specimens. Details of the marginal scutes were not recorded for a male and a juvenile. Category 'Other' is one female with a bridge ridge of marginal scutes 4-9 and one male with marginal scutes 3-9.

Bridge Ridge	Males Count	%	Females Count	%	Juveniles Count	%	Total Count	%
Weak	17	60.7	19	79.2	17	89.5	53	74.6
Medium	11	39.3	4	16.7	1	5.3	16	22.5
Strong	0	0.0	0	0.0	1	5.3	1	1.4
None	0	0.0	1	4.2	0	0.0	1	1.4
Totals	28		24		19		71	
3-7	2	7.4	2	8.7	3	16.7	7	10.3
3-8	19	70.4	16	69.6	14	77.8	49	72.1
4-7	4	14.8	2	8.7	1	5.6	7	10.3
4-8	1	3.7	2	8.7	0	0.0	3	4.4
Other	1	3.7	1	4.3	0	0.0	2	2.9
Totals	27		23		18		68	

Appendix U Frequencies and percentages of dark pigment on the plastron of male, female, juvenile and all *Psammobates geometricus* from live (South-western Cape) wet and dry Iziko Museum specimens. Category (Cat.) 1 represents 0, 10 & 20% black pigment, whereas categories 2, 3 and 4 each represents two pigments increments, 30 & 40%, 50 & 60%, and 70 & 80%, respectively.

	Cat. 1	%	Cat. 2	%	Cat. 3	%	Cat. 4	%	Totals
Male plastron	0	0.0	6	26.1	13	56.5	4	17.4	23
Female plastron	0	0.0	4	17.4	8	34.8	11	47.8	23
Juvenile plastron	1	5.6	7	38.9	7	38.9	3	16.7	18
Total plastron	**1**	*1.6*	**17**	*26.6*	**28**	*43.8*	**18**	*28.1*	**64**

Appendix V   Frequencies (none, less than, greater than or equal to three) and percentages of anterior (A) and posterior (P) marginal scutes serrated among groups (female, male and juvenile) for *Psammobates oculifer* (PO) and *P. geometricus* (PG). Data was collected from live specimens of *P. oculifer* and *P. geometricus* and wet and dry specimens from Iziko and Transvaal (*P. oculifer only*) museums.

Spp	Sex	A/P	0	%	< 3	%	3	%	> 3	%
PO	F	A	1	0.9	5	4.3	108	92.3	3	2.6
PG	F	A	13	59.1	3	13.6	6	27.3	0	0.0
PO	M	A	2	1.3	0	0.0	135	90.6	12	8.1
PG	M	A	14	58.3	7	29.2	3	12.5	0	0.0
PO	J	A	0	0.0	0	0.0	25	75.8	8	24.2
PG	J	A	0	0.0	2	11.1	11	61.1	5	27.8
PO	F	P	0	0.0	5	4.1	90	74.4	26	21.5
PG	F	P	11	55.0	0	0.0	4	20.0	5	25.0
PO	M	P	0	0.0	0	0.0	109	72.2	42	27.8
PG	M	P	12	48.0	0	0.0	12	48.0	1	4.0
PO	J	P	0	0.0	0	0.0	16	48.5	17	51.5
PG	J	P	0	0.0	0	0.0	5	25.0	15	75.0

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