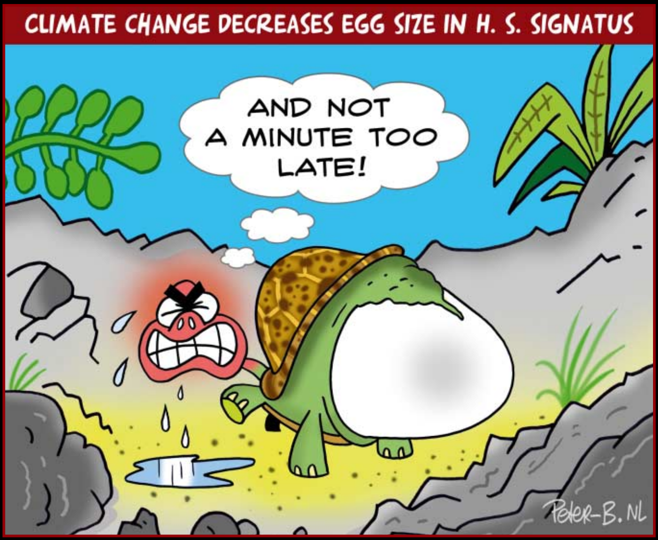
The ecology of the world's smallest tortoise, *Homopus signatus signatus*: effects of rainfall



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The ecology of the world's smallest tortoise, *Homopus signatus signatus:* effects of rainfall

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

March 2008

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Keywords

Aridification
Body condition
Growth
Herbivore
Morphology
Namaqualand
Reptile
Reproduction
Sexual dimorphism
Shrinking
Ticks

To my parents…

…who stimulated my interest in tortoises
by tolerating an ever-increasing collection of live animals

…who stimulated my interest in fieldwork
by enabling my first trip to South Africa

Abstract

Tortoises appear to be successful in arid ecosystems, where they depend on primary production for their predominantly herbivorous diets. The low primary production of arid regions is exacerbated by periodic droughts, so that iteroparous species such as chelonians require mechanisms to overcome resource shortages. The smallest of all tortoises, *Homopus signatus signatus*, occurs in a dry winter rainfall area in northwestern South Africa that is threatened with aridification due to regional climate change. *Homopus s. signatus* is listed in the South African Red Data Book and IUCN Red List of Threatened Species, yet its morphology and ecology, including traits that help cope with its dry environment, have been studied little. The conservation status of the taxon requires ecological data to take sound conservation measures. This study evaluates shell size, shape and colour pattern in a population of *H. s. signatus*, and reports responses of growth, tick infestations, body condition and reproduction to five years of rainfall variation.

The small body size of *H. s. signatus* probably translates to low resource demands, helping tortoises survive their low-productive environment. However, females were larger than males (absolute or scaled on carapace length) to accommodate clutches of single, relatively large eggs that are characteristic for this species. Egg size correlated to female size, and average egg size was similar in all years. Large eggs may be required to produce large hatchlings capable of surviving the harsh Succulent Karoo environment. To facilitate the production of large eggs at a small body size, female pelvic girdles allowed passage of eggs that were typically wider than the width of the pelvic canal. Furthermore, flexibility of the shell in a dorso-ventral plane enabled females to temporarily increase shell volume to accommodate eggs and follicles.

Annual rainfall and timing of rains seem to determine the primary production available to the tortoises. *Homopus s. signatus* accumulated resources when food was abundant (i.e., spring), contributing to high spring body conditions. In the dry season, tortoises probably reduced activity levels and opportunistically acquired resources to maintain relatively stable body conditions throughout the year. Opportunistic foraging may help females increase their body condition towards spring and, subsequently, produce large eggs or multiple clutches. Females may require more feeding time than do males, facilitated by the sexually different shell colour patterns.

In a drought year, tortoises had lower spring body conditions than in other years, yet some females produced eggs. Spreading reproductive investments may increase the chance that some offspring hatch when conditions are favourable (i.e., bet-hedging). However, allocations to reproduction during drought appear to occur at the expense of growth, which was often negative. Reproductive costs of males may also be considerable, perhaps as a result of courtship behaviour and male-male agonism, because male growth rates were lower than female growth rates (corrected for body size), and many males shrank during the drought. Shrinking in *H. s. signatus* seemed to be effected through flexibility of the shell, changing in shape and volume due to starvation, but may also include (reversible) bone resorption. Levels of tick infestations were negatively correlated with rainfall, and *H. s. signatus* males were particularly vulnerable due to the larger shell openings compared to females. Larger shell openings can facilitate locomotion and courtship behaviours, but tick infestations may counter these advantages by costs through loss of blood and tick-born diseases.

The projected aridification of the Succulent Karoo may increase the frequency of drought years. As a result, frequent low growth rates may increase the time for females to mature from 11–12 to 30 years. This would lead to smaller females (average and maximum sizes), with frequently low body conditions, producing smaller eggs and hatchlings. Furthermore, fewer females would reproduce in drought years so that fewer eggs and offspring would be produced. These results may partly be compensated by conservation measures (e.g., reducing mortality caused by road traffic) that increase survival of adult females and enhance reproduction over many years. However, since aridification may demand larger viable egg and hatchling sizes, the long-term survival of *H. s. signatus* requires drastic measures allowing populations to migrate to areas that will continue to receive sufficient rainfall in the future.

Declaration

I declare that *The ecology of the world's smallest tortoise, Homopus signatus signatus: effects of rainfall* 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.

Victor J.T. Loehr, March 2008

Acknowledgements

This study lasted from 2000 to 2008 and a large number of people have supported me. First of all, 15 field assistants helped me locate and measure tortoises in the field: P Abramsson (Sweden), M Blohm (Germany), T Harris-Smith (South Africa), C Hobson (U.S.A.), J Karlsson (Sweden), M Klerks (Netherlands), L Lagerström (Sweden), T Licitra (U.S.A.), F van Loon (Belgium), P van Putten (Netherlands), J Reyes (Mexico), I Schettler (Germany), F Schmidt (Germany), S Scholz (Germany), M van Tilborghs (Belgium), C Woodhead (U.S.A.). Without these volunteers (particularly M Klerks, F van Loon and F Schmidt who joined me more than once), I would not have been able to collect the extensive dataset on which this dissertation is based. Thanks to all!

The following organisations and private persons helped fund the project: Chelonian Research Foundation (Linnaeus Fund), National Research Foundation (South Africa), University of the Western Cape, Tortoise Trust, Dutch Foundation for the Advancement of Herpetology, Schildkrötenfreunde Österreich, Dutch Turtle and Tortoise Society, World Chelonian Trust, Basel Zoo, University of Colima, Seneca Park Zoo, M&W Blohm, J Bruekers, E Engin, C Hobson, G Hofstra, J Karlsson, M Klerks, T Licitra, K&C Loehr, F van Loon, B Sawey, I Schettler, J Schlömer, F Schmidt, S Scholz, R. Verhoeks, S&T Vinke, L&P Wolfs. I am indebted to all. In addition to the provision of financial support, several organisations donated or discounted research materials or software, for which I am grateful too: AnTech instruments, Barbour Threads, CamCode/ StatsDirect, Cellpack BV, Microscoop Service Rob Engelhard, Mulder-Hardenberg BV, Röbke Agenturen. Services were provided by Dr. van Niekerk hospital in Springbok (radiography – thank you Emelda Bezuidenhoudt) and Goegap Nature Reserve (storage of research materials).

During processing and interpreting my data, I was very grateful for information and (unpublished) data from the South African Weather Services and the following persons: G van Aardt, NR Bryson, KJ Field, H Heyne, IG Horak, C Schradin. I have also truly enjoyed the many visits and *braais* at Carsten Schradin's research station in Goegap Nature Reserve.

I consider myself extremely fortunate that my work was supervised by researchers the calibre of Retha Hofmeyr and Brian Henen. When I started the work, I had no idea that there was so much to learn! Sincerest thanks are extended to both. Also special thanks to my wife Dyana, who encouraged me to continue and finalise the dissertation, despite the fact that it meant that we did not have much time to spend together. It will be difficult to compensate this time loss in the future! In addition, I am grateful for her running the household during my long stays in South Africa.

This study was permitted by Northern Cape Nature Conservation (permit numbers 137/99, 019/2001, 152/2002, 168/2003, 158/2003, 633/2003) and the UWC Research Ethics Committee, and followed ASIH-SSAR-HL Guidelines for the use of live amphibians and reptiles in research.

My employer, the Ministry of Traffic, Public Works and Water Management (Netherlands), funded the printing of this dissertation.

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List of acronyms

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
BC	Body condition
BM	Body mass
CV	Coefficient of variation
EL	Egg length
EM	Egg mass
EV	Egg volume
EW	Egg width
F	Female
J	Juvenile
KW ANOVA	Kruskal-Wallis ANOVA
M	Male
PL	Plastron length
PW	Pelvic canal width
REV	Relative egg volume
RM ANOVA	Repeated measures ANOVA
SCL	Straight carapace length
SD	Standard deviation
SE	Standard error
SH	Shell height
SV	Shell volume
SW	Shell width

1 General introduction

1.1 Tortoises and their habitats

Chelonians are among the oldest vertebrates that exist today, having changed scarcely in their general appearance since they evolved during the Mesozoic era roughly 200 million years ago (Campbell 1990). Their morphology, characterised by the shell that is a composite of dermal bones and the endochondral axial skeleton (Kuchling 1999), apparently offers important evolutionary advantages that allowed chelonians to persist through substantial climatic and geologic changes over time. Ernst *et al.* (2000) currently recognise 288 species, but morphological and genetic evaluation may yet change this number (e.g., Branch 2007; Fritz & Havaš 2006). Species of chelonians can be found in saltwater, freshwater, and on land.

Among the chelonians, species in the family Testudinidae are typically referred to as tortoises (Kuchling 1999). All are terrestrial and the family currently includes 43 species, including one recently described *Homopus* species from Namibia (Branch 2007; Fritz & Havaš 2006). Extant Testudinidae inhabit most continents, except Australia and Antarctica (Ernst *et al.* 2000), and can be found in a wide variety of habitats (e.g., rainforest, savannah, steppe, desert), which emphasises further their evolutionary success. Features that all tortoises share, besides their *Bauplan*, are a life history of a long life-span, delayed maturity and iteroparous reproduction over several years or decades (Kuchling 1999). Additionally, tortoises are ectotherms and predominantly herbivores (Ernst *et al.* 2000). Both ectothermy and herbivory may facilitate success in arid habitats, because ectotherms have relatively low energy requirements (Louw & Seely 1982; Nagy 2001), and often the food source of herbivores is more abundant than that for higher trophic levels. However, arid-zone herbivores frequently face the challenge of low, and variable, quantities of nutrients obtainable from primary production, which is limited by low precipitation and droughts (Louw & Seely 1982).

1.2 Rainfall effects on tortoises

The morphology and ecology of tortoises have evolved through selection in current and past environments. The body size of tortoises differs over 1700-fold between the largest and smallest species (based on body mass, *Chelonoidis nigra* and *Homopus signatus*, respectively, Ebersbach 2001; Loehr 2002a). Because similar-sized species inhabit very different habitats (e.g., *Homopus areolatus*, *Psammobates oculifer* and *Homopus solus* live in Mediterranean, savannah and desert areas, respectively), size is likely the result of a complex interaction among phylogenetic, climatic, biotic and other variables. Adverse climatic conditions (e.g., dry and hot summers, cold winters) in the range of the steppe tortoise, *Testudo horsfieldii*, have probably contributed to its shell shape (i.e., dorso-ventrally flattened, rounded from a dorsal view, and small marginal scutes that do not extend laterally), which helps *T. horsfieldii* dig into the soil to find shelter (Bonnet *et al.* 2001). The small, flat and thin shell of the pancake tortoise, *Malacochersus tornieri*, helps individuals to retreat into narrow rock crevices, a prominent feature of the species' habitat (Moll & Klemens 1996). Besides environmental conditions, reproduction can also affect the development of tortoise shell sizes and shapes, leading to sexual differences. Female shells require sufficient space to accommodate eggs (Bonnet *et al.* 2001; Lambert *et al.* 1998), whereas male shells should accommodate locomotion (Bonnet *et al.* 2001), enable combating males to right themselves (Bonnet *et al.* 2001; Mann *et al.* 2006), and facilitate courtship behaviour (Willemsen & Hailey 2003).

Along with the size and shape of the shell, environmental conditions may affect how tortoise species allocate available resources. In arid and unpredictable regions in Africa, tortoises produce eggs that are large relative to their body size, perhaps because hatchlings may require a large body size to survive the harsh climate (Hofmeyr *et al.* 2005). However, within morphological and physiological constraints, tortoises may adjust to different resource availabilities. Like all chelonians, tortoises have indeterminate growth (Kuchling 1999) so adults may channel resources to growth, maintenance and reproduction when rainfall and primary production are high. During periods of resource shortages, reduced influx of water and nutrients may force individuals to trade off allocations. Desert tortoises (*Gopherus agassizii*) may exhibit extreme changes in nutrient flux by being opportunistic in the acquisition of resources, and by tolerating temporary surpluses and deficits in their energy, water and electrolyte balances (Henen 1997, 2002a; Nagy & Medica 1986; Peterson 1996a). This relaxation of homeostasis enables them to conserve nutrients, endure droughts and even allows females to produce eggs during drought years (Henen 1997). Nevertheless, *G. agassizii* females reduce reproductive effort in response to low rainfall and resource limitation (decreasing clutch frequency, Henen 1997; Turner *et al.* 1986), as do other tortoises: *Aldabrachelys gigantea* decreases clutch frequency, clutch size and egg size (Swingland & Coe 1978), *Chersina angulata* decreases clutch frequency (Hofmeyr 2004), and *Astrochelys radiata* decreases clutch size (Leuteritz & Ravolanaivo 2005). Furthermore, growth in desert tortoises appears to relate to rainfall and primary production (Berry 2002; Medica *et al.* 1975), but there are few evaluations of the relationship between resource availability and growth in tortoises. Despite the various physiological responses that may enhance survival, drought increases mortality in *G. agassizii* (Peterson 1994).

The potential to allocate resources depends on the quantity and quality of resources that an individual tortoise has acquired. A measure that reflects acquired resources is the body mass relatively to body size, or body condition (e.g., Jackson 1980). Body condition may correlate to rainfall and primary production (Hailey 2000), and may affect growth, survival (Shine *et al.* 2001) and reproduction (Henen 1997; Hofmeyr *et al.* 2005). Body condition may also be affected by ectoparasite infestations, because parasites use host resources. Besides direct infestations of tortoises by parasites such as fly larvae or ticks (McArthur 1996), some parasites act as vectors for secondary infestations of bacteria or viruses (Burridge *et al.* 2000a,b; Ergunay *et al.* 2007). The added resource sink that parasites represent may cause shifts in allocations and may affect host fitness when available resources for growth, maintenance and reproduction decrease, particularly when infestations coincide with low rainfall and food availability. Ultimately, infestations with parasites can affect population dynamics, as has been reported for *G. agassizii* infested with the bacterium *Mycoplasma* (Brown *et al.* 1994, 1999).

Mechanisms and trade-offs that tortoises use to survive periods of low rainfall and limited resources are not fully understood. Therefore, additional studies are required, especially for arid-region species that appear to tolerate drought conditions.

1.3 South African tortoises, and *Homopus signatus signatus* in particular

South Africa is a tortoise hotspot. Thirteen species occur within its borders, five of which are endemic (Ernst *et al.* 2000). Six South African taxa (*Homopus boulengeri*, *H. femoralis*, *H. signatus*, *Stigmochelys pardalis*, *Psammobates tentorius* and *P. oculifer*) inhabit arid regions with less than 500 mm of rain per year, although some species are not restricted to these arid regions (Branch 1998).

The genus of the padlopers, *Homopus*, contains five species of small tortoises (up to 168 mm straight carapace length; Boycott & Bourquin 2000), four of which are endemic to South Africa (Ernst *et al.* 2000). With the exception of the common padloper, *H. areolatus*, all *Homopus* are rock-dwelling and use crevices as retreats (Boycott & Bourquin 2000). The smallest in the genus is the speckled padloper, *H. signatus*, which reaches a maximum straight carapace length of only 110 mm, representing the smallest of all tortoises (Loehr 2004a). The speckled padloper occurs in the northwestern region of South Africa, its range stretching roughly from the Orange River south to Piketberg and from the Atlantic coast east to Calvinia (Baard 1994). The northern part of the range is inhabited by *H. s. signatus* (Namaqualand, southward towards the Olifants River), whereas *H. s. cafer* is found in the southern part (Fig. 1.1). Intergrades between the two subspecies are known as well (Boycott & Bourquin 2000; Morgan 1993). *Homopus s. signatus* is the subject of my dissertation.

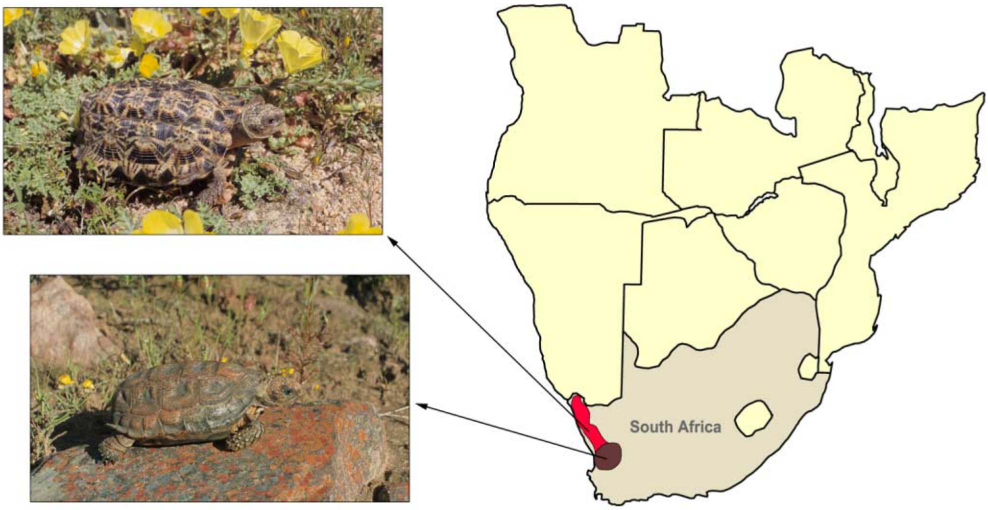

Figure 1.1 Distribution of *H. signatus* in South Africa after Branch (1998), with *H. s. signatus* (red) occurring in the north, and *H. s. cafer* (brown) in the south.

The habitat of *H. s. signatus*, the Succulent Karoo biome, is known for its high level of endemism. The Succulent Karoo was selected by Conservation International as one of the world's 34 Biodiversity Hotspots (Conservation International 2007). Rainfall is limited to 20—400 mm per year, and falls predominantly in winter, but most regions receive less than 150 mm per year (Cowling *et al.* 1999). In summer, low rainfall combined with high evapotranspiration contributes to the Succulent Karoo's arid nature. The distinct rainfall pattern supports vegetation characterised by leaf-succulents, and a diversity of annuals and geophytes emerging in spring (Milton *et al.* 1997). Consequently, primary production fluctuates strongly among seasons (Fig. 1.2), and annual plant production is related to the timing of the onset of winter rainfall and the occurrence of follow-up rains (Van Rooyen 1999).

While the Succulent Karoo is arid, climate models predict that the biome's rainfall will decrease further in the next decades as a result of regional climate change (Rutherford *et al.* 1999). Expected levels of rainfall will probably be unable to support vegetation in its current state, so this biome may undergo significant change (Rutherford *et al.* 1999). At this time, we lack sufficient information to understand how *H. s. signatus*, or other tortoise species, will respond to these climate and habitat changes.

1.4 Study rationale and research aims

Prior to this project, few studies on *H. signatus* had been conducted, and most publications deal with its morphology, taxonomy and distribution (Boulenger 1890; Bour 1988; Boycott 1986; Loveridge & Williams 1957). Although two studies (Bayoff 1995; Duerden 1907) attempted to link the shell colour patterns of South African tortoises, including *H. s. signatus*, to the habitats in which they occurred, there are no detailed analyses of morphology and colouration of *H. s. signatus* in light of environmental conditions and ecology. This is not surprising, because the ecology of *H. s. signatus* was virtually unknown, with only a single field study (Bayoff 1995) conducted previously. In that study, no active tortoises were found in summer (December and January), and all individuals encountered were hiding between rocks. This led Bayoff (1995) to believe that *H. s. signatus* aestivates in summer.

While we have limited knowledge on the ecology of *H. s. signatus*, the projected aridification of the Succulent Karoo requires ecological data urgently to facilitate conservation efforts. Currently, *H. s. signatus* is listed in the South African Red Data Book (Near Threatened, Branch 1988) and on species level in the IUCN Red List of Threatened Species (Lower Risk/near threatened, IUCN 2006). Since *H. s. signatus* inhabits an arid environment, this study will expand ecological understanding of this and other arid-region tortoises. Variation in rainfall and other resources may cause tortoises to shift resource allocations, so studies on the physiological and reproductive ecology are especially useful, including the potential effects of parasites. Understanding how tortoises cope with their arid environment may also help explain the morphology of *H. s. signatus*.

Figure 1.2 Contrasting vegetation conditions of the *H. s. signatus* study site in the wet season (above; September 2001) and the dry season (below; January 2004).

The overall aim of this study is to understand the ecology of *H. s. signatus*, particularly in reference to the importance of rainfall. This information can be used to enhance conservation efforts and would broaden understanding of reptile ecology in arid regions. This aim will be achieved through the following objectives:

1. Evaluating the shell size, shape and colour patterns of *H. s. signatus*, and interpreting the morphology in context of the species' ecology
2. Quantifying growth rates, body condition and reproductive output, and evaluating how variation in rainfall affects these parameters
3. Determining the level of tick infestations, and interpreting infestations in context of the tortoises' morphology and ecology
4. Formulating concrete recommendations to help conserve the species

In order to reach my research objectives, I conducted fieldwork on a natural population of *H. s. signatus* near Springbok, from 2000 to 2004. In all years, tortoise morphology, tick infestations, annual growth, body condition, and female reproduction were recorded in spring. In addition, body condition was monitored in all seasons from spring 2003 to 2004. The study period had considerable variation in annual rainfall (i.e., years with below- and above-average rainfall) and in rainfall timing.

1.5 Thesis organisation

Following this general introduction (Chapter 1), there are five research chapters, and one synthesis chapter. In Chapter 2, I describe the size, shape and colour pattern of *H. s. signatus* shells, and discuss the shell's function and evolutionary significance. Chapter 3 evaluates changes in shell size among years, and reports the frequent occurrence of negative growth or shrinking during drought. After this chapter, Chapter 4 describes how tick infestations differed among years (probably linked to rainfall) and groups (i.e., males, females and juveniles), and how infestations related to tortoise shell morphology. Chapter 5 demonstrates how the body condition of *H. s. signatus* related to rainfall, and evaluates the efficacy of two body condition indices for this species. Chapter 6 evaluates egg characteristics and reproductive strategies of *H. s. signatus* females over five years. Combining the results from all research chapters, Chapter 7 presents a new synthesis of *H. s. signatus* ecology and presents recommendations for the conservation of the taxon. Finally, Appendix 1 indicates all publications produced in this field study of *H. s. signatus*, including the ones on which this dissertation is based.

2 Shell characteristics and sexual dimorphism

A revised version of this chapter was published in African Journal of Herpetology.

Loehr, V.J.T., Henen, B.T. & Hofmeyr, M.D. 2006. Shell characteristics and sexual dimorphism in the Namaqualand speckled padloper, *Homopus signatus signatus*. African Journal of Herpetology 55: 1-11.

2.1 Abstract

There is little quantitative information regarding the two subspecies of the world's smallest tortoise, *Homopus signatus*. To help characterize the northern subspecies *H. s. signatus* and evaluate the development of shell size and colour patterns, I measured shell characteristics of wild juvenile, male and female *H. s. signatus*. When scaling shell dimensions on carapace length, male shell size represented an extension of juvenile shell size for shell height, width and volume, but not plastron length. The slope of plastron length scaled on carapace length was smaller for males than for juveniles or females, suggesting differential growth of the plastron. The smaller male plastron translates to large shell openings, perhaps to improve locomotion and to facilitate tail movement during copulation. Conversely, the slope of female shell height, width and volume (scaled) was larger than for juveniles or males, presumably providing more space to accommodate follicles and the large egg. Serration of the marginal scutes and shell colour changed with body size, and shell colour pattern differed between sexes. The carapace was darker at intermediate body sizes (large juveniles and small adults); the increase in dark appearance resulted primarily from widening of the dark pigment band around scute margins as growth laminae were added. Both the lighter shell colour and reduced serration of large adults may be due to shell wear; large adults may produce less dark pigment, and older laminae disappear due to flaking or peeling. Females had a darker overall colour, more rays and fewer speckles than did males. This dimorphism may relate to thermoregulation, gamete protection or intraspecific communication. Both male and female patterns may confer crypsis if the sexes use microhabitats differently.

2.2 Introduction

The Namaqualand speckled padloper, *Homopus signatus*, is the world's smallest tortoise (Loehr 2004a). It is endemic to southern Africa's west coast region (Boycott & Bourquin 2000; Branch 1998) and is associated with rocky habitat. Two subspecies are recognized, namely the northern subspecies *H. s. signatus* which occurs from the Orange River southward to Bitterfontein, and the southern subspecies *H. s. cafer* which occurs south from Klawer to Piketberg (Fig. 1.1, Boycott & Bourquin 2000).

Boycott (1986) described several morphological differences between the two subspecies. The two main distinguishing characteristics of *H. s. signatus* are serrated marginal scutes and a pronounced sulcate carapace (i.e., deep narrow grooves between the scutes) with sunken areolae (Boycott 1986). The carapace of *H. s. signatus* has an overall dark appearance and a light-brown background colour. The carapace has large, dark speckles, and sometimes rays of background colour. In contrast, the carapace background of *H. s. cafer* is orange-red or salmon-pink, with a pattern of finer dark stipples and short, thin black rays (Boycott 1986; Boycott & Bourquin 2000). Shell characteristics of *H. signatus* vary considerably, even within a single population (this study). A thorough analysis is needed to better understand the variation within subspecies and between subspecies and intergrade populations. In addition, detailed analyses may help to understand the ecological significance of shell characteristics.

Besides differences between the subspecies, there is sexual dimorphism in *H. signatus*. Males tend to be smaller than females, and have a concave plastron and large tail relative to that of females (Boycott & Bourquin 2000). Sexual dimorphism in chelonians covers a wide range of traits such as shell size, shape and openings, limb length, coloration, and head size (Ernst *et al.* 2000; Lagarde *et al.* 2001; Lambert *et al.* 1998; McRae *et al.* 1981; Tucker *et al.* 1995; Willemsen & Hailey 2003). Given the great variety of sexual dimorphism in other chelonians, we may expect additional differences between male and female *H. signatus*.

To help understand the morphology and sexual dimorphism of *H. signatus*, I examined shell dimensions, shape, and pattern within a natural population of *H. s. signatus*. Additionally, by studying males, females and juveniles, I assessed how morphology changes between juvenile and adult stages. I interpreted my results within the context of male and female behavioural and reproductive requirements, and relative to the ecological demands on the species.

2.3 Materials and methods

A population of *H. s. signatus* near Springbok (South African Coordinate System: Grid Cell 2917DB), South Africa, was monitored for 5 to 6 weeks in spring (August to October) every year from 2000 to 2004. Tortoises were located through methodical searches of the 3.6 ha study area (Loehr 2002a). I distinguished males from females by the large tail and concave plastron of males. Tortoises that were too small to confidently determine the sex were recorded as juveniles. Individuals were marked with unique combinations of black nail polish dots on the carapace (2000 to 2002), and from 2003 by notching marginal scutes (Cagle 1939).

2.3.1 Shell dimensions and shape

I used electronic callipers to measure, to the nearest 0.01 mm, straight carapace length (SCL, midline distance at the nuchal and supracaudal scutes), shell width (SW, where the shell was widest), shell height (SH, where the shell was highest), and plastron length (PL, midline distance at the gular and anal scutes). Shell volume (SV, cm^3) was estimated using a modified formula for an ellipsoid: $SV = \pi * SCL * SH * SW / 6000$ (Loehr *et al.* 2004) and mass was measured (± 0.1 g) with a digital balance.

