THE STATUS AND ECOLOGY OF THE LEOPARD TORTOISE (*GEOCHELONE PARDALIS*) ON FARMLAND IN THE NAMA-KAROO

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Submitted in fulfilment of the
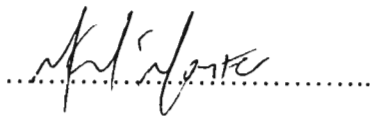academic requirements for
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Preface

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of Natal, Pietermaritzburg, from November 1997 to March 2001, under the supervision of Dr. Colleen T. Downs.

This study is the original work of the author and has not been submitted in any form for any diploma or degree to another university. Where use has been made of the work of others, it is duly acknowledged in the text. Each chapter is written in the format of the journal it has been submitted to.

Megan Kay McMaster

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March 2001

This thesis is dedicated to my father, the late Eric Ralph McMaster, *for his constant encouragement and belief in me, and to my brother, the late* Gregory Clifton McMaster, *for always making me smile.*

Abstract

The **Family Testudinidae** (Suborder Cryptodira) is represented by 40 species worldwide and reaches its greatest diversity in southern Africa, where 14 species occur (33%), ten of which are endemic to the subcontinent. Despite the strong representation of terrestrial tortoise species in southern Africa, and the importance of the Karoo as a centre of endemism of these tortoise species, there is a paucity of ecological information for most tortoise species in South Africa. With chelonians being protected in < 15% of all southern African reserves it is necessary to find out more about the ecological requirements, status, population dynamics and threats faced by South African tortoise species to enable the formulation of effective conservation measures.

The Leopard Tortoise (*Geochelone pardalis*) is the largest of the southern African species and has a wide distribution range, occurring in a variety of habitats. There is a paucity of ecological information about Leopard Tortoises in most of these habitats, especially arid and semi-arid regions. The broad aim of the study was to comprehensively investigate the ecology of Leopard Tortoises on farmland in the semi-arid Nama-Karoo biome, and use the ecological information to make recommendations for conservation.   An investigation was made to determine the population size, sex and age distributions, density, biomass, and morphometrics of Leopard Tortoises in the Nama-Karoo. It was predicted that Leopard Tortoises would either be similar in size to Leopard Tortoises in other habitats or larger in order to buffer the effects of extreme temperatures by decreasing the surface-to-volume ratio. In addition, it was predicted that Leopard Tortoises would have a smaller population size, and occur at a lower density and biomass per hectare than those tortoises in mesic habitats.

A total of 92 tortoises were caught, and 3899 observations made on Leopard Tortoises on 5500 hectares of farmland. Fourteen tortoises were radio tracked which allowed for repeated observations throughout the year. The population was skewed towards adults, and indicates a low hatchling recruitment. Female Leopard Tortoises were significantly larger than males with respect to all morphometric measurements. A male to female sex ratio of 1:1.6 was obtained, which was not significantly different from 1:1. A population estimate of 57.64 ± 3.99 tortoises for the 5500 ha area was obtained using a mark-recapture sampling method. Density of tortoises was extremely low at 0.017 tortoises.ha^{-1}, with a biomass of 0.002 kg.ha^{-1}. Population size, density, biomass and morphometrics were compared with Leopard Tortoise populations in other areas. Leopard Tortoises were larger in size in the semi-arid Nama-Karoo compared with Leopard Tortoises in other areas, probably a mechanism to reduce the effects of extreme temperature fluctuations, and were found at a much lower density. Knowledge of the home range size, home range overlap and seasonal change in home range is imperative to the understanding and conservation of the Leopard tortoise. Home range size, percentage overlap and mean daily distances moved were investigated for Leopard Tortoises as a function of season, gender and body mass. Home range and movement data were calculated for 36 Leopard Tortoises (22 females, 14 males), 14 of which were telemetered (8 females, 6 males), and 22 of which were recaptured 10 or more times (14 females and 8 males) over a period of two years. Mean (±SE) home range size for adult Leopard Tortoises was 205.41 ± 45.57 ha. Home range size was not significantly different between males and females, however females had larger home ranges than males. Mean home

range size of males was 133.27 ± 32.90 ha, and of females was 251.32 ± 70.56 ha. There

was a significant difference in home range size between telemetered tortoises (413.81 ±

89.46 ha), and those recaptured 10 or more times (72.79 ± 18.89 ha). It is suggested that

unacceptable variation in home range size estimations occur when radio telemetry is not

used to recapture tortoises throughout the year. No significant relationship between home

range size and body mass was found for all tortoises or between sexes. Significant

seasonal and gender variation existed in the seasonal home range sizes. Females had

larger home ranges than males in all seasons except spring. Mean daily distance moved

by Leopard Tortoises was 136.13 ± 8.94 m with males moving further overall daily than

females (males: 161.10 ± 11.8 m; females: 117.07 ± 12.87), but not significantly so.

Mean daily distance moved per season was significantly different between the sexes.

Females covered the largest mean daily distance in autumn and males in spring.

Considerable variation existed in the amount of home range overlap both within and

between sexes. Overlap percentages ranged from 5% to 90%, with home ranges most

frequently overlapping by 20%. Home range size and daily distances moved in the Nama-

Karoo are larger than for Leopard Tortoises in other habitats. This has strong implications

for the size of reserves needed in conservation efforts with regard to this and perhaps

other, species in arid or semi-arid areas.

Seasonal activity patterns of Leopard Tortoises were investigated as a function of

rainfall, sex, time of day, temperature and time after sunrise. It was predicted that due to

seasonal rainfall, and the subsequent increase in food available, the activity patterns of

Leopard Tortoises would vary greatly between seasons, but that the primary constraint on

activity levels within a season, would be ambient temperature. Type of activity, time of

day that the activity was performed, and amount of time spent performing each activity,

differed significantly between the seasons. There was no overall seasonal significant

difference between the sexes and the level of activity, however, in certain seasons and

with regard to specific activities, there were significant differences between the sexes.

Activity patterns were primarily bimodal in summer and autumn, and unimodal in winter

and spring, with non-thermoregulatory activities, for example walking and feeding, being

performed primarily in the afternoon. There was a significant positive correlation between

the number of tortoises caught and rainfall per season, but activity levels and the

percentage of tortoises walking and feeding was not correlated with seasonal rainfall. The

time of day that an activity was first performed in each season, was primarily a function

of the time after sunrise and only secondarily of temperature. The response of Leopard

Tortoise activity to rainfall, time of day, temperature and time after sunrise, is discussed.

With Leopard Tortoises being ectotherms, they rely largely on behavioural

thermoregulation to moderate the effects of daily and seasonal fluctuations in ambient

temperature on body temperature. Extensive use is made of refuges to facilitate this

behavioural thermoregulation. The Nama-Karoo experiences wide temperature

fluctuations both daily and seasonally, and therefore the types and seasonal use of refuges

by the Leopard Tortoise, in addition to the orientation of the exits and of the tortoises

within the refuges, was investigated. A wide variety of refuges were used, but *Lycium*

spp., Eberlanzia ferox (Doringvygie), *Opuntia ficus* (American Prickly Pear) and grass

clumps were preferred as refuges. There was seasonal variation in the use of these refuges

that further depended on whether the refuges were used as forms or shelters. Leopard Tortoises in spring and winter often remained in the same refuge for the entire season, or returned to the same refuge on consecutive nights.

There was seasonal and behavioural variation in a) compass direction that the tortoises were facing within a refuge, b) compass direction that exits of the refuges were open to, and c) portion of the shell of each Leopard Tortoise within a refuge that was exposed to sun radiation. Tortoises in winter and spring used these three factors to maximise the amount of solar radiation received on their carapace, while tortoises in summer and autumn used them to minimise solar radiation received. Therefore, using a combination of refuge type, exit orientation and tortoise orientation, Leopard Tortoises were able to passively thermoregulate and further control temperature fluctuations experienced in an extreme environment.

Leopard Tortoises on farmland in the Nama-Karoo had lower densities, larger body sizes and much larger home ranges than Leopard Tortoises in other habitat types. This is an important aspect to take into account when planning for the conservation of Leopard Tortoises in semi-arid areas, and may hold further implications for other arid or semi-arid tortoise species.

Activity patterns and patterns of thermoregulation allow for further understanding of the interactions between tortoises and their environment, habitat, and climate in the wild. In addition, it further aids in the understanding of the methods used by ectotherms to thermoregulate and manipulate body temperatures, especially when living in regions of unpredictable rainfall and extreme temperatures.

Acknowledgements

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Chapter One

General Introduction

The **Family Testudinidae** (Suborder Cryptodira) contains all the terrestrial tortoises, and is represented by 40 species worldwide (Boycott and Bourquin, 2000). The Family reaches its greatest diversity in southern Africa, where 14 species are known to occur, ten of which are endemic to the subcontinent (Baard, 1996; Boycott and Bourquin, 2000). South Africa supports more terrestrial tortoise species (33%) than any other country in the world, with eleven species occurring within its borders and nine of these species found in the Cape Province (Branch *et al.* 1995; Baard, 1996). Three species are endemic to the former Cape Province, a fourth is endemic to the former Cape Province and the adjacent regions of the former Orange Free State and Transvaal, and a further two are endemic to the former Cape Province and southern Namibia (Els, 1989). Thus at present, terrestrial tortoise species are strongly represented in southern Africa, with the Karoo region being a centre of endemism (Boycott and Bourquin, 2000). Despite the importance of the Karoo to the conservation of these tortoise species, the Karoo biome is inadequately protected (Lombard, 1995).

The greatest threats to South African land tortoises are those of habitat degradation, the encroachment of alien vegetation, overgrazing by stock animals and frequent veld fires (Baard, 1989; Boycott and Bourquin, 2000). The pet trade poses a further threat to many tortoise species especially within South Africa where an unknown number are illegally kept in captivity (Boycott and Bourquin, 2000).

While all land tortoises in South Africa are CITES Appendix II species, the present

numbers of many of the endemic land tortoises is unknown (Boycott and Bourquin, 2000). With chelonians being protected in less than 15% of all southern African reserves (Branch et al. 1995), it is necessary to find out more about the ecological requirements, status, population dynamics and threats faced by specific South African tortoise species to enable the formulation of effective conservation measures.

There is a paucity of information regarding the ecology of most tortoise species in South Africa with regard to behaviour, reproductive cycles, egg production, age structure, sex ratios, age specific fecundity and mortality, home range requirements, habitat use, the impact of natural and introduced predators, dietary and water requirements, and the effect of habitat disturbance by humans and domestic stock. Most of the data obtained, especially with regard to reproductive behaviour, are from captive animals (Els, 1989). Thus there is a need for a broad-based ecological study on wild populations of various tortoise species in the Karoo region and subsequent recommendations to the appropriate conservation organisations for the implementation of conservation measures to protect these populations.

