Seasonal movement and activity patterns of the endangered geometric tortoise, *Psammobates geometricus*

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ABSTRACT

SEASONAL MOVEMENT AND ACTIVITY PATTERNS OF THE ENDANGERED GEOMETRIC TORTOISE, *PSAMMOBATES GEOMETRICUS*

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Due to the critical status of *Psammobates geometricus* and the vulnerability of their habitat, there is a need to allocate areas for their protection. The aim of this study was to provide information on the space requirements and activity level of geometric tortoises to facilitate future conservation efforts. The thread-and-spool method was used to compare short-term movements, habitat utilisation, and activity patterns of male and female tortoises over 15 and 20 days respectively, in autumn and spring. Through radiotelemetry, the long-term movements of 10 male and 11 female tortoises were evaluated from April 2002 to April 2003. Locality data for the short-term and long-term studies were used to calculate the size of activity areas and home ranges as minimum convex polygons and fixed kernel estimates.

Male and female geometric tortoises were active throughout the year, and maintained a high level of activity in autumn and in spring. However, females were more active than males were in spring. Females may require more resources, particularly food, in spring when they produce eggs. Although males and females travelled similar distances in autumn and in spring, males displaced further than females displaced in both seasons. The movement path for males was often linear, perhaps because this path may enhance their opportunities to encounter females. Geometric tortoise males were substantially smaller than females, which may explain why the distances that males moved and displaced in spring were negatively correlated to environmental temperature. In autumn, when temperatures were lower than in spring, the distance travelled by males was not correlated to temperature. However, in autumn female displacement showed a positive correlation with environmental temperature.

Geometric tortoises showed large inter-individual variation in home range size, which may contribute to the fact that home range size did not differ among the three different habitat types: mature renosterveld, burned renosterveld and the old agricultural fields. Average home range size was 11.5 ha for 95% fixed kernel estimates, and 7.0 ha for minimum convex polygon estimates. Body size influenced the home range size of female geometric tortoises, but had no effect on the home range size of male tortoises. Females had larger home ranges than male tortoises had, possibly because females were larger, but reproductive requirements of females may have played a role. During the dry season, home range size increased when compared to the wet season. The larger home range during the dry season, which is associated with high temperatures, may be related to a reduction in resource availability. The fewer resources available, the greater the distance the tortoises would need to travel in order to acquire the necessary resources. The small home range in the wet season may indicate an abundance of resources, but it may also be that large pools of standing water restrict the movements of tortoises.

Understanding the spatial and habitat requirements of *P. geometricus* will help to assess the viability of populations in disturbed and highly fragmented areas, and contribute to the conservation efforts for this endangered species.

November 2005

DECLARATION

I declare that ***Seasonal movement and activity patterns of the endangered geometric tortoise, Psammobates geometricus*** is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

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Ulric Patrick van Bloemestein November 2005

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1 GENERAL INTRODUCTION

1.1 CHELONIANS

Amphibia, Reptilia, Aves and Mammalia are collectively called tetrapods. The Carboniferous Period brought about the beginning of reptile evolution with adaptations in morphology and behaviour to a terrestrial environment. The development of amniotic eggs by reptiles improved their chances of survival on land (Ferri 2002).

The most primitive turtle arose 210 million years ago (Late Triassic Period; Pough *et al.* 2001). Since turtles have a hard bony carapace, it makes them easily identifiable in fossil records (Pough *et al.* 2001). Extant turtles of the order Testudinata are divided into two clades, Pleurodira and Cryptodira, based on the movement or retraction patterns of the neck (Zug *et al.* 2001):

1. The Pleurodira can retract the head and neck by laying it to the side (left or right).
2. Cryptodira can retract the neck posteriorly into a medial slot within the body cavity.

Pleurodiran turtles have the pelvic girdle fused to the plastron and have a jaw closure mechanism with an articulation on the trochlear surface of the pterygoid. Cryptodira first appeared in the Cretaceous Period and have a characteristic flexible articulation of the pelvic girdle (Zug *et al.* 2001). Their jaw closure mechanism has an articulation on the trochlear surface of the otic capsule (Zug *et al.* 2001).

The Pleurodira consist of two extant clades Chelidae and Pelomedusoides, the latter consists of sister clades Pelomedusidae and Podocnemidae (Zug *et al.* 2001). Pelomedusidae has two genera and are small to moderately large (12 to 50 cm carapace length, Pough *et al*. 2001) with an oblong, moderately high-domed carapace (Zug *et al*. 2001). Podocnemidae has three genera and are moderately large (Zug *et al*. 2001), with extant forms reaching 90 cm (carapace length) and some extinct forms exceeded 2 m (Pough *et al.* 2001). Chelidae have 11 genera and all are aquatic species with a flattened skull and shell (Ferri 2002).

Combined molecular and morphological data support the recognized groupings of Cheloniidae with Dermochelyidae, Trionychidae with Carettochelyidae, Kinosternidae and Dermatemydidae, and Emydidae with Bataguridae and Testudinidae; each group forms a clade within Cryptodira (Zug *et al*. 2001). Chelydridae appears to be an ancient clade and a sister group to the other cryptodirans (Zug *et al*. 2001). Cheloniidae are sea turtles with a shell covered by large horny plates (Ferri 2002). Dermochelyidae has only one species, the leatherback turtle (*Dermochelys coriacea*), which has a carapace with a thick leathery skin and greatly reduced bony elements, mostly osteoderms (Pough *et al*. 2001).

The Trionychidae characteristically have a carapace, containing few bones covered with leathery skin (Ferri 2002). The Kinosternidae consists of two subfamilies Kinosterninae and Staurotypinae (Ferri 2002). Kinosterninae have a well-developed plastron that lacks an entoplastral bone; the plastron is usually hinged (Zug *et al*. 2001). Staurotypinae have a plastron with an entoplastral bone (Zug *et al*. 2001). The Dermatemydidae consists of a single species (*Dermatemys mawii*), which has a broad and flat carapace with no claws on the feet (Ferri 2002). The Carettochelyidae consists of a single species (*Carettochelys insculpta*); the carapace does not have epidermal scutes but a smooth epidermal skin (Ferri 2002).

The Emydidae consists of ten genera. With the exception of the genus *Terrapene*, the emydid carapace is rather flat, oval, and has a smoothed surfaced (Ferri 2002).

The Bataguridae has twenty-three genera and ranges from species that are semi-terrestrial to aquatic (Pough *et al*. 2001; Ferri 2002). The Testudinidae, the land tortoises, typically have well-developed, high-domed shells. The exception is the pancake tortoise *Malacochersus tornieri*, which has reduced bony components in its dorso-ventrally flattened shell. All tortoises have elephantine hind limbs (Zug *et al*. 2001).

1.2 TORTOISES

The Testudinidae are true land tortoises and form eleven genera, *Chersina, Geochelone, Gopherus, Homopus, Indotestudo, Kinixys, Malacochersus, Manouria, Psammobates, Pyxis,* and *Testudo,* and 45 species (Zug *et al*. 2001). Southern Africa has five genera (*Chersina*, *Geochelone*, *Homopus*, *Kinixys* and *Psammobates*), 14 species and 11 endemic species of tortoises (Boycott & Bourquin 2000). South Africa has the richest tortoise diversity of any country, having five genera and 13 species, with four of these species being endemic to South Africa. Four genera and eight species of tortoise can be found in the Northern and Western Cape Provinces (Branch 1998; Boycott & Bourquin 2000).

Not only does South Africa contain a wealth of tortoise species, it also has a great diversity of vegetation, including its own biome, the Cape Floral Kingdom. There are approximately 8 700 plant species in the Cape Floral Kingdom with the possibility of having the highest level of floral endemicity on any subcontinent (Low & Rebelo 1996). The tortoise diversity may be linked to the floral diversity. Most tortoises are herbivores and eat flowers, seeds, fruits, and foliage; a few tortoise species such as *Geochelone carbonaria* and those of the genus *Kinixys* are opportunistic omnivores (Boycott & Bourquin 2000; Zug *et al*. 2001). The importance of tortoises in an ecosystem is undervalued. Kerley *et al*. (1998) estimated that tortoises can have a high biomass in relation to other herbivores and are selective feeders. The impact of tortoises is considerable; they play a role in seed dispersal because they do not subject seeds to severe digestive processes (Kerley *et al*. 1998).

One of the more common southern African species is the angulate tortoise, *Chersina angulata*, which has a distribution paralleling the coastline from East London westwards to Cape Town and extending just north of the Orange River (Greig & Burdett 1976, Branch 1998, Boycott & Bourquin 2000). The largest tortoise of southern Africa is the leopard tortoise (*Geochelone pardalis*), which occurs in savannahs throughout much of Africa (Branch 1998). Tortoises of the genus *Homopus* have been studied little, although *Homopus signatus signatus*, the world's smallest terrestrial tortoise, is the subject of current studies (Loehr 2002, Loehr *et al*. 2004). The common padloper *Homopus areolatus* is endemic to South Africa, is restricted to southern and southwestern South Africa, and is found primarily in moister coastal regions (Boycott & Bourquin 2000). The hinged tortoises (*Kinixys* spp.) are found in northeastern regions of South Africa and adjacent countries (Boycott & Bourquin 2000). The activity of Speke's hinged tortoise (*K. spekii*) has been studied by and his colleagues (Hailey 1989, Hailey & Coulson 1996).

The genus *Psammobates* consist of three species: *P. geometricus*, *P. oculiferus*, and *P. tentorius* (Boycott & Bourquin 2000). *Psammobates tentorius* is endemic to southern Africa and consists of three subspecies, *P. tentorius tentorius*, *P. tentorius verroxii*, and *P. tentorius trimeni* (Boycott & Bourquin 2000). *Psammobates oculiferus* occurs over a large part of Namibia, Botswana, and the Northern Cape Province of South Africa; *P. oculiferus* is known, some times, as the Kalahari geometric tortoise (Boycott & Bourquin 2000). *Psammobates geometricus*, the geometric tortoise, has a small distribution and is found only in the southwestern portion of the Western Cape Province, South Africa (Boycott & Bourquin 2000). Three areas today support geometric tortoise populations, the Southwestern Coastal

Lowlands, Worcester-Tulbagh Valley, and Ceres Valley. These populations are isolated from one another by natural barriers such as mountain ranges (Baard & Mouton 1993).

1.3 THE GEOMETRIC TORTOISE

1.3.1 Historical overview

One characteristic that separates the genus *Psammobates* from others is the unique colouration pattern. It consists of a black background with bright yellow rays radiating from the centres of all the carapacial shields (Boycott & Bourquin 2000). These geometric patterns may be unique to individual tortoises, similar to that of fingerprints (de Villiers 1985). The cryptic colouration pattern and sedentary behaviour of this genus makes them extremely difficult to locate in the vegetation (Gardner *et al.* 1999).

Carolus Linnaeus first described the geometric tortoise in 1758 (Baard 1990). In 1960, the geometric tortoise was thought to be extinct. However, A. Eglis discovered a remnant population in 1972 (de Villiers 1985). Since the rediscovery, several nature reserves were established for the protection of the geometric tortoise (Baard 1993). The geometric tortoise has the smallest distribution of all South African tortoise species (de Villiers 1985) and *P. geometricus* do not occur in mountainous terrain (Greig 1984). The historical distribution of the geometric tortoise has never been extensive (Greig & Burdett 1976).

1.3.2 Status, Conservation and Threats

Psammobates geometricus is listed as Endangered in the IUCN Red Data Book (IUCN 2004) and the South African Red Data Book of reptiles and amphibians (Baard 1988). After the rediscovery of the geometric tortoise, immediate steps were taken to conserve it. The first reserve dedicated to the conservation of the geometric tortoise was opened on the farm Eenzaamheid (Greig & de Villiers 1982). The reserve grew from a 7.5 hectare in 1972 to a 28-hectare reserve (Greig & de Villiers 1982). From 1971 to 1982, six reserves where establish to protect the geometric tortoise. The largest reserve is the Elandsberg Private Nature Reserve (EPNR) and the second largest reserve is Voëlvlei Nature Reserve (Baard 1993). Today there are two private and five provincial nature reserves protecting the geometric tortoise (Boycott & Bourquin 2000). The largest reserve (EPNR) is 3 200 ha, of which 1 000 ha is suitable habitat (renosterveld) for an estimated 2 700 – 3 400 tortoises (Baard 1990; Boycott & Bourquin 2000).

Although there has been an improvement in the protection of the geometric tortoise, the reduced distribution has been attributed to many concerning factors (Baard 1993). The natural threat is far less detrimental than the unnatural threats to the geometric tortoise populations. The natural predators of geometric tortoises include baboons, jackals, mongoose, genets, ostriches, secretary birds, raptors, crows, and storks (Boycott & Bourquin 2000). Fire plays a part in the renewal process of renosterveld but fire can be destructive if not controlled. The unnatural threats to *P. geometricus* include unplanned and uncontrolled wild fires, invasive alien plants and the degradation and destruction of natural habitat by other human activities (e.g., agriculture and rural development; Baard 1993). The geometric tortoise is also highly desired in the illegal pet trade (Greig & de Villiers 1982; B.T. Henen, M.D. Hofmeyr & E.H.W. Baard, unpublished manuscript). Baard (1993) suggested that habitat destruction is now the main factor in the decline of geometric tortoise populations.

1.3.3 Habitat of the geometric tortoise

The geometric tortoise is restricted to a vegetation type known as renosterveld (Acocks 1975). The *P. geometricus* link to renosterveld may be the availability of specific food plants; geometric tortoises may have a specialized diet (Baard 1995;

Boycott & Bourquin 2000). West coast renosterveld or coastal renosterveld is part of the Cape Floristic Kingdom, and experiences a Mediterranean climate (hot and dry summers and cool, wet winters; Low & Rebelo 1996). West coast renosterveld is characterised by mid-dense to closed, cupressoid and small-leaved, mid-high evergreen shrubs, with regular clumps of broad-leaved, tall shrubs (Low & Rebelo 1996). About 3% of the original renosterveld remains, with the largest patches at the EPNR and Tygerberg Hills (Low & Rebelo 1996). Renosterveld grows on soils suitable for cultivation and the conversion of renosterveld to agricultural use is believed to be the major factor for the decline in geometric tortoises (Baard 1993).

1.3.4 Ecology of the geometric tortoise

Food, cover (or refugia) and nesting sites are important resources for geometric tortoises (Baard 1995). Geometric tortoises lay eggs from winter to mid summer (ca. July to January), producing clutches of up to five eggs and up to three clutches per year (M.D. Hofmeyr, M. Klein, B.T. Henen & E.H.W. Baard, unpublished manuscript). *Psammobates geometricus* may reach maturity at seven to eight years (de Villiers 1985). The maximum age for *P. geometricus* is about thirty years, although age estimation is problematic (Baard 1990). Female geometric tortoises are about 20% larger (carapace length up to 143 mm) and 100% heavier (body mass up to 680 g) than conspecific males (ca. 123 mm and 320 g, respectively; Baard 1990). Females have a more domed shell, shorter tails and less plastral concavity than do males (Baard 1990).

The colouration of geometric tortoises is cryptic and probably helps in predator avoidance (Gardner *et al*. 1999). Cryptic colouration may be enhanced by preferences for areas of high shrub or canopy cover, which geometric tortoises apparently prefer (Baard 1995). Baard (1988) reports a bimodal daily activity pattern for *P. geometricus*. The Mediterranean climate can cause large seasonal changes in the habitat (Baard 1993, U. van Bloemestein, pers. obs.); geometric tortoises probably avoid the flooded areas in winter, but may use the same locations during dry periods. Temperature may also affect the activity and movements of geometric tortoises. Temperature affects the activity patterns of other tortoise species (e.g., Hailey & Coulson 1996; Diaz-Paniagua *et al.* 1995).

1.4 RESEARCH DESIGN

1.4.1 Short-term movement studies

Many researchers used the thread trailing or thread-and-spool method with great success to determine the habitat use and movements of individual animals. The technique was first developed by Breder (1927) in an effort to obtain detailed data on the general behaviour and daily life of eastern box turtles (*Terrapene carolina*). Thread trailing provides detailed information on the length and location of individual animal movements (Hailey 1989; Hailey & Coulson 1996) and provides the means to follow paths as individuals move around obstacles that catch the thread (Claussen *et al.* 1997). This method would not be effective if there was little plant material to catch the thread (Claussen *et al*. 1997).

1.4.2 Long-term movement studies – a comparison

Radiotelemetry and thread trailing techniques can be used to ascertain animal home ranges. Home range is the area an animal normally travels in the course of its daily activities (Stickel 1950). Evaluating home ranges can include comparisons of geographic centres (the mean position of capture sites) used over time (Stickel 1989). Home range reflects habitat quality and population density (Stickel 1989; Diemer 1992).