2.3.2 Shell pattern and serration

Tortoises were photographed dorsally and ventrally using a Nikon Coolpix 880 digital camera. After all fieldwork was completed, I evaluated the digital images on a XGA computer screen. Photographs were evaluated for an individual's first capture, and were evaluated in a chronological sequence to avoid potential bias (e.g., this evaluation took several days, and bias could occur if groups or size classes were evaluated on different days). Photographs for tortoises captured in more than one year were compared for colour change. Boycott (1986) described sulcation of the *H. s. signatus* carapace, but I could not measure sulcation from the digital images. I used digital images to qualitatively evaluate shell colour and serration according to the following ten parameters:

1. Carapace colour (dark, light)
   This evaluation was based on an overall impression of whether the carapace appeared dark or light (Fig. 2.1a or 2.1b, respectively)
2. Carapace background colour (pale yellow, orange yellow, brown yellow)
   The colour underlying the black pigmentation was assessed from an overall impression of the costal and vertebral scutes (Figs. 2.1a to 2.1d).
3. Scute band (present, absent)
   The costal and vertebral scutes often had pigments that formed a dark band at the margins (Fig. 2.1a). For some animals, however, these margins had little dark pigment, so there was no dark band (Fig. 2.1b).
4. Scute rays (many, few, none)
   Using an overall impression of the costal and vertebral scutes, tortoise scute rays were scored as many (Fig. 2.1c), few (Fig. 2.1a) or none.
5. Speckle frequency (many, few, none)
   Using a visual impression of the carapace, speckle number was scored as many (Fig. 2.1d), few (Fig. 2.1a) or none.
6. Speckle size (large, small)
   Small, usually rounded, dots on the carapace were considered small (Fig. 2.1c), whereas larger blotches were recorded as large speckles (Fig. 2.1a).
7. Anterior serration (strong, weak)
   The first three marginal scutes, left and right sides, were considered strongly serrated if they had sharply pointed tips and serrations were deep relative to the size of the marginal scutes (Fig. 2.1a). I considered rounded scutes with shallow serrations as weakly serrated (Fig. 2.1b).
8. Posterior serration (strong, weak)
   I considered the last four marginal scutes (left and right) as strongly serrated if they had sharply pointed tips and serrations were deep relative to the size of the marginal scutes (Fig. 2.1a). Rounded scutes with shallow serrations were scored weakly serrated (Fig. 2.1b).

9. Plastron background colour (pale yellow, orange yellow, brown yellow)
   The colour underlying the black pigmentation was assessed from an overall visual impression of the plastron.
10. Plastron pigmentation (0–25, 25–50, 50–75, 75–100%)
   This was the percentage of the plastron surface area that was dark-brown or black.

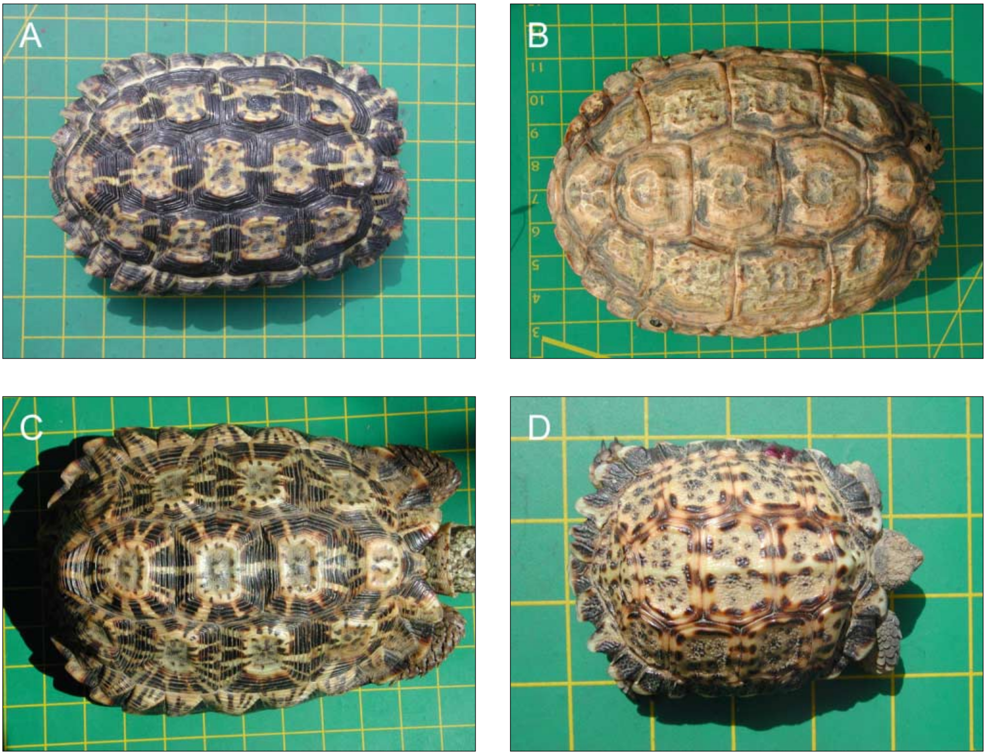

Figure 2.1 Tortoises indicative of carapace colour (a – dark, b – light), dark band on scute (a – present, b – absent), scute rays (a – few, b – none, c – many), speckle frequency (a – few, d – many), speckle size (a – large, c – small), and serration (a – strong, b – weak).

2.3.3 Statistical analysis

I summarized shell morphometrics and body mass as means and standard deviations. Some values were not parametric, so I used Kruskal-Wallis ANOVA, followed by Dunn's post hoc tests, to compare values among groups (males, females and juveniles). Shell dimensions were correlated to body size (SCL; data parametric when log-log transformed), so I used analysis of covariance (ANCOVA) to compare SH, SW, SV and PL among groups. In ANCOVA, if slopes were similar among groups, I tested for differences in elevation (*t*-tests; Zar 1999). However, if slopes differed among groups, I used Zerbe tests (Zerbe *et al.* 1982) to calculate the regions of SCL where the dependent variable differed between regressions.

I used χ^2 procedures to evaluate the frequencies of shell colour and serration. I used simple χ^2 tests (Zar 1999) to assess whether frequencies of parameters were homogeneous among categories (e.g., 50:50 for a dark or light carapace), and contingency table analyses to test for differences among the three groups (i.e., do the dark:light frequencies differ among the groups). Yates' corrections were applied when degrees of freedom equalled one. For each group, I used contingency table analyses to test for differences in frequencies among 10 mm size classes (e.g., 30 to 39.9 mm, 40 to 49.9 mm, and 50 to 59.9 mm SCL for dark:light frequencies in juveniles). All χ^2 tests were completed with average expected frequencies >5 (Zar 1999). The minimum criterion failed for the size class analysis of plastron pigmentation, so a rank of 1 to 4 was assigned to the pigmentation categories (0–25, 25–50, 50–75, and 75–100%). These ranks were evaluated with Kruskal-Wallis ANOVA. I used SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.) for Kruskal-Wallis and Dunn's tests, Microsoft Excel for contingency table analysis and ANCOVA (Zar 1999), and all statistical tests were considered significant if $P < 0.05$.

2.4 Results

2.4.1 Shell dimensions and shape

Males, females and juveniles differed in SCL, SH, SW, SV, PL and body mass (Table 2.1), and SH, SW, SV, PL and body mass correlated positively with SCL (all $t \geq 15.74$, df ≥ 50, $P < 0.001$). For SH (Fig. 2.2a), SW, SV and body mass, the slopes were steeper for females than for males and juveniles, although these slopes did not differ between males and juveniles. For PL, the males' slope was significantly lower than that of females and juveniles, whose slopes did not differ from one another (Fig. 2.2b). When slopes were similar between two groups, the elevations were also similar (Table 2.1).

There was consistency in the SCL (ca. 60 to 64 mm) at which male and female shell size and body mass diverged. The exception was shell width, where males and females did not differ until SCL = 70.4 mm (Table 2.1). The Zerbe regions included less than three data points of overlap between juvenile and either males or females, so I excluded the Zerbe comparisons with juveniles.

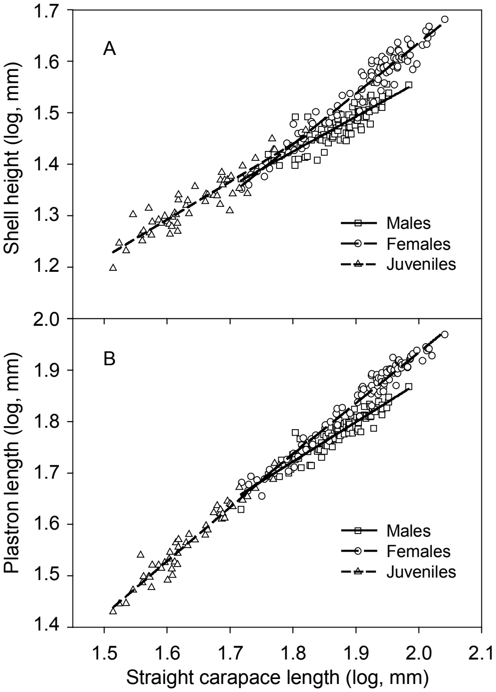

Figure 2.2 Relationships of shell height (SH, a) and plastron length (PL, b) to carapace length (SCL, log-log) of male, female and juvenile *H. s. signatus*.

Table 2.1 Mean (± SD) straight carapace length (SCL, mm), shell height (SH, mm), shell width (SW, mm), plastron length (PL, mm), shell volume (SV, cm^3), and mass (g), in a population of *H. s. signatus*. All measures differed among groups (Kruskal-Wallis ANOVA: all $H_2 > 129$ and $P < 0.001$) and all pairwise differences were significant (Dunn's tests, $P < 0.05$). Regression statistics (slope, intercept and coefficient of determination) are indicated for log-log relationships between all measures and SCL. For regressions against SCL, group had an effect on slopes (ANCOVA results for "Slopes" column: all $F > 10.0$, df1 = 2, df2 > 228, $P < 0.001$; Tukey's tests were used for pairwise post hoc analyses). When slopes were similar in post hoc analyses, regression elevations were also similar (ANCOVA: all $P > 0.1$). The column "Regions" indicates at what SCL female values were significantly higher than male values (Zerbe test: $P < 0.05$).

	Males	Females	Juveniles	Slopes	Regions
SCL	75.1 ± 8.28	81.9 ± 14.31	44.4 ± 7.02	–	–
Range (*N*)	52.2–96.4 (95)	52.3–110.0 (94)	32.7–60.0 (52)		
SH	29.9 ± 2.65	35.5 ± 6.31	21.2 ± 2.66	F > J ~ M	SCL > 62.4
Range (*N*)	23.5–36.2 (95)	22.5–48.0 (94)	15.8–28.2 (52)		
Regression	0.679, 0.202, 0.75	0.986, -0.337, 0.95	0.721, 0.139, 0.83		
SW	55.3 ± 5.10	61.3 ± 10.00	37.1 ± 4.53	F > J ~ M	SCL > 70.4
Range (*N*)	41.2–69.3 (95)	40.9–81.4 (94)	29.8–46.4 (52)		
Regression	0.757, 0.324, 0.84	0.894, 0.076, 0.95	0.756, 0.325, 0.95		
PL	60.2 ± 5.48	70.6 ± 12.36	37.9 ± 6.40	F ~ J > M	SCL > 60.6
Range (*N*)	42.6–73.8 (94)	45.2–93.1 (94)	26.9–52.3 (52)		
Regression	0.769, 0.338, 0.87	0.990, -0.046, 0.97	1.050, -0.152, 0.95		
SV	66.7 ± 18.47	101.1 ± 45.69	19.2 ± 7.87	F > J ~ M	SCL > 63.8
Range (*N*)	26.5–125.2 (95)	26.3–225.0 (94)	8.1–39.4 (52)		
Regression	2.44, -2.76, 0.94	2.88, -3.54, 0.99	2.48, -2.82, 0.98		
Mass	70.4 ± 19.14	109.7 ± 49.74	19.0 ± 7.53	F > J ~ M	SCL > 63.0
Range (*N*)	35.7–124.5 (90)	27.3–240.9 (94)	7.4–38.6 (51)		
Regression	2.44, -2.74, 0.91	2.89, -3.53, 0.98	2.43, -2.74, 0.96		

2.4.2 Shell pattern and serration

Most specimens had a dark band on the costal and vertebral scutes, many or few speckles on the carapace, and strongly serrated anterior and posterior marginal scutes (Table 2.2). The background colour of the plastron was most often pale yellow, with 25–50% dark pigmentation. The remaining characteristics were distributed evenly in the population. Within groups, the juvenile frequencies showed the most deviations from even distributions (Table 2.2), particularly towards dark carapaces with pale yellow background, few rays, few or many speckles, and strong serration. Juvenile plastrons were also pale yellow and had relatively little dark pigment. Most females had rays and pale yellow or brown yellow plastrons. Males also had pale yellow or brown plastrons, plus many speckles and strong serration of posterior marginal scutes (Table 2.2).

Table 2.2 Relative frequency (%) of shell characters in male, female and juvenile *H. s. signatus*. Frequencies within a group, and for all tortoises, that differed from a homogeneous distribution are noted with asterisks (*, ** or *** when $P < 0.05$, 0.01 or 0.001, respectively; simple χ^2 tests). Frequencies sharing a g superscript did not differ among groups (contingency table analysis) and frequencies with an s superscript had a significant size effect within that group ($P < 0.05$; contingency analysis for all characters except for plastron pigmentation, where I used Kruskal-Wallis ANOVA). Sample size refers to all characters except speckle size, where $N = 207$, 88, 69 and 50 for All, Males, Females and Juveniles, respectively.

Shell characteristics	All *N = 242*	Males *N = 98*	Females *N = 93*	Juveniles *N = 51*
Carapace				
Carapace colour				
Dark	55.37	43.88^{s}	62.37*^{g}	64.71*^{gs}
Light	44.63	56.12	37.63	35.29
Background colour				
Pale yellow	40.91*	34.69^{g}	30.11^{gs}	72.55***
Orange yellow	27.69	23.47	36.56	19.61
Brown Yellow	31.40	41.84	33.33	7.84
Scute band				
Present	66.53***	69.39***^{gs}	64.52**^{gs}	64.71*^{g}
Absent	33.47	30.61	35.48	35.29
Scute rays				
Many	35.12	32.65^{g}	47.31***	17.65*^{g}
Few	33.47	26.53	38.71	37.25
None	31.40	40.82	13.98	45.10
Speckle frequency				
Many	47.52***	51.02***^{g}	44.09^{s}	47.06***^{g}
Few	38.02	38.78	30.11	50.98
None	14.46	10.20	25.81	1.96
Speckle size				
Large	55.07	54.55^{g}	47.83^{gs}	66.00*^{gs}
Small	44.93	45.45	52.17	34.00
Anterior serration				
Strong	61.57***	58.16^{gs}	53.76^{gs}	82.35***^{s}
Weak	38.43	41.84	46.24	17.65
Posterior Serration				
Strong	64.05***	63.27**^{gs}	48.39^{gs}	94.12***
Weak	35.95	36.73	51.61	5.88

Table continues on next page

Shell characteristics	All *N = 242*	Males *N = 98*	Females *N = 93*	Juveniles *N = 51*
Table 2.2 continued from previous page				
Plastron				
Background colour				
Pale yellow	54.13***	41.84***^{g}	49.46***^{g}	86.27***
Orange yellow	7.85	8.16	9.68	3.92
Brown yellow	38.02	50.00	40.86	9.80
Pigmentation				
0–25%	26.45***	21.43^{g}	33.33^{gs}	23.53***^{g}
25–50%	35.12	31.63	30.11	50.98
50–75%	22.73	27.55	21.51	15.69
75–100%	15.70	19.39	15.05	9.80

Numerous group differences were recorded (Table 2.2). Carapacial colour was lighter in males than in females and juveniles, and the background colour of the juvenile carapace and plastron was pale yellow more often than in males and females. Compared to males and juveniles, females more frequently had rays on the carapace, but more often lacked speckles. The marginal scutes of juveniles showed strong serration more frequently than did those of adults.

Shell characteristics also changed with size (i.e., SCL). Overall, carapace colour showed opposite trends in juveniles (darkness increasing with size; $\chi^2 = 9.27$, df = 2, $P = 0.0097$) and males (darkness decreasing with size; $\chi^2 = 10.61$, df = 4, $P = 0.031$), and no size-related trend in females (Fig. 2.3). The background colour of the carapace changed from pale yellow in small females to orange and brown yellow in large females ($\chi^2 = 22.40$, df = 5, $P = 0.013$). Most juveniles had dark banding of the carapacial scutes (Fig. 2.4), but this banding decreased in frequency among larger males and females (for both, $\chi^2 \geq 14.62$, df ≥ 4, $P \leq 0.0055$). Although the frequency of speckles showed significant variation in females ($\chi^2 \geq 11.55$, df = 5, $P \leq 0.042$), there was no trend. The frequency of large speckles increased with body size for juveniles ($\chi^2 = 6.60$, df = 2, $P = 0.037$), and decreased with body size for

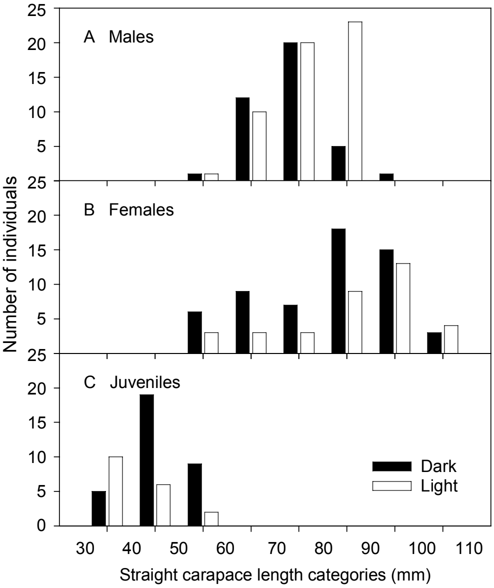

Figure 2.3 Size-class distribution of overall carapace colour (dark or light) for male (*N* = 93), female (*N* = 93), and juvenile (*N* = 51) *H. s. signatus* (a to c, respectively).

females (χ^2 = 15.08, df = 5, P = 0.010). The degree of serration of the anterior marginal scutes increased with increasing size of juveniles (Fig. 2.5; χ^2 = 8.06, P = 0.018). However, the anterior serration decreased as male and female size increased (Fig. 2.5; both $\chi^2 \geq 11.10$, df ≥ 4, $P \leq 0.049$). This adult pattern was consistent with changes observed in the serration of the posterior marginals (both $\chi^2 \geq 15.91$, df ≥ 4, $P \leq 0.0071$).

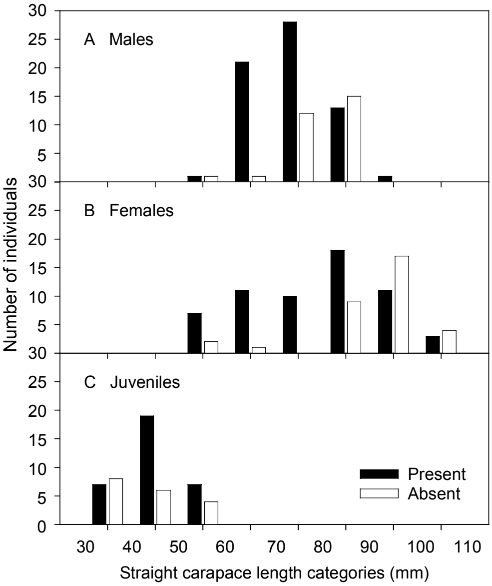

Figure 2.4 Size-class distribution of scute bands (present or absent) for male (N = 93), female (N = 93), and juvenile (N = 51) *H. s. signatus* (a to c, respectively).

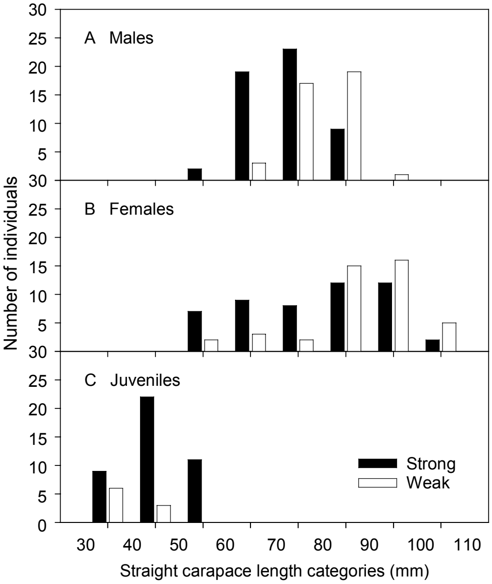

Figure 2.5 Size-class distribution of serration (strong or weak) for anterior marginal scutes of male (N = 93), female (N = 93), and juvenile (N = 51) *H. s. signatus* (a to c, respectively).

Forty-nine individuals were captured in three or more of the five field seasons and qualitative comparisons showed very few changes in their carapace patterns among years. However, three recaptured juveniles (SCL 40.1 to 41.4 mm) with large speckles showed drastic changes. From one year to the next, speckles on the areolae fused to form large black blotches, making it impossible to recognize the specimens from their carapace pattern. A smaller specimen (SCL 39.9 mm) showed less drastic changes, with a few speckles fading over time.

2.5 Discussion

2.5.1 Sexual dimorphism: shell shape

Sexual dimorphism in *H. s. signatus* is not restricted to a small SCL, concave plastron, and large tail in males compared to females. The shape of the shell showed differences too. The female shell showed the most deviations from the juvenile shape, with females developing a bigger shell (height, width, length and volume) in comparison to males and juveniles. In tortoises, sexual dimorphism results from the selection of traits that increase the reproductive fitness of males (e.g., enhanced mate-finding, copulation, and male-male combat abilities), or females (e.g., accommodating clutches) (Bonnet *et al.* 2001; Dodd 1997; Willemsen & Hailey 2003). *Homopus s. signatus* females produce large eggs relative to their body size, and large females produce larger eggs and possibly more clutches than do small females (Hofmeyr *et al.* 2005; Loehr *et al.* 2004). The shell dimensions of *H. s. signatus* females may reflect selection pressure on females to accommodate a large egg and follicles for subsequent clutches. Additionally, the sexes differed more in shell height than shell width (Table 2.1), emphasising that males can grow wide to increase size, and perhaps stability, while female shells also grow higher, potentially limiting their use of smaller crevices. The shell shape of males and females differentiated at SCL (60 to 70 mm) smaller than the minimum size for egg production in this population (SCL 84.1 mm; Loehr *et al.* 2004). The reproductive demands on female shell volume probably require early differentiation for a female shell to accommodate the large eggs and vitellogenic follicles at maturity. Early differentiation may also help females pass the large egg through the pelvic opening (Hofmeyr *et al.* 2005).

For many *H. s. signatus* shell traits, the male shell represents an extension of the juvenile condition. However, the male plastron does not continue to grow as rapidly as the juvenile or female plastron grows, relative to SCL. The relatively small plastron of males results in relatively large shell openings, a pattern also shown in *Testudo hermanni*, *T. horsfieldii*, *T. graeca*, and *T. marginata* (Bonnet *et al.* 2001; Willemsen & Hailey 2003). The large shell openings may help males during copulation, by accommodating the large tail and the hind limbs, and during locomotion (i.e., greater limb protraction and retraction; see Bonnet *et al.* 2001). Although the distinguishing characters in males may be detected at SCL of about 52 mm, plastron length began to differentiate between males and females at SCL of 60 mm. It is not known at what size range male *H. s. signatus* mature.

2.5.2 Sexual dimorphism: shell pattern

The carapace pattern of *H. s. signatus* has been described as black splashes on a light-brown or ivory background, sometimes forming a rayed pattern (Boycott 1986; Boycott & Bourquin 2000). My results confirm this characterisation, and add considerable detail regarding sexual dimorphism in the shell pattern.

Few studies have addressed sexual dichromatism in chelonians. The head and possibly limbs of male *Homopus areolatus*, *Callagur borneoensis*, *Batagur baska*, and *Kachuga* spp. change colour during the mating season (Ernst *et al.* 2000). In this study, females had a darker overall carapace colour, more rays, and less speckles than did males, dimorphism that may relate to ecological differences between sexes. The colour of male and female *H. s. signatus* may play a role in their thermal biology. Females are larger than males and the dark colour may help females to heat faster and overcome thermal lag. This may be advantageous when females reproduce (during the rainfall season in late winter and spring). Yet, we do not know if males and females have different absorptivities for solar radiation; more work is required. Lovich *et al.* (1990) found that melanistic and normal *Trachemys scripta* have very similar solar absorptivities and that melanism appears to have no thermoregulatory function in this species. Alternative adaptive explanations for the presence of dark colouration in chelonians are the protection of gametes from radiation, and intraspecific communication (see discussion by Lovich *et al.* 1990).

Shell colour may relate to predation risk (Gibson & Falls 1979) and rayed carapace patterns may help camouflage terrestrial chelonians (Pritchard 1979). Although Bayoff (1995) found no association of *H. s. signatus* carapace pattern and the rocks in the immediate vicinity for this same population, I consider *H. s. signatus* rather cryptic among the rocks and vegetation. The carapace pattern may be particularly cryptic in dead vegetation, where *H. s. signatus* were often found in spring (Loehr 2002a). The relative importance of rays and speckles to male and female shells probably contributes to the overall dark/light colour dimorphism between the sexes. The dimorphic shell colour and pattern may reflect different microhabitat use between males and females, as has been documented for other chelonians (Jones 1996; Lue & Chen 1999).

2.5.3 Size effects: shell pattern and serration

Body size contributed to the diversity in *H. s. signatus* shell patterns. The increasing darkness of the juvenile carapace with size may be related to widening of the dark pigment band as growth laminae are added, coupled with the increased incidence of large speckles. Rays result from the lack of pigment, at points along scute margins, extending across successively developing laminae. The small adults have the dark appearance of juveniles, but the dark appearance fades with size (and age) in adults, largely due to the dissipation of the dark scute band. This dissipation was similar for males and females, but background colour darkened with size in females, probably causing the greater overall dark appearance of females compared to males.

In large adults, the reduced dark appearance and reduced dark band may result from deterioration of the older laminae (Duerden 1907), as well as reduced melanin formation at the margins of new laminae. Both means of pigment reduction are probably due largely to the effects of age. However, females have higher growth rates than males (Chapter 3), so the larger female class may not equate to tortoises older than the largest males.

The changing shell pattern of juvenile and adult *H. s. signatus* also has methodological consequences. The shell changes associated with growth and ageing indicate that photography may have limited value for identifying adults recaptured over extended intervals (e.g., many years). The relatively rapid carapacial changes of juvenile *H. s. signatus* can render photography inadequate for identifying individuals recaptured after short time intervals (e.g., one year). Scute notching is a more reliable method for identifying recaptured *H. s. signatus*.

As with shell colour pattern, serration also appears to change through developmental stages. Serration was strong for juveniles and small adults, but decreased with size in males and females. Similar reductions are known from other chelonians, most notably *Heosemys spinosa* (Ernst *et al.* 2000). Strong serrations may provide juveniles some protection from predators, and the reduction of serration in adults may be the result of wear, especially in a rocky environment.

3 Growing and shrinking

A revised version of this chapter was published in Oecologia.

Loehr, V.J.T., Hofmeyr, M.D. & Henen, B.T. 2007. Growing and shrinking in the smallest tortoise, *Homopus signatus signatus*: the importance of rain. Oecologia 153: 479-488.

3.1 Abstract

Climate change models predict that the range of the world's smallest tortoise, *Homopus signatus signatus*, will aridify and contract in the next decades. To evaluate the effects of annual variation in rainfall on the growth of *H. s. signatus*, I recorded annual growth rates of wild individuals from spring 2000 to spring 2004. Juveniles grew faster than did adults, and females grew faster than did males. Growth correlated strongly with the amount of rain that fell during the time just before and within the growth periods. Growth rates were lowest in 2002–2003, when almost no rain fell between September 2002 and August 2003. In this period, more than 54% of the tortoises had negative growth rates for their straight carapace length (SCL), shell height (SH), and shell volume (SV); maximum shrinking for SCL, SH and SV was 4, 11 and 12%, respectively. The shell of *H. s. signatus* has some flexibility dorso-ventrally, so a reduction in internal matter due to starvation or dehydration may have caused SH to shrink. Because the length and width of the shell seem more rigid, reversible bone resorption may have contributed to shrinkage, particularly of the shell width and plastron length. Based on growth rates for all years, female *H. s. signatus* need 11–12 years to mature, approximately twice as long as would be expected allometrically for such a small species. However, if aridification lowers average growth rates to the level of 2002–2003, females would require 30 years to mature. Additionally, aridification would lower average and maximum female size, resulting in smaller eggs and hatchlings. These projected life history responses to aridification heighten the threat posed by the predicted range contraction of this red-listed species.

