THE ECOLOGY OF THE WORLD'S SMALLEST TORTOISE, *HOMOPUS SIGNATUS SIGNATUS*

UNIVERSITY OF THE WESTERN CAPE

Ph.D. Project Proposal

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Abstract

The Namaqualand Speckled Padloper (*Homopus signatus signatus*) is the smallest tortoise, making it an intriguing subject for study of life history and other ecological characteristics. The aim of my proposed study is to increase the understanding of the determinants of, and relationships between ecological patterns in chelonians, by placing traits of the world's smallest tortoise into the context of ecological analyses for many species. In addition, the study has a strategic aim: Knowledge on the ecology of this species will be of use in future conservation plans. Although the species is not currently endangered, several potential threats are present and conservation measures may be required in the future. Ecological data on *H. s. signatus* is almost completely lacking.

I will study a natural population near Springbok, Namaqualand, South Africa, focussing on the ecological aspects *population ecology*, *resource requirements* and *reproduction*. Fieldwork (2000 - 2004) will primarily be conducted in spring (September - October) but also in other seasons. I will use mark-recapture, thread-trailing and radio-tracking techniques to monitor individual tortoises. Ageing of specimens will be done by using scute rings, after determining if scute rings form annually in *H. s. signatus*. I will define microhabitats to study tortoise activity patterns in relation to their habitat. Weather data will allow analyses of relationships with temperature and rainfall, including the tortoises's seasonal activity cycle. I will also equip tortoises with small temperature loggers on their shell, to identify body temperature profiles. This will further increase the understanding how the tortoises use their habitat, and how they thermoregulate. I will determine the diet of *H. s. signatus* in relation to availability of food items, to identify preferences.

As a part of the reproductive studies, I will include data from a captive *H. s. signatus* colony. Wild tortoises will be radiographed and ultrasonographed to obtain information on clutches and eggs, and reproductive potential will be measured in captive tortoises. I will determine the age at maturity in the natural population.

My research will produce several papers that contribute to the understanding of chelonian ecological patterns. All data will be presented in a thesis, that may also be of interest to conservationists.

Key words

Ecology, *Homopus signatus signatus*, population characteristics, population dynamics, growth, habitat use, activity patterns, body temperature, diet, reproduction

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INTRODUCTION AND RESEARCH AIMS

Chelonians are long-lived, relatively conspicuous, and easily marked, measured and monitored creatures (Judd and Rose, 1983; Dodd, 1997; Hellgren et al., 2000). These characteristics make them excellent models to study life history and other ecological patterns in order to understand the underlying evolutionary drives, and to interpret their effects on populations (Congdon et al., 1993; Congdon and Sels, 1993; Kuchling, 1999; Hellgren et al., 2000). The Namaqualand speckled padloper (*Homopus signatus signatus*) is the world's smallest tortoise, measuring only around 10 cm (Ernst et al., 2000; Loehr, 2002b). It is endemic to the arid north-western part of South Africa (Branch, 1998; Boycott and Bourquin, 2000). The small size of this species makes it an intriguing subject for study of ecological traits in relation to the position of the species at the low end of the size range of all tortoises. The aim of my proposed research is to increase the understanding of the determinants of, and relationships between ecological patterns in chelonians, by placing traits of the world's smallest tortoise species into the context of ecological traits of other species.

Ironically, conservative life history patterns that ensured the survival of chelonians in the past 200 million years have made them vulnerable for anthropogenic impacts in recent times (Congdon et al., 1993; Congdon et al., 1994). As a result, my studies will also have an important strategic aim, as knowledge on the ecology of *H. s. signatus* will be of direct use in conservation efforts. Potential threats to the long-term survival of *H. s. signatus* include overgrazing, habitat alteration (including mining and accelerated climatic change), poaching, and vehicle traffic (Loehr, personal observation), although the species is not currently considered threatened or endangered. Until now, *H. s. signatus* has been poorly studied, with only one ecological study conducted in summer by Bayoff (1995). The presently available information is therefore inadequate for any comprehensive conservation efforts.