There are problems with thread trailing methods. First, the spool has a limited capacity that may run out before the tortoise enters a refuge. Second, the animal may become disturbed when changing the spool (Breder 1927). However, thread trailing facilitates gathering detailed information on habitat utilization (Breder 1927). Unlike thread trailing, radiotelemetry is a costly method of tracking animals (Claussen *et al.* 1997). However, with the use of radiotelemetry, the animal can be located at any time and animal movement can be studied over extended periods (Claussen *et al*. 1997). These features facilitate gathering many data points without frequent spool changes associated with thread trailing.

1.5 GENERAL AIMS

In my research, I am quantifying the short-term and long-term movements of male and female geometric tortoises. The aim of my research into these movements is to better understand the habitat use of *P. geometricus* in renosterveld. By assessing their movements and home ranges in different areas of the reserve, we can better quantify the habitat requirements of geometric tortoises. Such information is essential to develop an effective management programme (Gibbons 1986), which will help conserve this species.

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2 EFFECT OF SEX AND SEASON ON ACTIVITY AND MOVEMENT PATTERNS OF *PSAMMOBATES GEOMETRICUS*

2.1 INTRODUCTION

Animals may move to obtain food or water, find mates, shelter and nesting sites, bask and hibernate (Baard 1995; Claussen *et al*. 1997). Finding resources requires movement and consequently activity. The activity peaks of male and female spur-thighed tortoises (*Testudo graeca*) show differences due to critical phases in reproductive cycles, mate searching for males and nesting for females (Diaz-Paniagua *et al*. 1995). However, resources vary in space and fluctuate in time (Yeomans 1995). Weather conditions do not govern chelonian activity completely (Claussen *et al*. 1997). Studies conducted on *T. graeca* found that temperature, solar radiation, and population density can influence activity (Diaz-Paniagua *et al*. 1995). Home range size may depend on the productivity of the environment, the number of individuals within the habitat, and climatic conditions over time (Stickel 1950).

In addition, season plays an important part in the activity patterns of animals. Reptiles are ectothermic; they rely on external heat sources to elevate their body temperature. Activity in Speke’s tortoises (*Kinixys spekii*) is known to decline in the hottest part of the day (Hailey & Coulson 1996). Studies show that the seasonal activity of leopard tortoises (*Geochelone pardalis*) is related to both rainfall and temperature (Hailey & Coulson 1996). The environmental factors, which are important for tortoise survival may also, in high levels, limit movement and activity. Speke’s tortoises become active after rain and inactive in periods of high precipitation (Hailey & Coulson 1996). Thermoregulatory studies completed on *K. spekii* indicate increases in activity with increases in ambient temperature; however, further increases in ambient temperatures reduced tortoise activity because *K. spekii* were then in danger of overheating (Hailey & Coulson 1996).

A study of animal movement in the natural environment is critical in understanding the behaviour influencing the utilization of limited areas (home range) in the habitat (Stickel 1989). Through a better understanding of the space requirements of animals, effective and efficient methods of wildlife conservation can be implemented (Gibbons 1986). However, it is difficult to obtain detailed movement patterns from individual animals in their habitat. The use of the mark-recapture method is useful in population estimates and movement studies, but it is often difficult to recapture individuals in the wild (Pough *et al*. 2001). An expensive alternative, radiotelemetry, is available to follow individuals for long periods.

Thread trailing is a powerful technique for detailed movement studies of an animal (Breder 1927, Hailey & Coulson 1999). Thread trailing is cheaper than radiotelemetry and enables access to the exact path followed by an animal (Hailey & Coulson 1999). Consequently, it is possible to determine the extent to which a tortoise utilizes its habitat for resources and how individuals differ in habitat use. Although the thread-and-spool technique has been quite useful for detailed analysis of habitat utilization, it is however restricted by the length of thread in the container (Breder 1927).

Psammobates geometricus, known as the geometric tortoise, is restricted in distribution. The geometric tortoise is located in the southwestern coastal lowlands and low-lying parts of Worcester and Ceres Valleys of the Western Cape Province, South Africa (Baard 1988). This area experiences a Mediterranean climate consisting of dry summers and wet winters (Baard 1993). *Psammobates geometricus* is listed as Endangered in the IUCN Red Data Book (IUCN 2004) and the South African Red Data Book (Baard 1988). Understanding the special habitat requirements of *P.*

geometricus will help to assess the viability of populations in disturbed and highly fragmented areas, and contribute to the conservation efforts for this endangered species. With the use of thread trailing, the special needs can be determined for the geometric tortoise.

Psammobates geometricus is most active during autumn and spring (de Villiers 1985), which makes these periods important for study. I will focus on the sexual differences in movement, activity, and habitat use of *P. geometricus* for autumn and spring. In this chapter, I discuss the variability in activity for male and female geometric tortoises, and activity differences between autumn and spring 2002. I test for differences in distance moved, and the shape of the path followed within the habitat, by male and female geometric tortoises. I also test for influences of environmental factors on tortoise movement.

2.2 MATERIALS AND METHODS

2.2.1 Study site

The Elandsberg Private Nature Reserve (EPNR; 33° 26’ S; 19° 02’ E) has the largest known population of geometric tortoises. The reserve has a total area of 3 200 ha of which 1 000 ha consists of suitable habitat known as renosterveld (Baard 1993), making this the largest conserved area for the geometric tortoise. The reserve is located at the base of the Elandskloof mountain range, which forms part of the Cape Fold Mountains.

The EPNR is within the Fynbos Biome with two natural veld types occurring on the Reserve, West Coast Renosterveld and Mountain Fynbos. Fire is an integral part of Fynbos dynamics and several areas in the reserve show vegetation in various stages of post-fire succession. These burned fields have a low canopy cover of shrubs and contain plant elements needed by geometric tortoises (Baard 1990). The reserve is located on a wheat farm and previously cultivated lands were incorporated into the reserve. These old fields, covered mainly by grasses, are heavily grazed by the large herbivores in the reserve (Baard 1990).

Since renosterveld is the preferred habitat of geometric tortoises (Baard 1995), this veld type is well suited to study the local movement and activity patterns of *P. geometricus*. The geometric tortoise is regarded as extremely elusive due to its cryptic behaviour and colouration patterns (Gardner *et al*. 1999). Therefore, my study was done in a recently burned area (1998 fire) since it was easier to track tortoises in the sparse and patchy vegetation. The study area is surrounded by unburned renosterveld that graded into Mountain Fynbos in the eastern part of the reserve. The vegetation in the study area consisted of grasses, sedges, herbaceous plants, low shrubs, and clumps of taller *Leucadendron* species that exceeded one meter in height.

2.2.2 Study design

In April 2002, I surveyed the study area for tortoises and recorded the location (latitude and longitude) of each geometric tortoise with a handheld, global positioning system unit (Trimble GeoExplorer II). After capture, the tortoise was weighed to the nearest 0.1 g with an Ohaus digital balance, and its shell was measured to the nearest 0.1 mm with vernier callipers. The following shell measurements were recorded: straight carapace length from the nuchal to the supracaudal scute, the widest carapace width at marginal scutes six or seven, and shell height at the third vertebral scute. External morphological characteristics as described by Baard (1990), e.g., the plastral concavity and large tail of males, were used to distinguish males and females. Each tortoise received a unique identification number by filing shallow notches in specific marginal scutes.

I used the thread-and-spool method to study the activity and movement patterns of adult male and female *P. geometricus* over 15 days in autumn (22 April to 6 May 2002) and 20 days in spring (12 to 31 October 2002). The autumn sample consisted of three female and three male tortoises while the spring sample consisted of five females and four males. Two of the males and three females were studied in both seasons.

For the thread-and-spool method, I modified film canisters (average mass of 5.7 g) by cutting an opening into the side of the canister for the thread to unwind. The canister was attached with contact adhesive and duct tape to the tortoise's carapace (between the fifth vertebral and supracaudal scutes), and a spool of cotton thread (approximately 150 m) was placed inside the canister. Each study animal was also fitted with a radiotransmitter (ca. 18 g, Carapace Mount transmitters, AVM Instrument Company, Ltd.), attached between the anterior vertebral and costal scutes. The radiotransmitters allowed me to track and locate individuals that ran out of thread when moving long distances.

After processing the tortoise, each individual was returned to the exact position where it was captured. The position was clearly marked with a flag and the thread was tied either to a cane staked near the tortoise or to the plant used as refuge. I used different coloured thread for individual tortoises to help distinguish their paths when their movements overlapped. We excluded data from the first 24 to 48 hours to standardise starting dates and to minimise potential effects of tortoises responding to the handling disturbance.

All data were recorded in the late afternoon after the tortoises found refuge for the night and became inactive. If an individual was still in the open, I returned later to take measurements and when I could not record all the data before dark, I returned early the next morning before activity commenced. In the late afternoon, I recorded the GPS position of the tortoise, marked its position with a flag, and tied the thread to the vegetation of the new refuge. The thread was replaced when required, with minimal disturbance to the tortoise. Individual tortoises seldom moved from their refuges after the thread was replaced.

2.2.3 Data collected

2.2.3.1 Distance moved – thread length

The distance (m) each tortoise moved during the day was estimated by pacing the length of the thread between the previous and new refuge. I standardised my paces against a preset distance and initially verified the accuracy of the estimate by measuring the thread length after pacing the distance. A standardised conversion factor was then used to convert distances moved to meters. On a few occasions, movements of large game through the area broke the thread. The thread was then collected and measured with a measuring tape.

2.2.3.2 Displacement – point-to-point

In autumn, the daily displacement (m) of an individual tortoise was estimated by pacing the straight-line distance between the start (previous refuge) and the end (new refuge) positions. In spring, however, I used a Laser Rangefinder (Bushnell Yardage Pro 500) to measure displacement in meters.

2.2.3.3 Movement path (shape)

As a tortoise moves through the habitat, the thread leaves a trail and the shape of the path provides information on movement patterns and habitat utilisation. After visual inspection and walking the path, the path was assigned one of six shape categories (Table 2.1). These categories, except circular, represent a transition from linear, directional movement to apparent non-directional and random movements (e.g., criss-cross) in the habitat. Movement path was consistently evaluated in spring, so spring movement paths were statistically analysed.

Table 2.1. The different shape categories used to describe the daily movement paths of *Psammobates geometricus.*

Category	Description
Linear (L)	A nearly straight, directional movement
Semi-circular (SC)	A curved but directional movement with a semi-circular to semi-oval shape
Zigzag (Z)	A directional movement with random deviations to the left and right, but the path never or seldom crossed
Loops (LO)	A directional to random movement with many loops in the path
Criss-cross (CC)	A non-directional movement with the path crossing numerous times
Circular (C)	A more or less circular movement with the same starting and ending points

2.2.3.4 Refuge characteristics

I identified the refuge plant to the nearest taxon and measured the height and width of the plant to the nearest centimetre. When more than one plant species comprised the refuge, I recorded the dominant and subordinate species that contributed most to the cover. Each refuge was assigned a density index between one and five. A density of five indicated complete and dense cover with no tortoise exposure to sunlight while a density of one represented less than 20% cover.

2.2.3.5 Environmental data

An MCS 120-04EX data logger was used to collect meteorological data at the study site at 15-minute intervals (averaged over 15 minutes) for the duration of the study. I used thermocouples (MCS 151) to measure air temperature (shaded) and ground temperature in full sun and in shade. Solar radiation was recorded with a pyranometer (MCS 155-1; 95% of the full range of the solar spectrum) and humidity was recorded with a relative humidity probe (MCS 174). Except for ground temperatures, all environmental parameters were recorded at a height of 0.75 m. I recorded rainfall events during the study period but did not measure precipitation. For comparison, I obtained rainfall data for De Hoek weather station (33° 15’ S; 19° 03’ E), approximately 20 km north of the Elandsberg reserve, on the western side at the foot of the Elandskloof mountain range.

2.2.4 Data analysis

I attempted to use multivariate statistics (e.g., two-way repeated measures ANOVA and three-way ANOVA) to evaluate the data, but these methods worked in only a few instances because some data were nonparametric or had limited sample sizes. To overcome the problems inherent to small sample sizes, I analysed the data as daily parameters (e.g., % of tortoises active) and calculated average daily values (e.g., distance moved) for male and female tortoises and for the two sexes combined. The daily averages for 15 days in autumn and 20 days in spring were then used in most of the analyses. In almost every instance where individual data and daily means were compared, the results were similar.

2.2.4.1 Activity

I used daily movement data to classify individual tortoises as either active or inactive on each day of the study. When a tortoise was active (i.e., moved a detectable distance), a value of one was assigned while a value of zero was assigned to an inactive individual. The values of individual males and females were then used to calculate daily activity for each sex.

2.2.4.2 Distance moved – thread length

Inactive individuals were excluded when calculating daily averages for the distances moved by male and female tortoises. By including zero values, daily averages would have underestimated the distance active tortoises travelled.

2.2.4.3 Displacement – point-to-point

I used data for active individuals when calculating average daily displacement, including individuals with zero displacement for those returning to the same refuge.

2.2.4.4 Displacement-to-distance ratio

A displacement-to-distance ratio was calculated for each individual each day and daily averages were then calculated for the different sexes. Inactive tortoises were excluded from the analysis and a ratio of zero thus indicates that the tortoise returned to the same refuge. In general, small ratios indicate a more intense use of the habitat near the refuge, while a large ratio represents a large displacement away from the previous refuge.

2.2.4.5 Movement path (shape)

After sorting the frequencies of movement paths into six shape categories, I tested whether the frequencies were homogenous among categories for all tortoises, and for each sex (simple χ^2 tests). I also compared frequencies between sexes using χ^2 contingency tables (Zar 1999).

2.2.4.6 Refuge categorization

The refuge categories were simplified into grass, restio, sedge, and shrubs. The average and 95% confidence interval was calculated for refuge properties (e.g., height) in autumn and spring, and then for males and females. Additionally, the height, width, density and volume of the refuge types were compared for each season. Refuge volume was estimated using an ellipsoid formula (in litres, π x Height x Width^2 / 6000). Only one sedge was used as a refuge in autumn (for three consecutive nights) and spring (one night), so in each season there was no variance for sedge height, width, volume or density. Due to the lack of variance and small sample size for sedges, I excluded sedges from the analysis of variance comparing height, width, volume and density among refuge categories.

2.2.4.7 Environmental data

I used the data logger records to calculate daytime means, maxima and minima for air temperature, ground temperatures in the sun and the shade, solar radiation and relative humidity. I calculated daytime means, maxima and minima for the 12 hours from 07h00 to 19h00, to reflect environmental records during hours when tortoises were active. The daily means of tortoise data (e.g., distance moved) were compared to environmental data for each sex and season.

2.2.5 Statistical analysis

Statistical analysis was completed by testing for the effects of season and sex on tortoise activity, distance moved, displacement, and displacement-to-distance ratios. When a two-way ANOVA failed the test for normality or equal variance, I tested separately for the effects of season and sex. In autumn and spring, and for the combined seasons, daily averages of male and female parameters formed pairs. Thus, when data were parametric, I used a paired t-test to test for differences between sexes and a Wilcoxon Signed Rank Test when the data were non-parametric. When comparing variation within a sex but between seasons, I used a Student's t-test for parametric data and a Mann-Whitney Rank Sum Test as the non-parametric equivalent. When frequencies were evaluated among categories, contingency tables and chi-square analysis were used. Refuge characteristics were compared with ANOVA, often requiring data transformation or nonparametric ANOVA (Kruskal-Wallis). The effects of environmental parameters were tested using Pearson Product Moment Correlation (r, if parametric) and Spearman's Rank Order Correlation (r_s, if non-parametric) on distance moved, displacement, activity, and distance-displacement ratio data. Inspection of correlation matrices revealed relatively few significant relationships, which I subsequently characterised with linear regression analysis.

2.3 RESULTS

2.3.1 Activity

Daily activity was high, with 84% of geometric tortoises active on an average day in autumn or spring (Fig. 2.1). However, daily activity varied considerably in autumn (40 to 100%) and spring (56 to 100%), and all females were inactive on 27 April 2002 (see Distance moved on 26 April 2002). Nonetheless, a higher percentage of female than male tortoises were active in spring (W= -97.0; T+=4.0; T- = -101.0; $P<0.001$) and for the two seasons combined (W= -182.0; T+ = 35.5; T- = -217.5; $P=0.003$). The percentage of active females was similar to that of males in autumn (W=-16.0; T+=10.0; T-=26.0; $P=0.313$). There was no difference in activity between autumn and spring for males (T=297.5; N=15, 20; $P=0.37$), females (T=270.0; N=15, 20; $P=0.99$) or for the two sexes combined (T=288.0; N=15, 20; $P=0.56$).