3.2 Introduction

The tremendous variation in animal life histories reflects the complex interplay of intrinsic and extrinsic influences upon growth, reproduction, survivorship and other life history traits. Important extrinsic determinants of growth include among others, temperature (Atkinson 1996), water availability (Lorenzon *et al.* 1999), food availability (Dunham 1978) and food quality (Gauthier *et al.* 2006). Growth, survival and reproduction are often interdependent (Gauthier *et al.* 2006; Ricklefs 2006), and the effect of environmental variability on these life history traits may have far-reaching consequences for population dynamics and persistence. Recent studies showed that increasing spring temperatures advanced the breeding date of tree swallows over North

America (Dunn & Winkler 1999) but climatic variability may induce mismatches between food availability and requirements (Stenseth & Mysterud 2002), as has been shown for great tits (Visser *et al.* 1998). Severe winter conditions, which limit food availability, lower the growth rates of reindeer calves in Norway (Weladji & Holand 2003). To help us understand and conserve biodiversity, we must evaluate the relative impact of natural and human influences on animal life histories and populations.

Tortoises are long-lived species that grow slowly and may require more than a decade to reach sexual maturity (Aresco & Guyer 1999; Germano 1994). In reptiles, as in many animal groups, there is a positive correlation between age at maturity and longevity (Shine & Iverson 1995; Tinkle 1969), so that some costs associated with delayed maturity are offset by iteroparity (Kuchling 1999). Anthropogenic impacts, such as land development, climate change, road traffic, and collecting for consumption or the wildlife trade, challenge the success of life history strategies of tortoises, and contributed to the current listing of 33 tortoise species (ca. 60% of all tortoise species; Ernst *et al.* 2000) in the IUCN Red List of Threatened Species (IUCN 2006).

Given the constraints imposed by tortoise life histories, understanding growth patterns and their determinants is important to facilitate conservation. Incubation temperature influences post-hatching growth rates of some chelonians (Brooks *et al.* 1991; Demuth 2001), but little is known about the effects of environmental conditions on growth to maturity. Although Germano (1994) concluded that interspecific differences in growth rates among *Gopherus* spp. were not explained by different climatic conditions among the species' ranges, growth in desert tortoises (*Gopherus agassizii*) appears to be related to rainfall and primary production (Berry 2002; Medica *et al.* 1975). Desert tortoises respond remarkably to changing environmental conditions (Henen *et al.* 1998; Peterson 1996a,b), but it is not known how these physiological and behavioural responses relate to growth rates.

Growth is associated with a positive increase in the size of an animal but Galápagos marine iguanas, *Amblyrhynchus cristatus*, can shrink in years of food shortages (Wikelski & Thom 2000). In this species, shrinking appears to be an adaptive response to nutrient stress because individuals that shrank more had higher survivorship. A similar phenomenon has not been described for tortoises and would challenge current notions about the rigid nature of the tortoise shell.

The Namaqualand speckled padloper, *H. s. signatus*, is the world's smallest tortoise species (maximum straight carapace length 110 mm; Loehr *et al.* 2006), and is restricted to the arid winter rainfall area of the Succulent Karoo in northwestern South Africa (Boycott & Bourquin 2000). *Homopus s. signatus* lives in rocky terrain, where it retreats in crevices (Loehr 2002a), and has a herbivorous diet (Loehr 2006a). Female *H. s. signatus* produce one egg at a time and egg size is strongly correlated to body size and body condition (Hofmeyr *et al.* 2005). Body condition in turn is influenced by winter rainfall patterns (Loehr *et al.* 2007a); the rains in the austral winter fall primarily from May to August. Their relatively large egg (7.5% of body size) suggests that, compared to small hatchlings, large hatchlings may survive better in their harsh environment (Hofmeyr *et al.* 2005). Consequently, it is important to know how long *H. s. signatus* females require to grow large enough to produce viable offspring. The strong effects of rainfall and body size on the reproduction of *H. s. signatus*, together with recent threats of climate change to its restricted range (Rutherford *et al.* 1999), make it critical to understand how the environment influences growth in *H. s. signatus*.

I measured growth of *H. s. signatus* for a total of four 12-month growth periods, from 2000 to 2004. Here I report average growth rates for males, females and juveniles, the relationship of growth rates to rainfall, and a high incidence of shrinking during a particularly dry year.

3.3 Materials and methods

A population of *H. s. signatus* near Springbok, South Africa, was monitored annually for five to six weeks in each spring (August to October) from 2000 to 2004 (see Loehr 2002a for a site description). Each day the study site (3.6 ha) was traversed and inspected systematically by two to five experienced field workers who searched among rocks, under shrubs and open areas for tortoises. For each tortoise that we found for the first time in a year, I used electronic callipers to measure, to the nearest 0.01 mm, straight carapace length (SCL, midline distance at the nuchal and supracaudal scutes), shell width (SW, where the shell was widest), shell height (SH, where the shell was highest), and plastron length (PL, midline distance at the gular and anal scutes). Shell volume (SV, cm^3) was estimated using a modified formula for an ellipsoid: $SV = \pi * SCL * SH * SW / 6000$ (Loehr *et al.* 2004). My study design required repeatability of measurements throughout the study. Consequently, I collected most of the data and, to minimise variance, trained field crews to collect data consistent with my method. In addition, using digital callipers helped minimise reading errors. Although it was not feasible to quantitatively assess the repeatability of our measurements, a significant variation in measurement technique would have obscured the patterns that I detected. Tortoises that were too small to sex were recorded as juveniles. Each individual was marked with a unique combination of black nail polish dots on the carapace (2000 to 2002), and from 2003 by notching marginal scutes (Cagle 1939). The Springbok weather station, 2.5 km north of the study site, provided rainfall data.

I compared male, female and juvenile measurements (SCL, SH, SW, PL and SV) using one-way ANOVA (data ranked when required to meet parametric assumptions). Mean growth increments or growth rates of SCL, SH, SW, PL (mm yr^{-1}) and SV (cm^3 yr^{-1}) were calculated for each animal group, each 12-month growth period (e.g., spring 2000 to spring 2001), all groups combined and all periods pooled. My field method represented sampling with replacement, although by capturing several males and females in more than two consecutive years I was able to use repeated-measures tests also, albeit with greatly reduced sample sizes. I compared means among periods using ANOVA (two-way or one-way) for independent samples. I also report results from repeated measures ANOVA (RM ANOVA), on animals captured in all five years, in the rare instances when these added significant results beyond those of standard ANOVA.

When possible, I used two-way ANOVA or two-way RM ANOVA to simultaneously test for effects of animal group and period. If the data did not meet parametric assumptions, even after log- or rank-transformations, I used one-way ANOVA or one-way RM ANOVA on raw or transformed data, and in two instances, I used non-parametric Kruskal-Wallis tests. Student-Newman-Keuls (SNK) and Dunn's post hoc tests followed parametric and nonparametric ANOVA, respectively. To determine if growth increments were significantly different from zero, I used one-sample *t*-tests, or Wilcoxon tests if samples were non-parametric. I compared frequencies of negative growth rates among periods and groups by contingency table analysis (χ^2).

To account for body size differences in comparisons between males and females, and among growth periods, I used ANCOVA to compare linear regressions of growth increments (SCL, SH, SW and PL) on initial SCL, and growth of SV on initial SV (Zar 1999). ANCOVA was used only when regressions were statistically significant for the relevant groups or periods; in some cases log- or rank-transformation was necessary to comply with parametric assumptions. The slopes and elevations of regression lines were compared by ANCOVA (Zar 1999) followed by SNK post hoc tests for cases with more than two groups.

I assessed correlations between growth rates of the four 12-month growth periods and rainfall for the same periods, that is, from September to August. However, growth in herbivores will lag behind rainfall partly due to the time required for plants to respond to rain. High rainfall towards the end of winter (July to August) would probably not affect growth before September, so I also evaluated the effects of rainfall from August to July, and from July to June, on the growth of *H. s. signatus*. Effects of the rainfall periods and body size (SCL and SV) on growth rates were evaluated by multiple regression analysis. I used ANCOVA to evaluate whether male and female growth responded similarly to variation in annual rainfall. Because body size influenced growth rates, I used ANCOVA on the residuals (Clark *et al.* 2001; Hofmeyr *et al.* 2005) of growth scaled on body size. For all correlations of growth to rainfall, data were log- or rank-transformed when data were not parametric.

Differences were considered statistically significant at $P < 0.05$. I completed Wilcoxon's tests in StatsDirect 1.9.12 (Iain E. Buchan, UK), and ANCOVA, contingency table analysis and one-sample *t*-tests in Microsoft Excel according to Zar (1999). All other statistics were completed in SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.).

3.4 Results

Annual rainfall varied from 131 to 226 mm, and was below average (218 mm, for 1990 to 2004) in all years except 2001 (Fig. 3.1). The timing of the rains differed from year to year (Fig. 3.1); most notably, winter rainfall was nearly absent in 2003, when 79% of the annual rainfall fell in one month, August. In September 2003, I noted qualitatively that few annuals had germinated and that primary production was very low. In contrast, September 2001 had extraordinarily lush vegetation. Rainfall from September to August, the periods for which I recorded *H. s. signatus* growth, was 244, 183,

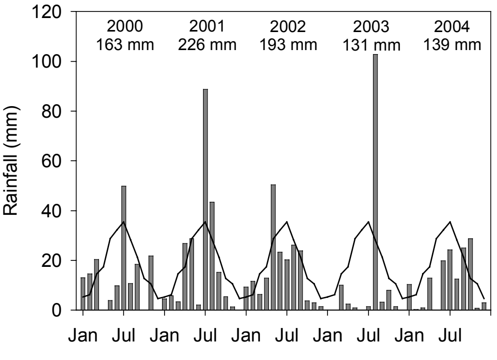

Figure 3.1 Monthly rainfall from 2000 to 2004 (bars), and long-term monthly averages (1990–2004; line), for Springbok, South Africa. Annual rainfall is indicated for 2000 to 2004.

150 and 94 mm, respectively, for the four growth periods. Rainfall for August to July (one month time lag) was 211, 200, 73, and 184 mm, respectively, whereas rainfall was 172, 268, 92, and 162 mm, respectively, for July to June (two month time lag).

There was considerable variation in tortoise shell measurements (Fig. 3.2a) and in the annual growth increments of shell dimensions (Fig. 3.2b). The mean percent change (± SD, N = 202, but N_{PL} = 201) in shell dimensions for all tortoises, expressed relative to the value at the beginning of the 12-month periods was 2.1 ± 4.7% for SCL, 1.6 ± 5.1% for SH, 2.1 ± 3.9% for SW, 2.2 ± 4.6% for PL, and 6.3 ± 13.6% for SV.

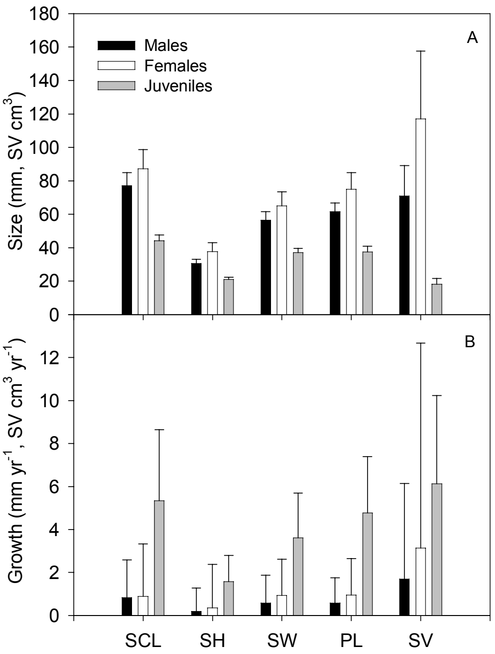

Figure 3.2 Mean straight carapace length (SCL), shell height (SH), shell width (SW), plastron length (PL), and shell volume (SV) of 51 male, 49 female and 12 juvenile *H. s. signatus* when they were first encountered (a), and mean annual growth of these parameters (b, sample sizes in Table 3.1). Error bars represent standard deviations. Each shell dimension differed among groups ($F_{2,109} \geq 52.91$, $P < 0.001$; SNK: F > M > J). Growth rates differed among groups for SCL, SH and PL (two-way ANOVA, $F_{2,190} \geq 8.82$, $P < 0.001$) and for SW and SV (Kruskal-Wallis tests, $H_2 \geq 9.16$, $P < 0.01$). Juvenile growth rates were significantly higher than those for males and females, which did not differ from one another, in all parameters (SNK or Dunn's: $P < 0.05$) except for SV, where juvenile rates were significantly greater than those of males but not females.

3.4.1 Growth variation among groups and periods

For the entire study, juvenile growth rates (in absolute terms) exceeded growth rates of adults (Fig. 3.2b). The exception was SV, which was similar for females and juveniles (Fig. 3.2b). Growth rates of male, female and juvenile *H. s. signatus* differed among periods (Table 3.1), with 2002–2003 tending to have low growth rates and 2001–2002 tending to have high growth rates. Annual increments for SCL and SH were consistently lower in 2002–2003 than in any other 12-month period. Male, female and juvenile PL growth was lower in 2002–2003 than in 2001–2002. Growth of male and female SW was higher in 2001–2002 than in the other periods, while growth of juvenile SW was lower in 2002–2003 than in other periods. The increase of male and female SV was higher in 2001–2002 compared to the other growth periods. For juvenile SV, annual differences in growth were significant, but post hoc tests were not significant.

Repeated measures analysis for males and females confirmed the differences among periods identified by independent ANOVA (two-way RM ANOVA, $F_{3,33} \geq 4.10$, $P \leq 0.014$), except

SH increments differed between only two periods (2002–2003 < 2001–2002), and PL growth tended to differ among growth periods ($F_{3,33}$ = 2.77, P = 0.057).

Table 3.1 Variation among mean annual growth rates (± SD, range; mm yr^{-1}) of the straight carapace length (SCL), shell height (SH), shell width (SW), plastron length (PL), and shell volume (SV, cm^{3} yr^{-1}) of male (M), female (F) and juvenile (J) *H. s. signatus*. Mean growth rates were considered negative (neg), positive (no mark) or not different from zero (ns) based on single sample *t*-tests or Wilcoxon tests. The statistics column indicates significant post hoc results from ANOVA$^{\#,@,*}$; see Fig. 3.2 for group effects. Interaction terms of two-way ANOVA were not significant ($P \geq 0.77$).

		2000–2001	2001–2002	2002–2003	2003–2004	Statistics
SCL	M	1.28 ± 1.75 -0.99 to 5.00	1.60 ± 1.80 -1.38 to 4.87	-0.11 ± 1.35^{ns} -3.39 to 3.76	1.04 ± 1.79 -0.78 to 7.61	02–03 < all
	F	1.13 ± 1.99 -1.07 to 6.34	2.30 ± 2.94 -0.34 to 11.02	-0.35 ± 1.64^{ns} -3.44 to 2.84	1.20 ± 2.34 -3.46 to 6.32	02–03 < all
	J	9.54 ± 2.28^{ns} 7.92 to 11.15	7.00 ± 3.37 3.13 to 11.55	2.48 ± 1.42 0.59 to 4.31	6.45 ± 1.03 5.86 to 7.64	02–03 < all
SH	M	0.45 ± 1.38^{ns} -1.65 to 3.48	1.01 ± 0.86 -0.43 to 2.65	-0.50 ± 0.80^{neg} -1.89 to 1.58	0.19 ± 0.79^{ns} -1.91 to 2.10	02–03 < all
	F	0.70 ± 1.68^{ns} -1.57 to 4.17	1.65 ± 1.83 -1.44 to 5.49	-0.53 ± 1.63^{neg} -4.57 to 2.55	0.16 ± 2.27^{ns} -4.48 to 3.83	02–03 < all
	J	2.10 ± 0.55^{ns} 1.71 to 2.49	1.87 ± 1.35 -0.02 to 3.76	0.78 ± 0.98 -1.17 to 1.75	2.66 ± 0.71 1.84 to 3.14	02–03 < all
SW	M	0.12 ± 1.57^{ns} -2.60 to 2.35	1.51 ± 1.09 -0.37 to 4.31	0.45 ± 1.07 -4.04 to 2.86	0.19 ± 1.20 -4.77 to 1.86	01–02 > all
	F	0.64 ± 1.06 -1.99 to 2.53	2.12 ± 2.39 -0.31 to 7.90	0.70 ± 0.99 -0.86 to 3.21	0.23 ± 1.39^{ns} -2.92 to 3.18	01–02 > all
	J	6.36 ± 0.07 6.31 to 6.41	5.29 ± 1.72 3.35 to 7.31	1.73 ± 0.69 0.92 to 2.62	3.38 ± 0.56 2.82 to 3.94	02–03 < all
PL	M	0.87 ± 1.95^{ns} -1.45 to 6.56	0.97 ± 1.23 -0.67 to 4.37	0.36 ± 0.77 -0.50 to 3.62	0.34 ± 0.82 -0.89 to 2.52	02–03 < 01–02
	F	0.47 ± 1.10^{ns} -1.30 to 3.53	1.94 ± 2.52 -0.13 to 9.18	0.67 ± 1.12 -0.70 to 3.81	0.64 ± 1.25 -0.77 to 3.65	02–03 < 01–02
	J	8.81 ± 2.72^{ns} 6.88 to 10.73	6.34 ± 1.63 4.49 to 7.89	2.53 ± 0.99 1.16 to 4.25	4.74 ± 1.64 3.32 to 6.53	02–03 < 01–02

Table continues on next page

		2000–2001	2001–2002	2002–2003	2003–2004	Statistics
Table 3.1 continued from previous page						
SV	M	1.67 ± 5.29^{ns} -5.89 to 12.10	5.67 ± 3.70 -0.39 to 11.77	-0.97 ± 3.34^{ns} -9.85 to 5.77	1.51 ± 3.18 -4.99 to 7.13	01–02 > all
	F	4.47 ± 7.18 -3.87 to 15.97	10.61 ± 9.67 -2.22 to 36.33	-1.61 ± 7.11^{ns} -24.84 to 9.85	1.78 ± 9.40^{ns} -20.11 to 16.97	01–02 > all
	J	9.41 ± 2.54^{ns} 7.61 to 11.20	8.24 ± 5.13 2.68 to 15.87	2.81 ± 1.82 -0.38 to 5.72	8.19 ± 1.32 6.67 to 9.02	none

Sample sizes for males, females, and juveniles were: 15, 14, 2 (2000–2001); 22, 23, 5 (2001–2002); 31, 34 (33 for PL), 7 (2002–2003); and 25, 21, 3 (2003–2004), respectively.

[#] Two-way ANOVA, rank-transformed; SCL $F_{3,190} = 8.25$, $P < 0.001$; SH $F_{3,190} = 8.79$, $P < 0.001$; PL $F_{3,189} = 2.68$, $P = 0.048$.

[@] One-way ANOVA: SV; males $F_{3,89} = 13.41$, $P < 0.001$; females $F_{3,88} = 10.07$, $P < 0.001$; juveniles $F_{3,12} = 4.29$, $P = 0.026$.

[*] One-way ANOVA: SW; males (rank-transformed) $F_{3,89} = 6.28$, $P < 0.001$; females (log-transformed) $F_{3,89} = 3.93$, $P = 0.011$; juveniles (rank-transformed) $F_{3,12} = 17.41$, $P < 0.001$.

3.4.2 Correlations of growth with body size

The growth of all body dimensions was strongly correlated to body size for males and females (Table 3.2), but not for juveniles (all periods combined, linear regressions, $F_{1,15} \leq 2.19$, $P \geq 0.16$). While ANOVA did not identify growth rate differences between males and females, compensation for body size effects using ANCOVA showed that female growth rates were higher than were those of males, that is, the elevations of growth regressions (when significant for males and females) were always higher in females than in males (Table 3.2; Figs. 3.3a–d).

Table 3.2 Regression statistics (± SE) for correlations between growth increments of the straight carapace length (SCL), shell height (SH), shell width (SW) and plastron length (PL) with initial SCL, and growth increments of shell volume (SV) with initial SV, for male and female *H. s. signatus*[*]. The l and r superscripts indicate regressions using log or rank transformations, respectively[#]. All regressions, except those with a ns label, were significant to at least $P < 0.05$[$]. When regressions were significant for both sexes, regression slopes did not differ between sex and female regressions always had higher elevations than did male regressions[&]. ANCOVA rows indicate SNK post hoc results ($P < 0.05$) when slopes or elevations differed between growth periods[@].

	Males			Females		
	Slope (SE)	Intercept (SE)	r^2	Slope (SE)	Intercept (SE)	r^2
SCL						
Combined	-1.98^{r} (0.37)	202.18 (29.21)	0.24	-0.16 (0.02)	14.87 (1.85)	0.39
00–01	-0.17 (0.04)	14.78 (2.78)	0.65	-0.19 (0.07)	18.07 (6.03)	0.40
01–02	-0.24 (0.06)	20.32 (4.52)	0.46	-0.20 (0.03)	20.33 (2.91)	0.65
02–03	-0.11 (0.03)	8.70 (2.23)	0.35	-0.11 (0.02)	9.16 (1.74)	0.49
03–04	-0.003^{l} (0.0007)	1.62 (0.06)	0.35	-0.19 (0.05)	18.27 (4.88)	0.39
ANCOVA	Elevation 02–03 < all others			Elevation 02–03 < all others		

Table continues on next page

	Males			Females		
	Slope (SE)	Intercept (SE)	r^2	Slope (SE)	Intercept (SE)	r^2
Table 3.2 continued from previous page						
SH						
Combined	-0.06 (0.02)	4.68 (1.25)	0.12	-0.08 (0.02)	7.17 (1.82)	0.14
00–01	-0.12 (0.03)	9.85 (2.58)	0.51	-0.16 (0.05)	15.53 (4.99)	0.42
01–02	-0.04 (0.04)	3.76 (2.89)	0.04 ns	-0.07 (0.03)	8.12 (2.70)	0.22
02–03	-0.04 (0.02)	2.73 (1.54)	0.13	-0.04 (0.03)	2.89 (2.33)	0.06 ns
03–04	-0.04 (0.02)	3.20 (1.91)	0.10 ns	-0.15 (0.06)	13.64 (5.24)	0.26
ANCOVA	Slope 00–01 steeper than 02–03					
SW						
Combined	-0.09 (0.02)	7.57 (1.43)	0.21	-0.002^{l} (0.0002)	1.55 (0.02)	0.30
00–01	-0.15 (0.03)	11.93 (2.57)	0.62	0.02 (0.04)	-1.15 (4.10)	0.02 ns
01–02	-0.10 (0.04)	9.28 (3.31)	0.22	-0.15 (0.03)	15.47 (2.72)	0.54
02–03	-0.08 (0.02)	6.44 (1.91)	0.26	-0.05 (0.01)	5.35 (1.21)	0.32
03–04	-0.04 (0.04)	3.55 (2.95)	0.27 ns	-0.11 (0.03)	10.24 (2.92)	0.38
ANCOVA	Elevation 01–02 > 00–01~02–03			Slope 01–02 steeper than 02–03		
PL						
Combined	-2.27^{r} (0.35)	225.08 (27.73)	0.31	-1.49^{r} (0.24)	178.92 (21.86)	0.30
00–01	-0.21 (0.03)	17.32 (2.46)	0.76	-0.03 (0.05)	2.75 (4.25)	0.02 ns
01–02	-0.17 (0.04)	14.00 (3.06)	0.48	-0.18 (0.03)	17.92 (2.30)	0.70
02–03	-0.08 (0.01)	6.88 (1.02)	0.59	-0.08 (0.01)	7.67 (1.17)	0.54
03–04	-0.07 (0.02)	5.97 (1.69)	0.33	-0.002^{l} (0.0004)	1.58 (0.04)	0.51
ANCOVA	Slope 00–01 ~ 01–02 steeper than 02–03 ~ 03–04			Slope 01–02 steeper than 02–03		
SV						
Combined	-0.15 (0.03)	12.96 (1.92)	0.28	-0.13 (0.02)	20.13 (3.17)	0.26
00–01	-0.24 (0.04)	19.25 (3.37)	0.69	-0.13 (0.05)	20.74 (6.52)	0.36
01–02	-0.14 (0.06)	16.01 (4.30)	0.23	-0.12 (0.05)	25.42 (5.93)	0.25
02–03	-0.12 (0.03)	7.94 (2.44)	0.32	-0.09 (0.03)	10.33 (3.74)	0.26
03–04	-0.11 (0.03)	9.92 (2.57)	0.33	-0.21 (0.05)	29.69 (6.50)	0.51
ANCOVA	Elevation 02–03 < all others, and 01–02 > all others			Elevation 01–02 > all others		

[*] See Table 3.1 for sample sizes

[#] Comparisons between sexes or among years used the same format (i.e., raw or transformed) across groups.

[$] More than half (27) had $P < 0.001$.

[&] ANCOVA between sexes: slopes $t \leq 1.86$, df ≤ 181, $P \geq 0.065$; elevations $t \geq 2.79$, df ≥ 26, $P \leq 0.0071$.

[@] ANCOVA among growth periods: for significant slope differences $F \geq 5.70$, df1 ≥ 2, df2 ≥ 71, $P \leq 0.0051$ except $t_{42} = -2.26$, $P = 0.029$ for male SH slopes; for significant elevation differences $F \geq 10.17$, df1 ≥ 2, df2 ≥ 64, $P < 0.0001$.

For many male and female regressions, there were differences among periods of growth, with steeper (more negative) slopes or higher elevations in 2001–2002 than in 2002–2003 (Table 3.2; Figs. 3.3a–d). In addition, elevations for SCL and male SV growth increments were lower in 2002–2003 than in all other 12-month periods, and elevations for male and female SV increments were higher in 2001–2002 compared to all other periods (Table 3.2). In males, SW regression elevations were higher in 2001–2002 than in 2000–2001 or 2002–2003, and the slopes of PL regressions were steeper in 2000–2001 and 2001–2002 than in 2002–2003 and 2003–2004 (Table 3.2). For some comparisons, statistical differences in elevation did not correspond to differences among intercepts (Table 3.2). This occurred because intercepts occurred outside the range of measured covariates (X values), and slight slope differences caused regression lines to cross before reaching the intercepts.

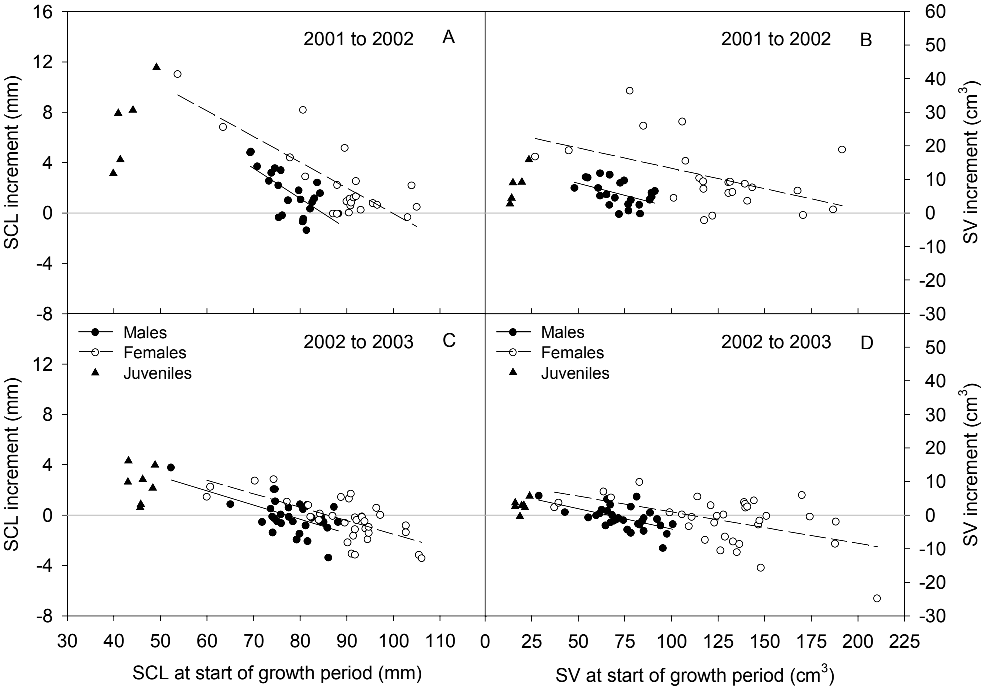

Figure 3.3 Correlations between growth increments (SCL, a and c; SV, b and d) and initial body size of *H. s. signatus*, for a 12-month period of good rainfall (2001–2002) and a 12-month period of very low rainfall (2002–2003). All regressions for males and females are significant ($F \geq 5.93$, df1 = 1, df2 ≥ 20, $P \leq 0.024$, $r^2 \geq 0.23$) and elevations of male regression lines are lower than those for females (ANCOVA, $t \geq 2.79$, df1 = 1, df2 ≥ 42, $P \leq 0.0071$). Slopes of male and female regressions are similar ($t \leq 0.49$, df1 = 1, df2 ≤ 61, $P \geq 0.63$).