RESEARCH OUTLINE

In my investigations, I will focus on three aspects of the ecology of *Homopus signatus signatus*: (1) Population ecology; (2) Resource requirements; and (3) Reproduction. These aspects allow a reasonably detailed analysis of the functioning of a species in its environment. Furthermore, they have been studied in a large number of other chelonians, and may form baseline information for conservation plans. I will collect my data in one natural *H. s. signatus* population, to limit the number of variables and to maximise sample sizes. For logistical reasons, most data collecting will be done in the spring season, but data from other seasons will also be included. Reproductive data will be supplemented with data gathered from a captive *H. s. signatus* colony.

1. POPULATION ECOLOGY

1.1. Population structure

1.1.1. Age distribution

For many chelonians it has been shown that the scute rings that form when the shell grows can reliably be used to estimate the age of a specimen, except in older individuals (reviewed in Germano and Bury, 1998). Scute rings form when periods of growth alternate with periods without growth, and usually result in one (true) scute ring being formed each year (Germano and Bury, 1998). It will be attempted to establish the age distribution of the investigated *H. s. signatus* population, after answering the question if scute rings form annually in this population. Until now, scute ring formation has not been studied in any padloper species. The age distribution of a population can provide information on the population's stability, and may reflect past events with demographic effects (Medica et al., 1975; Reese and Welsh, 1998).

1.1.2. Sex ratio

Males and females of sexually mature *H. s. signatus* are easily distinguished: Compared to females, males are small, have long tails, and have concave plastrons (Ernst et al., 2000). For many chelonian populations skewed sex ratios have been reported, and a variety of explanations have been proposed such as temperature dependent sex determination (Dodd, 1997), mortality differences between sexes (Hailey, 1990; Hellgren et al., 2000), sexual differences in immigration and emigration (Chen and Lue, 1998), sexual differences in the period of time required to mature (Lovich and Gibbons, 1990), and sampling biases (see also review in Lovich and Gibbons, 1990). In my study, I will determine if the sex ratio of the studied population is skewed, and interpret the causes and possible effects.

1.2. Population dynamics

Long-term studies are required to understand the population dynamics of long-lived organisms (Tinkle et al., 1981; Freilich et al., 2000; Congdon et al., 2000). Therefore, my study in this regard should only be considered a first exploration of the population dynamics of *H. s. signatus*. Monitoring of the population will continue after this study.

1.2.1. Natality and immigration

The *H. s. signatus* population will be an open population, resulting in four factors contributing to population growth or decline: natality, immigration, mortality, and emigration. I will monitor all four factors to assess population growth relationships and mechanisms. In addition, I will consider annual variation, and its possible causes.

1.2.2. Mortality and emigration

Several other mortality-related issues will be addressed:

Size-dependent mortality may be one factor affecting evolutionary development towards a species' body size (Willemsen and Hailey, 1999; Bodie and Semlitsch, 2000). I will investigate whether mortality in *H. s. signatus* is size-dependent, and I will furthermore evaluate sexual differences and their possible consequences for the sex ratio of the population.

Adult survival rates for chelonians are associated with age at maturity, with a lower age at maturity when adult survival rates are low (Shine and Iverson, 1995). I will compare adult survival rates with age at maturity (see also 3.1.1) in comparison to other chelonians.

1.2.3. Longevity

Combining age-composition and mortality data, I will be able to estimate longevity of *H. s. signatus* in the study population. Information on the longevity of long-lived, iteroparously reproducing species is required as a factor in the reproductive strategy of the species. Also the question if breeding senility (Kuchling, 1999) may exist in *H. s. signatus* will be addressed.

1.3. Population density

Some chelonian populations have high densities and are likely to have important impacts for the ecosystem in which they reside (Mason et al., 2000; Souza and Abe, 2000). The assessment of the density of a tortoise population is sometimes complicated as a result of bias due to temporarily varying capture probabilities (Freilich et al., 2000). In order to obtain a reliable estimate of the density of the *H. s. signatus* study population, this parameter will be measured in several years, and possible annual variation will be interpreted relative to environmental variation.