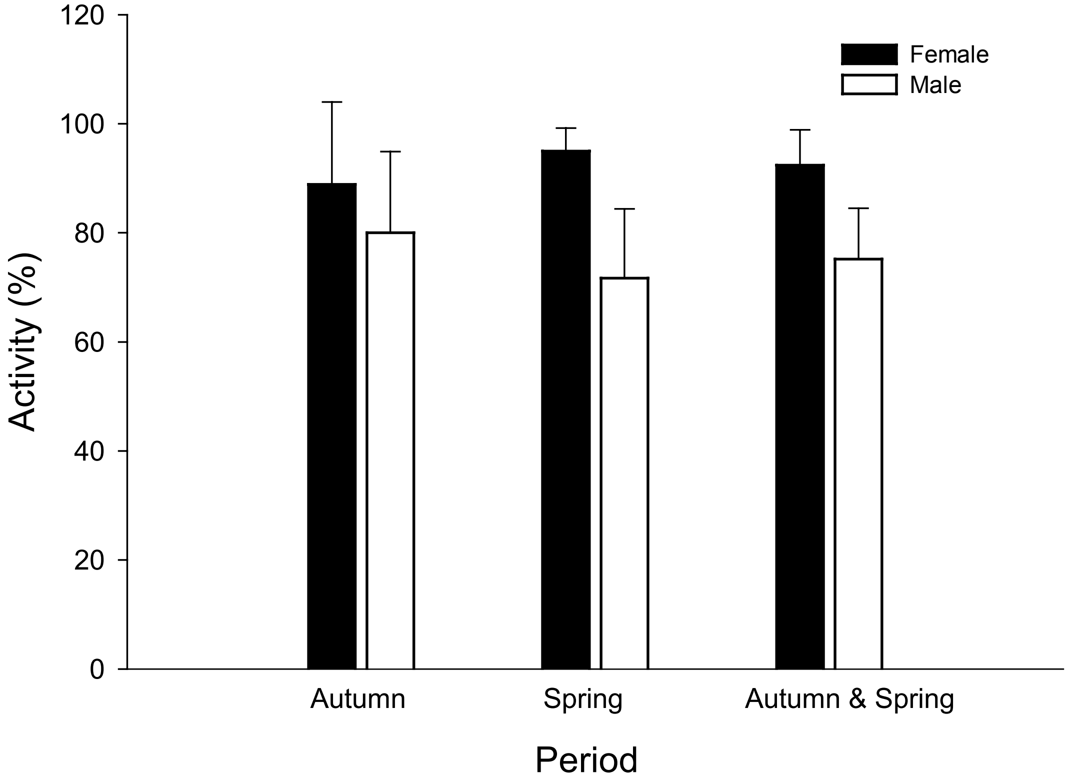

Figure 2.1. Percentage (mean ± 95% CI) of male and female geometric tortoises active each day in autumn, spring and the two seasons combined in 2002.

2.3.2 Movements

2.3.2.1 Distance moved

When active, geometric tortoises travelled 49.7 (± CI = 8.15, n=35) meters per day and moved longer distances in autumn than in spring (autumn: 62.2±13.6 m d^{-1}, n=15 and spring: 40.3±8.7 m d^{-1}, n=20, t_{33}=3.01, *P*=0.005). When considering both seasons, male geometric tortoises moved greater distances than females moved (paired t-test: t_{33}= 2.51; *P*=0.017; Fig. 2.2). When comparing seasonal movements for separate sexes, male geometric tortoises moved longer distances in autumn than in spring (Student's t-test: t_{33}= 2.86; *P*=0.007; Fig. 2.2). The same trend was apparent for females (Student's t-test: t_{32}= 2.23; *P*=0.033). There was no difference between the daily distances males and females moved in spring (paired t-test: t_{19}= 1.46; *P*=0.16), and the difference between sexes was not statistically significant in autumn (paired t-test: t_{13}= 2.06; *P*=0.061).

In a two-way ANOVA, distance moved differed among seasons (autumn>spring; $F_{1,201}$=13.9, P=0.00025) but not between sexes ($F_{1,201}$=1.56, P=0.21). In a separate two-way ANOVA, distances differed among individuals and days (using log transformation, individuals: $F_{9,161}$=5.68, *P*<0.001; days: $F_{34,161}$=2.79, P<0.001), with male #1121 moving further per day (88.3±18.6 m d^{-1}; n=31) than all others but female #1213 (45.8±16.2 m d^{-1}; n=16; all SNK post-hoc analyses at *P*<0.05). The distance travelled on 26 April 2002 (119.2±2.8 m, n=5) exceeded that on seven spring days (9 to 20 m d^{-1}; October 18, 20, 24, 25 and 28-30) and was preceded by cold rainy days on 23 and 24 April. The distance on 18 October 2002 (8.6±2.1 m) was lower than that on seven days in autumn and spring (44 to 67 m; 24 and 30 April, 3 and 4 May, 19, 22 and 23 October). The weather was cool and rainy on 18 October.

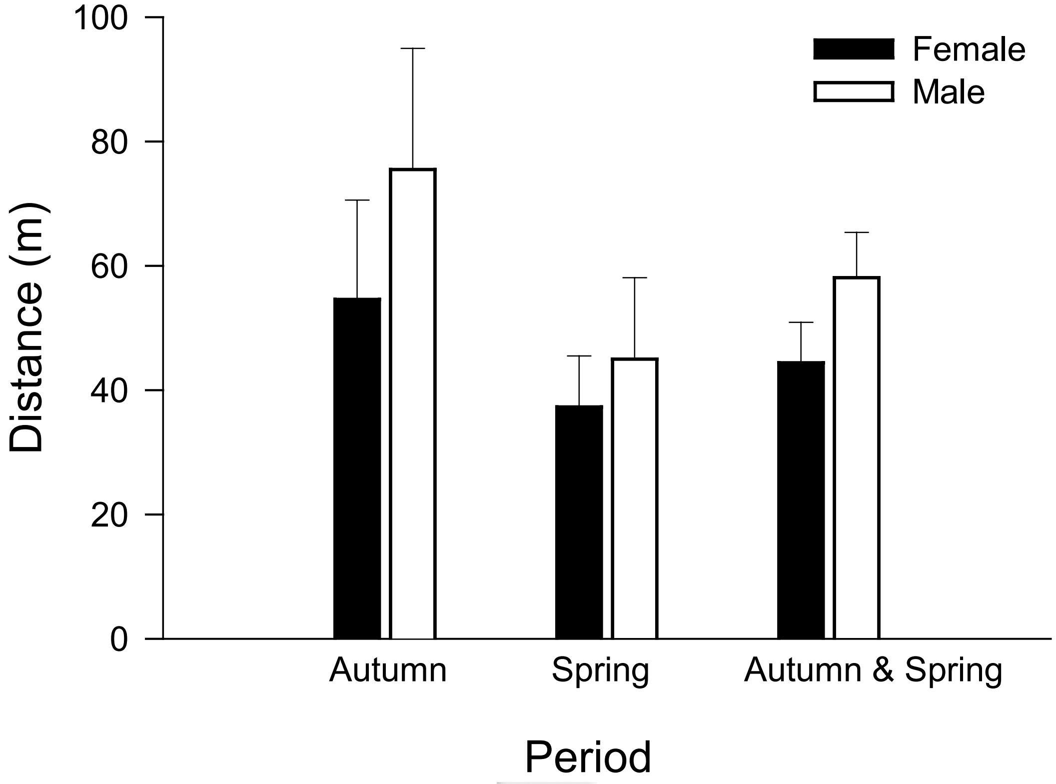

Figure 2.2. The average (± 95% CI) daily distance moved for male and female geometric tortoises, *P. geometricus*, for autumn (22 April – 6 May 2002), spring (12 – 31 October 2002), and for the two seasons combined.

2.3.2.2 Displacement

The distance female geometric tortoises displaced per day did not differ between the two seasons (Mann-Whitney Rank Sum Test: t_{32}= 1.96; *P*=0.058), however males had a greater displacement in autumn compared to spring (Student's t-test: t_{33}= 2.19; *P*=0.035; Fig. 2.3). When comparing the displacement of males and females, males displaced further in spring (Paired t-test: t_{19}= 2.90; P=0.009), autumn (Paired t-test: t_{13}= 3.33; P=0.005) and when the two seasons were combined (Paired t-test: t_{33}= 4.40; *P*<0.001). A two-way ANOVA confirmed the effect of sex (M>F, $F_{1,202}$=9.90, *P*=0.0019) and detected an effect of season (autumn>spring, $F_{1,202}$= 11.9, *P*=0.0070).

A separate two-way ANOVA detected effects of individuals ($F_{9,164}$=6.35; *P*<0.001) and days ($F_{34,164}$=2.04; *P*=0.002). Male #1121 displaced further (61.5±7.4 m d^{-1}, n=33) than all others did, and tortoises displaced further on 26 April (73.5±26.3 m, n=5) than during several days in spring.

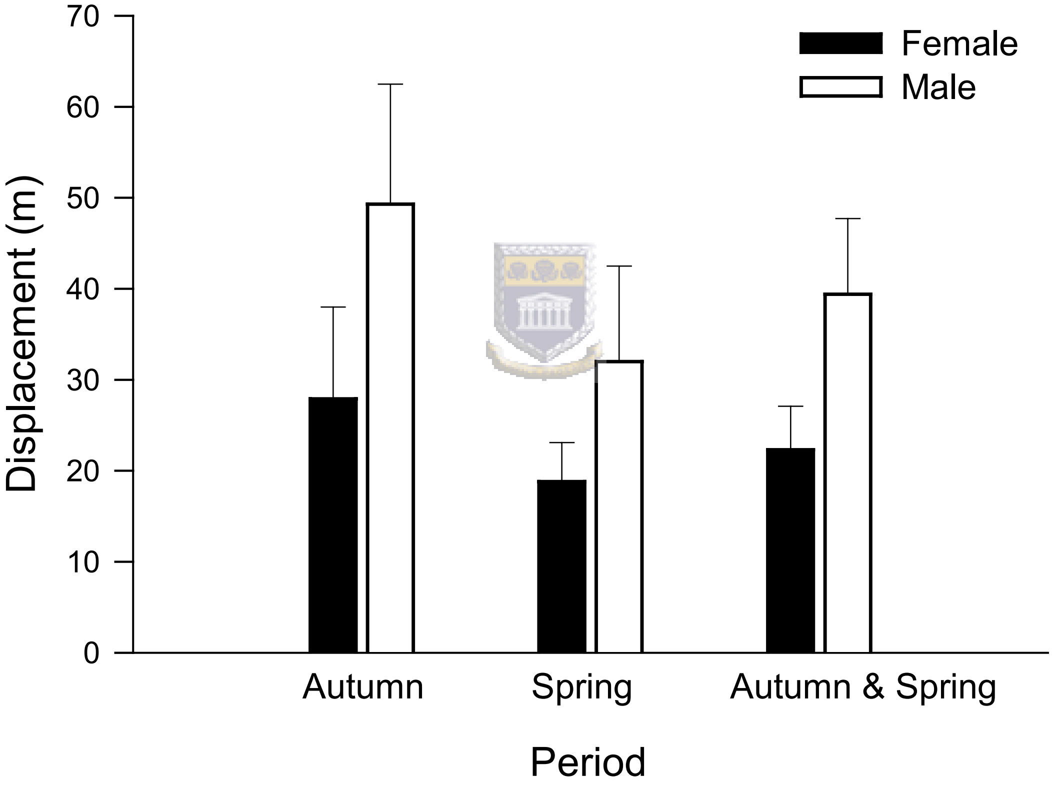

Figure 2.3. Displacement for male and female geometric tortoises, *P. geometricus*, for autumn (22 April – 6 May 2002), spring (12 – 31 October 2002), and for the two seasons combined.

2.3.2.3 Displacement-to-Distance Ratio

The mean (± CI) displacement-to-distance ratio for geometric tortoises was 0.556 ± 0.027, n=35. When comparing the displacement-to-distance ratios between seasons, the analysis revealed no difference for either females (t_{32}=0.49; *P*=0.62; Fig. 2.4), males (t_{33}=1.07; *P*=0.29) or all tortoises (t_{33}=0.53; *P*=0.60). The ratios were greater for males than for females in autumn (Paired t-test: t_{13}= 3.00; *P*=0.010), spring (Paired t-test: t_{19}= 3.72; *P*=0.001), and for the seasons combined (Paired t-test: t_{33}= 4.83; *P*<0.001).

ANOVA provided confirmation of some daily mean results and contradictions with other daily mean statistics. In one two-way ANOVA, males had higher ratios than did females ($F_{1,201}$=14.9, *P*=0.00016) but ratios did not differ between seasons ($F_{1,201}$=1.04, *P*=0.31). However, a separate two-way ANOVA detected significant effects of individuals ($F_{9,194}$=4.66; *P*<0.001) and season (spring > autumn; $F_{1,194}$=7.58; *P*=0.006). Two males had significantly higher ratios than did two of the females (0.691±0.078 and 0.644±0.125 versus 0.394±0.108 and 0.416±0.121, respectively). A third ANOVA confirmed that males had higher ratios than did females ($F_{1,169}$=19.0; *P*<0.001), but there was no effect of individual days ($F_{34,169}$=1.05, *P*=0.41).

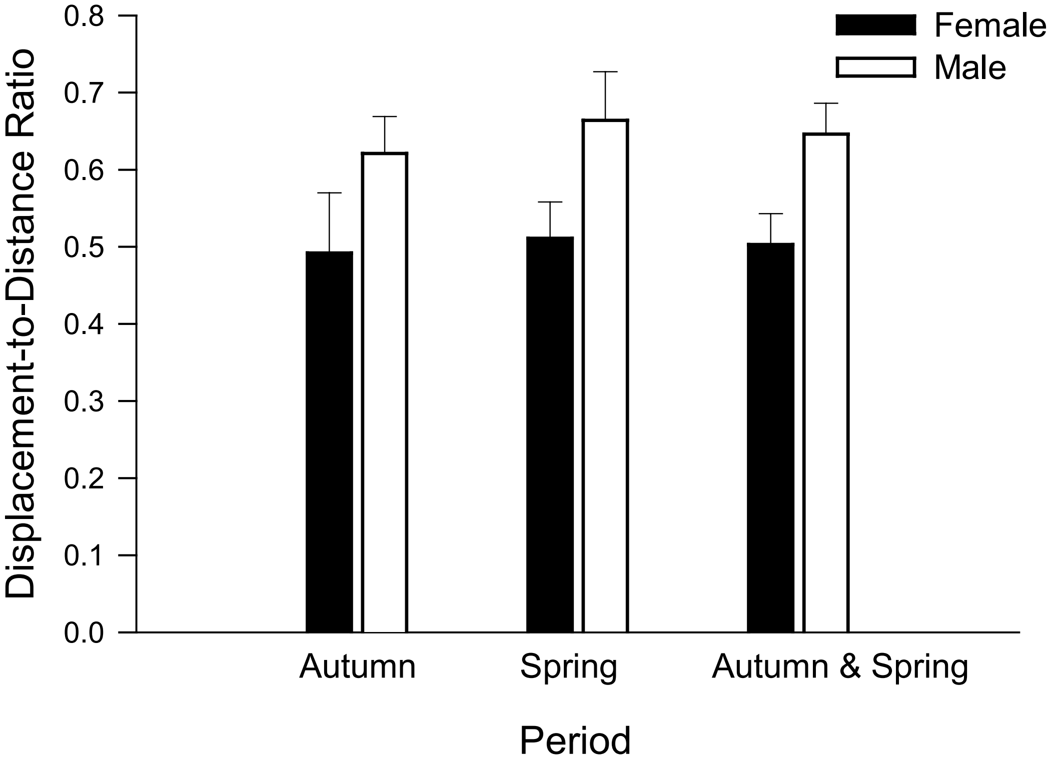

Figure 2.4. Displacement-to-distance ratio for male and female geometric tortoises, *P. geometricus*, for autumn (22 April – 6 May 2002), spring (12 – 31 October 2002), and for the two seasons combined.

2.3.2.4 Movement shapes

For all tortoises studied in spring, movement shapes were not random or homogeneously distributed (χ^2_5= 17.3, P<0.005); circular paths occurred infrequently (Fig. 2.5). Although shapes differed between males and females (contingency χ^2_5= 16.2, P=0.006), when considering sexes separately, female movement shapes did not differ from random (χ^2_5= 8.11, P<0.25). Male frequencies differed from random (χ^2_5= 23.9, P<0.001), with males tending to move more linearly and not in criss-cross patterns.