3.4.3 Negative growth rates (shrinking)

Many *H. s. signatus* individuals showed negative growth rates or shrinking, but the frequency of shrinking differed among growth periods (for SCL, SH and SV, $\chi^2 \geq 24.24$, df = 3, $P <$

0.001; for SW and PL, $\chi^2 \geq 9.91$, df = 3, $P \leq 0.019$). The lowest incidence of shrinking for SCL (18%, i.e., 9 of 50 tortoises), SH (16%), SW (8%), PL (8%), and SV (10%) occurred in 2001–2002 when average growth was positive for all body measures of all groups (Table 3.1). During this period, growth increments relative to body size differed between males and females (Figs. 3.3a–b) but the frequency of males and females with negative growth were similar (for all dimensions $P >$ 0.23). In fact, I recorded no sexual difference in the frequency of shrinking for any period or all periods combined (χ^2 = 0.017–3.63, df = 1, P = 0.057–0.90).

Shrinking was very common in 2002–2003. The SCL shrank in 57% of the tortoises and growth rates (i.e., the elevations of male and female growth regressions relative to body size) were lower than in all other periods (Figs. 3.3c–d; Table 3.2). Also, SH and SV often shrank in 2002–2003 (64% and 54% of the tortoises, respectively). Although the frequencies of SW and PL shrinking differed among growth periods, and were lowest in 2001–2002, the frequencies did not differ substantially among the other three periods (for SW 17–35%, for PL 21–33%). Juveniles rarely shrank; SH shrank for two juveniles (one in 2001–2002, one in 2002–2003) and SV shrank for one juvenile (2002–2003).

On average, tortoises with negative growth shrank 1% for SCL and SW, 3% for SH, 0.5% for PL, and 3% for SV in one year. The maximum shrinkage per year was 4% for SCL, 11% for SH, 8% for SW, 2% for PL, and 12% for SV. The mean growth increment for SH during 2002–2003 was less than zero in males (one-sample *t*-tests, $t_{30} = -3.47$, $P < 0.001$) and females ($t_{33} = -1.88$, $P =$ 0.034) (Table 3.1).

Of all adult tortoises with SCL that shrank during 2002–2003, 79% (i.e., 15 of 19 tortoises) had a positive SCL growth rate in the following year (2003–2004). Similar values for SH, SW, PL and SV were 68, 71, 43, and 70%, respectively. The 2003–2004 growth rates of adults that reversed negative 2002–2003 growth averaged 1.27, 1.18, 0.71, 0.23 mm yr^{-1} for SCL, SH, SW and PL respectively, and 3.80 cm^3 yr^{-1} for SV. In 2003–2004, all growth rates were larger than zero (one-sample *t*-tests, $t \geq 3.06$, df ≥ 4, $P \leq 0.019$; for PL $t_2 = 2.88$, $P = 0.051$).

3.4.4 Effect of rainfall on growth rates

No growth measure for males, and few growth measures for females and juveniles, was correlated to the September to August rainfall values. Regressions included SW and SV increments for females ($F_{1,90} \geq 4.48$, $r^2 > 0.047$, $P \leq 0.037$), and SW and PL increments for juveniles ($F_{1,15} \geq$ 6.77, $r^2 > 0.31$, $P \leq 0.020$).

All growth increments of males and females were correlated to the July to June rainfall (F = 4.04 to 40.97, df1 = 1, df2 $\geq$ 90, r^2 = 0.04 to 0.31, P = 0.047 to < 0.001). Most, but not all growth increments of males and females were also correlated with the August to July rainfall values (F = 12.98 to 26.44, df1 = 1, df2 $\geq$ 90, r^2 = 0.13 to 0.23, $P < 0.001$); the exceptions were the growth increments for SW and PL ($P > 0.23$). Juvenile growth was correlated to rainfall values for both periods ($F_{1,15}$ = 6.61 to 31.52, r^2 = 0.31 to 0.68, P = 0.021 to < 0.001), except for SH growth, which was correlated only to August to July rainfall ($F_{1,15} = 6.61$, $r^2 = 0.31$, $P = 0.021$).

Multiple regressions showed that body size and the July-to-June rainfall explained 30% to 56% of the variation in adult growth ($F > 19.40$, df1 = 2, df2 = 89 or 90, $P < 0.0001$). After correcting annual growth rates for body size effects, the regression of SV growth on rainfall was steeper for females than for males (Fig. 3.4), and the regression lines intersected at a rainfall of 165 mm and growth of -0.03 cm^3 $year^{-1}$. The lines for males and females intercepted zero growth at 165 and 164 mm rainfall, respectively. For juveniles, the combined effects of body size and the August-to-July rainfall values explained between 50% and 69% of the variation in growth ($F_{2,14} > 7.13$, $P < 0.0073$). Although growth increments of juveniles were not correlated to body size in simple regressions, SH and SV growth correlated with body size ($P \leq 0.033$) when I accounted for the effect of annual rainfall in the multiple regression analysis.

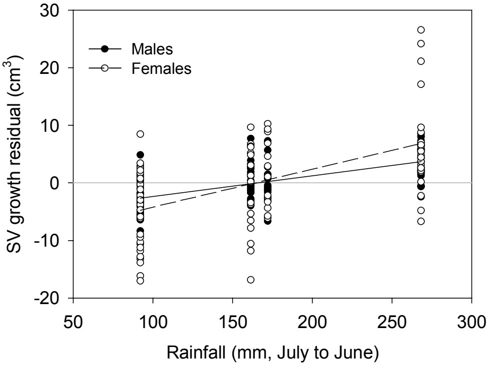

Figure 3.4 Correlations between the residuals of shell volume (SV) and rainfall (July-to-June) in male and female *H. s. signatus* (both $F \geq 38.34$, df1 = 1, df2 ≥ 90, $P < 0.001$, $r^2 \geq 0.30$). The slope of the female regression line was steeper than the slope of the male regression line (ANCOVA, $t_{181} = 2.56$, $P = 0.011$).

3.5 Discussion

3.5.1 *Growth rates of H. s. signatus*

As in many chelonians (Kuchling 1999), growth in *H. s. signatus* is indeterminate; the high growth rate of juvenile *H. s. signatus* decreased substantially but did not stop when individuals matured. The low growth rate in adults relative to juveniles is probably associated with changes in resource allocations at maturity. In contrast to juveniles, adults invest resources in reproduction, which may limit the resources that adults have available for growth (Stearns 1992). Adult growth correlated negatively with body size, with males and females reaching maximum SCL of 96 and 110 mm, respectively (Loehr *et al.* 2006).

The growth rates (SCL) of *H. s. signatus* tended to be low (2.5 to 9.5 mm yr^{-1} for juveniles and -0.4 to 2.3 mm yr^{-1} for adults) in comparison to other small terrestrial chelonians. Growth rates measured or modelled in *Terrapene carolina bauri* are about 11 mm yr^{-1} at ages 0–5 years and 0.1 to 7 mm yr^{-1} for ages 5–27 years (Ernst *et al.* 1998), and approximately 5 mm yr^{-1} for juvenile and 0 to 5.1 mm yr^{-1} for adult *Cuora flavomarginata* (Chen & Lue 2002). Growth rates for the tortoise *Testudo horsfieldii* range from 7 to 13 mm yr^{-1} for the 0–6 year age group and 4 to 7 mm yr^{-1} for ages 7–11 years (Lagarde *et al.* 2001), while in *Gopherus berlandieri* growth rates are about 12 mm yr^{-1} for the first four years and 4 to 9 mm yr^{-1} for ages 5–20 years (Germano 1994). The low growth rate of *H. s. signatus* is probably associated with the small size of the species and the harsh conditions in its environment.

Female *H. s. signatus* grew faster than did males of the same size. The single, large eggs that females produce, and the strong correlation between egg size and female size, suggest a selective advantage for large eggs and offspring in *H. s. signatus* (Hofmeyr *et al.* 2005; Loehr *et al.* 2004). The high growth rate of females, relative to males, may facilitate females reaching their large body size and ultimately the production of large, viable eggs.

The large variation in growth within groups (see Fig. 3.3) suggests that some individuals were more successful than others in acquiring and allocating resources for growth. This variation may result from different availabilities of resources in microhabitats, or it may reflect inherent individual variation (genotypic or phenotypic) in ability to gather and utilise resources from the environment. Inherent differences may provide material for selection when the environment changes.

3.5.2 Effects of rainfall on growth

The rainfall pattern in the habitat of *H. s. signatus* supports the growth of annual and perennial plants in autumn and winter, with most plants flowering in spring (Le Roux & Schelpe 1997; Loehr 2002b). The duration of the growth season depends on the timing of the rains, and may be long when rains start in autumn, or brief when rains start in midwinter (Van Rooyen 1999). In September 2003, when the first significant rains had fallen late, I noticed little plant growth, including known food plants for *H. s. signatus* (Loehr 2002b, 2006a), whereas the field site was covered by flowering annuals in September–October 2001 after regular rain showers since autumn. The amount and timing of rainfall is likely to influence foraging opportunities of herbivores, particularly animals such as tortoises, which rely mainly on herbaceous plants (Boycott & Bourquin 2000).

Homopus s. signatus growth rates appeared to lag behind rainfall events. Growth rates correlated with the amount of rain that fell just before and during the September to August growth periods. The high growth rate of *H. s. signatus* in 2001–2002 corresponds with good rains in late-winter 2001, which were followed by regular showers up to September 2002. In contrast, the extended drought from October 2002 to July 2003 explains the low growth rate in 2002–2003. The high rainfall of August 2003 was too late to influence growth measured in September 2003, but influenced growth measured for 2003–2004. This delayed effect of rainfall on tortoise growth is substantiated by the higher growth rate, despite lower rainfall during the growth period, in 2003–2004 compared to 2002–2003.

The effect of rainfall on SV growth was more pronounced in females than in males. In years with low rainfall, the growth rate of females decreased more than did male growth rate, and in years with higher rainfall, female growth rate increased more than did the growth rate of males (Fig. 3.4). A large proportion of females was gravid each year (Chapter 6), and the different effect of rainfall on the sexes probably reflects differences between male and female investments in reproduction; females tend to allocate more towards reproduction in wet years than in dry years (Grant *et al.* 2000; Henen 1997). In dry years, female *H. s. signatus* appear to invest most of their resources into egg production, at the cost of growth, while in years with higher rainfall, females have sufficient resources to channel towards egg production and growth.

3.5.3 Shrinking

Negative growth rates or shrinking occurred on a large scale in *H. s. signatus*, and was not just an aberration of a few individuals. There was large inter-individual variation in growth, which was partly due to body size differences, with juveniles being less prone to shrinking than were adults. Because of their small size, juveniles would have had lower total energy needs than adults had, which may have allowed juveniles to grow faster than adults did when resources were scarce. Additionally, juveniles probably had large somatic allocations, and little if any reproductive allocations, compared to adults. In adults, shrinking was not caused strictly by nutrient allocations to egg production as I found no differences in the frequency of shrinking between males and females. The highest incidence of shrinking coincided with an extended drought (2002–2003) when most adult *H. s. signatus* shrank. Nevertheless, there were incidences of shrinking in all the years, even when rainfall for the period was above average (i.e., 2001–2002). It thus appears if some variation in the growth rate of *H. s. signatus* can be ascribed to different capabilities of individuals to accrue resources for growth.

The marine iguanid *A. cristatus* may shrink up to 20% (snout-to-vent length, SVL) within two years (Wikelski & Thom 2000). Snout-to-vent length in lizards is determined by a composition of various tissues, such as bone and connective tissue, and shrinking in *A. cristatus* has been ascribed to the resorption of both soft tissue and bone. In tortoises, body size is determined by the bony shell, which is covered by a thin epidermal, horny surface (Kuchling 1999). In *H. s. signatus*, the bony layer of the carapace is thin, possibly to facilitate mobility in their rocky habitat, and the shell has some flexibility in a dorso-ventral plane (SH). Females require kinesis of the posterior shell elements to pass their large egg (Hofmeyr *et al.* 2005), and ontogenetic replacement of bony sutures with fibrous connections, as in the freshwater terrapin *Dogania subplana* (Pritchard 1993), may play a role in shell kinesis and shell flexibility in *H. s. signatus*.

The maximum annual SH loss (11%) of *H. s. signatus* was comparable to SVL shrinking in *A. cristatus*. A reduction in the internal mass of the tortoises (e.g., bladder and gut content, body reserves, and reproductive mass in females) probably contributed largely to shrinking in SH, and through the effect on SH, to shrinking of SV. The effect of shrinking was less pronounced on SCL, SW and PL, and body shape changes due to internal mass changes may partly explain reductions in these measures. However, the shell of *H. s. signatus* is fairly rigid in width and length (particularly PL; VJT Loehr, personal observation), suggesting that a loss of bone tissue is involved in the shrinking, as proposed for *A. cristatus* (Wikelski & Thom 2000).

Shrinking in *H. s. signatus* was reversible, as in marine iguanas. Wikelski & Thom (2000) viewed shrinking in marine iguanas as an adaptive response to low food availability in El Niño years because big adults that shrank more, lived longer. Recent information for adult desert tortoises (*G. agassizii*) indicates that carapace length can shrink 0.8% (ca. 1.9 mm) during a drought year (ca. 115 days of the activity period), and that this shrinkage was reversible (Field *et al.* 2007; KJ Field, personal communication). I do not have sufficient data on survivorship for *H. s. signatus*, but the growth subsequent to shrinking suggests that shrinking is a reversible effect of starvation.

3.5.4 Implications for conservation

Based on average growth rates and regressions for SCL in juvenile and female *H. s. signatus*, I estimate that females mature in 11–12 years (assuming a hatchling SCL of 33.8 mm, and SCL at maturity of 84.1 mm; Loehr 1999; Loehr *et al.* 2004). This period is unusually long; a chelonian the size of *H. s. signatus* would be expected to mature in approximately 5.5 years according to data for 35 chelonian species (Iverson 1992). The limited resource availability of the

Succulent Karoo probably limits the tortoises' growth rate and requires that females reach a relatively large size to produce viable offspring, the combination helping explain the long growth trajectory of *H. s. signatus*.

Climate models predict that the range of *H. s. signatus* will become substantially drier within the next 50–100 years (Rutherford *et al.* 1999), a scenario that holds serious consequences for this species. Based on the low growth rates of 2002–2003, *H. s. signatus* females may require up to 30 years to reach sexual maturity. Additionally, the SCL growth rate of females in 2002–2003 approached zero at SCL 86 mm, indicating that prolonged aridity would decrease the average and maximum size of females. Smaller individuals may be more vulnerable in the drier climate.

Shrinking may affect egg size and ultimately hatchling size of this species. Females that shrank in 2002–2003 produced smaller eggs (egg volume) in 2003 than in 2002 (paired *t*-test t_6 = 2.39, P = 0.054; VJT Loehr, unpublished data). Egg volume is correlated to SCL in *H. s. signatus* (EV = 0.19 SCL - 6.6, in cm^3; Hofmeyr *et al.* 2005) and the egg volume (10.99 cm^3) of an average sized female (92.6 mm) would decrease by 1% or 6%, respectively, when applying the average or maximum SCL shrinking rates for the dry year (2002–2003; see Table 3.1). In contrast, after maximum growth in a good year (2001–2002), egg volume would increase by 11%, so that the maximum difference in egg volume between a good and a bad year would be 17%. These egg sizes correspond to hatchling volumes of 8.05 and 9.74 cm^3, a difference of 21% (VJT Loehr, unpublished data from captivity).

Aridification of *H. s. signatus* habitat would impact the time hatchlings need to reach maturity, the size of females, the size of eggs and hatchlings, and probably the success of the eggs and hatchlings. Apart from the projected effects of aridification on the life history of *H. s. signatus*, climate change models predict that *H. s. signatus* would experience a range contraction and range displacement of more than 50% over the next decades (Erasmus *et al.* 2002). The prospects for *H. s. signatus* appear dire, and concerted conservation efforts are required to safeguard the future existence of the world's smallest tortoise.

4 Tick infestations

A revised version of this chapter was published in African Zoology.

Loehr, V.J.T., Henen, B.T. & Hofmeyr, M.D. 2006. Tick infestations in the Namaqualand speckled padloper, *Homopus signatus signatus* (Gmelin, 1789). African Zoology 41: 170-177.

4.1 Abstract

Many terrestrial chelonians are parasitised by ticks, but we have a poor understanding of what determines tick infestations on chelonian hosts. I counted ticks on *Homopus signatus signatus* during each spring in the years 2001–2004, and evaluated tick frequencies in relation to tortoise anatomy, climate, and microhabitat. Tortoises hosted *Ornithodoros compactus* and *O. savignyi*, and ticks seemed to prefer the hindlimbs, avoid the shell, and use the forelimbs and neck in intermediate frequencies. The number of ticks on the neck and forelimbs did not differ among males, females and juveniles, but for the hindlimbs and all body parts, males and females usually had similar tick numbers and adults often had more ticks than juveniles had. The number of ticks on the hindlimbs correlated with the body size of male and female tortoises, whereas the number of ticks on the forelimbs correlated with juvenile body size. Males and females had similar incidences of ticks despite sexual dimorphism in body size (female size > male size), and this may be due to the relatively large shell openings (soft skin exposure) of males compared to females. Body condition and microhabitat had no effect on the number of ticks. It is unclear why tick numbers on *H. s. signatus* increased in dry years. The adverse effects of drought on mammals may have caused ticks to switch from mammals to tortoises when preferred hosts were no longer available.

4.2 Introduction

In many ecosystems, parasitic species affect the population structure of hosts (Begon *et al.* 1990). Although chelonians host a variety of microparasites (e.g., viruses, bacteria, protozoa) and macroparasites (e.g., helminths, ticks) (McArthur 1996), few studies have linked the presence of parasites to ecological parameters of the host (Brites & Rantin 2004; Rechav & Fielden 1995; Robbins *et al.* 1998, 2001). In recent years, there have been heightened concerns about the effects of the primitive bacterium *Mycoplasma* on wild populations of desert tortoises, *Gopherus agassizii* (Brown *et al.* 1999; Lederle *et al.* 1997). *Mycoplasma* is the agent of upper respiratory tract disease syndrome, a suspected cause of declines in wild *G. agassizii* populations (Brown *et al.* 1994, 1999).

Ticks parasitise a wide variety of terrestrial chelonians (Burridge & Simmons 2003; Durden *et al.* 2002). Studies on tortoise ticks have focused on descriptions of new taxa or parasite-host relationships (Durden *et al.* 2002; Guner *et al.* 2004; Robbins *et al.* 1998; Robbins & Okatt 2000; Robbins & Platt 2001), and on tick ecology (Fielden & Rechav 1994; Labruna *et al.* 2002; Petney & Al-Yaman 1985; Rechav & Fielden 1995). Another aspect that has received attention is the potential for tortoise ticks to act as vectors in the transmission of heartwater disease (*Cowdria ruminantium*), a lethal disease of cattle and other livestock (Burridge *et al.* 2000a,b). Yet, the determinants of tick infestations on chelonians, and the relationships of ticks with the ecology of their hosts, have received little attention. Female *Rhinoclemmys areolata* hosted more ticks than males hosted, possibly because females are larger (Robbins *et al.* 2001). Thus, ticks may affect males, females and juveniles differently. In *Testudo graeca nikolskii*, males had more ticks than females had, perhaps due to the larger daily movements and home ranges of males (Robbins *et al.* 1998). While tick infestations in male and female *Geochelone pardalis* did not differ, tick abundance varied seasonally, probably resulting from fine-tuning of parasite life history to the activity cycle of the host (Rechav & Fielden 1995).

Homopus signatus signatus is a small tortoise from rocky terrain in South Africa, where it inhabits an arid environment (Boycott & Bourquin 2000), and most of the annual precipitation (ca. 245 mm) falls between March and August (Loehr 2004a). As much as 48% of all *H. s. signatus* hosted ticks in spring 2000 (Loehr 2002a), indicating that ticks may have an important impact on this population. I studied the tick loads on a population of *H. s. signatus* from 2001 to 2004. Due to differences in the morphology and ecology of males, females and juveniles (Loehr 2002a), I expected different tick infestations among sexes and tortoises of different size. In addition, I tested whether tick infestations were correlated with winter rainfall and the body condition of the host.

4.3 Materials and methods

Each spring (August to October) from 2001 to 2004, I studied *H. s. signatus* for 5–6 weeks at a 3.6 ha study site near Springbok, South Africa. This site has five different microhabitats: flower field (a level area with many annual plants), rocky hill (a steep hill with many rocks and shrubs, but few annuals), intergrade (a transition between flower field and rocky hill), rock slab (steep, bare granite slabs with very little vegetation), and river bed (a drainage line containing dense shrubs) (Loehr 2002a). Each spring I methodically searched the entire study site for tortoises, ensuring that I invested similar search efforts in all microhabitats. In 2004, I also used radiotelemetry to relocate five males and 10 females that had been equipped with radiotransmitters (mass < 12% of tortoise body mass; AVM Instrument Company, Ltd., Colfax, U.S.A.) in 2003. For each tortoise encountered, I recorded the microhabitat type and noted the group (male, female or juvenile). Males had large tails and concave plastrons, and tortoises that were too small to determine their sex were categorised as juveniles. In addition, I measured body mass (BM, ± 0.1 g) with a digital balance, and used digital callipers to measure (± 0.01 mm) the straight carapace length (SCL, along midline between nuchal and supracaudal), shell height (SH, where the shell was highest), shell width (SW, where the shell was widest), and plastron length (PL, along midline from the gulars to anal scutes). I used these measures to estimate shell volume (SV, cm^3) using a modified formula for an ellipsoid: $SV = \pi * SCL * SH * SW / 6000$ (Loehr *et al.*

2004), and estimated body condition as BM / SV. I also calculated the difference between carapace length and plastron length (SCL - PL, mm), indicating the size of shell openings and the degree of soft skin exposure. Each tortoise was marked with a unique combination of black nail polish dots on the carapace (2001 to 2002), and from 2003, by notching marginal scutes (Cagle 1939).

For the first capture of each tortoise in a year, I counted the number of ticks on the neck, forelimbs, and hindlimbs. In 2002, I removed all ticks from six female tortoises for identification at Onderstepoort Veterinary Institute, South Africa. Onderstepoort also identified two ticks that I collected, in 2003.

Most data had non-normal distributions, requiring non-parametric statistical tests. I report medians, and 25th and 75th percentiles, for the number of ticks on the different body parts, and for all body parts combined. I tested tick incidences for differences among body parts using Friedman's repeated samples ANOVA, followed by Dunn's post hoc tests. Tick numbers were compared among years, groups (males, females, juveniles), and microhabitats, using Kruskal-Wallis ANOVA and Dunn's post hoc tests. All tortoises were used in independent sample analyses, including the 15 telemetered animals that represented <20% of tortoises studied in 2004 ($N = 76$). I also analysed telemetered tortoises as part of repeated measures analyses (Wilcoxon tests) between years.

I used simple linear regression to scale morphometrics to carapace length and Spearman's correlations (r_s) to assess relationships between the number of ticks and tortoise size (SCL or SV), size of shell openings (SCL - PL), body condition, and winter rainfall (March to August). I used analysis of covariance (ANCOVA) to evaluate the slopes and elevations for the group regressions of shell opening size on SCL (Zar 1999). When slopes differed between groups, I tested for the regions of SCL where elevations differed (Zerbe *et al.* 1982). Rainfall data originated from the Springbok weather station, 2.5 km north of the study site.

4.4 Results

The 129 ticks (116 nymphs, and 13 adults) removed from six female *H. s. signatus* in 2002 belonged to the species *Ornithodoros compactus*, and the two ticks removed in 2003 were *Ornithodoros savignyi* nymphs. I found ticks on the soft skin of the neck (Fig. 4.1) and limbs, but none on areas with large scales or on the shell. The ticks were not firmly attached, and many moved when I handled the tortoises.

For all years combined, the median number of ticks on a tortoise was five (25th and 75th percentiles: 1 and 15 respectively, $N = 248$). Ticks were not evenly distributed among body parts for all years combined (Fig. 4.2; Friedman's ANOVA $\chi^2 = 112.9$, df = 2, $P < 0.001$), and within each year (all Friedman's ANOVA $\chi^2 \geq 14.63$, $P < 0.001$). In all but one year, the number of ticks was greater for hindlimbs than for forelimbs and neck. The only exception occurred in 2001, when the hindlimbs and forelimbs had similar numbers of ticks. In 2001, the number of ticks on the neck was smaller than that on the forelimbs and hindlimbs.

Within groups, tick numbers differed among body parts. The result was particularly strong for females ($\chi^2 = 64.01$, df = 2, $P < 0.0001$) and males ($\chi^2 = 75.18$, $P < 0.0001$) yet still significant

Figure 4.1 *Homopus s. signatus* neck infested with ticks (*Ornithodoros* sp.).

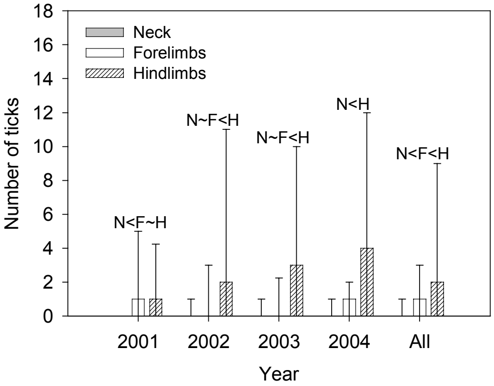

Figure 4.2 Median (± 25th and 75th percentiles) number of ticks on the neck (N), forelimbs (F), and hindlimbs (H) of *H. s. signatus* in 2001 to 2004. Sample sizes varied between 39–251 (neck), 76–383 (forelimbs), and 71–370 (hindlimbs). The letters N, F and H indicate post hoc results among body parts in a given year (Dunn's tests, $P < 0.05$).

for juveniles ($\chi^2 = 10.75$, $P = 0.0046$). For males, tick numbers on the hindlimbs exceeded tick numbers on the forelimbs and neck. Females had more ticks on the forelimbs and hindlimbs compared to the neck, while the forelimb and hindlimb numbers did not differ significantly from one another. Although tick numbers appeared highest on the forelimbs of juveniles, there were no significant post hoc results among forelimbs, hindlimbs and neck.

Among groups, tick numbers did not differ for the neck or forelimbs, but differed for the hindlimbs and for all body parts combined (Figs. 4.3a–b). For the entire body, tick numbers differed among groups for 2001, 2002 and all years combined (KW ANOVA $H_2 \geq 6.83$, $P \leq 0.033$), but not for 2003 ($H_2 = 5.92$, $P = 0.052$) or 2004 ($H_2 = 1.63$, $P = 0.44$). The Dunn's post hoc results for 2001 indicated that juveniles had fewer ticks than females had; for 2002 and for all years combined, juveniles had fewer ticks than males or females had. For the hindlimbs, tick numbers differed among groups for each year and all years combined (all $H_2 > 7.75$, $P < 0.025$). The post hoc results for hindlimbs indicated that juveniles always had fewer ticks than males had; juveniles had fewer ticks than females had in 2002, 2003, 2004 and all years combined. Males and females had similar numbers of ticks on their hindlimbs except in 2003 and for all years combined, when males had more ticks than females had. In essence, males and females tended to have similar numbers of ticks, while juveniles had fewer ticks.