Population densities of many species have shown decreases in recent decades (Turtle Conservation Fund, 2002). The density of my study population may serve as a reference for future monitoring, and I will use densities from 1991 and 1992 (Bayoff, 1995) to assess changes during the past decade.

1.4. Individual growth

If scute rings form annually in *H. s. signatus*, they can also be used to determine growth trajectories of individual tortoises (Germano, 1994; Lagarde et al., 2001). Such growth data may help to explain interacting parameters like age at maturity (and differences between sexes), and the sex ratio of the population. Furthermore, in a comparison with other species, growth data may explain adaptations to different habitats, including dietary composition (Hailey and Coulson, 1999). Also intraspecific growth variation as a result of fluctuating environmental conditions may occur.

Scute rings can also be used to estimate the age at maturity. This age is associated with a "growth shift" that is reflected by a marked growth decrease after reaching sexual (sub)maturity, as a result of a shift in resource allocation from growth to processes related to reproduction (Kuchling, 1999; Lagarde et al., 2001).

1.5. Tick infections

Tick infections in tortoises have received intensified research attention in recent years, partly due to spreading of heartwater disease by imported tick-infected African tortoises for the pet trade in the USA (Fielden and Rechav, 1994; Allan et al., 1998; Burridge et al., 2000; Robbins et al., 2001; Labruna et al., 2002). Apart from acting as vectors to transmit diseases, ticks may also affect tortoise health directly when present in large numbers. I will establish tick infection rates and fluctuations for the *H. s. signatus* population.

2. RESOURCE REQUIREMENTS

In the course of evolution, species will adapt to their environments through natural selection. Ultimately, a number of resources will be required for a species to function and persist in its habitat. Knowledge of such requirements is of special interest from a conservation point of view. In my study, I will characterise the habitat of *H. s. signatus*, and I will determine niche parameters related to habitat use, body temperature, activity patterns, and diet to identify how this species has adapted to its habitat.

2.1. Habitat characterisation

2.1.1. Topography

Homopus signatus signatus inhabits rocky habitat in northern Namaqualand (Branch, 1998; Boycott and Bourquin, 2000). Very few tortoises (*Malacochersus tornieri*, *Homopus boulengeri*, and the Nama padloper, *H.* species) live in rocky habitats (Boycott and Bourquin, 2000; Ernst et al., 2000), and these may show different strategies to persist. I will make comparisons between characteristics that are typical for *H. s. signatus* and published data for other rock-dwelling tortoises.

2.1.2. Vegetation

The vegetation type of *H. s. signatus* habitat is Succulent Karoo, consisting of small shrubs and other succulents (Le Roux and Schelpe, 1997; Branch, 1998). The area is renowned for its massive flowering of (mainly annual) plants in spring (Le Roux and Schelpe, 1997), and this may have resulted in the development of adaptive traits in *H. s. signatus* with regard to diet or other parameters. The investigation of such relationships will use stratified vegetation analysis among the five microhabitats at this site (See Research Design and Methods). This will include data from the South African Weather Services (located circa 2 km north of the site), as well as periodic placement of data loggers on site to measure temperature, humidity and wind speed.

2.1.3. Climate

The Namaqualand climate is strongly influenced by the cold Benguela Current along South Africa's west coast, and the direction of summer (easterly) and winter (westerly) winds (Branch, 1998). It is an arid winter rainfall area, with dry and hot summers. I will use historical and current weather data to understand how *H. s. signatus* has adapted to survive these climatic conditions.

2.2. Habitat use and space requirements

2.2.1. Activity areas and habitat utilisation

Chelonians may use their habitats in non-random patterns, utilising some areas more frequently or at other times than other areas (Dodd et al., 1994; Nieuwolt, 1996; Lue and Chen, 1999; Smith et al., 1999). Reasons for this can be found in spatial distributions of forage, retreats, or other requirements. I will look at habitat utilisation of *H. s. signatus* in spring, and I will determine activity areas (ranges used within a limited timeframe) for males and females in this time of the year.