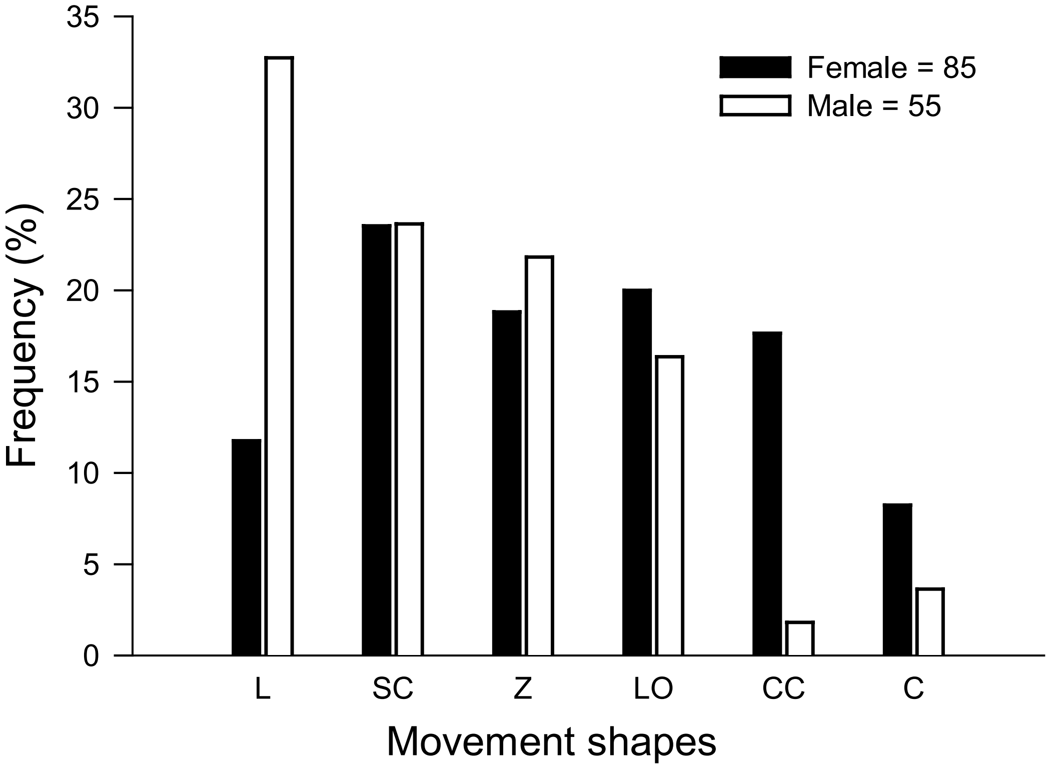

Figure 2.5. Relative frequency (%) of movement shapes for male (n=55) and female (n=85) geometric tortoises *P. geometricus*, in spring (12 – 31 October) 2002. Shapes include linear (L), semi-circular (SC), zigzag (Z), loops (LO), criss-cross (CC), and circular (C).

2.3.3 Refuges

The three main refuge types (shrubs, restio and grass; Table 2.2) differed in height (One-Way ANOVA: $F_{2,238}$=4.60; *P*= 0.0110), width ($F_{2,238}$=3.43, *P*=0.034) and volume ($F_{3,238}$=3.46; *P*=0.033). Student-Newman-Keul's (SNK, *P*<0.05) post hoc comparisons among the refuges indicated that grasses had larger volumes than did shrubs and restios, were taller than shrubs and were wider than restios. Shrubs were wider than restios. There was no difference in refuge class density (Kruskal-Wallis ANOVA: H_2=5.51, *P*= 0.064). Within spring, refuge height (H_2=2.63; *P*=0.269), width

(H_2=3.08; *P*=0.21), volume (H_2=4.93; *P*=0.085) and density (H_2=3.65; *P*=0.16) did not differ among plant types. For autumn refuges, we found significant differences in refuge height ($F_{2,73}$=17.4, *P*<0.0001), width ($F_{2,73}$=4.11; *P*=0.020), volume ($F_{2,73}$=17.3; *P*<0.0001) and density (H_2=6.61; *P*=0.037). Post-hoc results for autumn ANOVA indicate that all three categories differed in height and volume (grass>restio>shrub), and grasses had greater widths and densities than did restios.

Refuge height ($T_{76,165}$=10331.5; *P*=0.024), width ($T_{76,165}$=11279; *P*<0.00001) and volume ($T_{76,165}$=11045; *P*<0.00001) were greater in autumn than in spring (Table 2.2). In contrast, refuge density was greater in spring than in autumn ($T_{74,163}$=7454.5; *P*=0.010). Male geometric tortoises used refugia with greater densities than those used by females in spring (2.75±0.32 and 2.18±0.23; paired t_{19}=2.69; *P*=0.014) and both seasons combined (2.56±0.23 and 2.09±0.16, respectively; paired t_{34}=3.24; *P*=0.0027), but not during autumn (2.31±0.31 and 1.97±0.25, respectively; t_{14}=1.78; *P*=0.097). The height, width and volume of male refugia did not differ from those of female refugia (*P*>0.3 for all paired *t* or Wilcoxon signed rank tests).

Compared to grass refuges in spring, grass refuges in autumn were taller (Mann-Whitney: $T_{36,37}$= 1730.5; *P*<0.0001), wider (Student's t-test: t_{71}= 3.67; *P*<0.001) and more voluminous (Student's t-test: t_{71}= 7.14; *P*<0.0001); the density of grass refuges did not differ between autumn and spring ($T_{35,37}$=1283.5, *P*=0.95). Shrubs were taller (Mann-Whitney: $T_{23,81}$= 740.5; *P*<0.001) and had greater volumes (Student's t-test: t_{102}= 2.05; *P*=0.043) and densities (Mann-Whitney: $T_{23,80}$= 910.5; *P*=0.024) in spring than in autumn. Shrub refuges were wider in autumn than in spring (Mann-Whitney: $T_{23,81}$= 1465.5; *P*=0.044). Between seasons, restios differed in density (Mann-Whitney: $T_{16,46}$= 336.0; *P*=0.007; Table 2.2) but not height, width or volume (all *P*>0.15).

When considering season and sex (Table 2.3), geometric tortoises did not use refuge types randomly (3-way contingency χ^2_{10}=39.1; *P*<0.001). Grass use was greater in autumn than in spring (χ^2_3=18.9; *P*<0.001). Although shrub selection appeared to be high in spring, the result was not quite statistically significant (χ^2_2=5.88; *P*=0.053).

Refuge use in autumn was not random or homogeneous among categories; tortoises used few sedges and often used grasses (χ^2_3=28.5; *P*<0.001). In autumn, female refuge use was random (χ^2_3=7.51; *P*>0.05) while males used grasses more frequently than other refuge types (χ^2_2=16.7; *P*<0.001). Males used grasses more frequently than did females in autumn (χ^2_3=11.1; *P*=0.011) and both seasons combined (χ^2_3=13.2; *P*=0.004).

In spring, geometric tortoise refuges included few sedges and many shrubs (χ^2_3=78.3; *P*<0.001). Female tortoises used shrubs disproportionately in spring (χ^2_2=20.6; *P*<0.001) and for the seasons combined (χ^2_3=53.9; *P*<0.001). Male refuge use was homogenous among refuge categories in spring and both seasons combined (χ^2_2<5.4; *P*>0.05; males did not use sedges so the sedge category could not be included). In spring, refuge use did not differ between sexes (χ^2_3=4.94, *P*=0.18). Female geometric tortoises tended to utilise shrubs for cover more readily in spring than autumn (χ^2_3=8.88; *P*=0.031). However, males utilised grasses more frequently in autumn than spring (χ^2_2=12.7; *P*=0.002).

Table 2.2. Refuge height (cm), width (cm), volume (litres) and density (index from a low of one to a high of five) for geometric tortoises (*P. geometricus*). The values for the three main vegetation categories, plus sedges, include the mean, 95% confidence interval, and sample size.

			Shrub	Restio	Grass	Sedge	Totals
Height	Autumn	mean	21.9	32.8	42.2	43.0	34.3
		ci	7.8	7.2	5.6	0.0	4.1
		n	23	17	36	3	79
	Spring	mean	28.4	28.7	25.8	30.0	27.9
		ci	3.1	3.8	4.3	-	2.1
		n	81	47	37	1	166
	Total	mean	27.0	29.8	33.9	39.8	30.0
		ci	3.0	3.3	3.9	10.3	1.9
		n	104	64	73	4	245
Width	Autumn	mean	48.2	41.1	53.1	44.5	48.8
		ci	5.9	7.9	6.2	0.0	3.7
		n	23	17	36	3	79
	Spring	mean	43.7	37.3	38.1	31.0	40.6
		ci	4.4	4.0	5.0	-	2.7
		n	81	47	37	1	166
	Total	mean	44.7	38.3	45.5	41.1	43.2
		ci	3.7	3.5	4.3	10.7	2.2
		n	104	64	73	4	245
Volume	Autumn	mean	13.4	26.7	54.7	43.1	36.2
		ci	9.0	13.6	15.4	0.0	8.8
		n	23	17	36	3	79
	Spring	mean	27.5	16.2	13.9	14.6	21.2
		ci	11.8	4.1	6.5	-	6.0
		n	81	47	37	1	166
	Total	mean	24.4	19.0	34.0	36.0	26.0
		ci	9.4	4.6	9.4	22.7	5.0
		n	104	64	73	4	245
Density	Autumn	mean	2.1	1.6	2.3	3.0	2.1
		ci	0.34	0.39	0.35	0.00	0.21
		n	23	16	35	3	77
	Spring	mean	2.5	2.3	2.4	1.0	2.4
		ci	0.19	0.28	0.36	-	0.15
		n	80	46	37	1	164
	Total	mean	2.4	2.1	2.3	2.5	2.3
		ci	0.17	0.24	0.25	1.59	0.12
		n	103	62	72	4	241

Table 2.3. Refuge use represented as a percentage for geometric tortoises (*P. geometricus*) in autumn, spring and both seasons combined.

	Grass	Restio	Sedge	Shrub	n
Autumn					
Male	63.9	11.1	0.0	25.0	36
Female	30.2	30.2	7.0	32.6	43
Total	45.6	21.5	3.8	29.1	79
Spring					
Male	28.9	28.9	0.0	42.1	76
Female	16.7	27.8	1.1	54.4	90
Total	22.3	28.3	0.6	48.8	166
Totals					
Male	40.2	23.2	0.0	36.6	112
Female	21.1	28.6	3.0	47.4	133
Grand	29.8	26.1	1.6	42.4	245

2.3.4 Environmental parameters

Daytime air temperatures during autumn (19.1±1.38 °C, n=15) and spring (22.3± 1.55 °C, n=20) were rather mild (range=12.5 to 28.8 °C), and spring values were higher than the values in autumn ($t_{33}=3.15$, $P=0.0035$). For daylight hours, ground temperature in the shade, ground temperature in the sun, and radiation were also greater in spring than in autumn (Fig. 2.6, all $P<0.001$). However, relative humidity was greater in autumn than in spring (daylight hours: Student's t-test: $t_{33}=5.12$; $P<0.001$). Mean temperatures (ambient, ground shade and ground sun) and radiation were correlated to one another ($r_s=0.53$ to 0.92 and $P=0.037$ to $P<0.000001$, n=15 and 20 in autumn and spring, respectively), but inversely correlated to relative humidity ($r_s= -0.532$ or stronger, $P=0.04$ to $P<0.000001$).

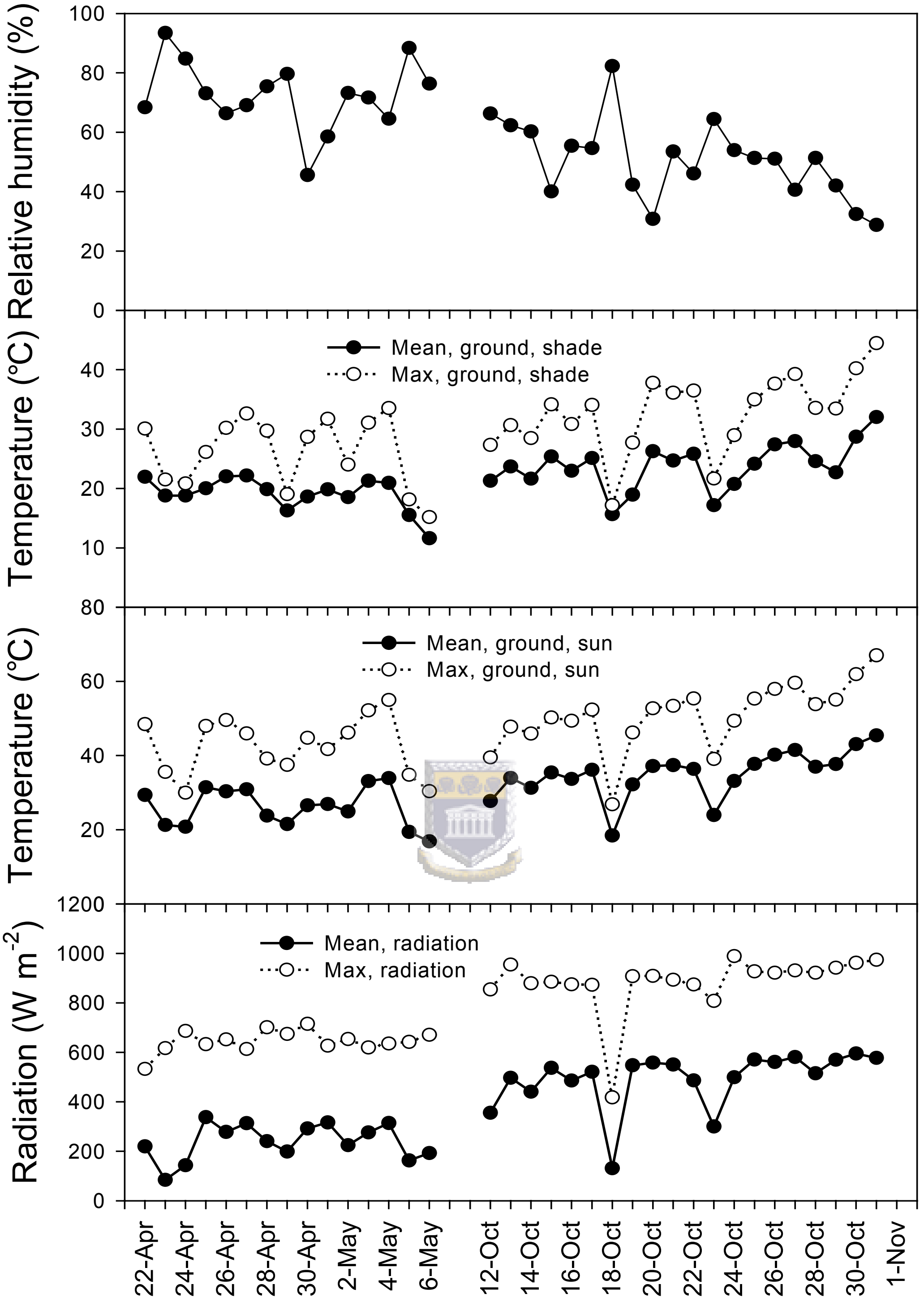

Figure 2.6. Autumn (22 April – 6 May 2002) and spring (12 – 31 October 2002) comparisons of relative humidity (%), shaded ground temperature (°C, mean and maximum), ground temperature in the sun (°C, mean and maximum) and solar radiation (W m^{-2}, mean and maximum). All values are for daytime (0700 to 1900), bracketing the activity of the tortoises.

2.3.5 Effect of temperature on distance moved and displacement

There were relatively few significant correlations between tortoise results and environmental data. Ground temperature in the sun (daylight hours) most consistently, compared to other environmental measures, revealed significant correlations and no spurious correlations. The few significant minima and maxima correlations tended to be spurious due to influential outliers. For the significant regressions, data for the cool rainy day of spring (18 October; Fig. 2.7) were outside the 95% prediction intervals. I excluded this day’s data from the final regression calculations.

The effect of ground temperature (in the sun) was statistically significant for males in spring; male tortoises demonstrated a decrease in distance moved with increased ground temperature (Fig. 2.7; Distance = 189 – 3.98T; r^2=0.519, $F_{1,17}$=18.4, *P*<0.0005). With increased ground temperature, female displacement increased in autumn (Displacement = -21.9 + 1.93T (r^2=0.351, $F_{1,12}$=6.50, *P*=0.026; Fig. 2.8a), and male displacement decreased in spring (Fig. 2.8d; Displacement = 149 – 3.23 T (r^2=0.523, $F_{1,17}$=18.7, *P*<0.0005).

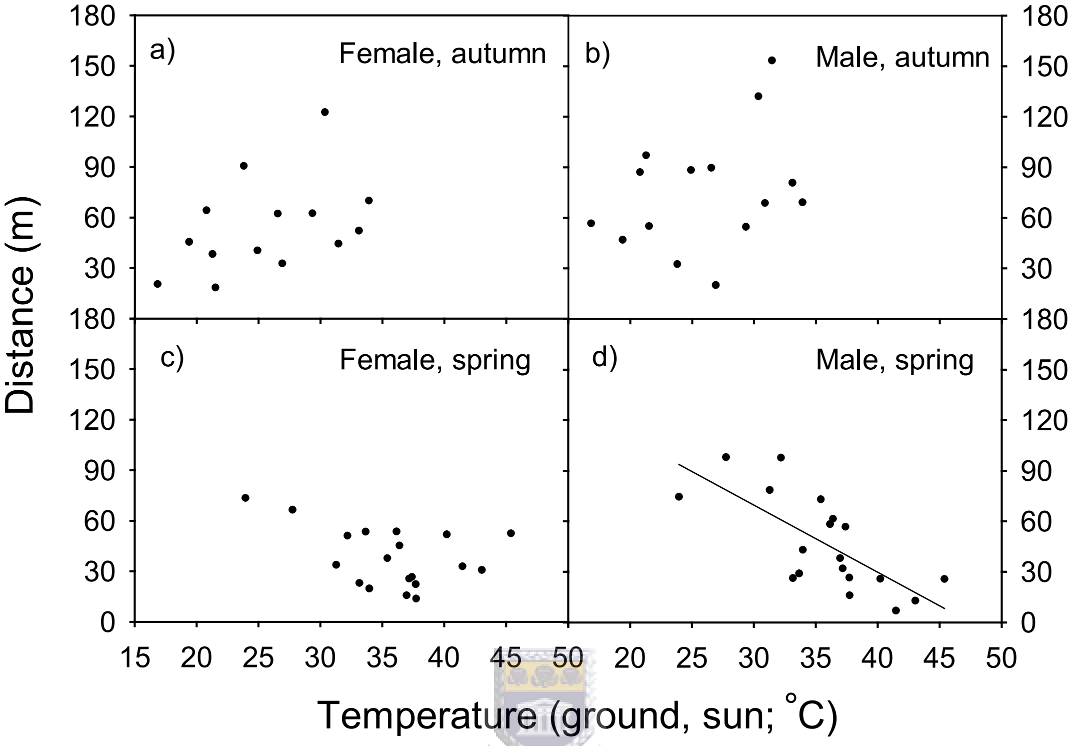

Figure 2.7. Relationship of distance moved and ground temperature (in the sun) for female (a, c) and male (b, d) geometric tortoises. Seasons include autumn (a, b; 22 April – 6 May 2002) and spring (c, d; 12 – 31 October 2002). When regressions were statistically significant, the regression line was included.