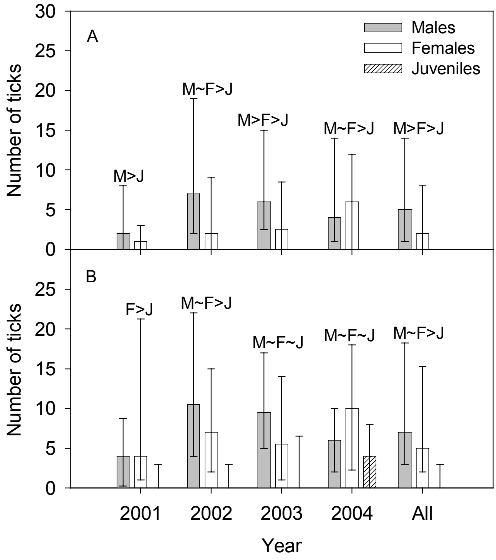

Figure 4.3 Median (± 25th and 75th percentiles) number of ticks on the hindlimbs (a), and all body parts (b) of *H. s. signatus* males, females and juveniles in 2001 to 2004. Sample sizes varied from 14–172 (males), 23–163 (females), and 2–48 (juveniles). Letters indicate post hoc results among groups (M, F and J) in a given year (Dunn's tests, $P < 0.05$).

For all years combined, some tick numbers correlated to measures of body size (SCL and SV) within each group. The numbers of ticks on male and female hindlimbs correlated positively with SCL and SV ($r_s = 0.18$ to 0.22, $P \leq 0.024$), and in juveniles tick number on the forelimbs and all body parts correlated with SCL and SV ($r_s = 0.42$–0.48, $P \leq 0.019$). Some tick numbers were also correlated with the size of shell openings (SCL - PL) in males and juveniles, but not in females. For males, the number of ticks on the hindlimbs correlated with the size of shell openings ($r_s = 0.18$, $P = 0.018$, $N = 165$), and for juveniles the numbers of ticks on the forelimbs correlated with the size of shell openings ($r_s = 0.28$, $P = 0.048$, $N = 49$). There were no other significant correlations between tick numbers and body size.

The size of the shell openings (SCL - PL) correlated with SCL for males ($y = 0.399x - 15.23$, $r^2 = 0.74$, $F_{1,75} = 214.2$, $P < 0.0001$), females ($y = 0.154x - 1.21$, $r^2 = 0.48$, $F_{1,73} = 68.6$, $P < 0.0001$) and juveniles ($y = 0.107x + 1.71$, $r^2 = 0.22$, $F_{1,39} = 11.1$, $P < 0.005$; Fig. 4.4). The slopes differed among groups (ANCOVA $F_{2,187} = 32.3$, $P < 0.0001$); the male slope was greater than female and juvenile slopes (Tukey's post hoc test, $P < 0.05$), but female and juvenile slopes did not differ from one another. Statistically, male shell openings were larger than female shell openings at SCL > 62.9 mm (Zerbe test, $P > 0.05$).

There were only a few annual effects on tick infestations. The number of ticks on the hindlimbs differed among years (all cohorts pooled; KW ANOVA, $H_3 = 9.96$, $P = 0.019$), with tick numbers being higher in 2004 than in 2001. For males, there was a weak annual effect for the number of ticks on all body parts combined ($H_3 = 8.17$, $P = 0.043$), but post hoc tests were not significant. The annual effects may have been linked to winter rainfall (March to August), which was lower in 2004 (70.6 mm) than in the earlier years (193.1, 139.5 and 117.9 mm in 2001 to 2003, respectively). The numbers of ticks on all body parts, for all groups combined, was inversely correlated with winter rainfall ($r_s = -0.14$, $P = 0.024$, $N = 249$). Additionally, for females and all groups combined, the number of ticks on the hindlimbs was inversely correlated with winter rainfall (females: $r_s = -0.16$, $P = 0.043$, $N = 162$; all: $r_s = -0.15$, $P = 0.0040$, $N = 370$).

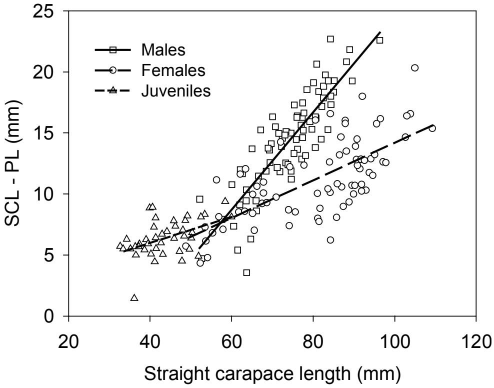

Figure 4.4 Relationship of shell opening size (estimated as straight carapace length minus plastron length, SCL - PL) to straight carapace length for male, female and juvenile *H. s. signatus*.

In 2004, the telemetered males had more ticks on their hindlimbs compared to non-telemetered males (Mann-Whitney, $T_{5,32} = 145.0$, $P = 0.028$), while telemetered females had fewer ticks on the hindlimbs compared to non-telemetered females ($T_{9,19} = 84.5$, $P = 0.025$). However, tick counts on recaptured tortoises did not differ between years (for each pair of years, Wilcoxon $W \leq 36.00$ and $P \geq 0.064$). Microhabitat had no effect on tick infestations (all KW ANOVA, $H_4 \leq 6.98$, $P \geq 0.14$) and tick numbers were not correlated with body condition (all $P > 0.3$).

4.5 Discussion

I found the soft ticks *O. compactus* and *O. savignyi* (family Argasidae) on tortoises but other tick species may also parasitise *H. s. signatus*. Ticks known from northern Namaqualand include the soft tick *Argas brumpti* (hosted by squamates and mammals), and hard ticks (family Ixodidae) *Ixodes rubicundus*, *Haemaphysalis zumpti*, *Rhipicephalus* spp., and *Hyalomma* spp. (all hosted by mammals) (Horak *et al.* 2000; Horak & Fourie 1992; Theiler 1962; Walker *et al.* 2000; IG Horak, personal communication). *Ornithodoros compactus* is a tick of tortoises, and parasitises other southern African tortoise species (*Homopus femoralis*, *Psammobates* spp.; Walton 1962). The genus *Ornithodoros* contains several other species that parasitise tortoises, such as *O. transversus* (parasitising *Chelonoidis nigra*; Robbins *et al.* 1998), *O. turicata* (parasitising *Gopherus* sp.; Kahn & Line 2005), and *O. moubata* (parasitising Testudinidae; Cumming 1998). *Ornithodoros* *savignyi* prefers mammalian hosts, especially domestic animals (e.g., cattle, sheep, goats, dogs; Cumming 1998; NR Bryson, personal communication). Bites of *O. savignyi* may result in severe toxicosis and death in animals (Kahn & Line 2005; NR Bryson, personal communication), but the effects of their bites are unknown for tortoises.

Many argasids endure the arid conditions of deserts by remaining beneath debris or the soil surface, or within burrows, for extended periods (e.g., months or years; Barnard & Durden 2000). *Ornithodoros savignyi* attacks its hosts from just below or above sandy soil (Kahn & Line 2005; NR Bryson, personal communication) and thus may access stationary *H. s. signatus* via the plastron or limbs, and probably frequently access the limbs of active tortoises. Once attached at adjacent suitable sites, this access route may contribute to the high incidence of ticks on the tortoise limbs. Ticks were not found on the thick distal scales of the limbs; perhaps for the same reason I found no ticks on the carapace or plastron. Ticks on these surfaces may become dislodged (Fielden & Rechav 1994), or have their cuticles abraded, as tortoises move through crevices, shrubs and rocky terrain.

The ticks may prefer soft skin surfaces for a combination of reasons. These surfaces are more amenable to piercing by feeding ticks, especially nymphs, due to their small size (Ernst & Ernst 1977; Robbins *et al.* 2001). Soft skin itself is inadequate for feeding without the availability of superficial vasculature. The inguinal pocket may offer a relatively stable microhabitat (temperature and humidity), little chance of abrasion or dislodging, and soft vascularised skin. Tick distributions on their hosts may also be influenced by tick pheromone signals (Fielden & Rechav 1994) and tick density (Petney & Al-Yaman 1985).

Body part differences in tick numbers may be complexly related to body size and differences in shell size and shell openings of males, females and juveniles. The correlations of tick numbers to body size for each group are probably related to increased areas of soft skin for tick attachment. Additionally, larger tortoises may move further, and encounter more ticks than smaller tortoises encounter. The relatively large shell openings of males, compared to females (SCL - PL ANCOVA and Zerbe test), help explain why males have as many or more ticks than do females. Also, the caudal opening of the shells are similar in size for both sexes (Hofmeyr *et al.* 2005), despite body size differences between males and females; the large tail of males requires large openings posteriorly, which predispose the hindlimbs to greater tick numbers. Both of these results indicate that ticks should have as much access to male soft skin as female soft skin. The juvenile pattern of tick attachment differed from adults, probably because of the small body size and small shell openings, especially posteriorly.

It is possible that different habitats influence tick infestations on chelonians (Robbins *et al.* 2001), but I found no effect of microhabitat on tick infestation. The tortoises move among the microhabitats (VJT Loehr, personal observation), obfuscating associations of tick incidences with microhabitats. Changes in a larger scale phenomenon, rainfall, may affect tick infestations, but the increased incidence of ticks in dry years was not effected through poor body condition. *Ornithodoros savignyi* is most active in dry weather, when it can move easily through the loose ground (NR Bryson, personal communication). The same is probably true for closely related *O. compactus*. In my study, increased tick infestations on tortoises in dry years may reflect higher activity of *Ornithodoros* spp. in those years. If *O. savignyi* made up much of the tick burden on *H.*

s. signatus, infestations may also reflect fluctuations in the population density of the usual tick hosts. Winter rainfall for 2003 is misleading because 87% of the rain fell late, in August. Shepherds probably altered their use of the study site in response to different rainfall and primary production (VJT Loehr, personal observation), and this may have caused *O. savignyi* to increase parasitism of *H. s. signatus* (i.e., host switching). Similarly, other tick species known from the area may have switched from decreasingly available mammalian hosts (e.g., rodents, elephant shrews, sheep, Horak *et al.* 2000; Horak & Fourie 1992; Theiler 1962; Walker *et al.* 2000; IG Horak, personal communication) to *H. s. signatus*. Although I did not evaluate population dynamics of mammals in my study site, the 2003–2004 "drought" nearly caused a local extinction of bush karoo rats (*Otomys unisulcatus*), whistling rats (*Parotomys* sp.), and striped mice (*Rhabdomys pumilio*) in nearby Goegap Nature Reserve (Schradin 2005; C Schradin, personal communication). The population densities for these rodents were still low in 2004 (C Schradin, personal communication). This effect of drought on local mammals supports the idea that host switching may explain the higher incidence of ticks on *H. s. signatus* in dry years.

5 Body condition

A revised version of this chapter was published in Journal of Arid Environments.

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.

5.1 Abstract

Homopus signatus signatus inhabits an arid region with unpredictable winter rainfall. To help understand the species' response to variation in rainfall, I measured spring body condition (BC) over five years and seasonal BC over 15 months. Total rainfall influenced BC but the timing and frequency of rain were important. In two successive years with low rainfall, BC was significantly lower in the year when most rain fell in late winter, than in the year with more frequent showers. Females tended to have a higher spring BC than males, perhaps because females nest in spring. The low spring BC of juveniles, relative to adults, may be ascribed to the juvenile shell that is less ossified than that of adults, giving juveniles a lower body mass to shell volume ratio. Seasonal fluctuations in BC were substantial; female body mass declined by 18% from summer to mid-winter but increased after the first rains to high values in spring. I compared two BC indices, the ratio of body mass to (1) carapace length and (2) shell volume. The latter index varied more among years and provides a ratio that closely approximates the body density of tortoises.

5.2 Introduction

Tortoises appear to be successful in many arid ecosystems (Ernst *et al.* 2000). Their long life-span, delayed maturity, and iteroparity imply that they have mechanisms to survive the droughts and food shortages that are characteristic of arid regions. Additionally, the tortoises' shells limit their mobility, emphasising their need to cope with adverse local conditions. The desert tortoise, *Gopherus agassizii*, can have low metabolic and water influx rates and these rates can increase considerably in response to rain (Henen *et al.* 1998; Peterson 1996a). In addition, desert tortoises are opportunistic in the acquisition of nutrients and water, allowing temporary surpluses and shortages in their energy, water and electrolyte balances (Henen 1997, 2002a; Nagy & Medica 1986; Peterson 1996a). This helps females reproduce in dry years (Henen 1997). Other terrestrial chelonians exhibit extended periods of inactivity, up to nine months per year, to overcome unfavourable climatic conditions (Lagarde *et al.* 2002; Plummer 2004).

Several studies have shown that body condition indices, based on body mass, correlate with fitness parameters such as survival (Shine *et al.* 2001) and reproduction (Dobson & Michener 1995). Body condition is associated with the reproductive output of several arid-zone tortoises

(Henen 2004; Hofmeyr *et al.* 2005; Loehr *et al.* 2004), and good body condition is critical for reproductive success of desert tortoises (Henen 1997, 2002a). Although body mass may be affected by various factors (e.g., body reserves, urinary bladder or gut contents, or reproductive state; see overview in Bonnet *et al.* 2001), body mass fluctuations help us understand the physiological responses of tortoises to arid habitats. Body condition indices are often expressed as body mass relative to a linear measure of body size, or as the residual of mass to body size (Bonnet *et al.* 2001; Hailey 2000; Jackson 1980; Keller *et al.* 1997; Schulte-Hostedde *et al.* 2005; Willemsen & Hailey 2002). Yet, body mass scaled on a linear measure of body size (usually straight carapace length in tortoises) might have limited value (Jacobson *et al.* 1993), especially when comparing animals with different mass-to-length relationships. To improve upon the unidimensional measures of body size, Nagy *et al.* (2002) accounted for group differences by using shell volume to correct for the effect of body size on body mass.

The Namaqualand speckled padloper, *Homopus signatus signatus*, inhabits the Succulent Karoo in the northwest of South Africa (Boycott & Bourquin 2000). The region is characterised by hot, arid summers and receives 20 to 290 mm of rain per year, mostly in winter. Leaf-succulents dominate the vegetation, but there are marked seasonal changes in vegetation composition, with annual forbs and geophytes emerging in winter and spring (Milton *et al.* 1997). *Homopus s. signatus* is a small tortoise and is found mostly on rock outcrops, where tortoises shelter in rock crevices or beneath vegetation (Boycott & Bourquin 2000; Loehr 2002a). This species feeds mainly on the leaves and flowers of small herbaceous plants (Loehr 2006a). Although *H. s. signatus* remains active throughout the year, it appears to be more active during the wet season than during the dry season.

The species' biology is closely linked to rainfall, but the relationship is not simple. Reproduction in females is seasonal and is related to both rainfall and body condition; females nest in late winter and spring (Boycott & Bourquin 2000). More than 73% of mature females were gravid in two successive springs when annual rainfall was below (163 mm) and above (226 mm) the annual mean (218 mm; Loehr *et al.* 2007b). In the drier year, gravid females had a higher body condition than non-gravid females (Loehr *et al.* 2004) and for both years, egg size was positively correlated with female body condition (Hofmeyr *et al.* 2005). Furthermore, annual growth rates correlate with rainfall (Loehr et al. 2007b).

Here I analyse annual variation in the body condition of male, female and juvenile Namaqualand speckled padlopers, over five successive years with a large variation in annual precipitation, to evaluate the relationship between body condition and rainfall. In addition, I evaluate seasonal variation in body condition over a 15-month period with below-average rainfall. Finally, I also assess the efficacy of two body condition indices, the ratio of body mass to (1) straight carapace length, and (2) shell volume.

5.3 Materials and methods

Each year from 2000 to 2004, I methodically searched for *H. s. signatus* over a five to six week period in spring at a 3.6 ha study site near Springbok, South Africa. The study periods were from 22 August to 22 September 2000, 5 September to 3 October 2001, 13 September to 6

October 2002, 4 September to 7 October 2003, and 2 September to 2 October 2004. For each tortoise I recorded the group (male, female or juvenile), and used digital sliding callipers to measure (to the nearest 0.01 mm) straight carapace length (SCL, midline between distal edges of the nuchal and supracaudal scutes), shell height (SH, where the shell was highest), and shell width (SW, where the shell was widest). These measures were used to estimate shell volume (SV, cm^3) with a modified formula for an ellipsoid: $SV = \pi * SCL * SH * SW / 6000$ (Loehr *et al.* 2004). I recorded field body mass (BM; ± 0.1 g, digital balance), and estimated body condition (BC) as BM / SV. Body mass was measured before the animal could urinate or defecate, but in the first year (2000) some juveniles urinated before they were weighed. I discarded body mass measurements for these individuals. From 2000 to 2002, I marked each tortoise with a unique combination of black nail polish dots on the carapace, whereas from 2003 to 2004, I notched the marginal scutes (Cagle 1939).

In September 2003, eight males and 11 females were equipped with radiotransmitters (mass < 12% of body mass; AVM Instrument Company, Ltd., Colfax, U.S.A.) to allow a "seasonal" or temporal evaluation of BC. These tortoises were tracked on 10–13 December 2003, and on 10–14 January, 11–12 February, 8–9 April, 1–2 June, 9–11 August, and 2–4 September 2004. Tortoises that died or were lost due to transmitter failure were replaced at the next opportunity. In September 2004, I removed the transmitters from the males and placed the transmitters on six additional females to track, along with the other telemetered females, on 30 October and 26–27 November 2004.

My sampling followed an independent design in spring 2000 to 2004, although radiotelemetry allowed me to use repeated measures (RM) ANOVA on a small subset of animals. In spring 2004, the BC of telemetered males and females did not differ from the BC of their non-telemetered counterparts (two-way ANOVA, $P > 0.05$). Therefore, I treated all spring values as independent samples.

Spring BC values were compared among groups and years (i.e., 2000 to 2004) using two-way analysis of variance (ANOVA). Because no data were available for juveniles in 2000, I performed two-way ANOVA on data for males and females from 2000 to 2004, and on data for all groups from 2001 to 2004. For the evaluation of seasonal changes in BC, I used a two-way ANOVA and RM ANOVA to evaluate the effects of sex and time (September 2003 to November 2004) on the BC of telemetered or opportunistically recaptured adult tortoises. All ANOVA tests were followed by Student-Newman-Keuls (SNK) post hoc comparisons.

To account for body size effects on BC, I scaled BM on SV and SCL by means of linear regression (BM on SCL regressions log-log transformed). Analysis of covariance (ANCOVA, followed by SNK post hoc tests) compared slopes and elevations of regression lines (Hofmeyr *et al.* 2005; Loehr *et al.* 2004; Zar 1999). If slopes differed, I used Zerbe tests (Loehr *et al.* 2006; Zerbe *et al.* 1982) to calculate the regions of SV or SCL where BM differed, unless regions included less than three data points of overlap (i.e., comparisons between juveniles and males or females). When regression slopes were similar and the elevations differed, I compared regression elevations using the adjusted mean Y (BM) for each group (Quinn & Keough 2002). Calculating the adjusted mean Y for each group ($Y_{g,adj} = Y_g - b_c [X_g - X_c]$) required the mean Y per group (Y_g), the common slope for all regressions combined (b_c), the covariate mean for each group (X_g) and the common covariate mean (X_c, the covariate mean of all groups combined). Data in BM on SV regressions that violated parametric assumptions were log-log transformed to meet normality and homoscedasticity assumptions before performing ANCOVA.

Records for rainfall and daily temperature data were obtained from the Springbok weather station, 2.5 km north of the study site. The topography at the weather station is similar to that at the study site. Therefore, I assumed that the site differences were insignificant. Linear regressions were used to evaluate relationships between spring BC and rainfall. I identified two rainfall periods of interest, and used simple regressions to assess if both periods had a significant effect on BC. The first period was from March to August and represented autumn and winter rainfall before the study period. Because there would be a delay before rainfall can change BC through its effect on seed germination, plant growth and foraging, I also evaluated the effects of March to July rainfall. This period was of particular importance to reflect field conditions in 2003 when most of the autumn-winter rains fell in August, just before the spring study commenced.

Mean temperatures were compared among years (January to December) and study periods by means of Friedman RM ANOVA, one-way ANOVA followed by SNK post hoc test, or Wilcoxon signed rank test. Finally, to evaluate if BC tended to change within any spring study period, I regressed BC against the date when the tortoise was captured in that spring (initial captures only, no recaptures).

ANCOVA analyses were done in Microsoft Excel (Quinn & Keough 2002; Zar 1999), and the other statistical procedures were completed in SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.); I considered differences significant at $P < 0.05$. I report BC as means and standard deviations.

5.4 Results

5.4.1 Rainfall and temperature

The annual rainfall (January to December) for all study years, except 2001, was below average for Springbok (218 mm for 1990–2004; Fig. 5.1). Rainfall was lowest in 2003, and 79% of the 2003 rain fell in one month, August. Total rainfall in 2004 was only slightly higher than in 2003, but in 2004 rainfall was distributed more evenly over several months. The March to August rainfall for each year from 2000 to 2004 was 95, 193, 140, 118 and 71 mm, respectively, and corresponding values for the March to July rainfall periods were 84, 150, 113, 15 and 58 mm, respectively. In 2001, but not in the other years, March to August and March to July rainfall exceeded the long-term averages (157 and 128 mm, respectively). Between

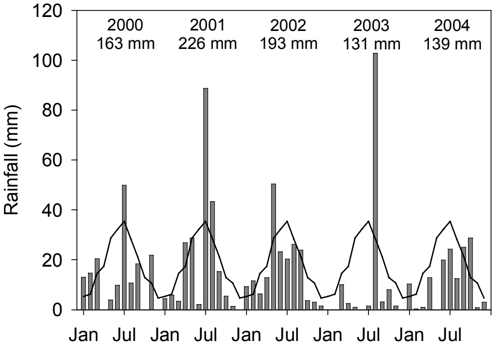

Figure 5.1 Monthly rainfall from 2000 to 2004 (bars), and long-term monthly averages (1990–2004; line), for Springbok, South Africa. Annual rainfall is also indicated for 2000 to 2004.

September 2003 and November 2004, when seasonal changes in BC were monitored, only 149 mm of rain fell (57% of the long-term average for these 15 months). Approximately 10 mm of rain fell in January 2004 (summer), a few days before locating the animals, but subsequent rainfall tended to be below average until spring 2004 (Fig. 5.1).

Daily maximum temperatures from January to December for 2000 to 2004 did not differ among years or from the 1990–1999 average (Friedman RM ANOVA $\chi^2 = 1.87$, df = 5, $P = 0.87$). Within the 2002 study period, the mean maximum temperature (24.1°C) was higher than in the other study periods (18.7, 18.5, 19.7, and 21.8°C in 2000, 2001, 2003 and 2004 respectively; one-way ANOVA, $F_{4,145} = 4.33$, $P = 0.0024$). The daily maximum temperature from September 2003 to November 2004 (mean = 23.4°C), the period when seasonal BC changes were monitored, was similar to the long-term average for this period (23.5°C; Wilcoxon signed rank test, $W = 2077$, $P = 0.71$).

5.4.2 *Body condition in spring*

Male and female *H. s. signatus* varied considerably in spring body mass (males: 74.0 ± 18.4 g, $N = 201$; females: 123.2 ± 44.7 g, $N = 196$) and shell volume (SV; males: 70.7 ± 17.7 cm^3, $N = 201$; females: 114.8 ± 41.7 cm^3, $N = 196$). The coefficients of variation (CV = SD / mean * 100%) were substantial, from 24.9 to 36.3%. Juvenile body mass (19.7 ± 7.2 g, $N = 51$) and SV (19.4 ± 7.0 cm^3, $N = 51$) also had high CV (36.8 and 36.3%, respectively).

Spring BC differed among groups ($F \geq 19.16$, df1 = 1 or 2, df2 ≥ 371, $P < 0.0001$) and years ($F \geq 5.84$, df1 = 3 or 4, df2 ≥ 371, $P \leq 0.0007$) (Fig. 5.2), but interactions between the two independent variables were not significant ($F \leq 1.82$, df1 = 4 or 6, df2 ≤ 387, $P \geq 0.094$). For all years combined, the BC of *H. s. signatus* females was higher than the BC of males, while the BC of juveniles was lower than that of the adults. The BC of male, female and juvenile *H. s. signatus* combined was lower in 2003 than in any other year.

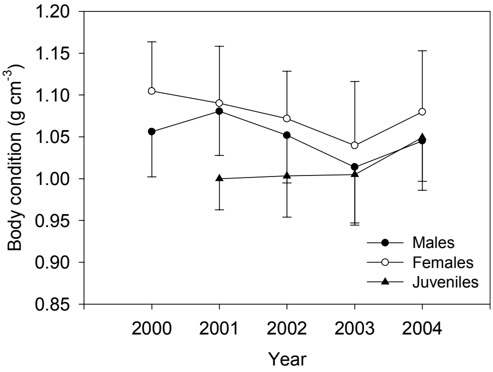

Figure 5.2 Mean body condition (± SD) for male ($N \geq 31$), female ($N \geq 30$), and juvenile ($N \geq 9$) *H. s. signatus* in spring (September–October) 2000 to 2004. For 2000, $N = 0$ for juveniles.

Analysis of covariance (ANCOVA) for regressions of BM on SV confirmed most of the ANOVA results. When the data (log-log) for all years were combined (with or without recapture data), the regression slopes of the groups did not differ, but females had higher elevations than males and juveniles had ($F \geq 8.00$, df1 = 2, df2 ≥ 225, $P < 0.001$). Within each year, groups had similar regression slopes (Table 5.1). In 2001 and 2002, however, female elevations were 6.8 to 8.5 g higher than juvenile elevations (adjusted mean BM in ANCOVA). In 2000, females had higher elevations than males (adjusted BM differed 5.6 g). The elevation for males was higher than the elevation for juveniles in 2001 (adjusted BM differed 5.3 g). In 2003 and 2004, the elevations of regression lines were similar for all groups. When comparing regression lines among years for each group, the slopes did not differ, but male and female regression lines had lower elevations in 2003 compared to all other years (Table 5.1). Adjusted BM means for males and females, respectively, were 2.5 to 4.5 g and 3.6 to 7.1 g lower in 2003. For juveniles, regression lines did not differ among years.

Table 5.1 Regression statistics (slope, intercept and coefficient of determination) for relationships between body mass and shell volume in male, female and juvenile *H. s. signatus*. All regressions were statistically significant with $F > 148.85$, df1 = 1, df2 ≥ 7, and $P < 0.001$. Regression elevations were affected by groups in 2000 to 2002 (see two columns on the right; for 2000 $t_{62} = 2.62$, $P = 0.011$; for 2001–2002 $F \geq 3.85$, df1 = 2, df2 ≥ 89, $P \leq 0.025$), and affected by years for males and females (see two rows at bottom, all; $F \geq 5.55$, df1 = 4, df2 ≥ 190, $P < 0.001$). Statistical analyses among groups in 2001 and 2002, and among years for females, were performed on log-log transformed data.

Year	Males	Females	Juveniles	Slopes	Elevations
2000	1.05, 0.34 0.96	1.06, 5.54 0.96	–	NS	F > M
2001	1.04, 2.50 0.95	1.07, 2.09 0.98	0.99, 0.11 0.98	NS	F > J, M > J
2002	0.97, 6.09 0.89	1.06, 1.44 0.97	0.93, 1.38 0.98	NS	F > J
2003	0.97, 2.93 0.93	1.00, 3.99 0.96	1.06, -0.68 0.98	NS	NS
2004	1.05, -0.27 0.97	1.02, 7.94 0.91	1.11, -1.23 0.96	NS	NS
Slopes	NS	NS	NS		
Elevations	all > 2003	all > 2003	NS		

5.4.3 Body mass and straight carapace length

For all years combined, regression slopes (log-log) of BM on SCL differed among groups (ANCOVA, $F_{2,442} = 30.45$, $P < 0.0001$; similar results were obtained when recapture data were excluded). The regression slope for females was steeper than the slopes for males and juveniles. Regression lines for males and females diverged at SCL > 60.6 mm (Zerbe test, $P < 0.05$). Within most years, regressions of BM on SCL had different slopes among groups (Table 5.2). In 2000, 2001, and 2003, female slopes were steeper than were the slopes for males, with regressions diverging at SCL of 61.6 to 66.0 mm (Zerbe tests, $P < 0.05$). In 2002, the female slope was steeper than the juvenile slope, but there was essentially no overlap between juvenile and female SCL. The regression slopes did not differ in 2004, but female regression lines had higher elevations than did the regression elevations for males and juveniles. Annual comparisons of regression lines within groups revealed very few differences (Table 5.2). Regression slopes differed among years for juveniles, but post hoc comparisons were not significant. Elevations differed only for males, with the elevations lower in 2003 than in 2001 or 2002.