2.2.2. Home range and spatial requirements

On a larger time-scale, the home range of *H. s. signatus* will be established. Tortoises may move to other sites in other seasons than spring, or they may move over larger distances. For some chelonians it has been documented that specimens move to different areas for hibernation or aestivation (Kaufmann, 1992; Buhlmann, 1995; Morales-Verdeja and Vogt, 1997; Lue and Chen, 1999). It is likely that also *H. s. signatus* will aestivate during the dry Namaqualand summer (Bayoff, 1995; V. Loehr, unpublished data), and my study will elucidate the spatial requirements of this species year-round.

2.3. Microhabitats, microclimates and body temperature profiles

I will define microhabitat types in the research area to focus on habitat use by the tortoises. These microhabitats will be characterised in terms of temperature (air, soil and refuge) and humidity, and tortoise body temperature profiles will be related to microclimates to establish how the animals regulate their body temperature, and what their preferred body temperature is (Hailey and Coulson, 1996; Willemsen and Hailey, 1999).

2.4. Climate and activity patterns

2.4.1. Seasonal cycle

It is unlikely that the harsh Namaqualand climate will allow year-round activity of *H. s. signatus*. As mentioned above, there is evidence that the species aestivates in summer (Bayoff, 1995). It may have its prime activity season in winter (Boycott, 1989) like the tortoise *Testudo kleinmanni*, another small tortoise from arid north Africa (Geffen and Mendelssohn, 1988). A more extreme cycle is known from a tortoise from an arid, but continental habitat, *Testudo horsfieldii*, exhibiting behavioural adaptations to survive and reproduce in an area that allows neither summer, fall nor winter activity (Lagarde et al., 2002). I will track a number of *H. s. signatus* to determine what seasonal activity cycle exists in this species. Furthermore I will use local people to gather additional data on activity.

Ambient temperature variation may affect the daily period that the tortoises can maintain sufficiently high body temperatures, which in turn could affect the annual activity cycle (Hailey and Coulson, 1996). Thus, annual body temperature variation will be investigated in the study population.

2.4.2. Daily activity in spring

Homopus signatus signatus is active in the spring season (personal observation), and I will conduct a detailed study on the daily activity pattern of *H. s. signatus* in spring. Activity types shown by the tortoises will be recorded, and interpreted in relation to microhabitat and weather conditions. Also the activity modus (unimodal, bimodal) will be determined. Body temperature profiles in spring will be related to behaviours (Litzgus and Brooks, 2000).

The tortoise *Malacochersus tornieri* from a rocky habitat in Tanzania, has been reported to show a high retreat fidelity (Moll and Klemens, 1996; F. Schmidt, unpublished data), possibly as a result of extreme adaptations to a specific retreat type. This may also be the case in *H. s. signatus* so I will analyse retreat use.

2.4.3. Environmental influences

An environmental factor that most likely will have an effect on the daily activity pattern of *H. s. signatus* in spring is the large variation in weather conditions between years. For instance, annual rainfall may vary as much as 225% between successive years (South African Weather Services, unpublished data), probably affecting seasonal activity levels (see Freilich et al., 2000). One example is the activity modus, which may shift from unimodal to bimodal depending on weather conditions (Willemsen, 1991; Díaz-Paniagua et al., 1995; Ramsay et al., 2002). In order to assess this variation, I will monitor spring activity in several years, and attempt to explain variation in terms of behavioural responses on varying weather conditions.

2.5. Diet

2.5.1. Diet in spring

Knowledge of the *H. s. signatus* diet is of importance as diet is one of the most direct factors contributing to the survival of a species in its habitat. Foraging by herbivorous tortoises may also have implications for the ecosystem by tortoises's potential to disperse seeds (Macdonald and Mushinsky, 1988; Moskovits and Bjorndal, 1990; Mason et al., 1999). I will determine the composition of the spring diet of *H. s. signatus*, including the plant parts (e.g., seeds) eaten.