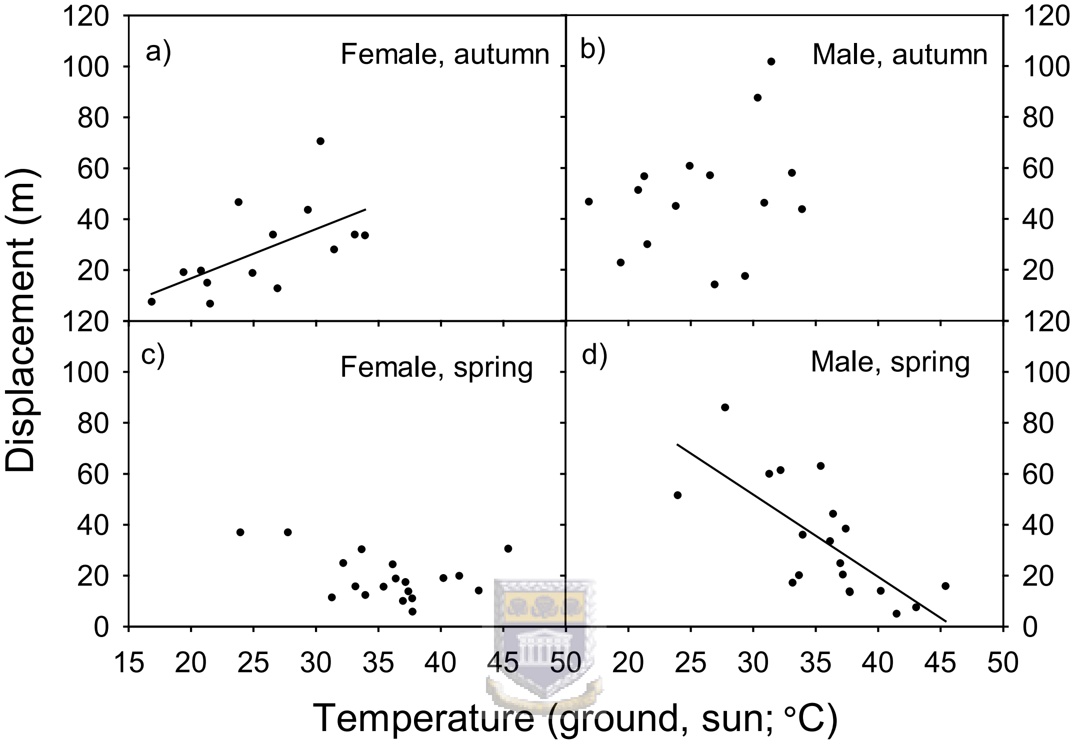

Figure 2.8. Relationship of displacement and ground temperature (in the sun) for female (a, c) and male (b, d) geometric tortoises. Seasons include autumn (a, b; 22 April – 6 May 2002) and spring (c, d; 12 – 31 October 2002). The regression line is indicated in each statistically significant relationship.

2.4 DISCUSSION

Although literature is available for the tortoise *P. geometricus* (Archer 1967; Greig 1984; Baard 1990, 1993, 1995; Baard & Mouton 1993), very few studies have investigated the movements and habitat use of this tortoise. Claussen *et al* 1997 stated that animals move within their habitat to obtain resources necessary for their survival. The distance an animal would travel is dependent on the heterogeneous distribution of these resources in the habitat (Brown & Brooks 1993). Baard 1995, indicated four main biological factors important for the survival of geometric tortoises in their habitat. The four factors are food, cover, nesting sites, and an open habitat that would not restrict the tortoises' movement.

Geometric tortoises are easily startled, which makes continuous observations as a means to determine activity of this tortoise almost impossible. With the use of thread trailing, I determined the daily habitat use of the geometric tortoises. With this method, the daily activity of tortoises can also be determined.

2.4.1 Individual effects

The activity level of geometric tortoises was high in both autumn and spring, compared to desert tortoises, which are active only about every third day (Nagy and Medica 1986). However, geometric tortoises showed high individual variability in movement for these two seasons of study. A few individual tortoises such as the male tortoise #1121 were found to move greater distances than others did. Although tortoise #1121 moved the greatest distance, there was very little difference in its body size compared to that of other males. It is unclear why such variability can occur in geometric tortoises. Therefore, it might be important to mention that the individual biological needs of a tortoise could determine the distance travelled in the habitat.

One possibility for variability in individual movements of *P. geometricus* is the availability of resources in the habitat. Lue & Chen 1999 found for box turtles (*Cuora flavomarginata*) that individual variability in activity and movement can be explained by the heterogeneous distribution of resources. Resources such as suitable nesting sites for females, food, water, and mating opportunities for males might alter the movement patterns of desert tortoises (Gibbons 1986). Additionally, Stickel (1950) found that individual needs of the box turtle (*Terrapene c. carolina*) would determine the distances travelled. Some turtles move to areas where resources are available and the productivity of the habitat is high (Kramer 1995). However, resources may not be evenly distributed in the habitat. Therefore, habitat quality may contribute to individual variability in activity and displacement in geometric tortoises. However, habitat quality was not measured in my study.

2.4.2 Sex effects

Diaz-Paniagua *et al*. (1995) found that sexual differences in *Testudo graeca* activity levels were related to their reproductive cycles. Due to differences in reproductive strategies during certain periods of the year, female *T. graeca* had higher activity levels than male tortoises (Diaz-Paniagua *et al*. 1995). Similarly, female geometric tortoises were more often active than male geometric tortoises. Not much is known about reproduction of geometric tortoises, but females are known to lay eggs between July and January (M.D. Hofmeyr, M. Klein, B.T. Henen, E.H.W. Baard, unpubl. manuscript). The spring study period falls within the egg-laying period for female geometric tortoises, therefore, compared to males, the greater female activity level in spring might be related to nest searching in the habitat.

In addition to differences in metabolic costs related to activities of each sex, it is possible that differences in metabolic costs are due to body size differences between female and male geometric tortoises. The greater activity level of female geometric tortoises, compared to males, was possibly due to greater foraging by females. Lagarde *et al.* (2003) suggested that the large home range of female *Testudo horsfieldi*, compared to male *T. horsfieldi*, is related to the large body size and energetic costs of egg production. Additionally, Henen (2002) indicated a higher energy demand in female desert tortoises due to egg production (field metabolic rates were correlated to the number of eggs produced). Therefore, a higher activity level for female geometric tortoises in spring may be related to an increase in foraging activity that is directly related to a greater metabolic demand (through egg production and large body size).

Female geometric tortoises had a smaller displacement-to-distance ratio than males. The small ratio indicates a more intense use of the immediate habitat. Female geometric tortoises explore and use a small activity area and males travel greater distances with a directional movement through the habitat. The differences can be related to mate searching by male geometric tortoises. Male tortoises may travel greater distances to increase encounters with females. Similarly, the distance *Testudo graeca* moved was related to body size, differences in reproductive strategies, and environmental factors such as temperature and rainfall (Diaz-Paniagua *et al*. 1995).

2.4.3 Seasonal effect

Boycott & Bourquin (2000) indicated that geometric tortoises are active throughout the year although the activity level drops during winter. Similar results were found for gopher tortoises, as activity was greatly reduced during winter (Diemer 1992). Although winter and summer seasons were not studied, I found no differences in activity for geometric tortoises between autumn and spring. Nevertheless, males and females travelled longer distances in autumn than they travelled in spring. Autumn represents the end of the dry season and these tortoises may have to travel longer distances to acquire resources. Baard (1995) indicated that the diet of geometric tortoises has seasonal changes related to seasonal changes in the vegetation. The seasonal changes in the vegetation may affect the availability and heterogeneous distribution of resources in the habitat. Male geometric tortoises displaced further in autumn than they did in spring. This may be related to mate searching behaviour, although it is not known when geometric tortoises mate.

Reproductive strategies and body size differences are important aspects affecting the distance travelled and activity of geometric tortoises. However, the environmental parameters, such as temperature and humidity, are important factors affecting Texas tortoises (Rose & Judd 1979) and geometric tortoises (this study).

2.4.4 Weather

Seasonal changes in climate have an important influence on daily activity levels of tortoises and turtles (Rose & Judd 1979; Diaz-Paniagua *et al*. 1995; Lue & Chen 1999; Lagarde *et al*. 2003). Hailey & Coulson (1996) found that male *Kinixys spekii* activity level would increase with ambient temperature, and activity would then decrease when the chances of overheating for the tortoise is high (at high ambient temperatures). A similar result may have occurred for the geometric tortoise. During the study, temperatures were higher in spring than they were in autumn. The displacement and distance moved by male geometric tortoises decreased at high ambient temperature in spring. The small body size of males may explain why movements decreased for males and not for females.

Radiation and ambient temperatures influence the activity of *Testudo graeca* (Diaz-Paniagua *et al.* 1995). In addition to ambient temperature changes, rainfall can influence the activity levels of tortoises (Rose & Judd 1975). Similarly, the activity level of *Terrapene carolina bauri* was correlated with warm temperatures, high humidity, and rainfall (Dodd *et al*. 1994). The responses of geometric tortoises to daily changes in weather were complex. The large movements on 26 April indicate a response to warm conditions, after low temperatures prevailed. A similar effect was detected in spring when movements were reduced on a particularly cold day in spring.

2.4.5 Refugia

The selection of refuges by the tortoise *Testudo hermanni* depends on the amount of cover provided by the vegetation (Hailey 1989). I found statistically significant differences seasonally for protection provided by the refuge. The refugia selected by the geometric tortoises were denser in spring but taller, wider and with a greater volume in autumn. The selection of a refuge by geometric tortoises may be due to seasonal changes in habitat quality. Therefore, the amount of protection provided by the vegetation may change between autumn and spring.

The refuge of a tortoise provides protection against environmental factors, such as temperature (Wright *et al*. 1988). Autumn temperatures were lower than spring temperatures, and geometric tortoises may use vegetation that provides the best protection for each season.

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3 ACTIVITY AREA AND HOME RANGE OF THE GEOMETRIC TORTOISE, *PSAMMOBATES GEOMETRICUS*

3.1 INTRODUCTION

Most animals limit their activities to familiar areas, which improve their ability to find the resources required for survival and reproduction (Pough *et al*. 2001). The space required by different species can differ substantially and the movement patterns of animals are interrelated with most aspects of their biology (e.g., temperature and water relations, energetics, reproduction, intra- and interspecies interactions). Space requirements and movement patterns of species provide critical information in the conservation and management of the species (Pough *et al*. 2001).

The space requirements of animals are tightly linked to the dispersion of resources in their habitat (Pough *et al*. 2001). Resource availability varies spatially and temporally, and animals may move large distances when resources are scarce. Throughout the year, animals may shift from one activity centre to another and the total area used during their daily activities constitutes their home range (Stickel 1950; Cox 1996). Since resources and the requirements of animals may differ through the year, home ranges should be determined over extended periods to include activities performed over an annual cycle. The space used over short periods is often termed activity areas to distinguish short-term space use from long-term home ranges.

The size of a species' home range is determined by many factors. Home range sizes tend to be smaller in densely populated areas than in sparsely populated ones (Stickel 1950). Food, shelter, habitat quality, mate seeking and other reproductive activities influence home range size (Stickel 1950; Stickel 1989; Diemer 1992). Body size may also influence the home range of individuals; larger body size would mean a greater energy requirement and a greater area travelled to acquire resources (Hailey & Coulson 1996a). Therefore, minimum geographic range size of individuals would tend to increase with body size (Gaston & Blackburn 1996). Although tortoises have lower energy requirements than mammals, their home ranges often have the same magnitude. Thus, home range size cannot be explained by energetic needs but rather by the distribution of resources (Hailey & Coulson 1996a).

Several methods are available to determine activity areas and home ranges of tortoises. Mark-recapture is commonly used, but the method provides limited information on movement patterns (Pough *et al.* 2001). Thread trailing allows continuous tracking of individuals and the method has been used in several studies to evaluate movement patterns and to determine activity areas (Stickel 1950; Hailey & Coulson 1996a; Claussen *et al.* 1997). The best method to obtain detailed information on movement is through radiotelemetry (Pough *et al*. 2001). Although radiotelemetry is a high-cost method it allows animals to be located at any time, provides more location points for each individual than the mark recapture approach, and can be used to monitor long-term and large-scale movements of animals (Claussen *et al*. 1997).

A variety of methods is available for calculating home range size; the oldest and most utilized method is the minimum convex polygon. Minimum convex polygons provide information on home range size but do not provide information on the intensity of use or the structure of a home range (Rodgers & Carr 1998). Bivariate normal models (e.g., Jennrich-Turner estimator, Dunn estimator) have been developed to provide more detail on the characteristics of home range shape, while contouring models (e.g., kernel methods) provides information on home range structure (Rodgers & Carr 1998). By combining information on home range size, shape and structure, one can estimate resources available to individuals in the population, identify interactions among individuals, and identify areas used by individuals for specific purposes (Rodgers & Carr 1998).

Psammobates geometricus is a CITES Appendix 1 species and is listed as Endangered in the IUCN Red Data List (IUCN 2004) and the South African Red Data Book (Baard 1988). The geometric tortoise is restricted to a vegetation type known as renosterveld (Baard 1995) and the destruction of renosterveld is the biggest threat to the continued existence of geometric tortoises (Baard 1993). Few studies have investigated habitat use of *P. geometricus* in their natural habitat and limited information exists on their home range size. Due to the critical status of the geometric tortoise and vulnerability of its habitat, there is a need to allocate areas for their protection and to implement more effective conservation measures. Information on the space requirements, and the way geometric tortoise use space, should facilitate future conservation efforts.

In this chapter, I will use minimum convex polygons and kernel density estimators to examine the effects of sex, body size, season, and habitat type on the home range and activity areas of geometric tortoises.

3.2 MATERIALS AND METHODS

3.2.1 Study site

Elandsberg private nature reserve (33° 26’ S; 19° 02’ E) is located at the base of the Elandskloof mountain range, which forms part of the Cape Fold Mountains. Elandsberg reserve falls within the Fynbos biome with two natural veld types occurring on the reserve, West Coast Renosterveld and Mountain Fynbos. Fire is an integral part of Fynbos dynamics and several areas in the reserve show vegetation in various stages of post-fire succession. Burned renosterveld has a lower canopy cover of shrubs and contains more plant elements needed by geometric tortoises than mature renosterveld does (Baard 1990). The reserve is located on a wheat farm and previously cultivated lands were incorporated into the reserve. These old fields are covered mainly by grasses, which are heavily grazed by the large herbivores in the reserve. Geometric tortoises at the Elandsberg reserve are located in mature renosterveld, burned renosterveld and the old fields, but not in Mountain Fynbos.

3.2.2 Data collection

In April 2002, I surveyed the study area for tortoises and used a Trimble GeoExplorer II to record the location (latitude and longitude) of each tortoise. After capture, I recorded the tortoise's body mass (BM) to the nearest 0.1 g with an Ohaus digital balance and used vernier callipers to record body parameters to the nearest 0.1 mm. The following morphometric measurements were recorded: straight carapace length (SCL) from the nuchal to the supracaudal scute, shell width (SW) across marginal scutes six to seven, and shell height (SH) over the third vertebral scute. External morphological characteristics, as described by Baard (1990), were used to distinguish males and females. Each tortoise received a unique number by filing shallow notches in specific marginal scutes.

Twenty-one adult geometric tortoises (10 males and 11 females) were fitted with carapace-mount radio-transmitters (AVM Instrument Company, Ltd), which allowed me to locate the individuals at regular intervals throughout the study. Six tortoises (three males and three females) were located in mature renosterveld (RV), seven tortoises (four males and three females) in burned renosterveld (BR), while eight tortoises (three males and five females) were in the old fields (OF). Six of the seven telemetered tortoises from the burned renosterveld formed a subset of the individuals used in the thread trailing study (see chapter 2).