Table 5.2 Regression statistics (slope, intercept and coefficient of determination) for relationships (log-log) between body mass and straight carapace length in male, female and juvenile *H. s. signatus*. All regressions were highly significant ($F > 181.95$, df1 = 1, df2 ≥ 7, $P < 0.001$). Groups had different slopes in four years (for 2000 $t_{61} = 2.01$, $P = 0.049$; for 2001–2003 $F \geq 6.28$, df1 = 2, df2 ≥ 87, $P \leq 0.0028$) and elevations in 2004 ($F_{2,76} = 46.16$, $P < 0.0001$). Male elevations differed among years ($F_{4,195} = 3.30$, $P = 0.012$).

Year	Males	Females	Juveniles	Slopes	Elevations
2000	2.59, -3.02 0.95	2.88, -3.50 0.97	–	F > M	–
2001	2.39, -2.65 0.94	2.92, -3.58 0.99	2.85, -3.43 0.96	F > M	–
2002	2.53, -2.90 0.86	2.89, -3.53 0.96	2.35, -2.61 0.97	F > J	–
2003	2.41, -2.71 0.94	2.83, -3.41 0.97	2.64, -3.08 0.97	F > M	–
2004	2.49, -2.83 0.94	2.78, -3.31 0.87	2.20, -2.34 0.96	NS	F > J ~ M
Slopes	NS	NS	[a]		
Elevations	2001 > 2003 2002 > 2003	NS	NS		

[a] Significant ANCOVA for effect of years ($F_{3,43} = 3.10$, $P = 0.037$), but post hoc tests not significant

5.4.4 Correlations with rainfall and capture date

Spring body condition correlated significantly with rainfall from March to July in males, females, and for all groups combined ($F \geq 9.34$, df1 = 1, df2 ≥ 194, $P \leq 0.003$). The correlation between body condition and rainfall from March to August was significant for males ($F_{1,199} = 7.76$, $P = 0.0059$), but not for females or all groups combined ($F \leq 1.39$, df1 = 1, df2 ≤ 446, $P \geq 0.24$). However, all relationships were weak ($r^2 \leq 0.13$). Juvenile BC in spring was not quite correlated with rainfall (March to August: $F_{1,49} \leq 3.82$, $P \geq 0.057$).

Regression results of BC scaled on capture date showed that the BC of *H. s. signatus* did not change during the 2000, 2001 and 2004 spring study periods (all $P \geq 0.14$). However, BC of all the groups combined increased 0.04 g cm^{-3} (ca. 4%) during spring 2002 ($F_{1,97} = 4.20$, $P = 0.043$, $r^2 = 0.041$; $N = 99$), and 0.07 g cm^{-3} (ca. 7%) in spring 2003 ($F_{1,109} = 8.95$, $P = 0.003$, $r^2 = 0.076$; $N =$

111). The correlation for 2003 was due mostly to BC increases for males (0.08 g cm^{-3}, ca. 8%, N = 53; regression $F_{1,51} = 5.66$, $P = 0.021$, $r^2 = 0.10$).

5.4.5 *Body condition among seasons*

The BC of male and female *H. s. signatus* appeared to change over time, being lowest in June 2004 (Fig. 5.3). Females lost about 31.7 g (18%) of their mass between January and June 2004. I used a two-way RM ANOVA on ranked data, excluding June and October 2004 because of small sample sizes for males (Fig. 5.3), to test simultaneously for BC differences between sexes and among sampling periods. Overall, there was no difference between males and females ($F_{1,128}$ = 0.15, P = 0.70) but there was a strong effect of time ($F_{7,128}$ = 7.59, $P < 0.0001$), with BC being higher in January than in September 2003, February 2004, and April 2004. The interaction term was strong ($F_{7,128}$ = 4.20, $P < 0.001$), suggesting that the relative position of BC means occasionally switched between sexes (Fig. 5.3). The two-way RM ANOVA design did not meet assumptions of normality ($P < 0.0001$) but the data met the assumptions of a two-way ANOVA design. The two-way ANOVA results confirmed that there were no BC differences between sexes ($F_{1,189}$ = 3.23, P = 0.074), that BC means changed with time ($F_{7,189}$ = 5.40, $P < 0.0001$; January BC higher than BC in September and December 2003, and February and April 2004), and that there was an interaction between the two factors ($F_{7,189}$ = 3.32, P = 0.0024). The post hoc tests within months indicated that males had, compared to females, a higher BC in February and April 2004 (SNK: $P \leq 0.011$).

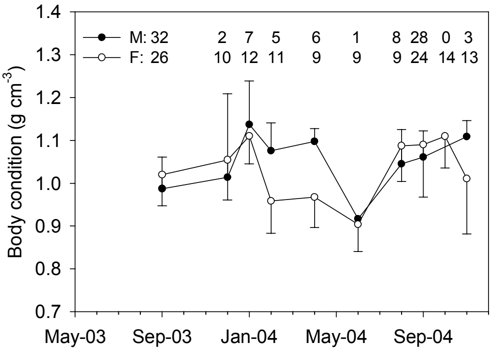

Figure 5.3 Mean monthly body condition (± SD) for male and female *H. s. signatus* between September 2003 and November 2004. Numbers in the panel represent sample sizes for males and females.

One-way RM ANOVA within each sex (data rank-transformed) allowed me to use the complete dataset for females. For females, the effect of time (sample month) was very strong ($F_{9,98}$ = 14.94, $P < 0.0001$). The BC means for all months, except February, were higher than the June BC mean. Furthermore, the four highest BC means (January, August, September and October 2004) did not differ from one another, but were higher than September 2003, and than February, April and November 2004. The December mean was higher than the means for September 2003, and February and April 2004. Data for males (rank-transformed) indicated that BC changed with time ($F_{7,51}$ = 6.31, $P < 0.0001$), but post hoc tests were not significant. The sole male measured in June 2004 had a low body condition (Fig. 5.3).

5.5 Discussion

Rainfall over the natural range of *H. s. signatus* is low and relatively unpredictable (Hofmeyr *et al.* 2005), as shown by the rainfall pattern from 2000 to 2004 (Fig. 5.1). This region has a distinct winter rainfall season and the cover of annuals and perennials reaches its highest densities in winter and spring (Le Roux & Schelpe 1997). When the rainy season starts early in autumn, seed germination and plant growth can occur over many months but if the first rains fall in mid-winter, the growth season may be short, resulting in small plants (Van Rooyen 1999) and low primary production. In many deserts, seeds require a minimum amount of precipitation for germination (ca. 26 mm in the Mojave Desert, Turner & Randall 1989). However the minimum amount required for Succulent Karoo plants has not been determined (Van Rooyen 1999). Furthermore, without "follow-up" rains to support plant growth after germination, seedling mortality can be high in desert plants (Van Rooyen 1999). Total rainfall plus rainfall frequency and timing probably influence primary production in the habitat of *H. s. signatus*. Although I did not quantify primary production, some annual contrasts were obvious. For example, the study site was densely covered with flowering annuals in September–October 2001, whereas a much smaller number of seedlings had barely initiated growth in September–October 2003.

5.5.1 Variation in body condition among spring seasons

Male and female tortoises had the lowest spring BC in the driest year, 2003, as consistently supported by ANOVA and ANCOVA. The likely cause is the low rainfall in autumn and winter 2003, and subsequent limited plant development. Although considerable rain fell in August 2003, the tortoises were unable to use this to increase their BC to the same level that I measured in other years during spring. The BC of the tortoises in September and October 2003 improved over time, probably because they consumed food plants that germinated and grew in response to the August rains. Changes in BC indices may reflect changes in the animal energy reserves (Schulte-Hostedde *et al.* 2005) or hydration state (Nagy *et al.* 2002). Because the animals would have been able to rehydrate after the August rains in 2003, the low BC in spring 2003, relative to the other years, probably reflects low energy or protein reserves (Henen 1997) due to the extended drought and lack of fresh food. In 2004, total rainfall was similar to 2003, yet tortoises had a higher BC in spring 2004. The explanation for this probably lies in the rainfall frequency; rainfall events were more evenly distributed throughout the rainfall season in 2004 than in 2003. Rainfall in the Succulent Karoo, through its effect on primary production, influenced the BC of the tortoises, but the weak correlations between rainfall and BC emphasise the complex relationship between primary production and rainfall.

The BC of the tortoises (all groups combined) also increased over the study period in spring 2002. The average maximum temperature during the 2002 study period was 2.3 to 5.6°C higher than that in 2000, 2001 and 2003, and this may have enabled tortoises to forage longer, improving their BC. In addition, higher spring temperatures may have stimulated plant growth, resulting in greater food availability.

The pattern of juvenile BC among spring seasons differed from the pattern in adults. Juvenile BC showed little annual variation, and appeared independent of rainfall (e.g., regressions of BC on rainfall were not significant). The low variation in juvenile BC among years may reflect sampling bias. Juveniles in poor condition may have had a lower level of activity compared to juveniles with higher BC, potentially lowering my chances to locate juveniles with low BC. Alternatively, I may have captured juveniles in good condition because mortality might be high for juveniles with a low BC. Mortality of juvenile desert tortoises from North America can be more than 50% per year and the survival of young tortoises is particularly threatened in dry years (Nagy *et al.* 1997).

5.5.2 Variation in spring body condition among groups

Spring is a favourable season for *H. s. signatus* because food is often readily available and ambient temperatures facilitate tortoise activity. As females nest in spring, female activity (e.g., activity time, feeding time) may facilitate rapid accumulation of reproductive mass. Males, on the other hand, may also invest time in other activities (e.g., finding mates), and this may explain the lower male BC. However, the BC difference between males and females was not strong (ca. 2 g) and the only within-year difference supported by ANCOVA results was for spring 2000.

While males and females appear to respond in a similar way to weather differences among years, the pattern for juveniles was different. For the spring seasons of 2001 and 2002, and for all years combined, males, females, or both sexes had a higher BC than juveniles. Because juvenile shells are less ossified than shells of adults, juvenile BM to SV ratios might be expected to be lower than that of adults. However, the BC of juveniles did not differ from adult BC in 2003 and 2004, the two years with the lowest rainfall. High mortality of juveniles with low BC in all years may explain these results, but the fact that some juvenile tortoises survived the poor conditions of 2003 and 2004 emphasises the ability of this species to endure its arid and unpredictable environment.

5.5.3 Seasonal variation in body condition

Large seasonal changes occurred in the BC of females, whereas the BC of males remained relatively stable except in June, but the June record was for a single male. Late rains in August 2003 and subsequent late germination of annual plants probably enabled the tortoises to maintain their BC from September to December, despite the low rainfall during this period. The small shower (10 mm) in January 2004, a few days before recapturing tortoises, may have allowed the tortoises to rehydrate and increase their BM, but there appeared to be no summer plant growth in response to this rain.

I observed an average BM loss of 18 ± 4.4% for females between January and June 2004, when virtually no rain fell except for 13 mm in April. Although this loss is quite substantial, it is much less than the losses that have been recorded for *G. agassizii* (up to 40%; Peterson 1996b). In fact, the physiology and behaviour of *H. s. signatus* may be attuned to maintain relatively stable BM through adverse conditions. It is not clear why the BC of females was lower than that of males in February and April 2004. This may be related to high activity levels of females during the dry months, when resources were scarce, but I have limited information about the activity patterns of the animals during this period.

Handling may cause desert tortoises to void and consequently decrease their survivorship (Averill-Murray 2002). I cannot exclude the possibility that the handling of females for a concurrent reproductive study may have affected their BC. While my protocol was designed to minimise stress to the tortoises, some females voided urine and may not have been able to replenish this loss. However, two opportunistically located females that I had not handled also had low body condition in February and June (0.92 and 0.80 g cm^{-3}, respectively).

Small but frequent showers from June to October 2004 stimulated plant growth and by early August, female BC increased to the same level as that of males. This increase in female BC coincided with substantial growth of vitellogenic follicles between June and October 2004 (MD Hofmeyr, BT Henen & VJT Loehr, unpublished data). Despite adverse conditions, *H. s. signatus* females reproduced each year between 2000 and 2004 (Loehr *et al.* 2004; Chapter 6).

5.5.4 Indices for tortoise body condition

In the present study, the BM to SCL regression slope for females was steeper than the slopes were for males or juveniles, in most spring seasons and for all years combined. These differences correspond to the wider, higher, and more voluminous shells in females compared to male and juvenile shells; female shells require more space to accommodate eggs (Hofmeyr *et al.* 2005; Loehr *et al.* 2006). The regression slopes for BM on SCL diverged at a small body size (SCL > 60.6–66.0 mm) indicating that SCL is not a good body size parameter to compare BC estimates among different *H. s. signatus* groups. Furthermore, when I compared BM to SCL regressions among spring seasons, I detected few differences, indicating that this ratio is less sensitive than the BM to SV ratio.

A BC index based on a one-dimensional measure of shell size can be plagued by high variation, non-linearity and incompatibility among groups (e.g., see Jacobson *et al.* 1993). Nagy *et al.* (2002) accounted for group differences by using SV rather than a one-dimensional measure to correct for the effect of body size on BM. Because the approximation of Nagy *et al.* (2002; SCL x SW x SH) overestimates the volume of the animal, the ratio of BM to SV (ca. 0.64 g cm^{-3}) does not approach a realistic density value (i.e., BM / SV ratio) for tortoises. My estimate of SV, based on a modified formula for an ellipsoid, provides a more reasonable estimate of body size because the BM to SV ratio of *H. s. signatus* approximates body densities of desert tortoises and pond turtles, 1.17 and 1.13 g cm^{-3}, respectively (Henen 1997, 2001; Loehr *et al.* 2004). The efficacy of this formula should be evaluated for other chelonian species.

6 Reproduction

6.1 Abstract

Tortoises are long-lived and require considerable amounts of nutrients for their iteroparous reproduction, yet many tortoise species inhabit ranges that are prone to droughts and resource limitations. Rainfall affects the growth rate and body condition of *Homopus signatus signatus*, a small, arid-zone tortoise that produces single-egg clutches in spring, while female body size and body condition affect egg size. To identify reproductive responses to variation in rainfall and to understand interactions among egg size, body size, body condition and rainfall, I studied egg production during five spring seasons. The percentage of females that were gravid differed among years and correlated with rainfall in the months prior to egg-laying. Gravid females had a higher body condition than non-gravid females had, presumably as a result of individual variation in the acquisition of resources causing some females to forfeit reproduction. Average egg size was similar among years, and egg volume represented up to 11.9% of female shell volume. The adult shell is somewhat flexible dorso-ventrally, and this may help females accommodate the large egg, as indicated by the larger shell height and volume in gravid females compared to non-gravid females. Egg width typically exceeded pelvic width, so females require morphological and physiological adjustments to the pelvis and shell during oviposition. It appears that large eggs have a selective advantage for *H. s. signatus*, possibly through the production of large hatchlings that can survive in their arid environment. Egg size did not quite correlate to maternal body size in dry years, when other determinants such as body condition seemed to outweigh the influence of body size. Since the range of *H. s. signatus* is threatened with aridification, the frequency of dry years with reduced production of large hatchlings may increase in the next decades. These impacts may challenge the long-term survival of populations.

6.2 Introduction

Iteroparous species need to cope with resource variability among reproductive bouts, and have developed various approaches to accommodate the great nutritional demands of reproduction to the amount of resources available. Examples of reproductive responses to resource variability among a wide variety of taxa include females adjusting clutch or litter size in reptiles (Seigel & Fitch 1985; Znari *et al.* 2002), mammals (Kenagy & Bartholomew 1985) and birds (Patten & Rotenberry 1999), changing the number of broods in reptiles (Ballinger 1977) and mammals (Kenagy & Bartholomew 1985), and producing different sizes of offspring in isopods (Brody & Lawlor 1984) and birds (Hipfner *et al.* 2005). Ultimately, reproductive strategies also involve trade-offs with other life history traits, such as offspring fitness and female survival.

Tortoises are long-lived, may produce eggs over several decades (Kuchling 1999), and many tortoise species inhabit regions where droughts may cause resource shortages (Ernst *et al.* 2000). Tortoises are mainly herbivorous, so their food availability is linked to rainfall through its promotion of plant growth. Tortoises use different reproductive strategies to cope with rainfall variability. For example, radiated tortoises, *Astrochelys radiata*, reduce clutch size in a dry year (Leuteritz & Ravolanaivo 2005) whereas desert tortoises, *Gopherus agassizii*, produce fewer clutches in response to low rainfall (Henen 1997; Turner *et al.* 1986). Desert tortoises endure an arid, unpredictable environment, and their physiology enables them to bet-hedge, producing some eggs even in drought years (Henen 1997; Turner *et al.* 1984).

The Namaqualand speckled padloper (*Homopus signatus signatus*) is a small, herbivorous tortoise occurring in the arid northwest of South Africa, where it is restricted to rocky terrain (Boycott & Bourquin 2000). This region is characterised by winter rainfall, and the amount of rain may fluctuate substantially among years (Milton *et al.* 1997). Female speckled padlopers produce single-egg clutches in spring, towards the end of the rainfall season, and thus do not adjust clutch size in response to resource availability (Hofmeyr *et al.* 2005; Loehr *et al.* 2004). Egg size correlates positively with body condition, which in turn is affected by rainfall (Hofmeyr *et al.* 2005; Loehr *et al.* 2007a). Egg size, and perhaps fecundity, is affected by female body size (Hofmeyr *et al.* 2005; Loehr *et al.* 2004, 2007b), and possibly by female shrinkage in drought years (Hofmeyr *et al.* 2005; Loehr *et al.* 2004, 2007b).

Long-lived organisms require long-term investigations to understand their reproductive patterns and the factors that affect their demography (Congdon *et al.* 1993, 1994). Loehr *et al.* (2004) presented a baseline for *H. s. signatus* reproductive parameters (e.g., female size at maturity, clutch size, egg size) and elaborated on the taxon's vitellogenic cycle, while Hofmeyr *et al.* (2005) focused on the relationships between body size, climate and reproductive output in southern African tortoises. Consequently, we do not yet understand the complex interactions among *H. s. signatus* egg size, body size, body condition and rainfall. Here I present data on egg production in *H. s. signatus* females over five successive spring seasons, with different levels of rainfall, to evaluate the females' reproductive response to variation in rainfall. In particular, I tested if rainfall or body condition affected female reproductive status (i.e., gravid or not gravid). Furthermore, I examined the relationships between egg size, female body size and body condition, and tested if these relationships culminated in variation in average egg sizes among years.

6.3 Materials and methods

6.3.1 Study design and field measurements

In each spring from 2000 to 2004, a 3.6 ha study site (see Loehr 2002a for a site description) was inspected for tortoises daily by two to five persons. Fieldwork occurred from 29 August to 21 September 2000, 7 September to 1 October 2001, 13 September to 7 October 2002, 5 September to 7 October 2003, and 2 September to 30 September 2004. For the first encounter of a female in a study period, I used digital sliding callipers to measure, to the nearest 0.01 mm, the straight carapace length (SCL, midline distance at the nuchal and supracaudal scutes), shell height (SH, where the shell was highest), shell width (SW, where the shell was widest), and plastron length (PL, midline distance at the gular and anal scutes). These parameters were used to estimate shell volume (SV, cm^3) for each individual through a modified formula for an ellipsoid: SV

= π * SCL * SH * SW / 6,000 (Loehr *et al.* 2004, 2006, 2007a,b). I recorded female body mass (BM, digital balance, to the nearest 0.1 g) on every capture, and I used the largest mass in a study period in all calculations. Female body condition (BC) was estimated as BM / SV. Ratios have drawbacks statistically (e.g., ratios are not always distributed normally, Sokal & Rohlf 1981) and misusing them can obfuscate important allometric results (Packard & Boardman 1987). Consequently, I also used the residuals of significant BM to SV regressions (BM residuals) as a body condition index (Clark *et al.* 2001; Hofmeyr *et al.* 2005). Each female was marked uniquely with combinations of black nail polish dots on the carapace (2000 to 2002), or by notching the marginal scutes (2003 and 2004; Cagle 1939).

I used thread-trailing to follow five to 13 females daily for one to four weeks throughout each study period from 2000 to 2002 (Loehr 2002a, 2004b). The thread-trailing device always weighed less than 10% of BM. In spring 2003, 11 females were equipped with radiotransmitters (transmitter mass < 11% of BM; AVM Instrument Company, Ltd., Colfax, CA, U.S.A.) and tracked daily throughout the spring 2003 and 2004 study periods. Three telemetered females were lost and replaced by others at the next opportunity.

6.3.2 Reproductive parameters

Homopus s. signatus can produce eggs at a SCL of 84.1 mm (Loehr *et al.* 2004). To verify the minimum size for reproduction, I evaluated the reproductive status of each female with SCL 75 mm or larger. Evaluation occurred by radiography (2000 to 2004). Females were radiographed dorso-ventrally (50 kV for 0.25 s at 50 mA; one to five tortoises on each radiograph) at the first encounter in a study period and when recaptured a week or longer after the previous capture date. Additionally, thread-trailed or telemetered tortoises were radiographed when their BM decreased substantially from one day to the next. On 21 and 22 September 2000, four *H. s. signatus* that had not been radiographed were scanned ultrasonographically (PIE 100 Veterinary Ultrasound scanner, curvilinear intravaginal probe; Philips, Maastricht, Netherlands) to determine if they contained eggs.

Radiographs were used to (1) assess if a female contained a shelled egg, (2) qualitatively assess the level of eggshell calcification, and (3) measure, to the nearest 0.5 mm, egg length (EL), egg width (EW) and the width of the pelvic canal (PW). Calcification was assessed qualitatively as one of three categories: lightly calcified (eggshell faint on the radiograph), heavily calcified (eggshell light-coloured and easily visible), or as intermediate calcification. There were eleven instances where gravid tortoises were radiographed twice in a study period. For eight females radiographed twice, daily BM measurements suggested the female did not lay the egg between radiographs (i.e., both radiographs showed the same egg). Sequential radiographs for two females showed progressive calcification of the eggshell, again indicating the same egg appeared in consecutive radiographs. For one female, the egg was less calcified on the second radiograph than on the first radiograph, so these were treated as two different clutches.

For multiple measurements of the same egg, I always used the largest values of EL and EW because egg size cannot be overestimated, but it can be underestimated when the egg's long axis is not parallel to the film plane (EL), or when the egg is asymmetrical in cross-sectional width (EW; although *H. s. signatus* eggs do not seem to show this asymmetry, Hofmeyr *et al.* 2005). The average differences between successive measurements of the same egg were 2.4% (EL) and 0.9% (EW). To be consistent, I also used the largest value for PW (average difference between measurements 3.2%).

Measurements of EL, EW and PW taken from radiographs were converted to actual dimensions by multiplying them with the ratio of PL to PL measured on the radiograph (Loehr *et al.* 2004). In this conversion, ratios were averaged for all tortoises on a given radiograph to obtain robust values, and to enable calculation of egg and pelvic canal dimensions of individuals for which radiograph PL could not be measured reliably. I used calculated egg dimensions to estimate egg volume (EV) for non-spherical eggs (Coleman 1991): $EV = \pi * EL * EW^2 / 6$ (cm^3). In addition, I calculated egg volume relative to female BM ($REV_{BM} = EV / BM$) and relative to female SV ($REV_{SV} = EV / SV$).

6.3.3 *Data analysis and statistics*

Although my sampling design was independent from 2000 to 2003, the 2004 sample contained eight (28%) telemetered females. These females had a larger SCL and SV than non-telemetered females had in 2004 (96.7 versus 90.2 mm, and 154.3 versus 124.1 cm^3, respectively; *t*-tests $t_{26} \geq 3.03$, $P \leq 0.0054$), but when they were combined with the non-telemetered females, SCL and SV of the 2004 sample did not differ from the other years (one-way ANOVA, $F \leq 0.83$, df1 = 4, df2 $\leq$ 145, $P \geq 0.51$). Therefore, I treated the combined 2004 sample as an independent sample in statistical analyses, and used repeated measurements (RM) tests for females captured in two or more years, when sample size allowed.

For each year, I calculated the percentage of females that were gravid, compared percentages by means of χ^2 tests, and correlated the percentages to rainfall. Rainfall data were provided for the Springbok weather station, 2.5 km north of the study site, by the South African Weather Services. I used rainfall from September to July for the test, based on the following considerations. Somatic growth in *H. s. signatus* appears to lag two months behind rainfall (Loehr *et al.* 2007b) and a similar lag may affect the beginning and end of the reproductive season. Ultrasound scanning showed that *H. s. signatus* females were gravid from September to November 2003 (MD Hofmeyr, BT Henen & VJT Loehr, unpublished data). Rainfall from September onwards may be channelled towards the reproductive investment of the next breeding season, instead of the current breeding season, and rainfall up to July probably influenced the percentage of females that become gravid by September. I also correlated the annual percentage of females that were gravid to the BC index and BM residuals to determine if body condition influenced the number of females that was gravid in a year. Within each year, I correlated the cumulative percentage of females that were gravid to the time (days) since the first female was radiographed, to serve as an index of the rate at which females became gravid. I used analysis of covariance (ANCOVA, followed by Student-Newman-Keuls or SNK post hoc tests) to compare the slopes and elevations of regression lines (Zar 1999), and to determine whether regression patterns differed among years.

Homopus s. signatus is an ectotherm, so the accumulation of reproductive mass towards, and the onset of, the egg-laying season may be influenced by environmental temperatures. This is particularly relevant for the cooler autumn and winter months, so I compared daily maximum temperatures for April to August (follicle development towards the next breeding season) and August (start of egg production), by means of Friedman RM ANOVA, followed by SNK post hoc tests. Temperatures were for the Springbok weather station.

I calculated averages for gravid and non-gravid female body dimensions, BM, and body condition (BC and BM residuals) in all years. Gravid and non-gravid averages were compared among years by two-way ANOVA, followed by SNK post hoc tests. Samples of SH and SV required log-transformation to meet parametric assumptions. Because SH and SW were correlated to SCL, I compared SH and SW differences among years and between groups (i.e., gravid and non-gravid) by means of ANCOVA. In addition, I compared gravid and non-gravid body condition using regressions of BM to SV, for each year. The latter comparisons were repeated after subtracting egg mass (assuming a density of 1 g cm^{-3}) from gravid female BM. If ANCOVA indicated significant slope differences, I determined the region of X (SV) where slopes differed from one another (Zerbe *et al.* 1982). For regression elevations that differed significantly, I compared elevations using the adjusted mean Y (BM) for each group (Loehr *et al.* 2007a; Quinn & Keough 2002).

Average egg dimensions, REV_{BM}, REV_{SV} and the difference between EW and PW were compared among years by means of one-way ANOVA and one-way RM ANOVA. The percentage of females for which EW exceeded PW was compared among years with a χ^2 test. I also correlated egg dimensions (i.e., EL, EW and EV) to body size (SCL or SV) and compared regressions among years using ANCOVA. Relationships between EW, PW and SCL were analysed by regression analysis and ANCOVA for all years pooled. Because body mass and egg size are correlated to female size (SV), a simple correlation of egg size to body condition (mass) represents multicollinearity. Consequently I used a residual analysis, with SV as the covariate, to evaluate if body condition (body mass residual) influenced the egg size (EV residual) (Hofmeyr *et al.* 2005). Subsequently, regressions between EV and BM residuals were compared among years (ANCOVA). Egg width and PW were also both correlated to female body size (SCL), so I used residual analysis (SCL as covariate) to correlate EW (residuals) to PW (residuals). Because it was ambiguous labelling EW residuals or PW residuals as dependent or independent variables, I assessed this relationship by means of Pearson's correlation (r_p).

ANCOVA analyses and χ^2 tests were done in Microsoft Excel (Quinn & Keough 2002; Zar 1999), and the other statistical procedures were completed in SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.); I considered differences significant at $P < 0.05$.

6.4 Results

The study duration, 2000 to 2004, was characterised by large variation in rainfall. Annual rainfall was below the long-term average (1990–2004, 218 mm) for all years except 2001 (Fig. 6.1). The year 2003 was driest, with 79% of the annual rains falling in August, just before the 2003 study period. The amount of rain that fell from 2000 to 2004, respectively, was 208, 200, 156, 47 and 82 mm for September to July, 141, 182, 141, 23 and 78 mm for October to July, and 130, 182, 136, 20 and 70 mm for November to July. Although I did not measure primary production, vegetation was most lush, with many flowering annuals, in September–October 2001, and poorest, with few annuals germinating, in September–October 2003.