Prior research

Studies on southern African tortoises in the past were largely based on the systematics and distribution of various species and included information on the morphometrics, colour variations and sexual differences within a species (Hewitt, 1933; Comrie-Grieg and Burdett, 1976; Broadley, 1981; Boycott, 1986; Boycott and Jacobsen 1988; Van den Berg and Baard, 1994). Other ecological information took the form of casual observations of tortoise behaviour and/or reproduction both in the wild and in captivity (Archer, 1948; Auffenberg, 1963; Jacobsen, 1978). A few life history studies on captive populations of the leopard tortoise (*Geochelone pardalis*) gave valuable insight into incubation periods, clutch size, number of clutches laid per season, and

the hatching, early growth and behaviour of hatchling tortoises (Archer, 1948; Jaques, 1969; Rall, 1988; Patterson *et al.*, 1989). Home range, movement patterns and homing ability of the leopard tortoise were investigated in savannah (Bertram, 1979a; 1979b), in valley bushveld (Weatherby *et al.*, 1995) and in the northern (Rall, 1985) and eastern (Grobler, 1982) Cape Province. Grobler (1982) also collected data on population size and peak activity periods of Leopard Tortoises. Hailey and Coulson (1996) studied the home range and distances moved by *G. pardalis* and *K. spekii* in Zimbabwe. A study on the home range overlap and competition between two sympatric genera *G. pardalis* and *Chersina angulata* was investigated by Mason and Weatherby (1995). Diets and food preferences of *G. pardalis* and *Psammobates oculifer* have been investigated and compared with each other (Milton, 1992; Rall and Fairall, 1993; Hailey, 1995). Thermoregulatory behaviour of *C. angulata, Homopus areolatus* and *G. pardalis* (Craig, 1973; Perrin and Campbell, 1981) have been investigated. Els (1989) investigated ecophysiological behaviour in *C. angulata* including home range, activity patterns and diet.

Predation of various tortoise species by a wide variety of predators has been frequently recorded, while fires, electric fences, vehicles and trampling by cattle and elephants are reported causes of mortality in Leopard Tortoises (Branch and Braack, 1987; Wright, 1988; Branch and Els, 1990; Malan and Branch, 1992; Burger and Branch, 1994; Malan and Crowe, 1996).

Apart from casual observations of captive tortoises, the social, sexual, feeding and seasonal behaviour of South African tortoises is virtually unknown. Auffenberg (1977) investigated chemical, visual, auditory and tactile communication in South African land tortoises and documented tortoises drinking from condensed water on their carapaces (Auffenberg, 1963), but a comprehensive behavioural study has yet to be done.

Aims of the study

The broad aim of the study was to comprehensively investigate the ecology of the Leopard Tortoise in the semi-arid Nama-Karoo. Due to a shortage of nature reserves in the Nama-Karoo, most land tortoises live on farmland in the Nama-Karoo and hence, the study was conducted on farmland in the Nama-Karoo. *Geochelone pardalis* was studied on a 26000 ha mixed commercial sheep and game farm named Wonderboom in the De Aar District, Nama-Karoo biome, South Africa (31°04'S, 23°41'E) (see Figure 1). Study site details are listed in more detail in each chapter.

Using ecological information gathered from this study, conservation recommendations will be made to local and legislative bodies in order to implement sound conservation strategies, and increase awareness of the rarity and endemism of tortoises in South Africa.

Each chapter has aims designed to ultimately gain broad ecological knowledge of Leopard Tortoises and add to the scientific knowledge of tortoises living in arid regions. Each chapter is presented in the format for manuscript submission

The population size, sex and age distributions, density and biomass, and morphometrics of the Leopard Tortoises are presented in Chapter 2. It was predicted that Leopard Tortoises in the semi-arid Nama-Karoo would be larger in size, have a smaller population size, lower density sand a lower biomass per hectare, than those found in wetter habitats.

Home range sizes, home range overlap and daily movement distances of Leopard Tortoises in the semi-arid Nama-Karoo and to compare these with regard to seasonal differences, tortoise gender and body mass are presented in Chapter 3. It was expected that home range sizes and daily distances moved would be greater in this semi-arid area compared with more mesic areas.

In Chapter 4 activity behaviour as a function of temperature, time of day, season and sex

are presented. It was predicted that due to seasonal rainfall, and the subsequent increase in the food available, the activity patterns of Leopard Tortoises would vary greatly between seasons, but that the primary environmental constraint on activity levels within a season would be ambient temperature.

Types and seasonal use of refuges, orientation of the exits and of tortoises within the refuges are presented in Chapter 5. It was predicted that the type of refuge used would differ seasonally and would differ according to the thermoregulatory requirements of the tortoises. In addition, it was predicted that tortoises would orientate themselves within a refuge with regard to the sun, in order to manipulate the amount of solar radiation received on the shell of the tortoise and therefore further aid in thermoregulation.

It was hoped that following these studies insight into the status of Leopard tortoise populations, their sex ratios and density on farmland in the Nama-Karoo would be obtained. The required home range sizes and the daily distances moved by Leopard Tortoises on Nama-Karoo farmland in conjunction with the density of tortoises per hectare can be compared to tortoises in other habitats, and gives an indication of the required size of conservation areas needed to protect Leopard Tortoise populations in this semi-arid area. Activity patterns and patterns of thermoregulation aided by indigenous plant refuges allows for further understanding of the interactions between tortoises and their environment, habitat, and climate in the wild. In addition, it further aids in the understanding of the methods used by ectotherms to thermoregulate and manipulate body temperatures, especially when living in regions of unpredictable rainfall and extreme temperatures.

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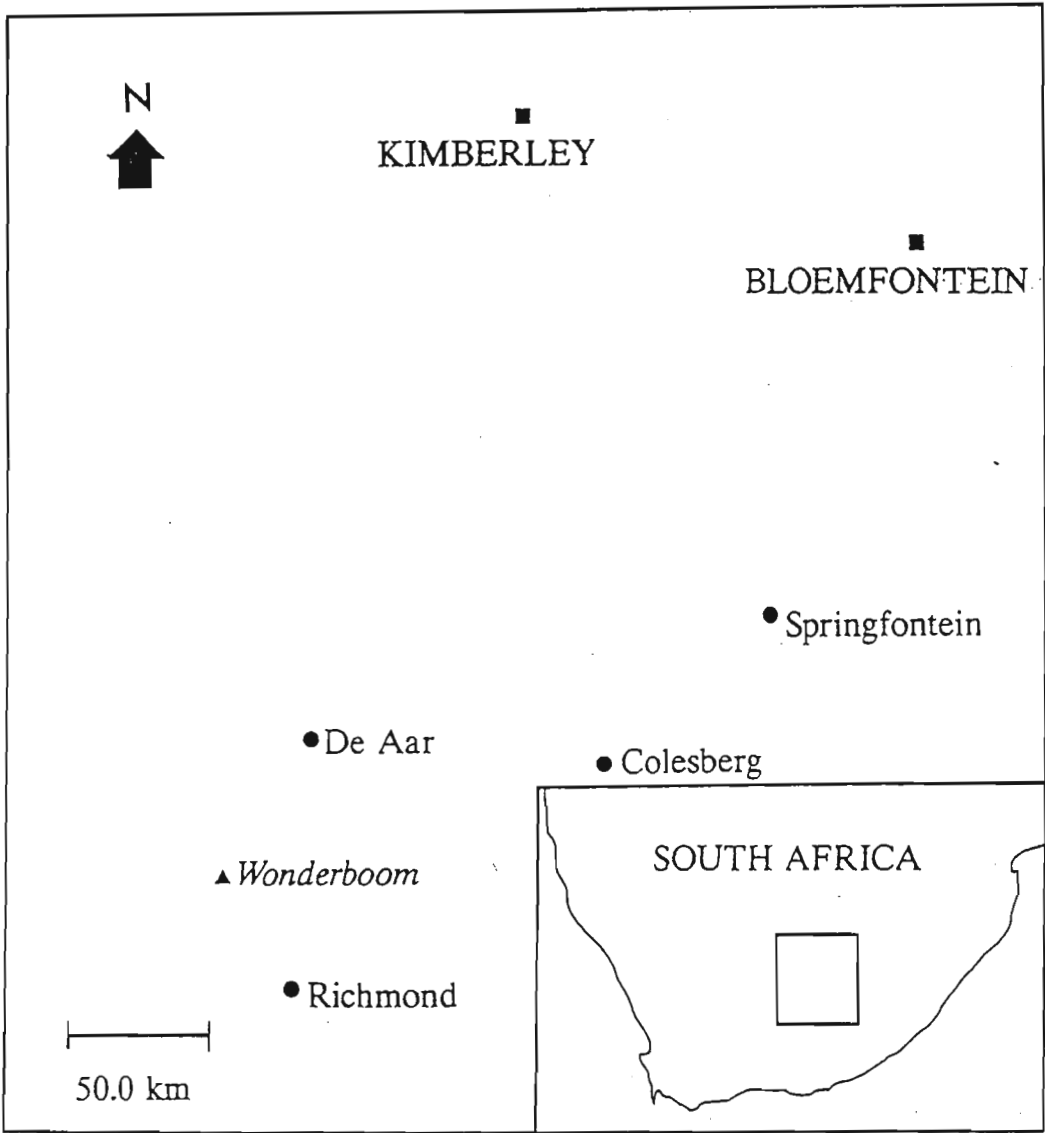
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List of Figures

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BLOEMFONTEIN

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SOUTH AFRICA

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Chapter Two

POPULATION ECOLOGY AND MORPHOMETRICS OF LEOPARD TORTOISES (*GEOCHELONE PARDALIS*) IN THE NAMA-KAROO

Megan K. McMaster and Colleen T. Downs

Formatted for submission to Herpetologica

Abstract

The leopard tortoise (*Geochelone pardalis*) is the largest of the southern African species and has a wide distribution range, occurring in a variety of habitats. There is a paucity of ecological information about leopard tortoises in these habitats. The aim of this study was to determine the population size, sex and age distributions, density, biomass, and morphometrics of leopard tortoises on farmland in the semi-arid Nama-Karoo. It was predicted that the leopard tortoise population would either be similar in average size to a leopard tortoise population in a different habitat or the population would be larger on average in order to buffer the effects of extreme temperatures by decreasing the surface-to-volume ratio. In addition, it was predicted that leopard tortoises in this semi-arid area would have a smaller population size, lower density and a lower biomass per hectare than those found in other regions.