2.5.2. Food availability and selection

Without knowing which, and how many food items are available, it is not possible to establish dietary preferences of the tortoises. If tortoises prefer some food items above others, this may provide clues how specimens actively maintain their nutrient or water balance (Rall and Fairall, 1993; Barboza, 1995; Mason et al., 1999). Vegetation analysis will be used to characterise the habitat, quantify food availability, and determine if *H. s. signatus* has dietary preferences.

3. REPRODUCTION

Chelonian life histories are characterised by delayed maturity, long lives, iteroparous reproduction, and low adult mortality (Kuchling, 1999). Within this strategy, interspecific variation exists. Information on reproduction in *H. s. signatus*, in combination with data on longevity and mortality (see 1.2) will allow me to compare life history strategies of this species with other chelonians, and to interpret these in terms of adaptation to its habitat.

3.1. Natural population in spring

3.1.1. Size and age at maturity

Most chelonians mature when they have reached approximately 70% of their maximum size (Shine and Iverson, 1995). I will determine if this is also the case in *H. s. signatus*, and I will also determine the age at maturity. I will do this by examination of scute rings (Lagarde et al., 2001), the minimum age of gravid females (using X-ray radiography and ultrasonography), and the minimum age of males displaying courtship or mating behaviour. Delaying the age at maturity provides a means for a species to allocate resources differently than to reproductive activity, but at the costs of potentially high mortality risks in the hatchling and juvenile stages. *Gopherus berlandieri* females exhibit relatively early maturation, possibly to counterbalance increased risk of predation and relatively high costs associated with reproduction in females of this small tortoise species (Hellgren et al., 2000). *Homopus signatus signatus* may exhibit similar mechanisms.

3.1.2. Clutch and egg characteristics

In the literature there has been much debate about a possible trade-off between clutch size and (optimal) egg size in chelonians, predicting that clutch size will vary at constant egg size as a result of evolutionary selection for optimal egg size (Brooks et al., 1992; Iverson and Smith, 1993; Iverson and Moler, 1997; Nieuwolt-Dacanay, 1997; Wallis et al., 1999; Kuchling, 1999). However, many of these studies showed that egg size also varies. Captive *H. s. signatus* produced single egg clutches (Loehr, 1999). I will assess whether wild *H. s. signatus* also produce only single egg clutches, and I will relate egg size to clutch size, female body size, and environmental parameters. Furthermore I will determine if females are capable of producing multiple clutches, as they did in captivity (Loehr, 1999).

3.1.3. Environmental influences

In the case of *H. s. signatus*, some environmental factors that could be of interest because they might result in interacting evolutionary selective pressures are the rocky habitat in which *H. s. signatus* lives (possibly affecting female body measurements), hatchling size required to survive the dry Namaqualand summer, and variable fecundity related to single or multiple clutching in an unpredictable environment. These factors will be considered in the analysis of reproductive strategies in *H. s. signatus*.

3.2. Captive breeding

3.2.1. Reproductive potential

Certain reproductive parameters are difficult to determine in a wild tortoise population during a relatively brief study period. Therefore I will supplement my reproductive data with information gathered from a captive population. This will help me quantify the reproductive potential of *H. s. signatus*, how reproductive potential relates to the small body size and *H. s. signatus* ecology, and how reproductive potential compares to that of other chelonians.

3.2.2. Conservation perspective

Many chelonians world-wide are threatened or even extinct in the wild (Turtle Conservation Fund, 2002). This situation has triggered initiatives to attempt conservation efforts by establishing reproducing captive "insurance" populations (Turtle Conservation Fund, 2002). Although *H. s. signatus* is not currently threatened or endangered, captive-breeding may become necessary for this or related species. I will evaluate the potential captive-keeping and breeding techniques for the conservation of *H. s. signatus*.