From April 2002 to April 2003, I located the telemetered tortoises at least once per month, while tortoises were located more often in April 2002 and in October to early November 2002. The mean number of location point per individual was 19.5 ± 4.8 (range: 5 – 24), with one male and one female having fewer than 15 location points. The home ranges of these two individuals were first evaluated against the mean for the sex in the same habitat type and season before including them in the analysis.

Because Elandsberg reserve does not have a weather station, I used rainfall and temperature data of De Hoek weather station (33° 15’ S; 19° 03’ E) in the analysis. Field notes on rainfall events supplemented this data. The climate at De Hoek, approximately 20 km north of the Elandsberg reserve, should be similar to the climate at the Elandsberg reserve, because De Hoek also lies on the western side at the foot of the Elandskloof mountain range.

3.2.3 Data analysis

Locality data collected through the thread trailing study (see Chapter 2) were used to calculate autumn (15 days, 22 April to 6 May 2002) and spring (20 days, 12 to 31 October 2002) activity areas for male and female geometric tortoises. The autumn sample consisted of three female and three male tortoises while the spring sample consisted of five females and four males. I used the locality data of the telemetered tortoises to calculate home ranges of males and females for the duration of the study (12 months) and for the wet and dry seasons.

The first good autumn rains fell in mid-April 2002, shortly after the study commenced. Elandsberg reserve received rain throughout winter 2002 and some rain was still recorded during spring sampling in October 2002. For the seasonal analysis of home ranges, I considered April to mid-October 2002 (6 months) as the wet season and the second six months from mid-October 2002 to April 2003 as the dry season. One locality point for each individual (recorded on 14 to 16 October) was included in both the wet and dry season data to represent the end locality of the wet season and the starting locality of the dry season.

I used ArcView version 3.1.1 in combination with the Animal movement extension to ArcView ver. 1.1 (Hooge & Eichenlaub 1997) and the Home range extension for ArcView ver. 0.9 (Rodgers & Carr 1998) to calculate the activity areas and home ranges of geometric tortoises. With the Animal movement program I calculated minimum convex polygons (MCP), 95% fixed kernel estimates (FK-95), and 50% fixed kernel estimates (FK-50); fixed kernel estimates were calculated with least square cross validation. The Home range program was used to calculate 95% Fixed Amean minimum convex polygons (MCP-95). All measurements for activity areas and home ranges are reported in hectares (ha).

The Trimble GeoExplorer II records latitude and longitude in degrees, minutes and seconds. Coordinates were converted into decimal degrees (DD) and saved as DBF 4 files before importing longitude (x-axis, positive value for East) and latitude (y-axis, negative value for South) data into ArcView.

$$\mathrm{DD} = \mathrm{deg} + \frac{\mathrm{min}}{60} + \frac{\mathrm{sec}}{(60)^2}$$

3.2.3.1 *Minimum convex polygon (MCP)*

When constructing a MCP, the outermost location points for an individual are connected to form a polygon with no internal angle greater than 180° (Rodgers & Carr 1998). The simplicity and ease of calculation made MCP the most common method for estimating home range (Rose & Judd 1975; Geffen & Mendelssohn 1988; Lagarde *et al.* 2003). This method, however, has many disadvantages, one being its sensitivity to sample size (Jennrich & Turner 1969; O’Connor *et al*. 1994). As the number of location points increases, the size of the home range estimate may increase indefinitely since MCP estimates the total area utilised (White & Garrott 1990). Minimum convex polygons may contain large empty areas and the size of the polygon is strongly influenced by outlying location points (Cox 1996). One approach to make polygons less sensitive to “outliers” is to compute “probability polygons” (White & Garrott 1990). Probability polygons exclude the farthest locations from a centre of activity, e.g., the arithmetic mean of the coordinates. The 95% Fixed Amean MCP is calculated from the 95% data points closest to the arithmetic mean of all the coordinates (Rodgers & Carr 1998).

In this study, I used MCP’s as an estimate of the size of activity areas and the home range of geometric tortoises to allow comparison with results of other tortoise species in the literature. I also calculated MCP-95 to evaluate the effect of “outliers” on the home range size.

3.2.3.2 Kernel Estimate

The kernel density estimator, first introduced by Worton (1989), produces the most accurate estimation of home range (Seaman & Powell 1996; Powell 2000). This procedure assumes that each location point is the centre of localized activity within the home range and superimposes a bivariate normal distribution (kernel) mathematically on each location point (Cox 1996). A grid is superimposed on the data and the density estimates at each grid intersection are used to calculate a kernel density estimator (Rodgers & Carr 1998). The kernel density estimator may have one or more peaks where observations are concentrated (Cox 1996; Seaman & Powell 1996). By drawing contour lines over the distribution, home range estimates are derived (Rodgers & Carr 1998).

Various kernels are available and the bandwidth of a kernel strongly influences the density estimate. Kernels with a narrow bandwidth emphasise the data structure, while kernels with a wide bandwidth reveal the general shape of the distribution (Seaman & Powell 1996). In the adaptive kernel procedure, the bandwidth varies to differentially smooth the overall distribution more along areas of low concentration and less along areas of high concentration (Cox 1996). In the fixed kernel procedure, a fixed bandwidth can be selected or a bandwidth can be chosen through the process of least squares cross validation (Seaman & Powell 1996). Through computer simulations, Seaman and Powell (1996) demonstrated that the adaptive kernel procedure overestimates the area of distribution. They found that the fixed kernel with least squares cross validation provides area estimates with very little bias and performed best of all the estimators tested.

For these considerations, I selected the fixed kernel density estimator with least square cross validation to estimate home range and activity areas of geometric tortoises. The wet and dry season home range data were subsets of the annual home range data. In my initial analysis, with least square cross-validation, the dry season home range estimates of individuals with large home ranges exceeded their annual home ranges. This was due to the large bandwidth generated from the smaller number of locality points for the dry and wet season subsets. To overcome this problem, I used the bandwidth generated for the annual data set of each individual, as a fixed bandwidth in the seasonal home range analyses of that individual. Inspection of the data showed that these estimates provide a realistic representation of seasonal relative to annual space use.

3.2.4 Statistical analysis

Statistical tests were completed with SigmaStat 2.0 and tests were considered significant at $\alpha = 0.05$. I first tested if the data meet parametric assumptions and used

$\log_{10}$ transformations to normalise data. When transformations did not work, non-parametric tests were used in the analyses. To facilitate interpretation of the results, however, I present parametric and non-parametric data as means ± 95% confidence intervals (CI). When analysing data, I used the Student's *t* test (t) to compare two independent samples. When comparing more than two independent samples, I used a one-way or a two-way ANOVA (F) when evaluating one or two effects (e.g., season and sex), respectively. When measurements were repeated on the same individuals, I used a one-way repeated measures ANOVA (F) or the Friedman RM ANOVA on ranks (χ^2) to evaluate a single effect. ANOVA's were followed with Student-Newman-Keul's analyses to assess differences among specific groups. The relationships of body measurements with home ranges or activity areas were tested with least squares linear regressions (r^2 and F).

3.3 RESULTS

3.3.1 Environmental conditions

Elandsberg reserve falls in a winter-rainfall region and rainfall is highest from April/May to August/September (Fig. 3.1a). Rainfall from April to September 2002 (wet season) was significantly higher than rainfall from October 2002 to March 2003 (dry season) at De Hoek (Wet: 79 ± 36 mm per month, Dry: 24 ± 16 mm per month; $t_{10} = 3.57$, $P = 0.0051$). Temperatures in the Western Cape fluctuate seasonally and De Hoek temperatures (Fig. 3.1b) were significantly higher during the dry season ($T_{max} = 30.1 \pm 3.1$ °C, $T_{min} = 15.3 \pm 3.0$ °C) than during the wet season ($T_{max} = 21.3 \pm 3.7$ °C, $t_{10} = 4.74$, $P = 0.00079$; $T_{min} = 9.8 \pm 2.3$ °C, $t_{10} = 3.72$, $P = 0.0040$).

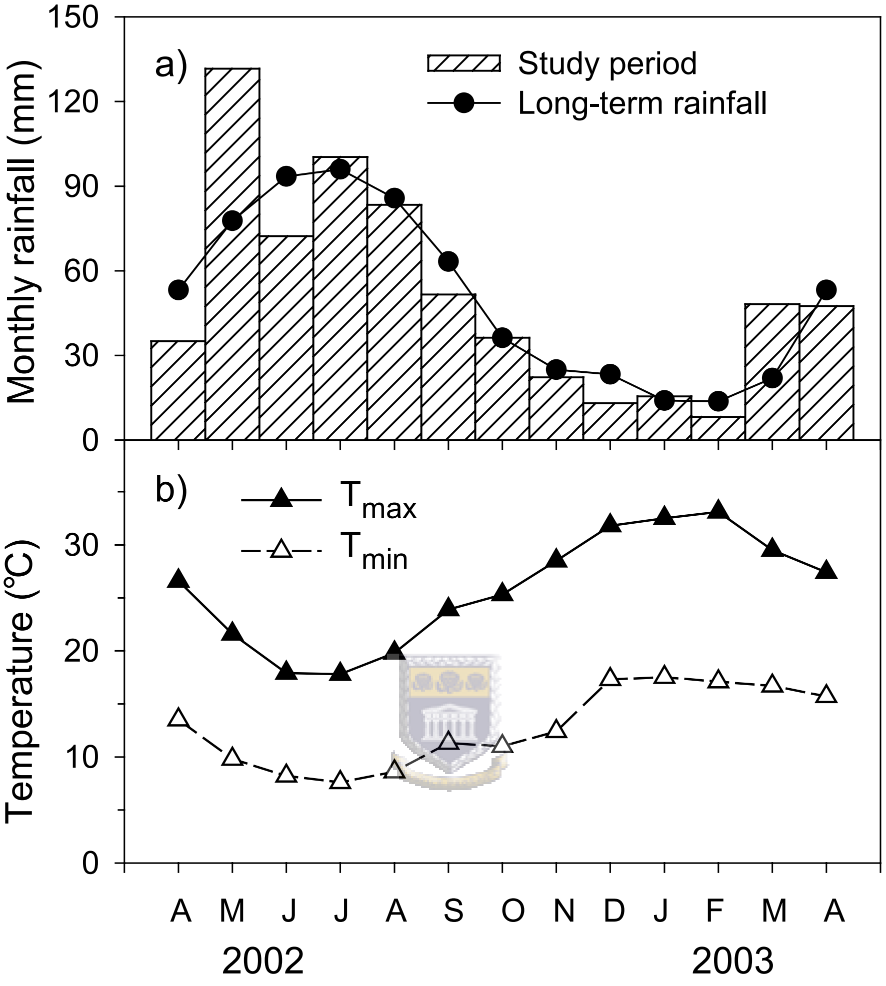

Figure 3.1. Monthly rainfall from April 2002 to April 2003 and long-term rainfall averages over 18 years at De Hoek (a). Mean monthly temperatures (b; maximum and minimum) at De Hoek.

3.3.2 Body parameters

Psammobates geometricus females are larger than males (Table 3.1). Straight carapace length, SW, SH, SV and BM of telemetered females were significantly larger than corresponding measures of telemetered males (all $t_{19} > 4.35$, $P <$ 0.00035). Females used in thread trailing were also larger than thread-trailed males (all $t_8 > 3.41$, $P < 0.0092$).

Table 3.1. Morphometric measurements of telemetered and thread-trailed female and male *Psammobates geometricus*. SCL is straight carapace length, SW is shell width, SH is shell height (all in mm), SV is shell volume (cm^3) and BM is body mass (g).

	Mean	**CI**	**Range**	**Mean**	**CI**	**Range**
Telemetered: Females (*N* = 11)				**Males (*N* = 10)**		
SCL	122.9	6.4	109.2 – 139.8	108.0	3.9	102.0 – 118.5
SW	93.4	3.6	83.8 – 102.3	77.1	2.4	73.2 – 83.6
SH	73.5	3.8	64.9 – 80.7	56.7	2.1	51.2 – 60.4
SV	447.1	60.9	315.1 – 585.9	248.0	23.6	203.8 – 304.6
BM	452.6	62.8	334.1 – 625.2	247.5	22.7	211.7 – 295.4
Thread trailing: Females (*N* = 6)				**Males (*N* = 4)**		
SCL	119.6	7.1	108.8 – 127.2	105.8	8.5	100.9 – 112.3
SW	92.0	4.2	86.6 – 96.6	75.9	3.1	73.9 – 78.5
SH	70.1	4.9	63.5 – 76.4	56.4	3.8	54.7 – 59.9
SV	406.4	67.6	313.3 – 483.9	238.1	43.4	215.9 – 276.5
BM	421.4	83.1	321.8 – 527.0	217.9	41.4	194.6 – 251.8

3.3.3 Body size effects

Body size of geometric tortoises influenced the size of their home range. For males and females combined, SCL, SW, SH, SV and BM had a positive effect on FK-50 (all $r^2 > 0.32$, $F_{1,19} > 8.92$, $P < 0.0076$) and on FK-95 (all $r^2 > 0.28$, $F_{1,19} > 7.38$, $P < 0.014$). Home ranges calculated as MCP and MCP-95 were not related to body size (all $F_{1,19} < 2.48$, $P > 0.132$).

For male geometric tortoises, body size had no effect on home range (all $F_{1,8} < 0.97$, $P > 0.35$). Inspection of the data showed that the home range of male #1121 was considerably larger than the home ranges of other males. Outliers have strong effects on regression analyses and outliers are often identified as data that fall outside two standard deviations of the group mean. The home range of male #1121 exceeded 7.8 or 2.6 standard deviations, respectively, of the group mean that excluded or included #1121. Nevertheless, after removing the data of male #1121, body size still had no effect on the home range of male geometric tortoises (Fig. 3.2).

There were limited effects of body size on the home range of female tortoises. Body mass influenced the FK-95 home range ($r^2 = 0.38$, $F_{1,9} = 5.40$, $P = 0.045$) while the relationships of FK-95 ($F_{1,9} = 4.65$, $P = 0.060$) and FK-50 ($F_{1,9} = 4.93$, $P = 0.054$) on SH just failed significance. The body parameters had no effect on home range areas determined as MCP and MCP-95 (all $F_{1,9} < 2.14$, $P > 0.18$). One female (#1242) had only five fixes from December 2002 to April 2003. When this female was removed from the data, the effect of body size on female home range became stronger. Apart from SW, all body parameters (SCL, SH, SV and BM) influenced the FK-95 home ranges (Fig. 3.2), while shell height influenced FK-50 and MCP, and BM affected FK-50 (all $r^2 > 0.41$, $F_{1,8} > 5.51$, $P < 0.047$). The relationship between FK-50 and SV ($F_{1,8} = 5.18$, $P = 0.052$), and the relationship between MCP-95 and SH ($F_{1,8} = 4.66$, $P = 0.063$), just failed significance.