A total of 92 tortoises were caught, and 3899 observations made on leopard tortoises on 5500 hectares of farmland. Fourteen tortoises were radio tracked which allowed for consistent observations throughout the year. The population was skewed towards adults, and indicates a low hatchling recruitment. Female leopard tortoises were significantly larger than males with respect to all morphometric measurements. A male to female sex ratio of 1:1.6 was obtained, which was not significantly different from 1:1. Leopard tortoises in this study were larger than leopard tortoises from other areas, but not greatly so. A population estimate of 57.64 ± 3.99 tortoises in a 5500 ha area was obtained using a mark-recapture sampling method. Density of tortoises was extremely low at 0.017 tortoises.ha^{-1}, with a biomass of 0.002 kg.ha^{-1}. Population size, density, biomass and morphometrics was compared with Leopard Tortoise populations in other areas. Semi-arid areas appear support a lower population size and density of leopard tortoises.

Introduction

Southern Africa has the greatest diversity of land tortoises (Family: Testudinidae) in the world, hosting 14 species (33%) of the world's 40 species (Boycott and Bourquin, 2000). Most of these southern African species are restricted in distribution and occur in arid to semi-arid areas in the Cape region, South Africa (Boycott and Bourquin, 2000). The leopard tortoise (*Geochelone pardalis*) is the largest of the local land tortoises, and has the widest distribution over central and southern Africa, occurring in habitats ranging from grassveld, savannah, tropical bushveld and arid to semi-arid Karoo (Boycott and Bourquin, 2000).

Despite there being such great diversity of land tortoises in South Africa, and despite the leopard tortoises' conspicuous size and wide distribution, very little ecological information has been collected on South African tortoises or on the leopard tortoises themselves (Branch 1984; Branch and Braack, 1987).

The majority of early data regarding leopard tortoise population ecology and morphometrics have been derived from observations of captive individuals (Archer, 1948; Jaques, 1969; Rall, 1988), or casual observations in the field of various ecological aspects (Rall, 1985). However, a few studies have been made regarding sex ratios, population estimates, density, mortality and morphometrics of leopard tortoises in various habitats (Grobler, 1982; Burger and Branch, 1994; Mason *et al.* 2000).

The aim of this study was to determine the population size, sex and age distributions, density and biomass, and morphometrics of leopard tortoises on farmland in the semi-arid Nama-Karoo. It was predicted that the leopard tortoise population would either be similar in average size to a leopard tortoise population in a different habitat or the population would be larger on average in order to buffer the effects of extreme temperatures by decreasing the

surface-to-volume ratio. In addition, it was predicted that leopard tortoises in this semi-arid area would have a smaller population size, lower density and a lower biomass per hectare than those found in other regions, due to the lower productivity per hectare compared with mesic habitats.

Methods

Geochelone pardalis was studied in a 5500 hectare area in the De Aar District, which is situated in the Nama-Karoo biome, South Africa (31°04'S, 23°41'E). The area comprises mixed commercial sheep and game farms of 26000 ha with the vegetation classified as grassy dwarf shrubland (Palmer and Hoffman, 1997). The average annual rainfall is low (200 - 400 mm), although the area has its highest rainfall in late summer and autumn. Daily temperatures are variable and range from 5° to 39°C in spring and summer, and from -5° to 26°C in autumn and winter. Spring was from September to November; summer from December to February; autumn from March to May; winter from June to August.

Leopard tortoises were located by riding transects on horseback in the study area twice daily. Date, time, type of activity and the geographical position of all tortoises was recorded using a handheld Trimble Navigation GeoExplorer II Geographical Position System (GPS) unit (U.S.A.). Individual tortoises were marked using a coded sequence of notches filed into their marginal scutes following Branch (1984). All tortoises were sexed, weighed and various morphometric characteristics were recorded. Measurements (using a measuring tape accurate to 1 mm) were taken of curved carapace length, width and side; straight carapace length, width and height; and the distance between the two front marginal shields (see Appendix 1). Tortoises were broadly placed into age classes based on size, being either

adult, subadult or hatchlings. If male tortoises weighed < 5 kg, and females < 10 kg, they were considered to be subadults. However, some males so classified as subadults, were later found to be sexually active.

In addition to chance sightings, eight females and six males were fitted with unique-frequency radio transmitters (see Chapter 3). Telemetered Leopard Tortoises were located twice daily for three month periods from October 1997 to April 1999. The GPS position and behaviour of the tortoises were recorded on every occasion. In addition, each individual was followed for a continuous eighteen hour period once every three months, and its behaviour and GPS position recorded every 15 minutes. All statistical tests were calculated using STATISTICA software (Statsoft, Tulsa, USA).

The population size of leopard tortoises was estimated using the Jolly-Seber mark-recapture equation (following Zar 1984). The density of leopard tortoises was calculated as a function of a 5500 ha area using a) the total number of tortoises caught, b) the estimated population size and c) the number of male and female tortoises. Similarly, leopard tortoise biomass (total mass of tortoises per hectare) was estimated for all tortoises, as well as for males and females using mean body mass.

Results

Number, sex and age distribution of tortoises captured

Observations of leopard tortoise activity were made on 3958 occasions over the total search time of 2615 man-hours. The number of leopard tortoises caught and the number of observations per season with regard to the sex and age distributions of the tortoises are shown in Table 1. A total of 92 Leopard tortoises were caught, 40 males and 52 females. A total of

62 adults were captured, 26 subadults and only 4 hatchlings (Table 1). A male to female sex ratio of 1:1.3 was obtained. This was not significantly different from a sex ratio of 1:1 ($X^2 =$ 0.818, df=1 , $p = 0.37$).

The majority of Leopard tortoises were caught in spring and summer, males being caught more frequently in spring and females more frequently in summer (Table 1).

Number of observations in Table 1 included observations of both recaptured and telemetered tortoises. The majority of teopard tortoises were observed in summer and spring, with a similar number of observations of male and females in summer and spring (Table 1). The majority of adults were observed in spring and summer, however observations of subadults were more frequent in spring and winter (Table 1). Hatchlings were never recaptured, so capture and observation frequencies were the same (Table 1).

Morphometrics

Differences in male and female leopard tortoises' morphometric characters are shown in Table 2. Females were significantly larger than males with respect to all morphometric measurements (Table 2). Overall mean body mass of all leopard tortoises was 11.1 ± 4.0 kg. Males weighed significantly less than females, being almost half their weight (Table 2). However, male body mass ranged up to 15.9 kg, while females weighed up to 18.8 kg. Similarly, males had a significantly smaller straight carapace length compared with females (Table 2).

Body mass and total carapace length were plotted as a frequency distribution to illustrate differences in size between the sexes (Figures 1 and 2). Male carapace length was negatively skewed, while female carapace lengths were mainly 40 cm in size (Figure 1). The frequency distribution of male body mass was negatively skewed compared to the

females, with females distinctly larger in body mass than males (Figure 2).

Population size and density

Using the Jolly-Seber method of population estimation, a population size of 57.64 ± 3.99 tortoises was estimated. In addition, 98% of tortoises marked were recaptured at least twice.

Density was calculated over 5500 ha as a) 0.017 tortoises.ha^{-1} using the total number of tortoises caught, b) 0.010 tortoises ha^{-1} using the estimated population size and c) 0.007 males ha^{-1} and 0.009 females ha^{-1} using estimated population size.

Biomass was 0.002 kg.ha^{-1} for all tortoises using the mean mass (Table 2), 0.001 kg.ha^{-1} for males and 0.003 kg.ha^{-1} for females, using their respective mean masses.

Discussion

Number, sex and age distribution of tortoises captured

Most tortoises captured, and the highest number of observations, were in spring and summer. Leopard tortoises were active earlier and for longer periods in warmer temperatures (refer to Chapter 4), and therefore more easily sighted. In addition, tortoises in spring, summer and autumn drank and fed at livestock watering points, where they were easily visible. In winter, tortoises hibernated and retreated to refuges where they were cryptically hidden and easily overlooked (refer to Chapter 5). Radio telemetry allowed for the location of tracked tortoises year around, hence the availability of observational data during autumn and winter.

The low number of hatchlings caught may be because of the difficulty of sighting them in the field, but may also indicate a population skewed towards adults. This implies a lack of juvenile recruitment, which may be a result of high predation, low egg fertility or high

juvenile mortality. Further investigation is needed to determine whether there is a paucity of

juveniles and hatchlings in the population or whether they were merely overlooked in

sampling. No juvenile leopard tortoises were found in the Mountain Zebra National Park, and

it was concluded that predation on juveniles caused the population to consist primarily of

adults (Grobler, 1982). However, other factors may have caused the population to be skewed

towards adults, such as fences limiting the immigration of adults out of the Park. Meek

(1985) reported that many populations of land tortoises have age and size frequencies skewed

towards large and older individuals in conjunction with low recruitment rates of 1-5%.

There was an insignificant difference in the 1:1.6 sex ratio of males: females in the

population of leopard tortoises in the present study. Grobler (1982) found a significant

difference with a sex ratio of 1:1.75 males: females. Both *Gopherus polyphemus* and *Testudo*

hermanni showed apparent seasonal differences in the sex ratio obtained (Hailey *et al.*, 1984;

Diemer, 1992). Similarly, *G. polyphemus* showed that sex ratios differed according to habitat

type (Breininger *et al.*, 1994). Thus the proportion of males to females obtained in a sample

may be biased by the season or habitat type in which individuals were sampled.

Morphometrics

Female leopard tortoises were significantly larger than males with regard to all morphological

characters. Males had a mean body mass of 7.6 ± 3.3 kg and a mean straight carapace length

shorter than females who weighed 15.2 ± 5.3 kg (Table 2). Female leopard tortoises in

Thicket Biome were also larger than the males, however, they were of a much smaller size,

having a mean straight carapace length of 33.23 cm, with males measuring 27.73 cm (Mason

et al., 2000).

Boycott and Bourquin (2000) stated that adult leopard tortoises usually weigh between

10 -20 kg, and can have a carapace length of 75 cm. Male leopard tortoises in the Mountain
Zebra National Park weighed 10.5 kg on average, with the largest weighing 18.4 kg, while the
females weighed a mean of 12.2 kg ranging up to 16.4 kg (Grobler, 1982).