RESEARCH DESIGN AND METHODS

In 2000, I initiated an ecological study of *Homopus signatus signatus* from which the study I propose here is a continuation and elaboration. As a result, I will be able to backup my choice of research design and methods by several trials that have already been conducted in the field. Drs. M.D. Hofmeyr and B.T. Henen, my current supervisors, have been involved in all of the previous studies. Some of the results that I have gathered in the previous years will form part of my thesis. The focus of my studies will be the spring season, but additional short fieldwork will be conducted in other seasons.

Study site and fieldwork schedule

Fieldwork will be conducted in and around a 3 ha research site near Springbok, Namaqualand. This site was previously used by Bayoff (1995), and by myself in 2000, 2001, and 2002. It supports a *H. s. signatus* population (Loehr, 2002b), and facilities are available for housing, radiography and miscellaneous research activities. A weather station is 2 km from the site; it holds many decades of weather data. It appears that the site represents “typical *H. s. signatus* habitat”, in comparison with descriptions in the literature (Boycott, 1989; Branch, 1998; Boycott and Bourquin, 2000).

The fieldwork periods that I will include in my thesis are:

(Early) spring	Summer	Autumn
August - September 2000 September - October 2001 September - October 2002 September - October 2003 September - October 2004	January 2004	April 2005[1]

[1] If body temperature loggers provide circumstantial evidence for autumn activity

General recordings

Throughout the fieldwork periods, 1 - 5 persons will methodically inspect the research area for *H. s. signatus* during the activity period of the species, which will be identified initially. I will log the number of daily searching hours and times. For each tortoise encounter, we will record the sex, shell dimensions and aberrations, mass, number and location of ticks, tortoise temperatures (inguinal, carapace and plastron surfaces), behaviour and microhabitat features. Microhabitat information will include soil temperature, distance (cm) to closest obstacle (any object large enough to hide or obscure the specimen from direct view), type of obstacle (rock, vegetation type), obstacle height (cm), geographic orientation and dorsal cover (%), and sun and shade soil temperatures near the tortoise. Furthermore, additional location information (latitude and longitude) of each tortoise will be measured with a GPS instrument.

In order to maximize the number of tortoises captured and observed during the fieldwork, and to identify tortoise refuge use and walked trails, thread-trailing and radio-telemetry methods will be applied. In 2000 - 2002 approximately five male and five female tortoises were equipped with thread trailing devices (Loehr, in press). In September 2003, six adult male and six adult female tortoises will be equipped with radio transmitters (giving a signal for one year), by means of quick-setting (60 s) epoxy. Tortoises will be selected that were located at approximately the same site in the three previous years (2000 to 2002).

In the previous years all tortoises have been uniquely marked by means of dots of black nail polish on the carapace, and they had their carapace and plastron characteristics photographed on digital images. As a more permanent marking technique I will notch tortoise marginal scutes from 2003 onwards (Cagle, 1939).

All tortoises will be promptly released at their points of capture when ambient temperatures are not dangerous.

As a supplementation of the temperature data provided by the weather station, dataloggers (HOBO, various types, Onset Computer Corporation, USA) will be used to measure ambient and microhabitat (including hiding place) temperatures year-round.

Population ecology

Each encountered tortoise will also have its scute ring number counted on the anterior left costal scute by two researchers to verify estimates. To allow for additional interpretations and comparisons with previous and future ring counts, digital images will be made using a macro lens. Across year comparisons will be used to verify and calibrate the use of scute ring counts to quantify age. Furthermore, we will estimate the number of scute rings formed prior to maturation (and possible growth rate changes) in adult tortoises. Combining scute ring data with the general recordings described above, I will address research problems regarding population ecology.

Resource requirements

(Micro)habitats and activity

When the research area was first used, I defined five microhabitats (flower field, rocky hill, dry river bed, intermediate flower field - rocky hill/river bed, and rock slab), differing in slope, presence of rocks, and vegetation (Loehr, 2002b). The tortoises distributed disproportionally in the microhabitats, and thread-trailing was used to determine the daily distances that the tortoises moved and their activity ranges. Also, I evaluated spring activity patterns (hiding, basking, walking, feeding, combat, mating, and digging for egg-laying), and retreat use (deep rock crevice with and without concealed entrance, shallow crevice with and without concealed entrance, under vegetation, and dorsally exposed retreat). Beginning September 2003, radio-telemetry will be used to continue the monitoring of activity patterns along the same design, to increase sample size and to identify annual variation. Additionally, I will focus on microhabitat use by characterising microhabitats in greater detail (see General Recordings), to determine if tortoises prefer exposed or concealed sites for their activities, and what types of concealment or cover are preferred. Radio-tracked tortoises will be located once daily at various times of the day and in various order.