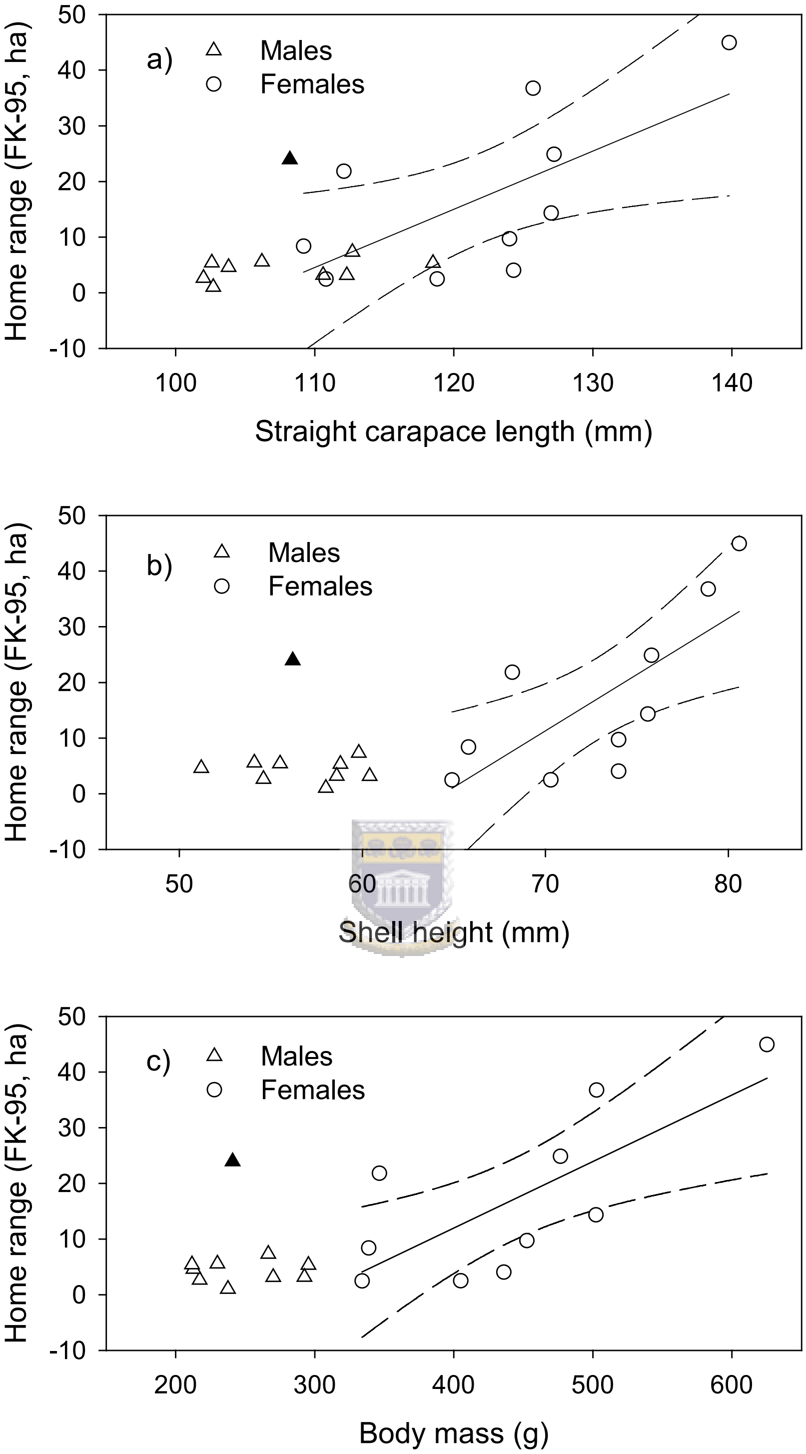

Figure 3.2. The relationship of 95% fixed kernel home ranges and straight carapace length (a), shell height (b), and body mass (c) of male and female geometric tortoises. Female data exclude #1242 and the solid triangles indicate male #1121. Regression lines (± 95% confidence intervals) are indicated for significant relationships: FK-95 = 1.05 SCL - 110.5; FK-95 = 2.03 SH - 130.5; FK-95 = 0.12 BM - 35.9.

3.3.4 Fixed kernels and minimum convex polygons

Home range size was significantly influenced by the method used to estimate the area (χ^2 = 56.57, *P* << 0.0001, d.f. = 3; Table 3.2). The FK-95 estimate gave the largest home range, followed by MCP**,** MCP-95 and FK-50. The method also influenced the size of activity areas in spring (χ^2 = 25.50, *P* << 0.001, d.f. = 3; FK-95 > MCP > MCP-95 > FK-50) and in autumn ($F_{3,15}$ = 7.20, *P* = 0.0032; FK-95 > MCP = MCP-95 = FK-50).

Table 3.2. Mean (± CI) home ranges and activity areas (hectares) of male and female *Psammobates geometricus*. Areas are presented as 95% fixed kernels (FK-95), 50% fixed kernels (FK-50), minimum convex polygons (MCP) and 95% minimum convex polygons (MCP-95).

	N	**FK-95**	**CI**	**MCP**	**CI**	**MCP-95**	**CI**	**FK-50**	**CI**
Home range	21	11.49	5.52	6.98	3.59	6.11	3.43	1.59	0.69
Activity area									
Spring	9	5.28	8.32	1.59	2.08	1.36	1.80	0.66	0.90
Autumn	6	2.39	2.23	1.14	1.02	0.95	0.85	0.51	0.59

3.3.5 Spring and autumn activity areas

Activity areas of tortoise individuals showed great variation in spring (FK-95 range: 0.35 – 34.03 ha; MCP range: 0.15 – 8.72 ha; MCP-95 range: 0.15 – 7.53 ha; FK-50 range: 0.09 – 3.77 ha) and in autumn (FK-95: range: 0.10 – 5.65 ha; MCP range: 0.014 – 2.43 ha; MCP-95 range: 0.014 – 2.26 ha; FK-50 range: 0.021 – 1.43 ha; Fig. 3.3). Large inter-individual variation was apparent within each sex (Table 3.3), particularly for male tortoises in spring. The large variation for males in spring was due to the large activity area of male #1121 (see Fig. 3.3). For male #1121, FK-95 (34.03 ha) was nearly 25 times larger than the second largest activity area for males in spring. Male #1121 also had the largest activity area of the males in autumn.

Season and sex had no effect on the spring and autumn activity areas of geometric tortoises (Two-way ANOVA: for season, all $F_{1,11} < 0.23$, $P > 0.64$; for sex, all $F_{1,11} < 0.44$, $P > 0.52$). After removing male #1121 from the data, season had no effect on activity areas (all $F_{1,9} < 0.15$, $P > 0.70$), but females used larger areas than males did for FK-95 ($F_{1,9} = 9.57$, $P = 0.013$), FK-50 ($F_{1,9} = 11.00$, $P = 0.0090$), MCP ($F_{1,9} = 6.39$, $P = 0.032$) and MCP-95 ($F_{1,9} = 6.71$, $P = 0.029$).

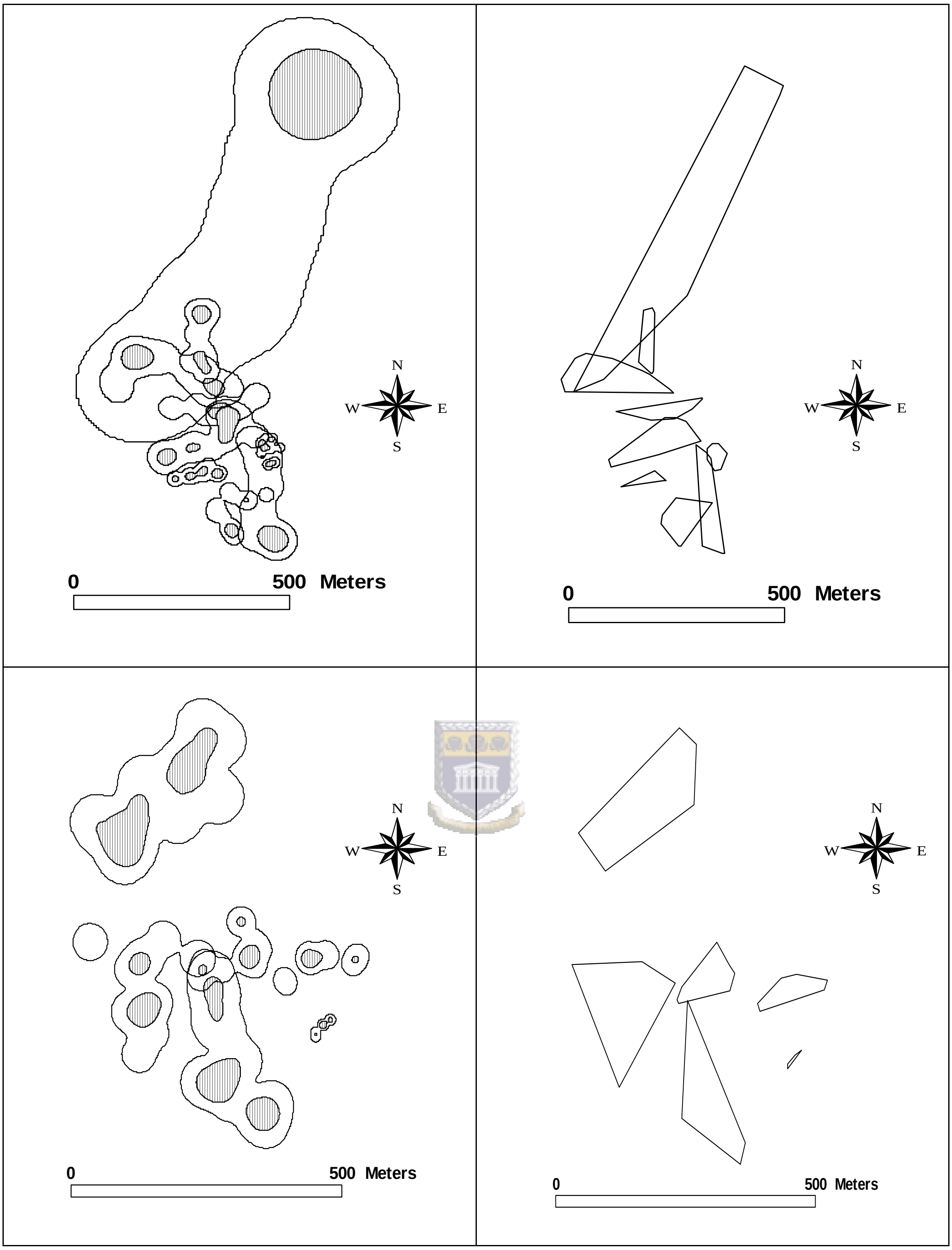

Figure 3.3. Spring (top) and autumn (bottom) activity areas (hectares) of male and female geometric tortoises presented as 95% (open) and 50% (hatched) fixed kernel estimators with least square cross validation (left) and as minimum convex polygons (right). Note the large home range of male #1121 in the spring season (top frames).

Table 3.3. Mean (± CI) activity areas (hectares) of female and male *Psammobates geometricus*. Areas are presented as 95% fixed kernels (FK-95), 50% fixed kernels (FK-50), minimum convex polygons (MCP) and 95% minimum convex polygons (MCP-95).

	N	**FK-95**	**CI**	**MCP**	**CI**	**MCP-95**	**CI**	**FK-50**	**CI**
Spring									
Female	5	2.15	1.39	0.85	0.68	0.73	0.64	0.34	0.23
Male	4	9.19	26.36	2.52	6.58	2.16	5.70	1.06	2.88
Autumn									
Female	3	2.62	3.48	1.34	1.87	1.02	1.05	0.51	1.03
Male	3	2.17	7.53	0.95	3.22	0.88	3.01	0.52	1.96

3.3.6 Annual home range

Average home range size for 21 male and female geometric tortoises varied greatly among individuals (FK-95: 1.02 – 44.93 ha; FK-50: 0.17 – 5.55 ha; MCP: 1.00 – 31.38 ha; MCP-95: 0.52 – 29.11 ha; Table 3.2; Fig. 3.4).

Habitat had no effect on the home range of geometric tortoises (Two-way ANOVA: all $F_{2,15} < 0.59$, $P > 0.56$; Table 3.4), but females had larger home ranges than males had for FK-50 ($F_{1,15} = 4.96$, $P = 0.042$) and almost passed significance for FK-95 ($F_{1,15} = 4.12$, $P = 0.061$). The effect of sex on home range was not significant for MCP or MCP-95 (all $F_{1,15} < 1.26$, $P > 0.28$). After removing the data for male #1121, the FK-95 estimators of females was larger than the estimators were for males ($F_{1,14} = 5.68$, $P = 0.032$).

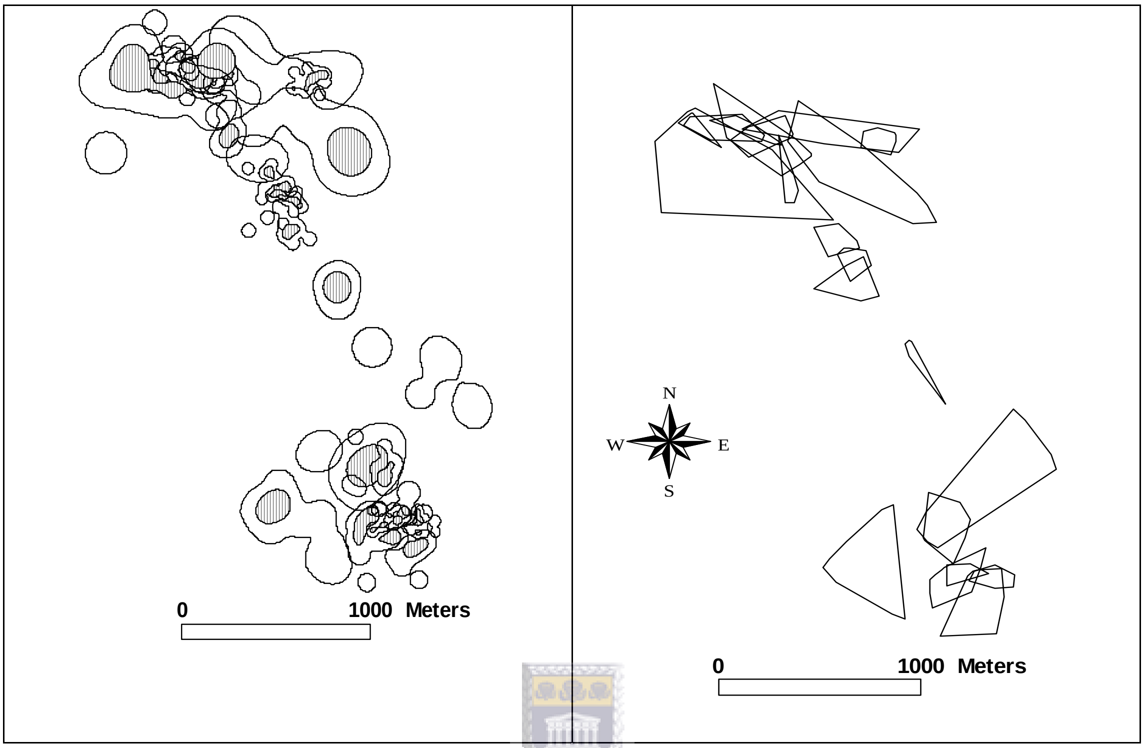

Figure 3.4. Home range (hectares) of individual geometric tortoises over 12 months, presented as fixed kernel estimators with least square cross validation (left; 95% kernels are open and 50% kernels are hatched) and as minimum convex polygons (right).

Table 3.4. Home ranges (mean ± CI; hectares) of male and female geometric tortoises in three different habitat types, burned renosterveld (BR), old fields (OF) and mature renosterveld (RV). Home ranges are presented as 95% fixed kernels (FK-95), 50% fixed kernels (FK-50), minimum convex polygons (MCP), and 95% minimum convex polygons (MCP-95).

	N	**FK-95**	**CI**	**MCP**	**CI**	**MCP-95**	**CI**	**FK-50**	**CI**
Female	11	16.29	9.58	8.77	6.26	7.91	5.86	2.21	1.12
Male	10	6.21	4.63	5.01	4.16	4.13	4.12	0.90	0.69
BF	7	10.46	8.20	7.82	6.29	6.83	6.47	1.54	1.19
OF	8	12.53	10.31	7.85	8.45	6.96	7.88	1.71	1.48
RV	6	11.29	17.50	4.85	6.89	4.13	6.41	1.48	1.72
Female–BF	3	11.33	24.32	6.36	14.75	5.88	14.85	1.76	3.04
Female–OF	5	17.67	16.43	11.31	14.58	10.13	13.67	2.38	2.45
Female–RV	3	18.95	56.56	6.96	23.98	6.22	22.20	2.39	5.10
Male–BF	4	9.81	15.27	8.92	12.84	7.55	13.54	1.38	2.36
Male–OF	3	3.97	6.34	2.08	3.55	1.67	3.06	0.60	0.99
Male–RV	3	3.64	2.07	2.74	2.62	2.05	1.58	0.58	0.17

3.3.7 Wet and dry season home range

Season influenced the area geometric tortoises used when comparing home range size over the entire year, the dry season, and the wet season with a one-way RM ANOVA (Tables 3.2 and 3.5). Annual home range and home range during the dry season were larger than the area used during the wet season for FK-50 ($F_{2,38} = 5.07$, $P = 0.011$) and for FK-95 ($F_{2,38} = 31.84$, $P << 0.0001$; Fig. 3.5). For MCP-95 and MCP, the home range for the year was larger than both the dry and wet season home ranges, while the home range of the dry season was larger than that of the wet season (MCP-95: $F_{2,38} = 31.48$, $P << 0.001$; MCP: $F_{2,38} = 28.11$, $P << 0.0001$).

3.3.8 Short-term and long-term area use

When comparing long-term space requirements (annual, wet and dry seasons) with short-term space use (autumn and spring activity areas), there was a significant effect of period (One-way ANOVA: FK-95: $F_{4,71} = 4.75$, $P = 0.0019$; FK-50: $F_{4,71} = 4.20$, $P = 0.0041$; MCP: $F_{4,71} = 7.04$, $P = 0.000078$; MCP-95: $F_{4,71} = 6.890$, $P < 0.001$; Fig. 3.6). For all determinations, home ranges for the year and for the dry season were larger than the activity areas were in spring and in autumn (all $P < 0.033$). There was no difference between wet season home range and the activity areas in spring and autumn.

Table 3.5. Home ranges (mean ± CI; hectares) of male and female geometric tortoises in the wet season (April to October 2002) and in the dry season (October 2002 to April 2003). Home ranges are presented as 95% fixed kernels (FK-95), 50% fixed kernels (FK-50), minimum convex polygons (MCP), and 95% minimum convex polygons (MCP-95).