Consequently, female leopard tortoises seem to be consistently larger than the males
irrespective of habitat, however, the mean mass and total lengths vary between sites. Ideally,
age must be taken into account. A site with a greater juvenile recruitment in the leopard
tortoise population, will also have a lower mean for morphometric measurements. Although
Boycott and Bourquin (2000) report a wide range of sizes, one expects that leopard tortoises
would be larger in a more extreme environment in order to buffer the effects of extreme
temperatures by decreasing the surface-to-volume ratio. While Leopard tortoises in this study
were larger than those in other habitats, which may indicate that body mass increases in areas
with larger temperature variation, age should be taken into account before absolute
conclusions can be drawn. Leopard tortoises do, however, have the largest body mass and
size compared with other desert chelonians both in South Africa and in other deserts (Meek,
1985; Diemer, 1992; Boycott and Bourquin, 2000).

Population size and density

The population size of leopard tortoises was estimated to be 57.64 ± 3.99 tortoises. Leopard
Tortoise density was extremely low at 0.017 tortoises.ha^{-1} using all tortoises caught and 0.010
tortoises.ha^{-1} using the population estimate. Leopard tortoises in the Addo Elephant National
Park had a population of 85 tortoises per 100 ha (ie 0.85 tortoises.ha^{-1}) which is an order of
magnitude larger than the density found in the present study (Branch and Braack, 1987).

The biomass calculated for leopard tortoises in the present study was an extremely
low (0.002 kg.ha^{-1} for all tortoises, and 0.001 males.ha^{-1} and 0.003 females.ha^{-1}). In

comparison, leopard tortoises in the Addo Elephant National Park had a biomass of 6.02 kg.ha^{-1} (Mason, *et al.* 2000).

Thus it seems evident that density is strongly influenced by habitat type and productivity. The density of *G. polyphemus* was found to be influenced by habitat type (Breininger et al. 1994) and environmental effects (Kushlan and Mazzotti, 1984) while extreme environmental conditions influenced the density of *G. agassizzi* (Freilich *et al.* 2000).

There were seasonal influences on the number of leopard tortoises that were captured or observed due to a decrease in activity in cooler months, with tortoises retreating into refuges and becoming harder to find. Radio telemetry allows for an unbiased sampling period across all seasons. The low number of hatchlings captured could indicate a low juvenile recruitment, perhaps due to high predation pressure on eggs or hatchlings. However, other factors may result in a low hatchling count, for example hatchlings are more difficult to locate, or they may be migrating out of the area through fences that adults cannot penetrate.

Leopard tortoises in this study have larger females than males and are larger in overall size compared to other populations. In addition, they are found on this study site at very low densities and biomass compared to leopard tortoises in other habitats. This has implications for the conservation of this species in semi-arid areas, as they seem to have very low recruitment rates and the habitat can only support a low density of individuals. This must be taken into account when planning a conservation area for tortoises distributed in arid and semi-arid regions.

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List of Figures and Tables

Table 1: Number of Leopard Tortoises caught and the number of observations of these tortoises per season with regard to sex and age distributions

|	Spring	Summer	Autumn	Winter	Total
Tortoises captured*	34	53	4	1	92
Captured males	20	17	3	0	40
Captured females	14	36	1	1	52
Captured adults	20	39	2	1	62
Captured subadults	13	12	1	0	26
Captured hatchlings	1	2	1	0	4
Number of Observations[†]	1208	1240	637	814	3899
Observed males	498	523	264	316	1601
Observed females	710	717	373	498	2298
Observed adults	964	1063	521	588	1121
Observed subadults	243	175	115	226	758
Observed hatchlings	1	2	1	0	4

*Capture is the first sighting and marking of a tortoise.

[†] Observations is the repeated sighting of all of the marked tortoises.

ble 2: Differences in morphological characters between female and male Leopard Tortoises found in the Nama-Karoo.

| orphological Character	Males					Females					t
	Mean	SE	Min	Max	N	Mean	SE	Min	Max	N	
irved carapace length (cm)	47.5	11.0	6.2	63.0	39	55.9	7.4	22.5	69.5	51	-6.06***
irved carapace width (cm)	45.4	10.9	6.5	61.7	39	54.6	7.2	22.0	66.5	51	-6.47***
arapace side (cm)	32.8	7.8	5.0	46.6	39	39.1	5.4	15.5	49.0	51	-6.00***
raight carapace height (cm)	16.8	4.6	2.4	27.0	32	20.5	3.2	7.0	26.0	48	-5.20**
raight carapace length (cm)	35.4	10.3	5.2	47.0	23	42.8	4.7	28.0	49.5	35	-3.05**
raight carapace width (cm)	23.0	6.3	4.5	31.0	23	30.3	4.6	21.0	43.0	35	-6.09***
ont marginal shield gap (cm)	7.2	1.9	1.3	12.0	39	8.3	1.4	3.2	11.0	51	-4.31**
ass (kg)	7.6	3.3	4.4	15.9	32	15.2	5.3	5.6	18.8	43	-7.33***

< 0.005**, $P < 0.0001$***
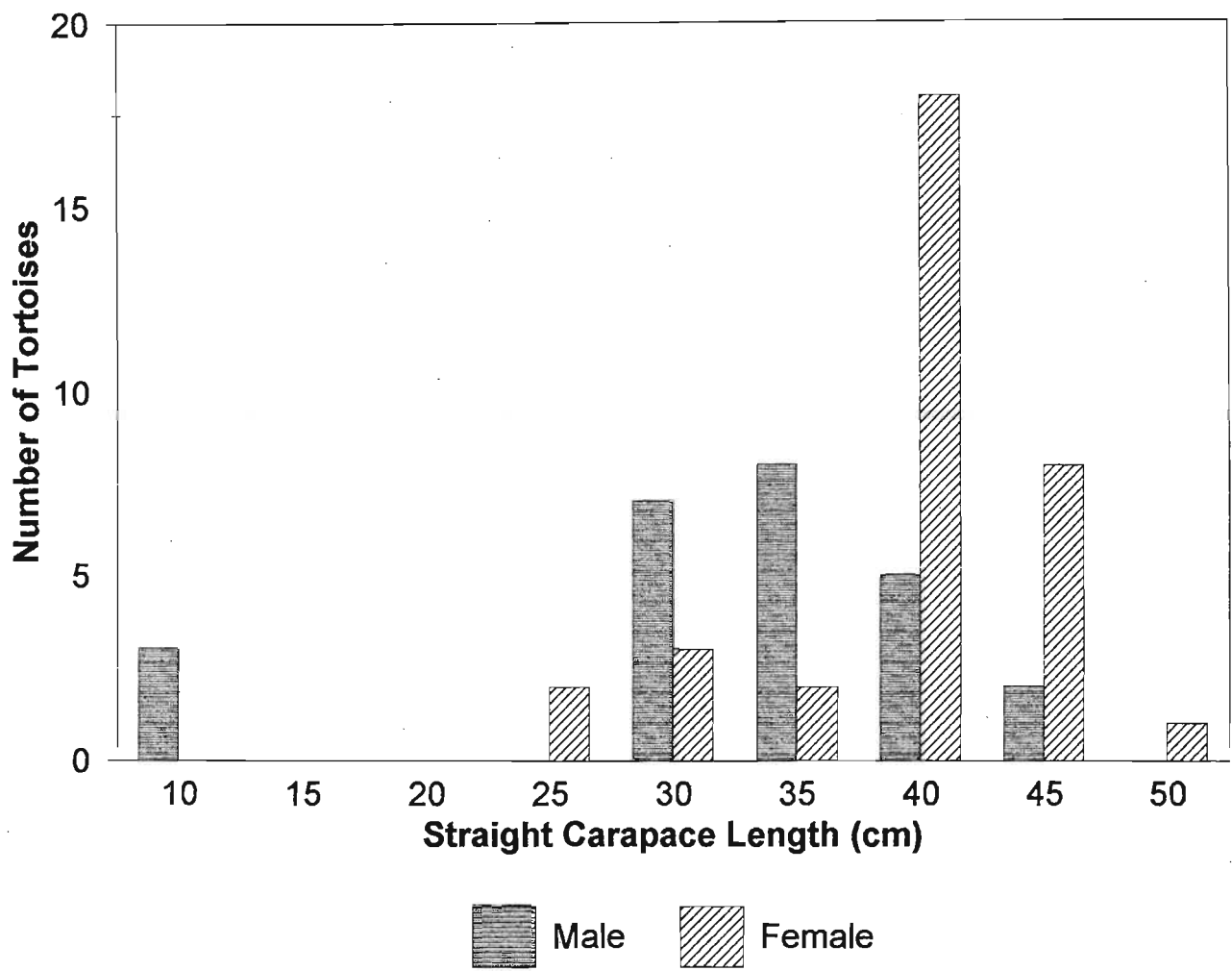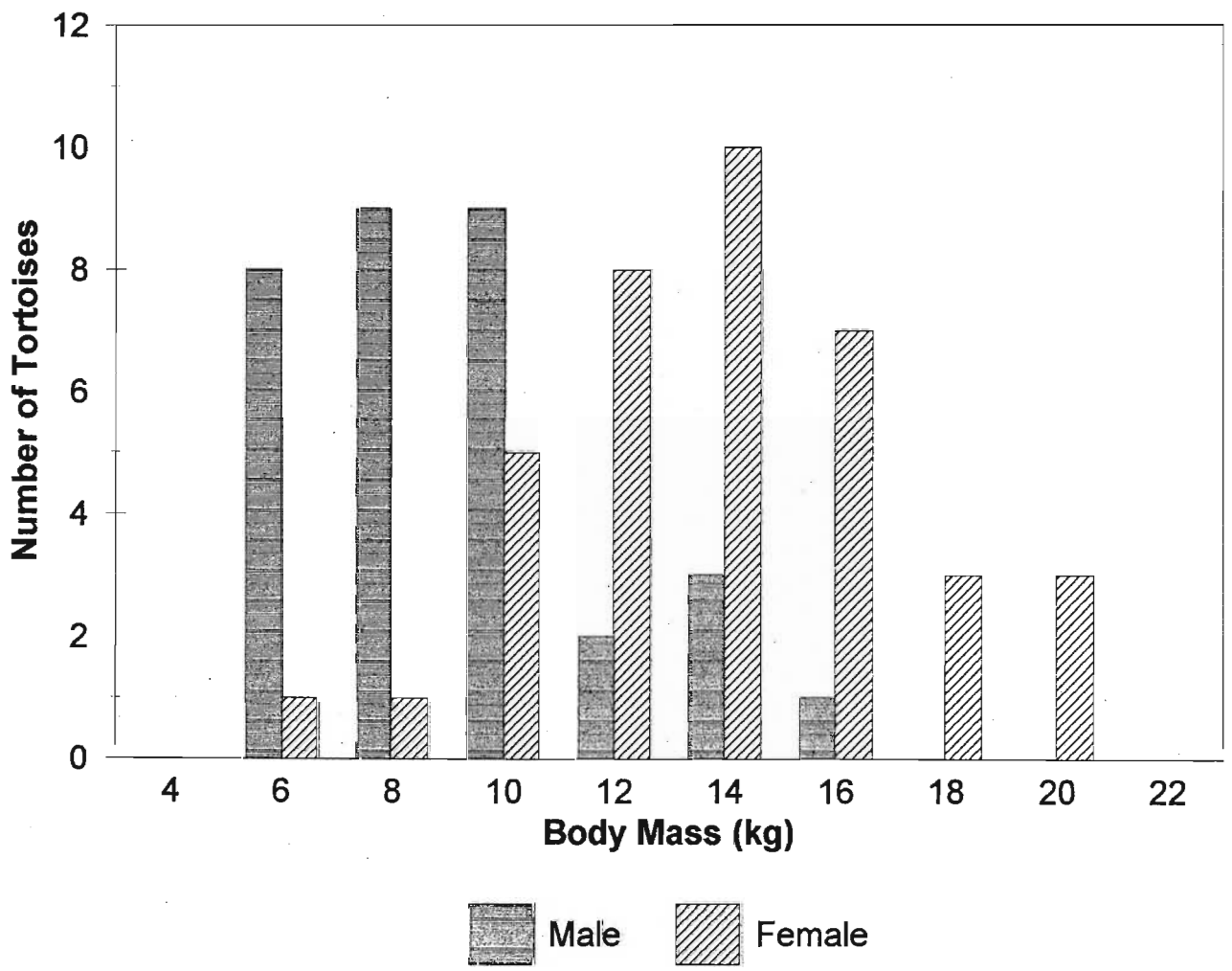
Appendix 1: Morphometric measurements taken from individual Leopard Tortoises