Radio-telemetry will also allow to track aestivating tortoises in summer 2004, to measure annual space requirements and home ranges. In case tortoises will not be aestivating in January 2004, I will track all specimens daily as in spring. Drs. M.D. Hofmeyr and B.T. Henen consider tracking specimens between my fieldwork periods, and this would generate additional information regarding the annual activity cycle. With the help of a group of local people who are already aware of the *H. s. signatus* research project, and who have provided help in the past years, I will also distribute a *H. s. signatus* sightings form among approximately 50 - 100 local people (including farmers) who are in the veld frequently. I will ask them to note the date, time and location for all *H. s. signatus* they see between October 2003 and September 2004. If a reasonable number of forms are returned, this might provide data on the activity cycle of the species.

Body temperatures

Recording of body temperatures will be renewed after having started this in spring 2001. During fieldwork periods, inguinal, carapace and plastron surface (and vicinity soil) temperatures will be measured by means of hand-held infrared thermometers (Convir Pyropen L, Calex Electronics Limited, UK. In order to obtain body temperature profiles between fieldwork episodes, the six male and six female radio-tracked tortoises will be equipped with small weatherproof temperature data loggers (Thermochron iButtons, 16 mm diameter and 6 mm height, feature up to 2048 measurements and delayed start option) in September 2003. The dataloggers will be glued on the carapace by means of quick-setting epoxy, and data will be read (and memories reset) in October 2003 (end of 2003 fieldwork), and January and September 2004. If temperature data in September 2004 indicate a high probability of activity in autumn 2004, measurements will be prolonged with an extra fieldwork period in April 2005. This would also increase information on the annual activity cycle of *H. s. signatus*. In September - October 2003, I will compare data logger temperatures of the radio-tracked specimens with manually measured carapace temperatures, to establish the relationship between these two variables. This relationship will be used to calculate carapace temperatures from data logger temperatures during the rest of the year. Dataloggers and infrared thermometers will be calibrated before application and after removal against readings for standard mercury thermometers.

The following data logger measuring schedule will be used:

Radio-tracked specimens

Specimen	Sex	Start measurements	Specimen	Sex	Start measurements
4 September - 7 October 2003, measuring frequency 30 minutes			*13 January - 18 January 2004, measuring frequency 10 minutes*		
1 - 6	Male	04-09-03 12:00 hrs	1 - 6	Male	13-01-04 12:00 hrs
7 - 12	Female	04-09-03 12:00 hrs	7 - 12	Female	13-01-04 12:00 hrs
9 October 2003 - 11 January 2004, measuring frequency 90 minutes			*19 January - 7 September 2004, measuring frequency 180 minutes*		
1 - 6	Male	09-10-03 12:00 hrs	1 - 6	Male	19-01-04 12:00 hrs
7 - 12	Female	09-10-03 12:00 hrs	7 - 12	Female	19-01-04 12:00 hrs

Diet

In spring 2000 the composition of the diet of *H. s. signatus* was established by faecal analysis. Faeces from encountered specimens were collected and dried, together with samples from most plant species in the research area. Faecal samples were compared with the identified references by means of a dissecting scope. In spring 2003 and 2004 I will determine dietary preferences of the tortoises, comparing focal feeding observations with vegetation analysis. Binocular-aided focal observations will be made by two field personnel who will follow and observe a (radio-tracked) tortoise for an entire day, twelve times during each study period. Each food item will be recorded, and it will be attempted to estimate the number of bites and plant parts eaten for each species. These data will be compared to the availability of plant species, as determined by analysis of abundance and cover, at ground level, in six to ten plots in each of the five major microhabitat types on site.