	N	**FK-95**	**CI**	**MCP**	**CI**	**MCP-95**	**CI**	**FK-50**	**CI**
Wet season	20	6.69	3.21	2.74	2.34	1.43	0.77	1.32	0.62
Female	10	9.66	5.86	4.34	4.89	1.99	1.53	1.85	1.12
Male	10	3.72	2.51	1.14	0.46	0.86	0.47	0.79	0.60
Dry season	20	11.16	5.66	4.88	2.41	4.02	2.24	1.97	1.03
Female	11	14.84	9.03	5.20	3.10	4.64	3.06	2.81	1.75
Male	9	6.66	6.87	4.49	4.62	3.27	4.01	0.95	0.66

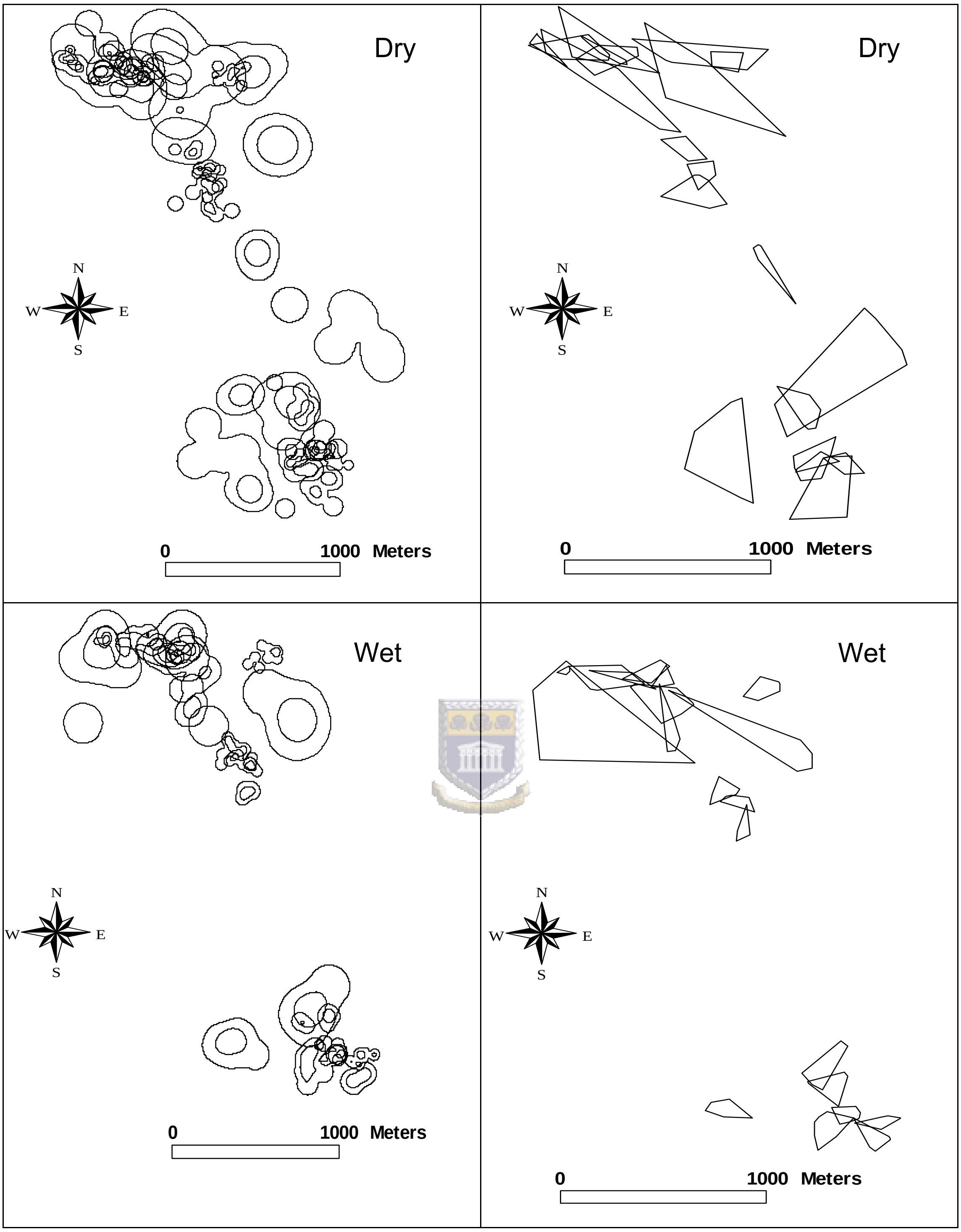

Figure 3.5. Home ranges (hectares) of male and female geometric tortoises in the dry and the wet seasons, presented as 95% (open) and 50% (hatched) fixed kernel estimators (left) and as minimum convex polygons (right).

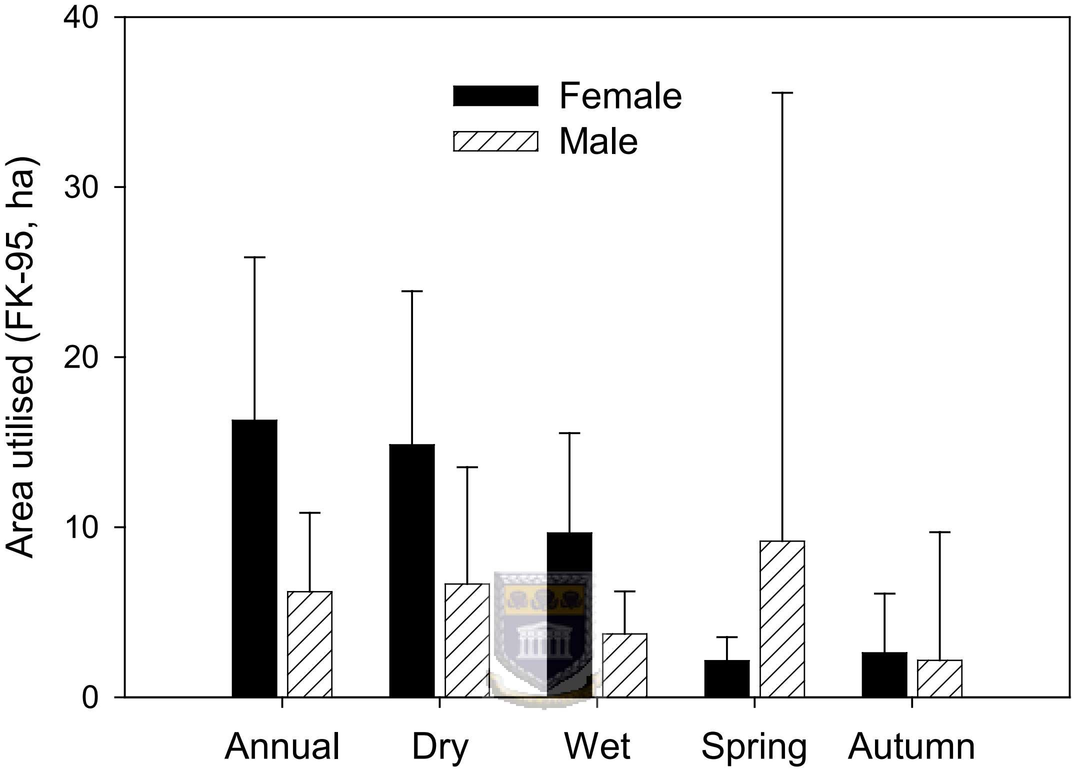

Figure 3.6. Mean area (± 95% CI) that female and male geometric tortoises used over an annual cycle, during the dry and wet seasons (six months), and for short periods in spring (20 days) and autumn (15 days). Areas have been calculated as 95% fixed kernels. Spring values for males included data for male #1121.

3.4 DISCUSSION

3.4.1 Space utilisation and the habitat

Psammobates geometricus exhibited great individual variation in activity area and home range size. The FK-95 annual home range estimates ranged from 1.02 to 44.93 ha and the MCP home range size varied between 1.00 and 31.38 ha. Large inter-individual variation in home ranges have been reported for several other tortoise species, e.g., *Gopherus polyphemus* (MCP = 0.16 to 2.88 ha; Diemer 1992), *Testudo kleinmanni* (MCP = 2.0 to 47.5 ha; Geffen & Mendelssohn 1988), and *Testudo horsfieldi* (MCP = 18 ± 19 ha, mean ± SD; Lagarde *et al.* 2003). Lagarde and co-authors (2003) concluded that the home range of *T. horsfieldi* was considerably larger than the home ranges of many Testudinidae species, with most other species having home ranges of only a few hectares.

Geometric tortoises utilized relatively large areas through the year, but most individuals tended to utilise a smaller core area. Studies on the tortoise *T. kleinmanni* found that individuals would have a large home range and a smaller preferred core area in which they acquire the necessary resources for their survival (Geffen & Mendelssohn 1988). Reproductive strategy and habitat quality are all factors that can affect the size of geometric tortoise home ranges. Nevertheless, this study and others have shown that individuals in the same habitats, and of the same sex, vary widely in their space use.

The distribution of resources in the habitat may alter the size of the home range. Several authors suggested that variation in home range size of individuals could be attributed to the heterogeneous distribution of resources in the habitat (Nieuwolt 1996; Hailey & Coulson 1996a; Lue & Chen 1999). If the productivity of the habitat is low, there is an increase in home range size, whereas an increase in habitat productivity will result in a smaller home range (Harestad & Bunnell 1979; Stickel 1989; Diemer 1992).

There was no difference in home range size of geometric tortoises among the three different habitats. Therefore, the large variation in home range size cannot be attributed to differences in habitat quality among the habitat types. This lack of significance, however, should be viewed with caution because sample sizes in the different habitat types were small. Additionally, on a finer scale the mature and burned renosterveld were both heterogeneous in composition and structure, complicating an evaluation of the effect of habitat type.

Males and females may require different resources from the environment and Brown & Brooks (1993) found that resources related to reproduction affect the space use for the turtle *Chelydra serpentina*. Rose & Judd (1975) attributed the movements and area used by the tortoise *Gopherus berlandieri* to an assortment of factors, which included the availability of food and shelters. Although habitat type does not seem to be an important factor affecting the home range size of the geometric tortoise, seasonal changes in habitat quality may influence seasonal changes in the tortoises' home range size.

3.4.2 Effects of body size and sex

Female geometric tortoises were considerably larger then males were. The home range of geometric tortoises was correlated to the body size of individuals, which can explain the sex related differences in area use. The body size effect on home range may be explained by a greater energy requirement of larger animals, resulting in larger movements and a larger home range (Hailey & Coulson 1996a; Gaston & Blackburn 1996). However, although body size influenced the home range size of female geometric tortoises, body size did not influence the home range size of males.

This may be due to the small body size range for males compared to females, or body size may not be a factor that influences home range size of geometric tortoise males. The fact that male #1121 had an exceptionally large home range while this tortoise had an intermediate body size indicates that body size is not an important factor in the space use of adult geometric tortoise males.

In several tortoise species, females are larger than conspecific males, which is also the case for *Testudo hermanni.* The low body temperature of *T. hermanni* females relative to the body temperature of males has been explained by the thermal lag in large females (Meek 1988). The larger body size of female geometric tortoises may have the effect that females take longer than males to overheat, allowing females to remain in the open for longer, and to range over larger areas, when environmental conditions are unfavourable. Hailey & Coulson (1996b) proposed that the low body temperature of the tortoise *Kinixys spekii* provides a wider safety margin before overheating, relative to species that maintain higher temperatures.

Factors other than body size may contribute to the large home ranges of female geometric tortoises compared to conspecific males. For *T. horsfieldii*, the larger female home range size was attributed to females requiring a larger foraging area to meet their energy requirement for the production of eggs (Lagarde *et al*. 2003). The high energy demands of egg production and availability of suitable nesting sites may help explain the large home ranges of geometric tortoise females.

3.4.3 Seasonal effects

Geometric tortoises were found to have larger home ranges in the dry season than in the wet season. The dry season was associated with unfavourable environmental conditions such as high temperatures, low rainfall and a limited availability of herbaceous plants (personal observations). In *G. polyphemus*, the home ranges of the tortoises increased when herbaceous groundcover decreased (Auffenberg & Iverson 1979). Geometric tortoises may thus have to utilize larger areas to acquire the necessary resources during the dry season.

The wet season was associated with increased rainfall and milder temperatures. The higher rainfall had a positive effect on plant growth (personal observations), resulting in a better habitat quality when compared to the dry season. The increased availability of water and improved habitat quality in the wet season may explain the relatively small home ranges of geometric tortoises in the wet season. According to Kramer (1995), a small home range may reflect an abundance of resources in the habitat. The small home range of geometric tortoises in the wet season may also be the result of flooding caused by increased rainfall. These flooded areas create water barriers that may restrict the movements of geometric tortoises in their habitat.

In addition to habitat quality, geometric tortoises' home range size may be influenced by temperature. Rose & Judd (1975) found that high temperatures limit the activity levels of the tortoise *Gopherus berlandieri.* Although I did not record activity levels of geometric tortoises during the warmest months, the large home ranges in the dry season indicate that these tortoises remained active during the warm months. Baard (1990) reported that the activity patterns of geometric tortoises differ between summer and winter, and that geometric tortoises are active earlier in the day during summer than during winter.

Several studies have shown that tortoises exhibit seasonal changes in reproductive strategies that can alter the size of a home range (Geffen & Mendelssohn 1988; Diemer 1992; Lagarde *et al*. 2003). Geometric tortoise females produce eggs during winter and nest mainly in spring to early summer (M.D. Hofmeyr, M. Klein, B.T.

Henen & E.H.W. Baard, unpublished manuscript). Spring nesting may help explain the large home ranges of geometric tortoise females in the dry season.

3.4.4 Comparison of methods

The home range size of *P. geometricus* was influenced by the method used for home range calculation. The 95% and 50% fixed kernel estimates produced the largest and the smallest home range sizes, respectively, with the MCP estimates falling between the two extremes. These results caution against comparing home ranges of different species without considering the method of home range estimation.

Many authors suggested that MCP home ranges might overestimate home range size because the polygons can enclose large empty areas (White & Garrott 1990; Kaufmann 1995; Cox 1996). The research of Seaman and Powell (1996) demonstrated that fixed kernel estimates with least square cross validation provide reliable estimates of home range size. Fixed kernel estimates may also contain empty areas and for geometric tortoises fixed kernel estimates were larger than MCP estimates were. Long time intervals separated the sequential locality points of geometric tortoise individuals and it is reasonable to assume that the animals used the areas adjacent to each locality point. I thus propose that the 95% fixed kernel estimates provide the best estimate of geometric tortoise home range size.

The kernel estimates of geometric tortoises were influenced by body size, season, and sex. In contrast, the MCP estimates only showed a strong effect for season. It thus appears if the kernel estimates provided better information to explain the biology of the geometric tortoise than the MCP estimates did.

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4 CONCLUSIONS AND RECOMMENDATIONS

Individual variability in movement and home range size for *P. geometricus* was high in the different seasons and throughout the year. The large variation can in part be explained by differences in body size. Larger females had a larger home range size than smaller females, and females, who are the larger sex, had larger home ranges than males. Body size was also implicated in the effect of temperature on the distances that males and females displaced in autumn and spring. The smaller-sized males appear to be more sensitive to overheating, because males moved shorter distances when temperatures increased during the warmer spring season. Because of the changes in environmental conditions between autumn and spring, the selection of a refuge by the geometric tortoise depended on the amount of protection the refuge provided. Sufficient cover is thus a critical requirement in the habitat of geometric tortoises.

In spring, females moved more often than males, but active males travelled greater distances than females did. Male geometric tortoises would move great distances probably to increase female encounters. Therefore, males tended to have more linear movements through the habitat than females. The more random movement shapes of females was possibly linked to foraging activities because females may have greater energy needs to produce eggs and may have specific nutritional requirements related to reproduction. The home range size for geometric tortoises was larger in the dry season than in the wet season, which corresponds with the greater distances that males and females travelled in autumn, relative to spring. The reason may be that resources are scarce in the dry season and tortoises need to travel greater distances to satisfy their requirements. The larger movements in the dry season may also be related to reproductive activities. The large home ranges of geometric tortoises during the dry season should be considered when protected areas are allocated for these tortoises.

The distribution of geometric tortoises is intimately linked to the distribution of renosterveld. Since remaining renosterveld is fragmented and often degraded, it is important to know how these factors influence the biology of this tortoise. In this regard, this study provided no clear-cut answer. There was no difference in the space use of geometric tortoises in mature renosterveld, burned renosterveld, and the old agricultural fields. These results, however, were confounded by small sample sizes.

This study provided important information about the space requirements and space use of geometric tortoises during different times of the year. This study also indicated that more work is required specifically in the following fields:

1. Larger numbers of tortoises should be transmittered and studied in disturbed and natural habitats to evaluate the effects of disturbance on the movement patterns of geometric tortoises.
2. It is important that the dietary needs of geometric tortoises are evaluated to assess if disturbed habitats can provide in their needs. If these tortoises, particularly females, have very specific requirements, these elements should be present in the protected areas.