caught in the Nama-Karoo. Abbreviations: CCL = Curved carapace length; CCW =

Curved carapace width; CS = Carapace side; SCH = Straight Carapace Height; SCL =

Straight carapace length; SCW = Straight carapace width; FMSG = Front marginal

shield gap
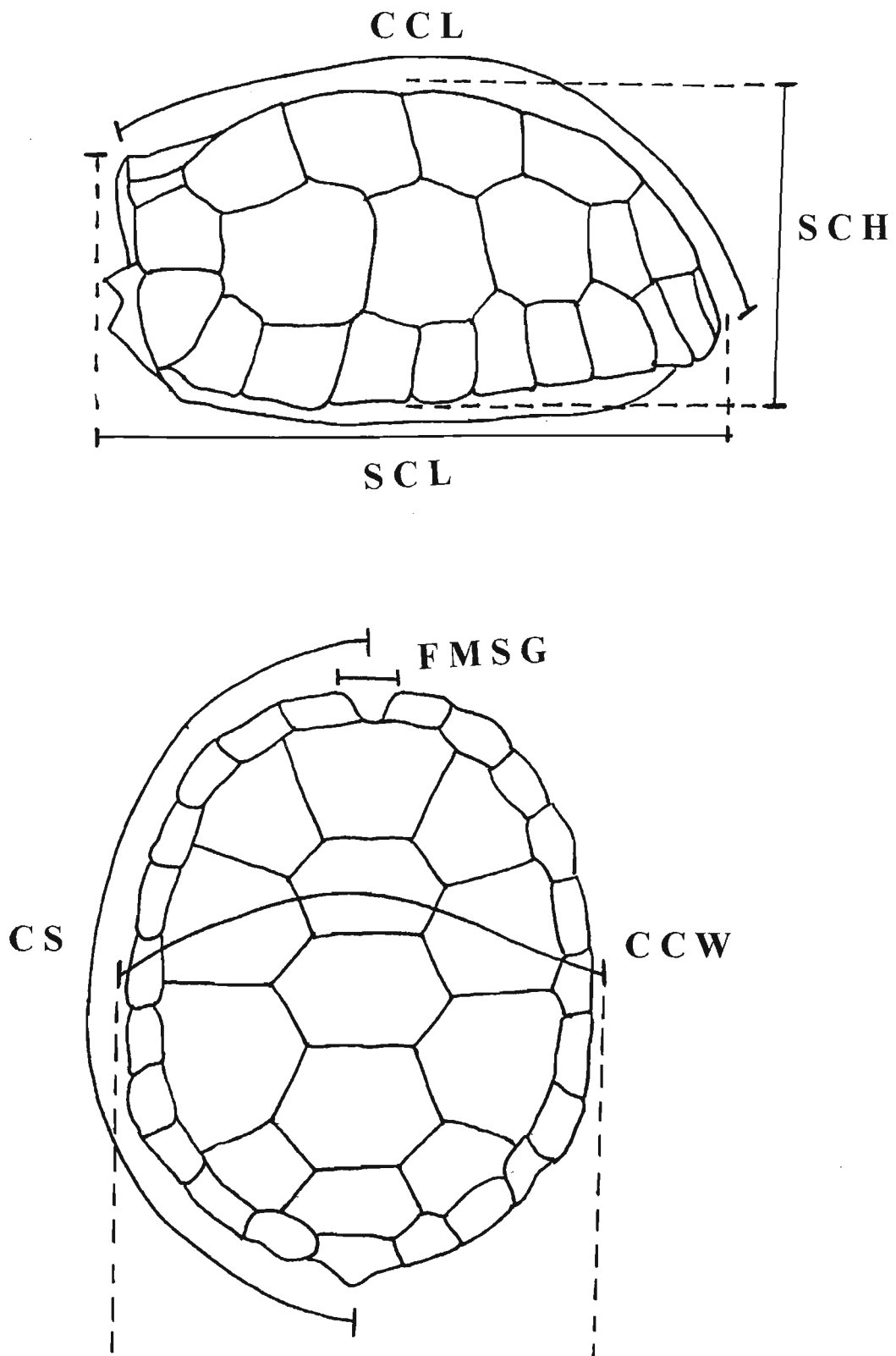
Chapter Three

Home range and Daily Movement of Leopard Tortoises (*Geochelone pardalis*) in

the Nama-Karoo

M. K. McMaster & C. T. Downs

Abstract

Knowledge of the home range size, home range overlap and seasonal change in home range is imperative to the understanding and conservation of the leopard tortoise (*Geochelone pardalis*). The leopard tortoise is the largest of southern Africa's 14 tortoise species, and occurs in a variety of habitats from arid and semi-arid areas to wetter grassveld, savannah and bushveld. Home range size, percentage overlap and mean daily distances moved were investigated in the Nama-Karoo, as a function of season, gender and body mass. Home range and movement data were calculated for 36 leopard tortoises (22 females, 14 males), 14 of which were telemetered (8 females, 6 males), and 22 of which were recaptured 10 or more times (14 females and 8 males) over a period of two years. Mean (±SE) home range size for leopard tortoises was 205.41 ± 45.57 ha. Home range size was not significantly different between males and females. Mean home range size for males was 133.27 ± 32.90 ha, and for females was 251.32 ± 70.56 ha. There was a significant difference in home range size between telemetered tortoises (413.81 ± 89.46 ha), and those recaptured 10 or more times (72.79 ± 18.89 ha). No significant relationship between home range size and body mass was found for all tortoises or between sexes. Significant seasonal and gender variation existed in the seasonal home range sizes. Females had larger home ranges in all seasons except spring. Mean daily distance moved by leopard tortoises was 136.13 ± 8.94 m with males moving further overall daily than females (males: 161.10 ± 11.8 m; females: 117.07 ± 12.87), but not significantly so. Mean daily distance moved per season was significantly different between the sexes. Females covered the largest mean daily distance in autumn and males in spring. Considerable variation existed in the amount of home range overlap both within and between sexes. Overlap percentages ranged from 5% to 90%, with home ranges most frequently overlapping by 20%. Home range size and daily distances moved by *G. pardalis* in the Nama-Karoo are larger than for leopard tortoises in other habitats.

Introduction

In order to initiate the correct conservation measures needed to protect land tortoises (Family: Testudinidae) in South African nature reserves, it is imperative to understand the size of their home ranges, the amount of home range overlap that can occur between individuals, and the change of home range in different seasons (Geffen and Mendelssohn 1988; Lambiris et al. 1989).

Tortoises are widely reported to have defined home ranges, but the home range sizes of some tortoise species have been found to be much larger than seems necessary to fulfill a tortoises' biological requirements (Geffen and Mendelssohn 1988; Bertram 1979a, 1979b; Lambiris et al. 1989). In addition, tortoises in arid areas have been reported to have larger home ranges than those tortoise species found in higher rainfall areas (Geffen and Mendelssohn 1988; Deimer 1992). This suggests that the home range size of a tortoise may be correlated with resource availability in an area, where the limiting resource may be food, water, mates, shelter or minerals (Rose and Judd 1975; Geffen and Mendelssohn 1988; Hailey and Coulson 1996).

Chelazzi and Calzolai (1986) suggested that tortoises evolved a stable home range to facilitate more efficient thermoregulation. Home range size and overlap between individuals of different sexes and ages can also give an indication of the social organisation and reproductive behaviour of a species (Geffen and Mendelssohn 1988; Els 1989; Lambiris et al. 1989; Diemer 1992).

Despite all land tortoises in South African being listed as CITES Appendix II species, very little is known about their home ranges or movement patterns (Boycott and Bourquin 2000). The leopard tortoise (*Geochelone pardalis*) is the largest of the

South African tortoises and is found in a wide variety of habitats ranging from savannah to semi-arid ecosystems (Boycott and Bourquin 2000). Daily movement distances have been investigated in *G. pardalis* in savannah grassland (Bertram 1979b) and woodland (Hailey and Coulson 1996) with preliminary estimates of their home ranges being reported in thornveld (Rall 1985) and valley bushveld (Mason and Weatherby 1995).

The aim of this study was to determine the home range sizes, home range overlap and daily movement distances of leopard tortoises in the semi-arid Nama-Karoo and to compare these with regard to seasonal differences, tortoise gender and body mass. It was expected that home range sizes would be greater in this semi-arid area compared with mesic areas.

Methods

Geochelone pardalis was studied on a 5500 ha area of a mixed commercial sheep and game farm of 26000 ha in the De Aar District, Nama-Karoo biome (31°04'S, 23°41'E). The vegetation type is classified as grassy dwarf shrubland (Palmer and Hoffman 1997). Although the area has its highest rainfall in late summer and autumn, the average annual rainfall is low (200 - 400 mm). Temperatures range from 5° to 39°C in spring and summer, and from -5° to 26°C in autumn and winter. The seasons were classified as follows: spring months were September to November; summer from December to February; autumn from March to May; winter from June to August.