Daily maximum temperature from April to August for 2001 was 0.5–2.2°C lower than were temperatures for the same period in the other years (Friedman RM ANOVA χ^2 = 11.73, df = 4, P = 0.019). Furthermore, daily maximum temperature in August 2000 was 3.5–6.8°C higher than August temperatures in the other years (Friedman RM ANOVA χ^2 = 16.48, df = 4, P = 0.0024).

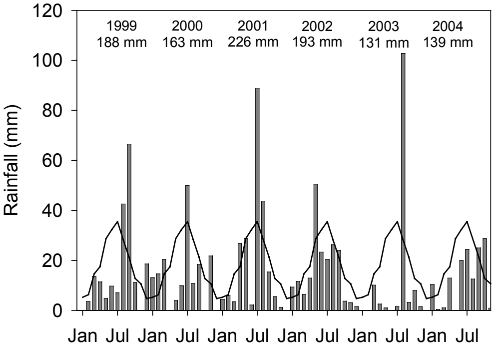

Figure 6.1 Monthly rainfall from 1999 to 2004 (bars), and long-term monthly averages (1990–2004; line), for Springbok, South Africa. Annual rainfall is indicated for 1999 to 2004.

The smallest female that contained a shelled egg had a SV of 89.4 cm^3 (SCL, SH and SW = 81.2, 35.1 and 59.9 mm, respectively). Data for smaller females were not included in subsequent analysis. The measurements of the smallest gravid female relative to values of SV, SCL, SH and SW for the largest female were 40, 74, 73 and 74%, respectively.

6.4.1 Gravid females

The reproductive status of 65% (40 of 62) of *H. s. signatus* females was assessed in more than one year (Table 6.1). One female was gravid in five successive years. The percentage of females that were gravid differed among years. From 2000 to 2004, the percentages were 72, 75, 65, 36, and 50%, respectively (χ^2 = 13.96, df = 4, P = 0.0074). This difference weakened when the year with the lowest percentage of gravid females (2003) was removed (χ^2 = 6.63, df = 3, P = 0.085).

Table 6.1 The number and status of *H. s. signatus* females assessed during one or more years over the five-year study period.

Assessed in	Total	Gravid in					
		0 years	1 year	2 years	3 years	4 years	5 years
5 years	7	0	1	1	1	3	1
4 years	7	0	2	1	2	2	
3 years	13	2	0	10	1		
2 years	13	6	5	2			
1 year	22	9	13				

Annual percentages of gravid females correlated positively with rainfall from September to July (linear regression, $F_{1,3} = 92.76$, $P = 0.0024$, $r^2 = 0.97$). The percentages did not correlate with average BC in each year, although the relationship had a strong correlation coefficient (linear regression, $F_{1,3} = 5.54$, $P = 0.10$, $r^2 = 0.65$). When I used average BM residuals as the body condition measure, calculated from a BM to SV regression using all of the data, the correlation seemed to strengthen ($F_{1,3} = 6.85$, $P = 0.079$, $r^2 = 0.70$) despite the small sample size.

Within each study period, the cumulative percentage of females that were gravid increased over time and correlated with my number of days in the field (linear regressions, $F \geq 51.27$, df1 = 1, df2 ≥ 5, $P < 0.001$). The annual regression lines differed from one another. The regression slopes were similar (ANCOVA, $F_{4,29} = 0.56$, $P = 0.69$), but the elevations for 2000 and 2002 were higher than in the other years, while the elevations for 2001 and 2004 exceeded the elevation for 2003 ($F_{4,33} = 20.36$, $P < 0.001$).

6.4.2 Gravid versus non-gravid females

Gravid and non-gravid females had similar mean SCL and SW (two-way ANOVA, $F \leq 2.89$, df1 = 1, df2 ≤ 140, $P \geq 0.091$), but SH, SV and BM were larger in gravid than in non-gravid females (Table 6.2). Post hoc results within years indicated that SH and BM differed between gravid and non-gravid females in 2000, whereas post hoc results for SV were not significant for any year. None of the parameters differed among years, but female size spanned a broad range. Scaled on SCL, SW of gravid and non-gravid females was similar in each year and for all years combined (ANCOVA slopes and intercepts, $F \leq 1.55$, df1 = 1, df2 ≤ 124, $P \geq 0.11$). The regression for SH on SCL was not significant in 2000, but elevations of regression lines for gravid females exceeded those for non-gravid females in 2002 and for all years combined (ANCOVA, $F \geq 2.87$, df ≥ 31, $P \leq 0.0073$). Significant regressions for SW or SH did not differ among years (ANCOVA slopes and intercepts, $F \leq 1.90$, df1 ≤ 4, df2 ≤ 80, $P \geq 0.12$).

Table 6.2 Means, standard deviations, and ranges of shell dimensions, body mass (BM, g), body condition (BC, g cm^{-3}), and BM residual (g) of gravid and non-gravid female *Homopus s. signatus* from 2000 to 2004. Sample sizes are italicised. Shell dimensions include straight carapace length (SCL, mm), shell height (SH, mm), shell width (SW, mm), and shell volume (SV, cm^3). None of the shell size parameters or BM differed among years[@], but SH, SV and BM were larger in gravid than in non-gravid females[#]. Body condition and BM residual were larger in gravid than in non-gravid females, and larger in 2001 than in 2003[&].

	2000	2001	2002	2003	2004
Non-gravid	*7*	*6*	*12*[$]	*25*[$]	*14*[$]
SCL	89.51 (5.22)	90.93 (2.87)	92.34 (4.84)	90.43 (6.13)	92.40 (5.43)
	84.80–99.30	87.90–95.58	83.98–102.67	78.20–102.62	83.64–104.61
SH	37.81 (2.94)	39.52 (3.09)	39.31 (2.41)	39.50 (3.01)	39.78 (2.63)
	33.10–40.90	35.19–44.10	36.11–43.36	35.67–46.24	35.76–43.97
SW	66.79 (6.15)	67.30 (4.81)	68.52 (3.41)	67.99 (4.55)	68.52 (4.30)
	60.80–77.70	62.51–75.97	62.14–73.75	59.69–77.15	60.14–75.70

Table continues on next page

	2000	2001	2002	2003	2004
Table 6.2 continued from previous page					
SV	119.43 (23.95)	127.54 (22.76)	130.94 (18.98)	128.50 (25.59)	132.94 (22.60)
	90.68–158.77	105.84–167.67	103.59–170.00	92.66–186.23	95.97–182.32
BM	128.79 (20.67)	141.38 (16.40)	138.95 (25.66)	137.42 (25.22)	136.32 (25.88)
	103.80–161.10	122.30–163.90	108.50–193.40	83.30–198.70	107.10–194.10
BC	1.09 (0.05)	1.12 (0.09)	1.06 (0.06)	1.06 (0.10)	1.06 (0.09)
	1.01–1.14	0.98–1.21	0.94–1.14	0.83–1.31	0.91–1.21
BM residual	-3.27 (4.45)	1.36 (10.84)	-4.24 (9.04)	-5.30 (10.85)	-4.90 (11.15)
	-9.62–1.29	-15.57–12.33	-19.59–11.63	-29.57–20.36	-24.17–16.52
Gravid	*18*	*18*	*22*[$]	*14*[$]	*14*
SCL	93.29 (6.34)	94.16 (6.88)	92.28 (6.48)	91.04 (5.59)	91.68 (6.48)
	84.10–110.00	86.50–109.27	81.72–106.06	81.17–102.28	82.07–102.85
SH	40.75 (2.84)	40.81 (2.99)	41.11 (2.97)	40.45 (2.91)	39.86 (2.52)
	36.70–48.00	37.27–47.16	36.56–49.16	35.10–45.18	35.39–45.10
SW	69.72 (4.91)	69.75 (5.78)	69.00 (4.74)	69.64 (4.95)	68.50 (5.65)
	60.70–81.40	60.46–83.07	62.06–77.05	59.90–77.35	57.99–76.17
SV	140.42 (29.33)	142.28 (32.30)	138.72 (28.81)	135.50 (24.41)	132.46 (25.91)
	101.30–225.04	105.62–224.14	99.07–210.35	89.36–179.28	88.19–182.85
BM	158.04 (31.61)	160.08 (31.10)	148.29 (25.42)	148.02 (18.39)	150.69 (29.48)
	113.10–240.90	110.50–230.90	114.20–203.80	118.80–177.80	97.40–211.70
BC	1.13 (0.07)	1.13 (0.08)	1.10 (0.06)	1.07 (0.07)	1.14 (0.06)
	1.03–1.26	1.03–1.25	0.98–1.21	0.95–1.20	1.05–1.25
BM residual	5.35 (9.19)	5.56 (9.16)	0.11 (8.19)	-3.32 (8.48)	5.83 (8.60)
	-8.36–26.81	-8.55–23.17	-15.08–17.04	-19.29–12.07	-4.89–20.53

[$] Sample sizes for BM, BC and BM residual of non-gravid females in 2002, 2003 and 2004 were 11, 23 and 11, respectively. Sample sizes for the BM, BC and BM residuals of gravid females in 2002 and 2003 were 20 and 13, respectively.

[@] Two-way ANOVA, $F \leq 0.43$, df1 = 4, df2 ≤ 140, $P \geq 0.79$.

[#] Two-way ANOVA, $F \geq 4.43$, df1 = 1, df2 ≥ 128, $P \leq 0.037$.

[&] BC: Two-way ANOVA, factor Year, $F_{4,131} = 2.60$, $P = 0.039$; factor Gravid/Non-gravid, $F_{1,131} = 7.00$, $P = 0.0092$; interaction, $F_{4,131} = 0.83$, $P = 0.51$. BM residual: Two-way ANOVA, factor Year, $F_{4,131} = 2.57$, $P < 0.041$; factor Gravid/Non-gravid, $F_{1,131} = 12.24$, $P < 0.001$; interaction, $F_{4,131} = 0.97$, $P = 0.42$.

The mean BC and BM residual (calculated from annual regressions of BM to SV) differed between gravid and non-gravid females, and among years (Table 6.2). Post hoc tests indicated that gravid females had a higher BC and BM residual than non-gravid females had, particularly in 2000 (BM residual) and 2004 (BC and BM residual). BC and BM residuals were lower in 2003 than in 2001. Regressions of BM on SV showed that gravid females were heavier than were non-gravid females in 2000, 2004, and for all years combined (i.e., regression elevations were 8.3, 10.5 and

7.2 g higher, respectively; ANCOVA, $F \geq 2.63$, df ≥ 22, $P \leq 0.048$). Regression lines for non-gravid females were similar among years (ANCOVA slopes and elevations, $F \leq 1.64$, df1 = 4, df2 ≤ 52, $P \geq 0.18$), whereas regression lines of gravid females had lower elevations in 2003 than in 2000 and 2001 (8.7 and 8.9 g lower, respectively; ANCOVA, $F_{4,77} = 3.29$, $P = 0.015$).

When BM minus egg mass was scaled on SV, the 2000 and 2004 differences between gravid and non-gravid females disappeared (ANCOVA slopes and elevations, $F \leq 0.84$, df1 = 1, df2 ≤ 22, $P \geq 0.37$). For 2002, the regression slope of non-gravid females was steeper than was the regression slope of gravid females (ANCOVA, $F_{1,28} = 4.47$, $P = 0.044$), and lines diverged at BM > 135.7 g (Zerbe test, $P < 0.05$). For 2003 and for all years combined, regression elevations were higher for non-gravid than for gravid females (8.4 and 3.9 g higher, respectively; ANCOVA, $F \geq 5.69$, df1 = 1, df2 ≥ 33, $P \leq 0.020$). The annual difference within gravid females persisted, but the regression elevation was lower in 2003 than it was in 2000, 2001 and 2004 (9.7, 9.2 and 8.8 g lower, respectively; ANCOVA, $F_{4,76} = 3.80$, $P = 0.0072$).

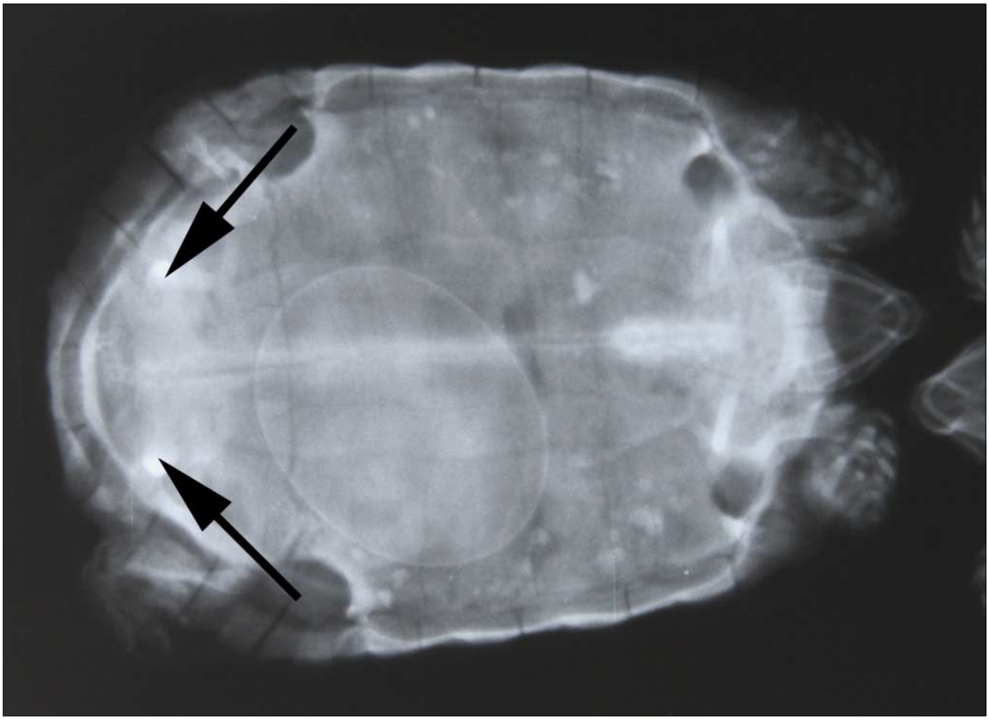

Figure 6.2 X-ray radiograph of gravid female *H. s. signatus* demonstrating the large egg relative to body size (egg length is 34.3 mm). The arrows indicate the locations where I measured the width of the pelvic canal.

6.4.3 Egg size

Egg size was large compared to the body size of gravid females (Fig. 6.2). On average, EL represented 38, 86 and 49%, and EW 27, 61 and 35%, of SCL, SH and SW, respectively. Egg volume averaged 8.3% of female SV (REV$_{SV}$), and 7.5% of BM (REV$_{BM}$). Mean egg dimensions were similar among years for randomised block ANOVA (Table 6.3), and for repeated measures analyses for females gravid in two or more years (one-way RM ANOVA, $F \leq 2.20$, df1 = 4, df2 $\leq$ 37, $P \geq 0.089$).

Egg width correlated with female SCL, but only in 2000, 2001, 2002 and for all years combined (linear regressions, $F \geq 18.34$, df1 = 1, df2 $\geq$ 14, $P < 0.001$). Regression slopes and elevations were similar among years (ANCOVA, $F \leq 0.77$, df1 = 2, df2 $\leq$ 53, $P \geq 0.50$). In addition, EV correlated with SV over all years and for each year, except 2004 (linear regressions, $F \geq 5.74$, df1 = 1, df2 $\geq$ 12, $P \leq 0.034$; for 2004: $F_{1,12} = 2.21$, $P = 0.16$), with similar regression slopes and elevations among years (ANCOVA, $F \leq 0.60$, df1 = 3, df2 $\leq$ 66, $P \geq 0.62$). EL did not correlate to SCL in any year or for all years combined ($F \leq 2.64$, df1 = 1, df2 $\leq$ 83, $P \geq 0.13$) although the analysis for 2000 was close to the criterion ($F_{1,14} = 4.50$, $P = 0.052$).

Table 6.3 Means, standard deviations, and ranges of eggshell dimensions in *H. s. signatus* from 2000 to 2004. Egg dimensions include egg length (EL, mm), egg width (EW, mm), egg volume (EV, cm^3), egg volume relative to female body mass (REV$_{BM}$, %), egg volume relative to female shell volume (REV$_{SV}$, %) and EW minus pelvic width (EW - PW, mm). None of the parameters differed among years[@]. Sample sizes are presented in italics.

	2000	2001	2002	2003	2004
	16[#]	*18*[#]	*23*[#]	*14*[#]	*14*[#]
EL	34.96 (1.53)	34.24 (2.19)	35.54 (2.37)	34.06 (2.38)	34.86 (2.11)
	32.28–38.91	30.74–38.34	31.82–43.03	29.14–37.27	31.70–38.21
EW	24.75 (1.55)	25.09 (1.65)	24.94 (1.46)	25.04 (1.68)	25.00 (2.09)
	22.20–27.35	22.40–28.62	22.78–27.52	22.72–27.96	19.32–27.71
EV	11.27 (1.67)	11.36 (1.88)	11.64 (1.80)	11.26 (1.89)	11.52 (2.17)
	8.97–14.42	8.37–15.37	8.83–14.68	7.87–14.10	6.19–14.99
REV$_{BM}$	7.19 (0.67)	7.18 (0.89)	8.06 (1.23)	7.81 (1.16)	7.80 (1.64)
	5.93–8.57	5.82–8.75	5.05–10.38	5.85–10.48	5.14–10.86
REV$_{SV}$	8.15 (0.89)	8.15 (1.24)	8.86 (1.28)	8.38 (1.54)	8.86 (1.82)
	6.41–9.57	6.17–10.61	5.47–10.86	6.15–11.88	5.95–11.75
EW - PW[$]	1.85 (1.26)	2.25 (1.31)	1.96 (1.31)	1.34 (2.23)	2.08 (2.02)
	-1.00–2.99	0.50–4.23	0.50–5.01	-2.96–3.50	-1.51–5.53

[#] Sample sizes for REV$_{BM}$ and REV$_{SV}$ in 2002 and 2003 are 21 and 13, respectively, and for PW - EW 15, 15, 20, 12 and 14, from 2000 to 2004, respectively.

[@] EL, EW and EV: One-way ANOVA, $F_{4,80} \leq 1.42$, $P \geq 0.23$; REV$_{BM}$ and REV$_{SV}$: One-way ANOVA, $F_{4,77} \leq 2.19$, $P \geq 0.078$; EW - PW: One-way ANOVA, $F_{4,71} = 0.58$, $P = 0.68$.

[$] EW exceeded PW in 14, 15, 20, 9 and 12 females, in 2000 to 2004, respectively.

Significant regressions of EV on SV and BM on SV allowed scaling of EV residuals on BM residuals for 2000 to 2002, to evaluate the effect of female body condition on EV. The 2003 regression of EV on SV was not significant after removing a data point for which no BM value was available in the corresponding BM on SV regression. Regressions of EV residuals on BM residuals were significant in 2000 and 2001 ($F \geq 4.79$, df1 = 1, df2 ≥ 14, $P \leq 0.044$), but not in 2002 ($F_{1,19}$ = 0.31, P = 0.58). The 2000 and 2001 regressions did not differ from one another (ANCOVA, $F \leq 0.051$, df1 = 1, df2 ≤ 30, $P \geq 0.82$).

In 2001 and 2002, EW exceeded PW in all females. In 2000, 2003 and 2004, EW exceeded PW in 93, 75 and 86% of the females, respectively (Table 6.3). Annual percentages did not differ significantly (χ^2 = 8.65, df = 4, P = 0.071). In all years, EW exceeded PW by about 5 to 9% (Table 6.3). However, EW ranged from 3.0 mm narrower to 5.5 mm wider than PW. Both EW and PW were correlated to SCL (Fig. 6.3), and regression lines had similar slopes (ANCOVA, $F_{1,148}$ = 0.0034, P = 0.95). The elevations of the regressions differed, EW being 1.95 mm (8.4% of PW) larger than was PW (Fig. 6.3).

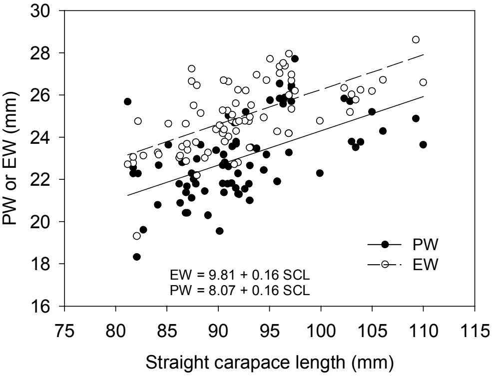

Figure 6.3 Relationships between egg width (EW), the width of the pelvic canal (PW), and straight carapace length of *H. s. signatus*. Linear regressions were significant ($F_{1,74} \geq 31.87$, $P < 0.001$, $r^2 \geq 0.30$) and regression elevations differed (ANCOVA, $F_{1,149}$ = 68.36, $P < 0.001$).

The residuals of EW and PW were also correlated (Fig. 6.4). The latter correlation showed that females that had a small PW, relatively to their body size (SCL), produced eggs that were also small relatively to SCL, whereas females with a large PW compared to SCL produced relatively large eggs.

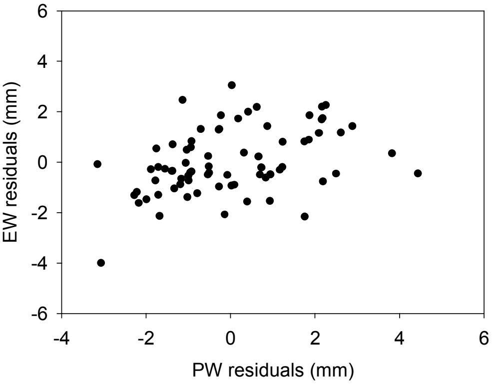

Figure 6.4 Relationship between the residuals of egg width (EW) and the residuals of the pelvic canal width (PW) in *H. s. signatus*. Egg width residuals and PW residuals correlated significantly (Pearson correlation, r_p = 0.39, $P < 0.001$).

6.5 Discussion

Rainfall differed substantially among years and included a drought year when reproduction of *H. s. signatus* decreased significantly. Nevertheless, egg production occurred in all years. This pattern is consistent with desert tortoises, *G. agassizii*, which tend to produce eggs every year, although some females forgo egg production after dry winters (Henen 1997; Turner *et al.* 1984). *Homopus s. signatus* had low body condition in September–October 2003 (Loehr *et al.* 2007a; this study) and many females' shells shrank during the preceding drought, probably as a result of decreasing body reserves (Loehr *et al.* 2007b). The fact that some females were able to channel resources towards reproduction under dry conditions suggests that these individuals were well suited to cope with occasional drought.

6.5.1 Body condition

Vitellogenesis in tortoises is a long-term process (Kuchling 1999), so that past environmental conditions affect whether or not a female produces a shelled egg in spring. *Homopus s. signatus* females appear to initiate a new vitellogenic cycle in spring, and possibly in other seasons (Loehr *et al.* 2004). Gravid females had a higher spring body condition than non-gravid females had, reflecting individual differences in the acquisition and accumulation of resources in the period preceding the egg-laying season. In *G. agassizii*, females with low non-lipid energy (probably low protein reserves) and total body water prior to the reproductive season forfeited egg production, presumably to ensure their own survival (Henen 1997). Similarly, non-gravid *H. s. signatus* females with low body condition may have skipped reproduction in order to survive.

Body condition differences between gravid and non-gravid females were most pronounced in 2000 and 2004. These two years were preceded by years with little rainfall until late winter, 50 and 15 mm for January to July 1999 and 2003, respectively, while the 1990–2004 average is 140 mm (South African Weather Services, unpublished data). Some females may have forfeited egg production in 1999 and 2003 in order to survive while accumulating resources towards the next egg-laying seasons, spring 2000 and 2004, respectively. Consequently, these females may have reached a higher body condition in 2000 and 2004 compared to females that used much of their resources for reproduction in 1999 and 2003. The similar body conditions of gravid and non-gravid females in other years may have resulted from (a) high rainfall allowing non-gravid females to increase their body condition to the same level as in gravid females (2001 and 2002), or (b) drought causing equally low body conditions in gravid and non-gravid females (2003).

The large egg produced by *H. s. signatus* may explain most of the body condition differences between gravid and non-gravid females. The simple body condition index that I used (i.e., based on body mass) is potentially affected by factors such as body reserves, urinary bladder or gut contents (Bonnet *et al.* 2001), but patterns revealed by comparisons between gravid and non-gravid females suggest that reproductive mass was an important contributor. In 2000 and 2004, gravid females had acquired roughly the mass of one egg in excess of body mass of non-gravid females, because gravid and non-gravid body conditions were similar after subtracting egg mass. In 2002, the body condition of large, non-gravid females was higher than was the body condition of gravid females, excluding egg mass, suggesting that large non-gravid females may have contained reproductive mass (e.g., ovarian follicles, soft-shelled eggs) that could not be detected by X-ray radiography. The 2002 study period started relatively late, and some females that I recorded as non-gravid may have produced an egg before the fieldwork commenced. Apparent reproductive mass in large, non-gravid females possibly represented additional clutches (Loehr *et al.* 2004), while smaller non-gravid females may not have been able to produce more than one clutch. Unfortunately, my study design did not allow measurement of annual clutch frequency. In 2003, non-gravid females of all sizes may have contained reproductive mass, since their body mass was higher than the egg-free mass of gravid females. The numerical difference between non-gravid and gravid female body masses in 2003 was within the range of the mass of an egg (6.19–15.37 g, assuming a density of 1 g cm^{-3}; Table 6.3), so some females that I recorded as non-gravid may have produced an egg later in the season.

6.5.2 Response to rainfall

Homopus s. signatus produces single-egg clutches, so the females' ability to vary annual reproduction is limited to clutch frequency and egg size. Each year, some females produced eggs, but annual percentages of females that were gravid varied. Although I did not radiograph females throughout the entire egg-laying season (ca. August to November; MD Hofmeyr, BT Henen & VJT Loehr, unpublished data), low rainfall during the months when females could accumulate reproductive mass prior to the egg-laying season appeared to result in low percentages of gravid females, particularly in 2003. The effect of rainfall likely materialised through its influence on food availability (i.e., primary production) and female body condition. The rates at which females became gravid (i.e., the regression slopes for the cumulative frequency of gravid females over the duration of the field season) were similar among years, but there were annual differences in the percentage of females that were gravid. The relatively high percentage of gravid females early in spring 2000 and 2002, compared to other years, may be related to high rainfall in the preceding summers, and the high temperatures in August 2000. However, the relatively late start of the 2002 study period may have contributed to a high initial proportion of gravid females. The delay in egg production in 2003 was probably caused by the drought that preceded the laying season, but females eventually responded to the August rainfall and produced eggs.

6.5.3 Egg size

Several characteristics suggest that a large egg size has a selective advantage for *H. s. signatus*. The eggs are large compared to female size; relative egg volume (7.5% of body mass) exceeds that of the other African tortoise genera that include single-egg clutching taxa (2.7 to 6.5%, Hofmeyr *et al.* 2005). My study showed that relative egg volume can reach 10.9% of body mass, or 11.9% of shell volume, for some individuals. In addition, egg width of most females exceeded pelvic width so that females require morphological and physiological adjustments to the pelvis, carapace and plastron during oviposition (Hofmeyr *et al.* 2005). Pelvic kinesis at oviposition appeared to accommodate a maximum EW - PW difference of 5.5 mm, a difference that was not related to body size.

Additional indications for the importance of large eggs for *H. s. signatus* include the large female shell volume relative to males, before and after scaling on SCL (Loehr *et al.* 2006), and the tendency of females with high body condition to produce larger eggs than did females with low body condition (Hofmeyr *et al.* 2005; this study). Furthermore, the onset of egg production is delayed in *H. s. signatus*; although females become reproductively active at a relative size similar to that in other chelonians (i.e., ca. 70% of maximum SCL, Kuchling 1999), *H. s. signatus* requires approximately twice as long as expected, for its body size, to reach size at maturity (Loehr *et al.* 2007b). Finally, egg size correlates with female body size (Hofmeyr *et al.* 2005; Loehr *et al.* 2004) in all but the driest years (i.e., 2003 and 2004). This suggests that in dry years other determinants outweighed the effect of body size. Body condition may have affected egg size in dry years. However, average egg size was similar among years despite significant variation in spring body condition, so egg size may be affected most by the body condition throughout vitellogenesis.