Reproduction

Radiography

Adult female tortoises have been and will be examined for calcified eggs by the use of x-rays at the Springbok hospital, during all fieldwork episodes. Egg measurements will be taken and calculated from the radiographs. Females will be released at the location of capture on the same day as temperatures permit.

Ultrasonography

In order to maximize reproductive data collection, Drs. M.D. Hofmeyr and B.T. Henen have conducted ultrasound scans in the field in 2000. Although it will not be part of my research project, this collaboration will continue and the radio-tracked specimens in my study population will be used for continued ultrasound data collection.

EQUIPMENT, BUDGET AND PLANNING

The following list describes the equipment needed for carrying out the research project, including the financial costs involved. Eco-volunteers will be used to assist in the field, and all fieldworkers will fund international travel expenses, housing, food, and salary themselves. For the previous projects on *Homopus s. signatus* much of the expensive equipment (balances, digital callipers, ambient temperature data loggers, infrared thermometer, GPS device, et cetera) has been purchased. Some other equipment (laptop and pocket computers, digital camera, additional GPS device, infrared thermometer, et cetera) will be provided by myself. This will reduce considerably the costs for the current project.

In 2002, the Chelonian Research Foundation has granted a Linnaeus Fund Award, and the Dutch Foundation for the Advancement of Herpetology an additional grant, for an intended study on *H. s. cafer*. Circumstances forced me to abort this study, but both organisations have decided that the remaining budget would also be spent wisely on further *H. s. signatus* research. In addition, funding has been raised among various European turtle societies, and private individuals, resulting in a total available budget of US$ 2,550.

In November 2002 a screensaver on turtles of Africa has been included in the catalogue of a German publisher, likely resulting in some budget (estimated US$ 150). Various funding organisations in Europe and the USA have been approached to cover the remaining costs (US$ 3,719). When funding would turn out to be insufficient, the participants will cover the costs of national travel expenses, and I will fund the receiver and antenna for the radio-tracking privately. The minimum amount of funding that still is to be found is US$ 819.

Equipment	**Costs (US$)**
Radio transmitters (12 pcs.)	2,500
Receiver	1,000
Antenna	200
Thermochron iButtons (12 pcs.)	180
Connecting kit and software for iButtons	15
Batteries	50
Subtotal	*3,945*

Further budget and total is estimated as following:

Material/services	**Costs (US$)**
National travel expenses (Sep/Oct 2003+ 2004)	1,700 (Jan 2004 and Apr 2005 will be funded by myself)
X-raying	150
Quick-setting epoxy	20
Printing forms	20
Subtotal	*1,890*
Various expendable supplies	10% of budget
Total	*6,419*

The following table presents the proposed time line.

Activity	**Period**
Review and finalisation Ph.D. proposal	April 2003
Fund raising	January 2003 - August 2003
Applying for research permits	April 2003
Ordering equipment	April 2003
Data processing 2002 study	October 2002 - August 2003

Activity	Period
Fieldwork	September - October 2003 (6 weeks) January 2004 (1 week) September - October 2004 (5 weeks) April 2005 (1 - 3 weeks, depending on activity)
Data processing 2003 - 2005 studies	October 2003 - July 2005
Writing Ph.D. thesis	January 2004 - July 2005
Preparing manuscripts for publication	January 2005 - July 2006

DISSEMINATION OF RESULTS

The preceding research period (2000 - 2002) has already resulted in several papers (Loehr, 2002a, 2002b, in press), and some results have been and will be presented orally (symposium of the Herpetological Association of Africa in Stellenbosch, South Africa, 2001; Congress for Chelonian Conservation in Saly, Senegal, 2003). Upon completion of the proposed continuation, all results will be aggregated in several more comprehensive publications. This implies that fewer publications may be produced in the mean time, not to compromise possibilities of producing higher quality papers. I will present all of my results gathered between 2000 - 2005 in a Ph.D. thesis.

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