Leopard tortoises were located by riding transects on horseback in the study area twice daily. Date, time, individual marking, body mass, sex and activity

behaviour were recorded for all tortoises sighted and recaptured. To facilitate location and recapture, eight female and six male tortoises were fitted with unique-frequency radio transmitters (locally made by the University of Natal Electronics Centre, powered by a lithium battery, with a ¾ wavelength stainless steel tracer wire antennae, potted in moulded PVC tubing and attached to the carapace with dental acrylic). Telemetered tortoises were tracked with Yaesu transceivers and a Yagi antenna. The geographical positions of all tortoises were recorded using a Trimble Navigation Geoexplorer II Geographical Position System (GPS). Data were then downloaded into PATHFINDER (an interface program) and the inbuilt satellite error corrected for using data available on the Internet from Telkom and Eskom, before being transferred into Geographical Information System (GIS) ARCVIEW for further analysis.

Telemetered leopard tortoises were located twice daily for three month periods from October 1997 to April 1999. The GPS position and behaviour of the tortoises were recorded on every occasion. In addition, each individual was followed for a continuous eighteen hour period once every three months, and its behaviour and GPS position recorded every 15 minutes.

Home ranges were calculated for the 14 telemetered tortoises, in addition to all tortoises that had been recaptured 10 or more times (referred to as non-telemetered tortoises). Home ranges were plotted using the minimum convex polygon method (chosen for its relative accuracy in calculating the actual size of home ranges (Rose and Judd 1975)), and the area of each polygon calculated using ARCVIEW. In addition, home ranges were calculated per telemetered tortoise for each season and further compared with regard to tortoise gender.

The overlap between tortoise home ranges was only calculated for telemetered

tortoises. The overlap between two tortoises was calculated as a percentage of the total home range of each tortoise, following Geffen and Mendelssohn (1988). Therefore there were two overlap percentages per pair of telemetered tortoises.

The daily distances moved were calculated for all telemetered tortoises using ARCVIEW, and further analysed with regard to tortoise gender and season.

All statistical tests were calculated using STATISTICA software (Statsoft, Tulsa, USA).

Results

Home ranges were calculated for 36 leopard tortoises (22 females, 14 males), 14 of which were telemetered (8 females, 6 males), and 22 of which were recaptured 10 or more times (14 females, 8 males) (see Appendices 1 & 2).

Home range sizes

The mean home range for all leopard tortoises was 205.41 ± 45.57 ha ($n = 36$), however, the frequency distribution was positively skewed with the majority of leopard tortoises having home range sizes of less than 100 ha (Figure 1a).

The home range sizes of males and females were not significantly different (ANOVA; $F = 1.62$, $p = 0.21$). The mean ($\pm$SE) home range size for males was 133.27 ± 32.90 ha ($n = 14$) and for females was 251.32 ± 70.56 ha ($n = 22$), however, the frequency distribution for both males and females was positively skewed and most tortoises had home ranges less than 100 ha (Figure 1b and 1c, respectively).

There was a significant difference between the home range sizes of leopard tortoises that were telemetered and those that were only recaptured 10 or more times

(ANOVA: $F_{1,34}$ = 20.86, p << 0.001). Telemetered leopard tortoises had a mean (±SE) home range size of 413.81 ± 89.46 ha compared to a mean (±SE) home range size of 72.79 ± 18.89 ha for recaptured tortoises. Home range frequency distributions for telemetered tortoises indicated that the majority of tortoises had home ranges between 100 to 200 ha and between 300 to 400 ha (Figure 2). Male home range sizes of telemetered tortoises were most frequently distributed between 100 to 300 ha around a mean (±SE) of 220.21 ± 49.75 ha, while the home range sizes of female telemetered leopard tortoises showed a positively skewed frequency around a mean of 559.01 ± 132.87 ha (Figure 2). There was no significant difference between the home range sizes of male and female telemetered tortoises (ANOVA: $F_{1,14}$ = 4.44, p = 0.057), but there was a trend suggesting a difference.

The mean (±SE) home range sizes of male and female leopard tortoises that were not telemetered was 68.06 ± 27.83 ha and 75.49 ± 25.81 ha, respectively. Non-telemetered tortoises (both males and females) had home ranges that were positively skewed, with most tortoises having home ranges less than 100 ha (Figure 3). There was no significant difference between the home range sizes of male and female non-telemetered leopard tortoises (ANOVA: $F_{1,22}$ = 0.34, p = 0.85).

Home Range Size and Body Mass

The body masses of both telemetered and non-telemetered leopard tortoises were normally distributed around a mean (±SE) of 11.30 ± 0.62 kg (Figure 4). There was no significant relationship between home range size and body mass for all tortoises ($F_{1,34}$ = 0.07, R^2 = 0.002, p = 0.79).

The body mass of male and female leopard tortoises were negatively skewed

around means (±SE) of 8.01 ± 0.59 kg and 13.39 ± 0.62 kg, respectively (Figure 4).

There was no significant relationship between body mass and home range size for

males or females (Males: $F_{1,12} = 0.12$, $R^2 = 0.09$, $n = 14$, $p = 0.30$; Females: $F_{1,20} =$

0.37, $R^2 = 0.02$, $p = 0.55$).

Neither the telemetered nor the recaptured leopard tortoises showed a

significant relationship between home range size and body mass ($F_{1,12} = 0.13$, $R^2 =$

0.95, $p = 0.28$; $F_{1,20} = 0.33$, $R^2 = 0.02$, $p = 0.57$, respectively).

Seasonal Differences in Home Range Size

Home range size was calculated per season for telemetered tortoises only.

Telemetered tortoises had a mean (±SE) home range of 77.66 ± 18.40 ha in spring,

271.31 ± 95.72 ha in summer, 143.60 ± 36.99 ha in autumn and 8.64 ± 3.07 ha in

winter. There was a significant difference in home range sizes between spring and

winter ($t = 3.26$, $n = 12$, $p < 0.01$), summer and winter ($t = 2.75$, $n = 12$, $p = 0.02$), and

autumn and winter ($t = 3.16$, $n = 12$, $p < 0.01$).

Seasonal and gender differences in the mean (±SE) and range of home range

sizes are shown in Table 1. Females had larger mean (±SE) home range sizes in all

seasons except spring, and had a greater range of home range sizes in all seasons

(Table 1). Tortoises of both sexes had their largest home range in summer and their

smallest in winter, with some females not moving at all in autumn and winter (Table

1). Home range sizes of male and female tortoises were significantly different (Table

1). There was a significant difference in the home range sizes of females when spring,

summer and autumn were tested against winter, and between spring and autumn

(Table 1). Similarly, male seasonal home ranges were significantly different between

winter and spring, summer and autumn (Table 1).

Home Range Overlap

Following Geffen and Mendelssohn (1988), a matrix was derived showing the percent

overlap between two telemetered tortoises taking into account the overlap as a

percentage of each tortoises' complete home range (Table 2). The amount of overlap

that two tortoises had with the rest of the telemetered tortoises was tested using a t-test

and significant differences indicated with an asterix in Table 2. Table 2 illustrates the

enormous variation in the amount of overlap between tortoises and the individual

variation in the amount of overlap. For example, Leopard Tortoise 70 and Leopard

Tortoise 7 showed a significant difference in the amount that Tortoise 70 overlapped

with all other telemetered tortoises, compared with the amount that Tortoise 7

overlapped with other tortoises (Table 2). In contrast, both Tortoise 9 and Tortoise 70

showed very little overlap with the other tortoises (Table 2).

Individual variation in the amount of overlap showed no pattern with regard to

the sex of the individual. Males and females overlapped in varying degrees to other

males and females irrespective of gender. Thus leopard tortoises in the Nama-Karoo

have defined home ranges, but do not hold or defend territories.

The mean (±SE) percentage overlap of home range for each individual with all

the others is shown in Figure 5. Certain individuals, for example Tortoises 22, 23 and

57 (all females) have very high mean (±SE) overlap, with their home ranges

overlapping more than 50% with all other home ranges (Figure 5). However, there is

no separation of males and females based on mean overlap, as some males had home

ranges that overlapped with many others (e.g. Tortoise 62), whereas some females

overlapped with very few other tortoises (e.g. Tortoise 70).

A plot of the number of times a certain percentage overlap of home range occurs, shows a positive skewness in the frequency distribution, with the greatest percent overlap of leopard tortoise home ranges occurring at 10% and 20% (Figure 6).

Daily Distances Moved

Calculations of distances moved daily were determined exclusively for telemetered tortoises. The overall mean (±SE) daily distance moved by leopard tortoises was 136.13 ± 8.94 m.day^{-1}.

Leopard tortoises in spring moved a mean (±SE) distance of 209.80 ± 29.53 m.day^{-1}, 145.37 ± 11.34 m.day^{-1} in summer, 150.19 ± 17.82 m.day^{-1} in autumn and 21.06 ± 4.12 m.day^{-1} in winter. Mean (±SE) and range differences in the daily distances moved by male and female telemetered tortoises in each season are shown in Table 3. Overall, male tortoises walked further on average than females, however, the range of distances moved by females was greater (Table 3). Male tortoises moved the greatest daily distances in spring, and then summer, with the lowest distances moved in winter (Table 3). In contrast, females moved the greatest daily distances in autumn, then summer, with the lowest distances moved in winter (Table 3). Mean daily distance moved per season was significantly different between the sexes across all seasons (Table 3).

These differences between the sexes are most likely because males are searching for mates in spring and summer, hence the greater daily distances covered in these seasons, as compared to females who moved the largest distances in autumn.

Discussion

Home Range Sizes

Leopard tortoises in this study were found to have distinct home ranges with a mean

size of 205.41 ± 45.57 ha. As expected this was much greater than the home range

size of leopard tortoises in other habitats. Leopard tortoises in savannah grassland had

a home range of 1.6 km^2 (160 ha) (Bertram 1979b), a home range of 106.4 ha in

valley bushveld (Kerley et al. 1999), and 26 ha in woodland (Hailey and Coulson

1996).

This suggests that home range size may be influenced by habitat type. Rose

and Judd (1975) suggested that home range size was larger where resources were

scarce or widely scattered. Diemer (1992) found that tortoises living in semi-arid and

arid areas have considerably larger home ranges than species living in more temperate

areas, due to habitat quality. This may explain the much larger home range size of the

Leopard Tortoises in the Nama-Karoo, a semi arid area.