Homopus s. signatus offspring size is correlated to egg size (Loehr 2006b), and a large hatchling size might be required to survive the arid environment of the Succulent Karoo (Hofmeyr *et al.* 2005). Relative egg size among several African tortoise taxa, including *H. s. signatus*, is associated with unpredictability of rainfall (Hofmeyr *et al.* 2005). Moreover, large eggs and large hatchlings may enhance survivorship even in mesic environments (Landers *et al.* 1980). While low rainfall appeared to affect reproductive output in *H. s. signatus*, drought did not affect egg size. The lack of variation in egg size in response to different levels of rainfall is not unusual for arid-adapted chelonians, such as *G. agassizii* (Averill-Murray 2003), *A. radiata* (Leuteritz & Ravolanaivo 2005) and the desert box turtle *Terrapene ornata luteola* (Nieuwolt-Dacanay 1997). While *A. radiata* females produce smaller clutches in low rainfall years, and some *T. o. luteola* females forfeit reproduction in response to a dry spring, the offspring of these species, and *H. s. signatus*, probably face strong challenges to survival. A large size may help offspring surmount these challenges. In the Aldabran giant tortoise, *Aldabrachelys gigantea*, egg mass, clutch size and clutch frequency correlated to rainfall (Swingland & Coe 1978), but this large-bodied species produces large eggs, in absolute terms, so that a smaller egg in low rainfall years might still produce viable offspring.

Besides the large shell volume in female *H. s. signatus*, compared to males (Loehr *et al.* 2006), a comparison of the shell dimensions of gravid and non-gravid females suggests an additional means for females to accommodate the relatively large egg. Differences in SH and SV may be related to the pliable nature of female shells (see also Hofmeyr *et al.* 2005). The shell of *H. s. signatus* has some degree of flexibility dorso-ventrally, and SH and SV may decrease as a result of a reduction of internal matter, possibly due to starvation, in dry years (Loehr *et al.* 2007b). Similarly, an increase of reproductive matter in gravid females may have caused SH and SV to increase compared to non-gravid females. This flexibility would help females accommodate the large egg, and possibly follicles for subsequent clutches. Spring 2000 and 2002 followed relatively wet summers (Fig. 6.1) that may have allowed females to develop several clutches. Indeed, three gravid females contained follicles of preovulatory size in 2000 (Loehr *et al.* 2004), and 2000 and 2002 coincided with the strongest SH and SV differences between gravid and non-gravid females.

6.5.4 Capital or income breeding

Tortoises rely on reproductive mass accumulated during the long period of vitellogenesis to produce eggs (Kuchling 1999). This may be seen as a form of capital breeding, with follicles developing outside the egg-laying season representing the "capital". However, when rainfall and primary production during the egg-laying season are abundant, resources acquired during this period may also contribute to follicular growth, representing an income breeding component. Using this interpretation of capital and income breeding, *Gopherus agassizii* uses a mixture of capital and income breeding (Henen 2002b, 2004). Females accumulate reproductive mass (capital) before winter to produce eggs the ensuing spring (Henen 1997; Turner *et al.* 1986). When environmental conditions permit (e.g., high rainfall and primary production), females use resources acquired in the egg-laying season (income) to produce additional clutches (Henen 1993, 2002b, 2004; Mueller *et al.* 1998; Wallis *et al.* 1999). The steppe tortoise, *Testudo horsfieldii*, also appears to mix capital and income breeding strategies (Henen 2004). *Homopus s. signatus* required rainfall between egg-laying seasons to increase their body condition (Loehr *et al.* 2007a) and females likely allocated some resources to follicular growth at that time (capital breeding). Ultrasonography shows that this species can accommodate considerable capital; one female that was scanned in 2000 contained as many as four large follicles close to preovulatory size (Loehr *et al.* 2004), representing the highest clutch frequency recorded for the species (four eggs, data from captivity, Loehr 2006b). However, 12 females (86% of the sample) contained follicles measuring 40–80% of preovulatory size (Loehr *et al.* 2004), requiring females to continue accumulation of resources in the nesting season (income breeding) if they were to ovulate these follicles that season. When environmental conditions disable follicular growth, small follicles may become atretic as occurs in desert tortoises (Rostal *et al.* 1994).

6.5.5 Aridification

The population's egg production seemed strongly influenced by individual and environmentally induced variation. One female was gravid in all five years, but each year, even when rainfall was abundant, several females appeared to forfeit reproduction. Drought may be detrimental to egg production in *H. s. signatus* (i.e., 2003) as it is for desert tortoises (Henen 1997; Turner *et al.* 1984). In addition, drought may decrease egg size in *H. s. signatus* because egg size is related to body condition, although average egg size was constant among years in this study. Because the range of *H. s. signatus* is threatened with aridification as a result of regional climate change (Rutherford *et al.* 1999), years of low reproduction may occur more frequently in the next decades. Populations of *H. s. signatus* appear challenged by the negative effects of arid conditions, and ultimately aridification, upon growth rates (Loehr *et al.* 2007b), body condition (Loehr *et al.* 2007a) and reproduction. The projected aridification of the habitat of *H. s. signatus* will increase the importance of large offspring, causing concern about the prospect of a reduction in the number of large eggs and hatchlings produced in dry years.

7 General discussion and recommendations for conservation

7.1 Ecological patterns in *H. s. signatus* and in other tortoises

Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1972). *Homopus signatus signatus* is confined to rocky terrain over a small range in the arid northwest of South Africa (Boycott & Bourquin 2000). The ecological parameters investigated in this study help explain how *H. s. signatus* copes with environmental conditions in its arid habitat, particularly variable in rainfall. Despite being the smallest of all tortoises (Loehr 2004a), the species is a typical representative of the Testudinidae family in the sense that it is highly modified for terrestrial life (Branch 1998), has a long life-span, delayed maturity, iteroparous reproduction (Kuchling 1999; Loehr *et al.* 2004, 2007b), and a predominantly herbivorous diet (Ernst *et al.* 2000; Loehr 2002b, 2006a). Therefore, understanding the ecology of *H. s. signatus* also expands our knowledge of ecological patterns in tortoises in general, and arid-zone tortoise species in particular.

7.1.1 Determinants of body size

Homopus s. signatus is a small tortoise, and its small size may provide it with certain advantages in its environment. First, developing and maintaining a small body requires few resources, which would be advantageous in an arid, low-productive environment (e.g., Capellini & Gosling in press; Louw & Seely 1982; Yom-Tov & Geffen 2006). Secondly, small retreats such as rock crevices and small shrubs are accessible only for small species such as *H. s. signatus* (Loehr 2002a). These potential advantages of a small size are supported by the body sizes of other rock-living tortoises (*Malacochersus tornieri*, *Homopus* spp. except *H. areolatus*), which are all small (110-178 mm, Boycott & Bourquin 2000; Ernst *et al.* 2000). Among this group, the two largest rock-dwelling species, *M. tornieri* and *Homopus femoralis*, occupy the highest rainfall, or most productive, habitats (Hofmeyr *et al.* 2005; Müller 1996).

Countering the advantages of a small body size, female *H. s. signatus* appear to experience selective pressures for a larger body size to produce larger eggs (Hofmeyr *et al.* 2005; Loehr *et al.* 2004; Chapters 2, 3, 6). Hatchling body mass correlates with egg mass in captive *H. s. signatus* (Loehr 2006b), as do hatchling masses for several other chelonians (Brooks *et al.* 1991; Roosenburg 1996; Roosenburg & Kelley 1996; Rowe 1995; Steyermark & Spotila 2001), so large eggs may be important to produce large *H. s. signatus* hatchlings. Survival may correlate to chelonian hatchling size (Janzen 1993; Valenzuela 2001), but this relationship is not always present (Congdon *et al.* 1999; Kolbe & Janzen 2001). In *H. s. signatus*, high hatchling body mass may reflect body reserves to overcome periods of low rainfall and food availability. A second pressure that might require a large hatchling size is predation. Small *H. s. signatus* had serrated posterior marginal scutes (Chapter 2), potentially deterring predators. Since withstanding predation would require large hatchling dimensions rather than a large body mass, hatchling dimensions might also correlate to egg size.

Trade-offs in response to these contrasting selection pressures on the size of female *H. s. signatus* probably contributed to sexual size and shape dimorphism, i.e., females growing larger than males (Chapter 2), and to the relatively high growth rates in females (Chapter 3). Nevertheless, it appears that egg production would benefit from a larger female size than was obtainable within the trade-off, because the females used several mechanisms to facilitate the production of large eggs at a relatively small body size. The larger width of the rigid-shelled egg compared to pelvic canal width (Chapter 6) shows that females require shell kinesis during oviposition (Hofmeyr *et al.* 2005). Shell kinesis may be hormonally induced (Hofmeyr *et al.* 2005), and the endocrine system may play a role in the determination of the chelonian egg size (Bowden *et al.* 2004). Indeed, explanations of chelonian egg size, along pelvic width or anal gap size, may benefit from inclusion of a possible role of the endocrine system (Bowden *et al.* 2004). A second means that allows female *H. s. signatus* to produce large eggs at a relatively small body size is the flexible shell that may temporarily increase in height and volume to accommodate a large egg and follicles (Chapter 6). This flexibility is probably not hormonally linked to reproduction, as it was also apparent in males and non-gravid females when their shell size shrank during drought (Chapter 3). However, the level of shrinking was more pronounced in females than it was in males.

Although females benefit from a flexible shell that allows the development of large eggs and follicles, the evolutionary pathway is not clear. Several rock-living tortoises (e.g., *Homopus solus*, *M. tornieri*) have reduced shell ossification, possibly to help them climb steep rock faces and shelter in rock crevices (Branch 2007; Ireland & Gans 1972; Loveridge & Williams 1957; Moll & Klemens 1996), or as a reduction of unnecessary investment in shell, replaced by protection by rocks (Loehr 2002a). A reduced ossification will probably increase shell flexibility. Although *H. s. signatus* shells are well-ossified compared to *H. solus* and *M. tornieri* shells (Branch 2007), bones are relatively thin in comparison to other South African tortoises (MD Hofmeyr & BT Henen, personal communication). Therefore, the relatively thin and flexible shell may have evolved to benefit the tortoises through locomotory, sheltering, energetic, and reproductive advantages simultaneously. The mechanism for flexibility in *H. s. signatus* shells remains unknown, however, the shell of the South American terrapin *Platemys platycephala*, which also produces relatively large, single, hard-shelled eggs, has a flexible lateral suture that expands in gravid females (Métrailler 2006). In *H. s. signatus*, I have observed similar expansions of carapacial sutures during oviposition (Hofmeyr *et al.* 2005), and these sutures may play a role in shell kinesis at other times.

Shell size and volume were not the only sexual differences in *H. s. signatus*. Males had smaller plastrons compared to females of the same size, probably to help males locomote and copulate (Chapter 2). The investigation of tick infestations suggests that the smaller male plastron involved a cost, as the larger shell openings correlated to higher tick infestations (Chapter 4). Besides the direct effect of parasitism (loss of blood), ticks are known vectors for diseases (e.g., heartwater disease, Peter *et al.* 2000). It is not known if tortoises are susceptible to such tick-born diseases, but various snakes (*Bitis gabonica*, *B. nasicornis*, *Naja naja*, *N. nigricollis*, *Pituophis melanoleucus*) appear to be susceptible (Kiel *et al.* 2006), so the costs of a small male plastron in *H. s. signatus* might be considerable. In addition to increased tick infestations, large shell openings may involve costs through increased risk of predation and evaporative water loss.

7.1.2 Coping with an arid habitat

The Succulent Karoo receives winter rainfall but dry and hot summers (Le Roux & Schelpe 1997). Life-forms in arid ranges either desynchronise active life stages from periods of unfavourable conditions (e.g., through phenological adaptation, aestivation, or seasonal migration, Baker 1978; Harder 2001; Le Roux & Schelpe 1997), or endure such periods through morphological, physiological or behavioural traits that decrease resource requirements or accommodate temporary shortages (e.g., Cain III *et al.* 2005). Both strategies can be found among tortoises, with *Testudo horsfieldii* aestivating and remaining inactive for up to 9 months per year (Lagarde *et al.* 2002), and *Testudo kleinmanni* and *Gopherus agassizii* adjusting their dry season activity levels to rainfall events (Geffen 1989; Medica *et al.* 1980). Moreover, physiological traits (e.g., tolerating anhomeostasis of the *milieu intérieur*, Peterson 1996b), help *G. agassizii* overcome the unpredictable resource availability in spring and summer (Henen 1997; Nagy & Medica 1986; Peterson 1996a). This study helps understand how *H. s. signatus* acquired and allocated resources to deal with periodic drought in the Succulent Karoo.

Homopus s. signatus gathered nutrients and increased body condition when winter rainfall promoted plant growth (i.e., March to July/August, Chapter 5). If rainfall continued in spring, persistent plant growth allowed tortoises to maintain and improve their body condition (Chapter 5). Many Succulent Karoo plants have quite shallow root systems, so that primary production decreases rapidly when rainfall ceases (Esler & Rundel 1999). Nevertheless, tortoises were able to maintain a relatively stable body condition from 2003 to 2004; female body mass decreased 18% despite rainfall being approximately half of the long-term average, whereas body mass of *G. agassizii* may decrease 40% during drought (Peterson 1996b). Ectothermy, small body size and associated low resource requirements probably contributed to a relatively constant body condition. Tortoises may also have reduced their activity level in the dry season, similar to *T. kleinmanni* and *G. agassizii.* Bayoff (1995) observed inactive *H. s. signatus* in December and January, and under laboratory conditions inactive individuals can have two- to six-fold lower metabolic rates than active individuals have at similar temperatures (Schmidt 2003). This reduction approximates the decrease in field metabolic rates of up to 90% measured in *G. agassizii* when tortoises were inactive during drought (Henen 1997, 2002b). Dehydrated forage and drinking water from occasional summer showers (e.g., January 2004) may have enabled *H. s. signatus* to eat in the dry season (see also Henen 1997). Because the occurrence of summer rains is unpredictable, resource acquisition in the dry season may require tortoises to withstand temporary electrolyte and water imbalances (Henen 1997; Nagy & Medica 1986; Peterson 1996a,b). *Homopus s. signatus* feeds on a wide range of plant species (Loehr 2002b, 2006a), which may have improved their opportunities to find food in the dry season.

Resources acquired in the rainfall season likely yielded most of the annual nutrient budgets for growth, maintenance and reproduction. However, tortoises appeared to be opportunistic in the acquisition of resources in other seasons, because growth and reproduction correlated to annual rainfall (excluding months that could not provide resources immediately due to the time-lag between rainfall and food acquisition, Chapters 3 and 6). The habitat of *H. s. signatus* demands a relatively large egg, requiring females to accumulate considerable mass towards the egg-laying season (e.g., females had higher spring body condition than males had; Chapter 5). The long-term vitellogenic process may allow females to acquire resources in two rainfall seasons, at the start of a vitellogenic cycle, and prior to ovulation and egg production (Loehr *et al.* 2004). Opportunities for females to gather additional resources during the dry season in between these two periods might help them produce a large egg, or possibly more than one clutch (Loehr *et al.* 2004), in the following egg-laying season. Selective advantage for females producing large or several eggs might lead to sexual differences in behaviour. Although males and females displayed similar behaviours at the population level in spring 2000 (Loehr 2002a), I hypothesise that male and female behaviour and activity levels differ on a longer time-scale, favouring more feeding behaviour and possibly longer active periods in females (see also Keswick *et al.* 2006; Lagarde *et al.* 2002). These potential differences between *H. s. signatus* sexes might be facilitated by the different carapacial colour patterns of males and females (Chapter 2), through thermoregulatory or crypsis advantages.

Despite their low body condition in the drought year 2003, several females succeeded to produce at least one egg of the same size as in wetter years, and non-gravid females appeared to contain reproductive mass (i.e., ovarian follicles, Chapter 6). This ability of *H. s. signatus* females to produce an egg after a drought is similar to *G. agassizii* females reproducing despite drought (Henen 1997, 2002b; Turner *et al.* 1984). In response to the unpredictable habitat of *G. agassizii* in the Mojave Desert, females produce eggs every year to enhance the possibility that some offspring will encounter favourable conditions for survival (bet-hedging, Henen 1997, 2002b). Similarly, desert box turtles (*Terrapene ornata luteola*) produce eggs at low rainfall (Nieuwolt-Dacanay 1997), but species that experience unpredictable yet fairly high rainfall such as *Gopherus berlandieri* (Hellgren *et al.* 2000) and *Pseudemydura umbrina* (Kuchling & Bradshaw 1993) do not appear to use a bet-hedging strategy. The arid Succulent Karoo has relatively predictable rainfall compared to the Mojave Desert (Desmet & Cowling 1999), but the fact that female *H. s. signatus* allocated scarce resources to reproduction during drought suggests that this biome favours bet-hedging in tortoises as well. *Homopus s. signatus* also spread reproductive bouts within a breeding season, by producing one egg at a time (Chapter 6), which is an additional way of increasing the chance that some offspring will hatch when conditions are favourable. In *Chersina angulata* and *Psammobates tentorius tentorius*, spreading small reproductive investments throughout the breeding season may be advantageous for female survival (Hofmeyr 2004; Leuteritz & Hofmeyr 2007). Each reproductive investment was large for *H. s. signatus* females (i.e., large relative egg size), suggesting that the distribution of single eggs over several clutches was mostly a consequence of small body size, probably in combination with advantages for hatchling survival.

The growth rates of *H. s. signatus* were low compared to similar-sized chelonians, apparently due to the low-productive environment of *H. s. signatus* (Chapter 3). Male and female growth correlated to rainfall, but drought caused a stronger decrease of female growth than male growth, presumably because resource allocations to eggs increasingly inhibited female growth (Chapter 3). Nevertheless, males had lower growth rates than had females, corrected for body size, suggesting that the male reproductive strategy or behaviour also required considerable amounts of their limited resources. For *G. agassizii* in high rainfall years, male field metabolic rates exceeded female rates in late summer and autumn (after egg-laying); the higher rates of males may have reflected larger home ranges than females, male-to-male agonism, and expenditures to court and mate (Henen *et al.* 1998). *Homopus s. signatus* males display aggression towards, and fight with, other males (Loehr 2002a,c). Also, male courtship behaviour includes prolonged periods of following potential mates in spring (in captivity, Loehr 1999, and in the wild, VJT Loehr, personal observation). These behaviours probably elevate resource demands in male *H. s. signatus*.

7.1.3 Contributions to tortoise ecology in general

Several characteristics of *H. s. signatus* are consistent with other tortoise species. Examples are sexual dimorphisms that may facilitate male and female behaviours (Chapters 2 and 4), a slow and indeterminate growth pattern (Chapter 3), opportunistic use of resources to allow reproduction under arid conditions (Chapters 6 and 7), and production of similar-sized eggs despite variation in environmental conditions (Chapter 6). However, other characteristics provide new insights in the ecology of tortoises and perhaps other reptiles.

This study demonstrates that viable egg size may have significant influence on the morphology and ecology of tortoises, and traits that I found in *H. s. signatus* may also have developed in other (especially small) taxa living in environments that demand large eggs. One trait, flexibility of "outwardly rigid" chelonian shells (i.e., without plastral or carapacial hinges) may enable accommodation of large eggs and follicles. Other authors have noted shell flexibility in chelonians (*G. agassizii*, Field *et al.* 2007; *P. platycephala*, Métrailler 2006; *G. berlandieri*, Rose & Judd 1991), but this appears to be the first analysis of its ecological significance in a natural population (Chapters 3, 6, 7). A second trait that helped female *H. s. signatus* produce large eggs is the apparent flexibility of the pelvic girdle (Chapter 6). This trait may benefit chelonians that produce large eggs, but may not be restricted to chelonians (e.g., Squamata: *Ptenopus garrulus*, Hibbitts *et al.* 2005).

The presence of sexual dichromatism in the shell of *H. s. signatus* may relate to egg production through behavioural differences between males and females (Chapters 2 and 7), and shows that detailed analysis may be necessary to reveal the presence of sexually different colour patterns in chelonian shells. It is well-recognised that male and female chelonians may differ in their activities, behaviours and habitat use (Jones 1996; Keswick *et al.* 2006; Lagarde *et al.* 2002; Lue & Chen 1999), yet most reports of sexual dichromatism deal with species for which sexual differences are easily perceived (e.g., colouration differences of the soft body parts in the mating season, Ernst *et al.* 2000). Analysing shell colour patterns of male and female chelonians may help identify and understand ecological differences between sexes.

A final result of this study that likely extends to other taxa is the observation that a taxon with a relatively low conservation listing (*H. s. signatus*, Lower Risk/near threatened, Branch 1988; IUCN 2006) may in fact be at survival risk, due to regional climate change, and aridification (Chapters 3 and 6, paragraph 7.2); lack of information may also produce inaccurate conservation assessments. The Succulent Karoo is a biodiversity hotspot, and limited or inaccurate information calls for continued and intensified ecological work on *H. s. signatus* and other taxa.

7.2 Conservation implications and recommendations

Homopus s. signatus is listed in the South African Red Data Book (Branch 1988) and in the IUCN Red List of Threatened Species (species level, IUCN 2006). Although the literature mentions that *H. s. signatus* can be common in suitable habitat (Baard 1994; Boycott 1989), there are no published quantitative evaluations of population sizes. Moreover, it is not quite clear what defines suitable habitat and how this is distributed within the subspecies' range. Furthermore, some individuals in the Richtersveld and near Pofadder have atypical morphologies or shell colour patterns (Bauer & Branch 2001; Branch *et al.* 2007) and might not represent the subspecies *H. s. signatus*. The range of *H. s. signatus* is threatened with aridification as a result of regional climate change (Rutherford *et al.* 1999), and the sum of range shift and contraction is expected to exceed 50% over the next decades (Erasmus *et al.* 2002). This threat requires evaluation of the ecological effects of aridification on the long-term survival of the taxon, and work to quantify the taxon's habitat requirements, range, and population sizes and status. The current study demonstrates how the ecology of *H. s. signatus* is linked to rainfall, and can help formulate sound conservation measures.

The time to maturity for female *H. s. signatus* is more than 10 years and will increase with aridification (Chapter 3). Moreover, a drier habitat may cause females to produce smaller eggs and offspring (Chapters 3 and 6), requiring longer periods to mature. Longer growth periods would likely increase juvenile mortality, so fewer individuals would enter adulthood. There are no life-tables for *H. s. signatus*, but effects of drought on reproduction indicate that reproductive females may not be able to compensate for increased mortality in the juvenile stage if populations are to be maintained. Low rainfall appeared to result in fewer gravid females (Chapter 6). In addition, females seemed to accumulate fewer reserves during drought, as indicated by their low body condition (Chapter 5), so that clutch frequency may also decrease. Eventually, populations require increased adult survival and reproduction over a long life-span to counter increased juvenile mortality, reduced egg size and reduced clutch frequency.

Although preliminary results indicate that adult survival may not be directly affected by a period of drought (VJT Loehr, unpublished data), several other threats appear to challenge adult tortoises. *Homopus s. signatus* is a small animal, making it vulnerable to predation. In addition, tortoise survival may be affected by overgrazing, various forms of land use (e.g., agriculture, mining), road traffic (road victims, Fig. 7.1) and (illegal) collecting for the wildlife trade. Controlling and alleviating some of these threats may improve sustainability of populations, especially if the largest individuals, which are most important for the production of large eggs and hatchlings, survive longer.

Regulations to prevent overgrazing, maintain pristine land and control the collection of wild animals, are already in place in the range of *H. s. signatus* (G van Aardt and EHW Baard, personal communication) so that potential improvements should be sought in periodic evaluation and further development of regulations, and in adequate enforcement. Reducing the number of tortoises killed by road traffic is important for populations near busy roads. Stretches of road that directly border rocky habitat could be provided with barriers, for example concrete blocks of circa 30 cm high to restrict *H. s. signatus* and other tortoises from crossing the road. However, since

Figure 7.1 Adult male *H. s. signatus* killed by road traffic, a common sight near Springbok, South Africa, in spring.

Figure 7.2 Concrete, mesh-covered gutter to allow herpetofauna to cross a tar road near Hilversum, Netherlands. The mesh ensures that the gutter will have a non-threatening microclimate for fauna. Note the concrete blocks that guide fauna to the gutter entrance.

barriers would effectively isolate subpopulations, barriers should ideally be accompanied with structures that allow safe road circumvention (e.g., culverts or mesh-covered gutters integrated in the road surface, Fig. 7.2, Guyot & Clobert 1997; Kruidering *et al.* 2005).

Conservation efforts should not target adult survival exclusively because egg and hatchling sizes may drop below the minimum required to survive the dry season in the Succulent Karoo. This effect is particularly relevant because the current large hatchling size probably helps tortoises survive periods of unfavourable conditions (drought), and the intensity and frequency of such periods may increase due to aridification. Conserving this taxon requires drastic measures to ameliorate the effects of aridification on *H. s. signatus*. There appear to be two ways to accomplish this, (1) by helping tortoise populations move gradually through corridors into areas that should receive sufficient rainfall in the future, or (2) by translocating populations to higher rainfall areas. The first option is preferred, because it involves natural ecosystem processes, whereas the second option might have unpredictable effects (e.g., adaptability of the tortoises to the selected area or effects on resident species) and might benefit only a single taxon.

The first step to be taken would be to select, or establish, and connect conservation areas that represent rainfall gradients or corridors. This step is in line with the conservation target of the Succulent Karoo Ecosystem Programme (SKEP) to create or expand protected areas while taking into account key climatic gradients (SKEP 2007). Secondly, population movements should be monitored over the next decades to evaluate whether migration occurs into previously uninhabited areas, so that translocations can be considered as a last resort. In addition, I recommend that several populations of *H. s. signatus* be monitored to detect changes in population composition (i.e., density, size range) and dynamics (i.e., mortality, recruitment of mature females).

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Appendix 1. List of publications arisen from this field study

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.

Loehr, V.J.T. 2002. Diet of the Namaqualand speckled padloper, *Homopus signatus signatus*, in early spring. African Journal of Herpetology 51: 47-55.

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. 2003. Annual temperature fluctuation in the natural habitat of the Namaqualand speckled padloper, *Homopus signatus signatus*. Radiata 12: 25-27.

Loehr, V.J.T. 2004. A new thread-trailing method for small tortoises in densely structured habitats. Turtle and Tortoise Newsletter 2004: 13-14.

Loehr, V.J.T. 2004. Growth of the Namaqualand speckled padloper, *Homopus signatus signatus* (Reptilia: Testudinidae). African Zoology 39: 309-313.

Loehr, V.J.T. 2006. Natural diet of the Namaqualand speckled padloper (*Homopus signatus signatus*). Chelonian Conservation and Biology 5: 149-152.

Loehr, V.J.T. In press. Annual variation of the relative humidity in a rock crevice in the natural habitat of the Namaqualand speckled padloper, *Homopus signatus signatus*. Radiata.

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 and sexual dimorphism in the Namaqualand speckled padloper, *Homopus signatus signatus*. African Journal of Herpetology 55: 1-11.

***Loehr, V.J.T., Henen, B.T. & Hofmeyr, M.D. 2006. Tick infestations in the Namaqualand speckled padloper, *Homopus signatus signatus* (Gmelin, 1789). African Zoology 41: 170-177.

***Loehr, V.J.T., Hofmeyr, M.D. & Henen, B.T. 2007. Growing and shrinking in the smallest tortoise, *Homopus signatus signatus*: the importance of rain. Oecologia 153: 479-488.

***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.

*** Publication on which this dissertation was based

Tortoises appear to be successful in arid ecosystems, where they depend on primary production for their predominantly herbivorous diets. The low primary production of arid regions is exacerbated by periodic droughts, so that iteroparous species such as chelonians require mechanisms to overcome resource shortages. The smallest of all tortoises, *Homopus signatus signatus,* occurs in a dry winter rainfall area in northwestern South Africa that is threatened with aridification due to regional climate change. *Homopus s. signatus* is listed in the South African Red Data Book and IUCN Red List of Threatened Species, yet its morphology and ecology, including traits that help cope with its dry environment, have been studied little. The conservation status of the taxon requires ecological data to take sound conservation measures. This study evaluates shell size, shape and colour pattern in a population of *H. s. signatus*, and reports responses of growth, tick infestations, body condition and reproduction to five years of rainfall variation.