There was a great range and a positively skewed distribution of home range

sizes of leopard tortoises, with most recaptures having home ranges less than 100 ha.

However, this was influenced by sample size, indicated by the significant difference in

home range sizes between telemetered and non-telemetered leopard tortoises. Non-

telemetered tortoises had home ranges under 100 ha in size, while telemetered

tortoises had a mean home range size of 413.81 ± 89.46 ha.

White and Garrot (1990) stated that a fault of estimating home range size

using minimum convex polygon method is that the more positions one records for

each tortoise (i.e. the greater the sample effort), the greater your home range will be.

While this may explain why the telemetered tortoises had larger home ranges, the home range size calculated for telemetered tortoises in this study was more accurate and realistic, as, due to the higher sampling effort, seasonal home ranges could be calculated for the telemetered tortoises.

In counter argument to this finding, Rose and Judd (1975) found that other methods of home range estimation exaggerate home range size, while the minimum convex polygon method reflects home range stability and gives a conservative estimate of real home range size. In addition, Diemer (1992) found no significant difference between telemetered and non-telemetered tortoises, and this suggests that differences in home range size in the present study is not because of differences in sample effort.

As such, home ranges that are estimated using a small number of recapture points may be highly inaccurate if home range stability is only reached with recapture sizes over 100. This is especially relevant when comparing seasonal changes in home range which leads to further inaccuracy when using small sample sizes to estimate home range size. The present study supports that telemetry as a technique gives a more accurate estimate of home range size. Seasonal differences in the capture of non-telemetered tortoises can lead to highly inaccurate home range sizes that are biased to being larger in seasons when tortoises are more active and thus recaptured more frequently. Telemetry allows for recaptures throughout the year, irrespective of whether tortoises are hibernating or not, and as such, gives much more accurate home range sizes.

No significant difference was found between male and female leopard tortoises, whether they were telemetered or not, however, home ranges were smaller

in males than in females. There was also no significant relationship between body mass and home range size, despite females being larger than males. The difference between male and female home range size appears to be highly variable between species and is often habitat specific (Hailey 1989; Diemer 1992). Male leopard tortoises in valley bushveld had home ranges that were significantly smaller than female home ranges (Mason and Weatherby 1995). Els (1989) found no significant difference between male and female home ranges of the Angulate tortoise *(Chersina angulata)*, however, Branch (1984), found that male Angulate tortoises had significantly larger home ranges than females.

Seasonal Variation in Home Range Size and Daily Distances Moved

There was large seasonal and sexual variation in home range sizes and daily distances moved. Leopard tortoises in the present study moved an average of 136.13 m.day^{-1}, males moving 161.10 m.day^{-1} and females 117.07 m.day^{-1}, as compared to leopard tortoises in valley bushveld whose males walked 92.61 m.day^{-1} and females 76.97 m.day^{-1} (Mason and Weatherby 1995). Tortoises in summer and autumn had larger home ranges than in spring and winter, however, tortoises moved the greatest daily distances in spring and autumn. Tortoises in winter (males, females and both sexes combined) had a significantly smaller home range than all the other seasons. Male and female leopard tortoises had significant differences in both home ranges and daily distances moved.

Male leopard tortoises had smaller home ranges than females in all seasons except spring. Similarly, male tortoises moved greater distances in spring and summer than females. This is similar to leopard tortoises in valley bushveld where male

leopard tortoises had smaller home ranges, but moved greater distances than females

(Mason and Weatherby 1995). The larger home range and greater distance travelled

by male leopard tortoises in spring is probably a consequence of mating activity or

males searching for mates, while females may range widely searching for nesting sites

in autumn.

Geffen and Mendelssohn (1988) found that home range use in the Egyptian

tortoise (*Testudo kleinmanni*) differed significantly between seasons, but not between

sexes. In addition, *T. kleinmanni* had the greatest mean travel distance in spring, and

the shortest in summer (Geffen and Mendelssohn 1988). Geffen and Mendelssohn

(1988) concluded that the greater male activity is because of the search for mates.

Hailey (1989) states that *T. hermanni* show a shift in seasonal home range that

is probably due to physiological reasons or food resources. Similarly, giant tortoises

(*Geochelone gigantea*), showed striking seasonal shifts in home range due to changes

in food availability (Gibson and Hamilton 1983), while Dean and Milton (1999),

stated that leopard tortoises moved from hills into valley bottoms in search of water.

Home Range Overlap

There was great individual variation in the amount of overlap that occurred in home

ranges. Leopard tortoises had distinct home ranges and therefore some individuals

would not have overlapping home ranges simply because of spatial separation.

However, individuals of different sizes and sexes had overlapping home ranges to

varying degrees across all seasons. The percentage overlap was most frequently 20%

or less, but some individual home ranges overlapped by more than 90%.

This indicates that while leopard tortoises have distinct home ranges, they do

not hold territories. Similarly, the home ranges of *T. kleinmanii* showed large percentages of overlap and indicated a lack of defence of territories and resources (Geffen and Mendelssohn 1988). Many tortoise species have been widely reported as having home ranges which are stable in time but not defended, as indicated by a large degree of overlap in home ranges (Rose and Judd 1975, Chelazzi and Calzolai 1986, Els 1989, Hailey 1989). *Gopherus polyphemus* showed sexual differences in overlap, with female home ranges not overlapping, but male home ranges overlapping with other home ranges of both sexes (Diemer 1992).

In conclusion, it was found that leopard tortoises in the semi-arid Nama-Karoo do have larger home range sizes and a greater daily movement distance than those leopard tortoises in other habitat types. There was a significant difference in the home range size of telemetered vs non-telemetered tortoises. This has implications for the accuracy of estimating home ranges using a low number of recaptures, especially with the influence of seasons on activity and thus recapture probability. In comparison to leopard tortoises in other habitats, the larger home range size used by leopard tortoises in the Nama-Karoo, in conjunction with the low density and population size (see Chapter 2), has great implications with regard to the conservation of leopard tortoises in semi-arid regions (as well as other semi-arid tortoise species). The variation in home range size both seasonally and with regard to habitat type must be taken into account when planning conservation efforts for tortoises in semi-arid areas and when planning the size of reserves.

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Gopherus berlandieri, in South Texas. Herpetologica 31: 448-456.

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List of Figures and Tables

ible 1: Differences in mean home range area (ha) between seasons and sexes of both telemetered and non-

telemetered Leopard Tortoises in the Nama-Karoo.   .

	Males					Females					
:asons	Mean	SE	Min	Max	N	Mean	SE	Min	Max	N	t
·ring	108.20	38.43	1.47	239.74	6	54.74	11.58	3.25	104.35	8	7.45***
mmer	100.37	34.47	12.63	229.53	6	417.82	159.47	45.67	1247.51	7	6.02***
ıtumn	88.99	36.11	17.98	238.29	6	190.40	57.96	0	412.47	7	6.83***
inter	4.44	2.71	0.73	12.48	4	10.73	4.33	0	36.72	8	3.01*
/erall	81.96	17.99	0.73	239.74	22	159.38	47.42	0	1247.51	30	8.46***

$< 0.01*$, $P < 0.005**$, $P < 0.0001***$

Table 2: Home range overlap matrix showing the percent overlap between two telemetered Leopard Tortoise's (*Geochelone pardalis*) home ranges in the Nama-Karoo. (* indicates $p < 0.05$ for t-tests)

	7	9	11	13	14	15	17	18	22	23	50	57	62	70
7	-	0.44*	20.11	56.10	17.8*0	3.711*	26.29*	6.67*	89.71*	100*	15.37*	69.18	65.03	0*
9	4.71*	-	0*	23.44*	0*	0*	39.86	0*	56.86*	100*	0*	0*	22.01*	0*
11	16.16	0*	-	8.34	0	41.32*	10.15	0.915	44.01*	30.04*	18.00	44.50	3.89	0*
13	90.68	3.55*	16.78	-	20.17*	1.29*	26.92*	11.83*	96.50*	99.35*	23.72*	83.47*	84.10	0*
14	44.39*	0*	0	31.12*	-	0	0.46	18.47	89.92*	64.56*	0.76	86.73*	39.31*	0*
15	4.79*	0	66.41*	1.036*	0	-	0	1.17	32.18*	8.01*	18.72	30.22*	0*	7.24*
17	36.99*	5.25*	17.78	23.44*	0.262	0	-	0	29.72*	77.70*	13.52	15.81*	34.57*	0*
18	14.95*	0*	2.55	16.39*	16.59	2.04	0	-	50.45*	65.69*	0	71.28*	69.21*	0*
22	48.59*	2.88*	29.66*	32.34*	19.53*	13.49*	11.44*	12.20*	-	75.37	9.92	69.04	41.47*	0*
23	29.93*	2.812*	11.18*	18.39*	7.75*	1.85*	16.52*	8.78*	41.65	-	5.49*	33.25	27.50*	0*
50	42.95*	0*	62.60	41.01*	0.86	40.51	26.86	0	51.19*	51.26*	-	57.80*	21.77*	0*
57	44.66	0*	35.75	33.34*	22.45*	15.10*	7.25*	20.55*	82.29	71.72	13.35*	-	45.32	0*
62	67.11	2.12*	5.00	53.70	16.27*	0*	25.35*	31.90*	79.01*	94.84*	8.04*	72.45	-	0*
70	0*	0*	0*	0*	0*	6.58*	0*	0*	0*	0*	0*	0*	0*	-

Table 3: Daily distance moved between seasons within sexes of Leopard Tortoises in the Nama-

Karoo.

Seasons	Males					Females					t
	Mean	SE	Min	Max	N	Mean	SE	Min	Max	N	
Spring	294.39	34.70	0	2315.60	180	120.75	47.53	0	7948.02	171	8.71***
Summer	144.47	13.09	0	1316.71	241	146.09	17.53	0	2578.79	302	2.64*
Autumn	128.65	19.42	0	1694.31	132	164.91	26.89	0	3170.37	193	6.63***
Winter	15.72	5.96	0	504.58	108	23.94	5.46	0	582.41	200	4.38**
Overall	161.10	11.86	0	2315.60	661	117.07	12.87	0	7948.02	866	8.33***

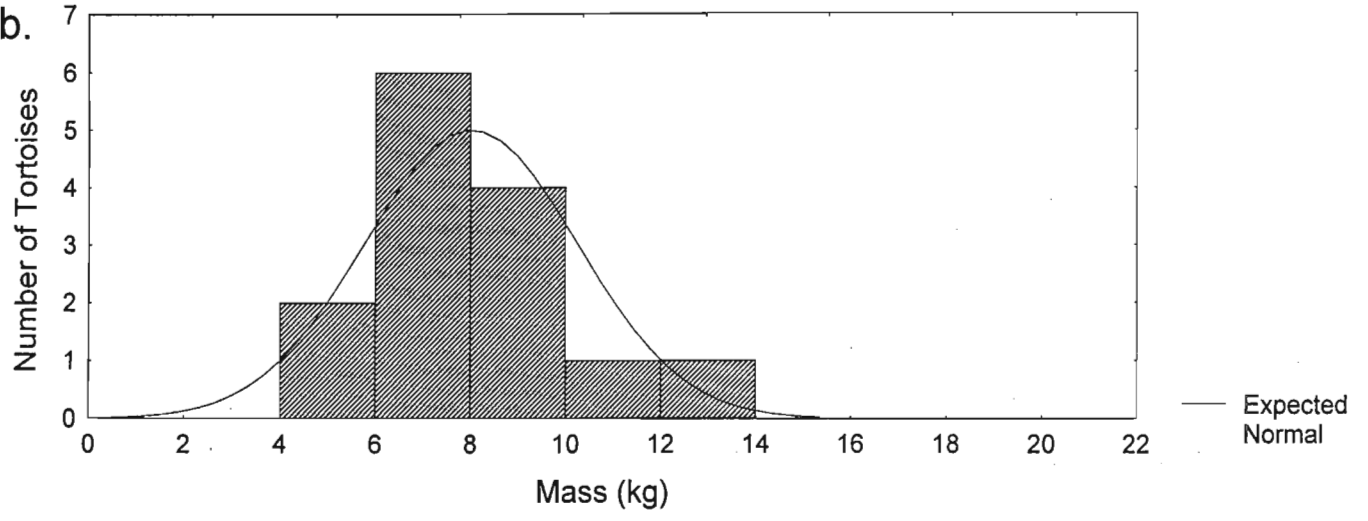$P < 0.01$*, $P < 0.005$**, $P < 0.0001$***
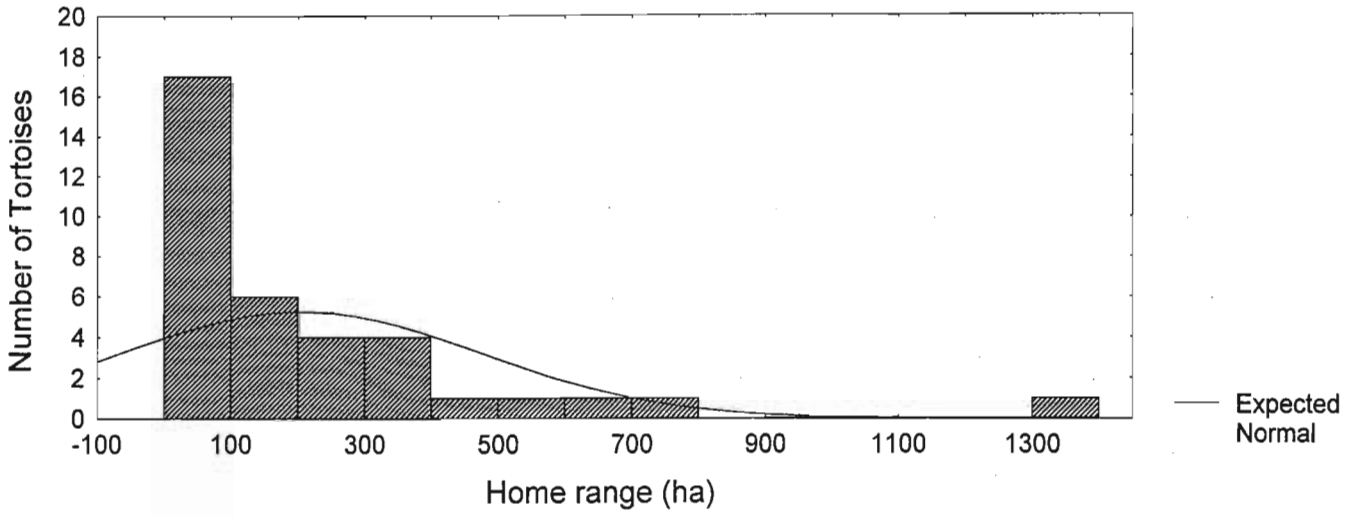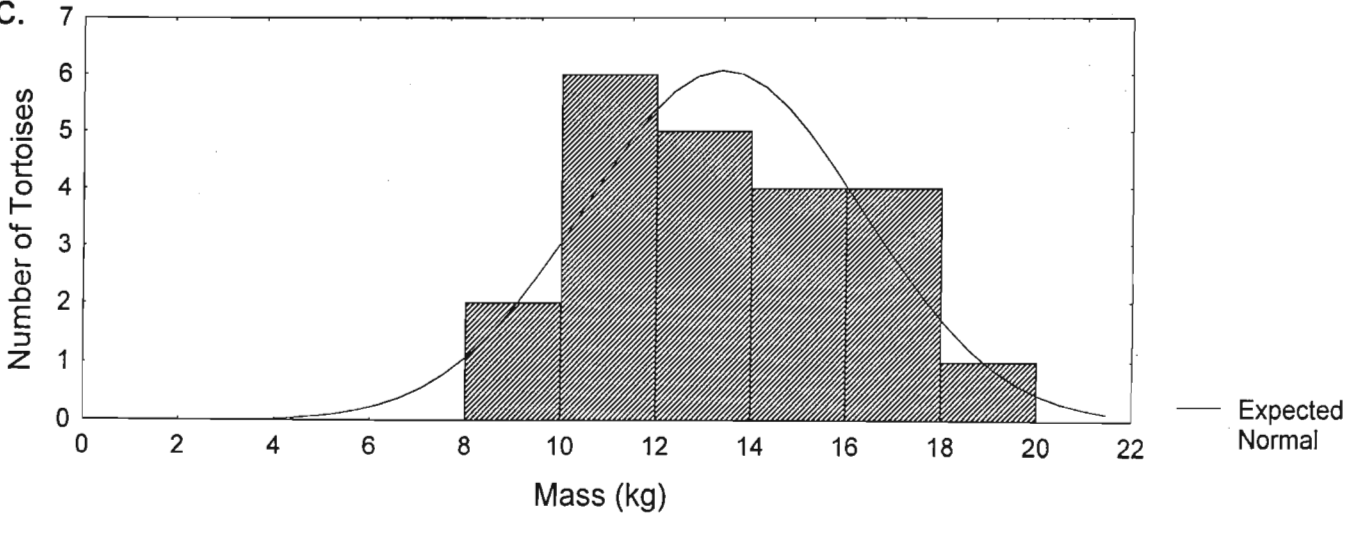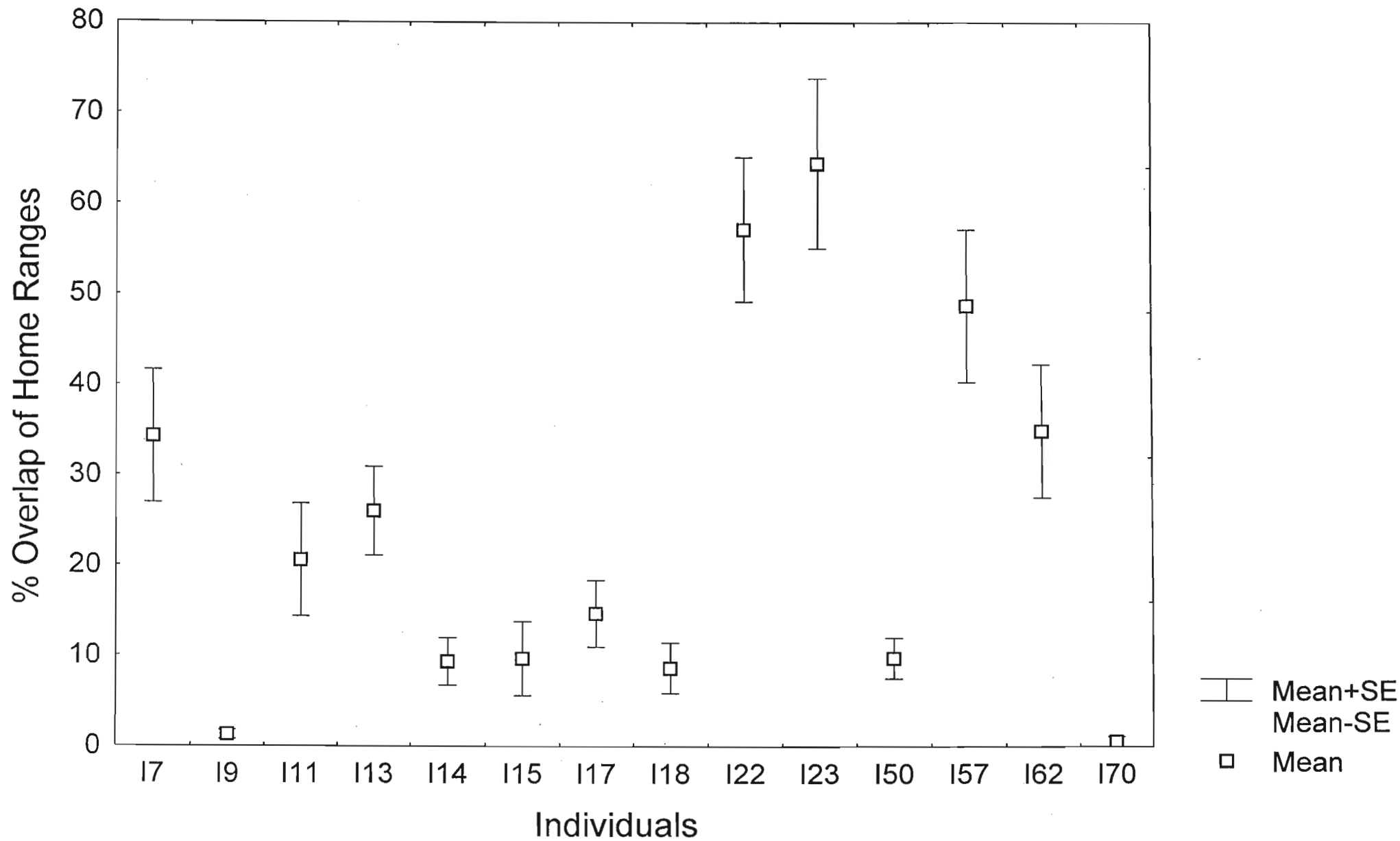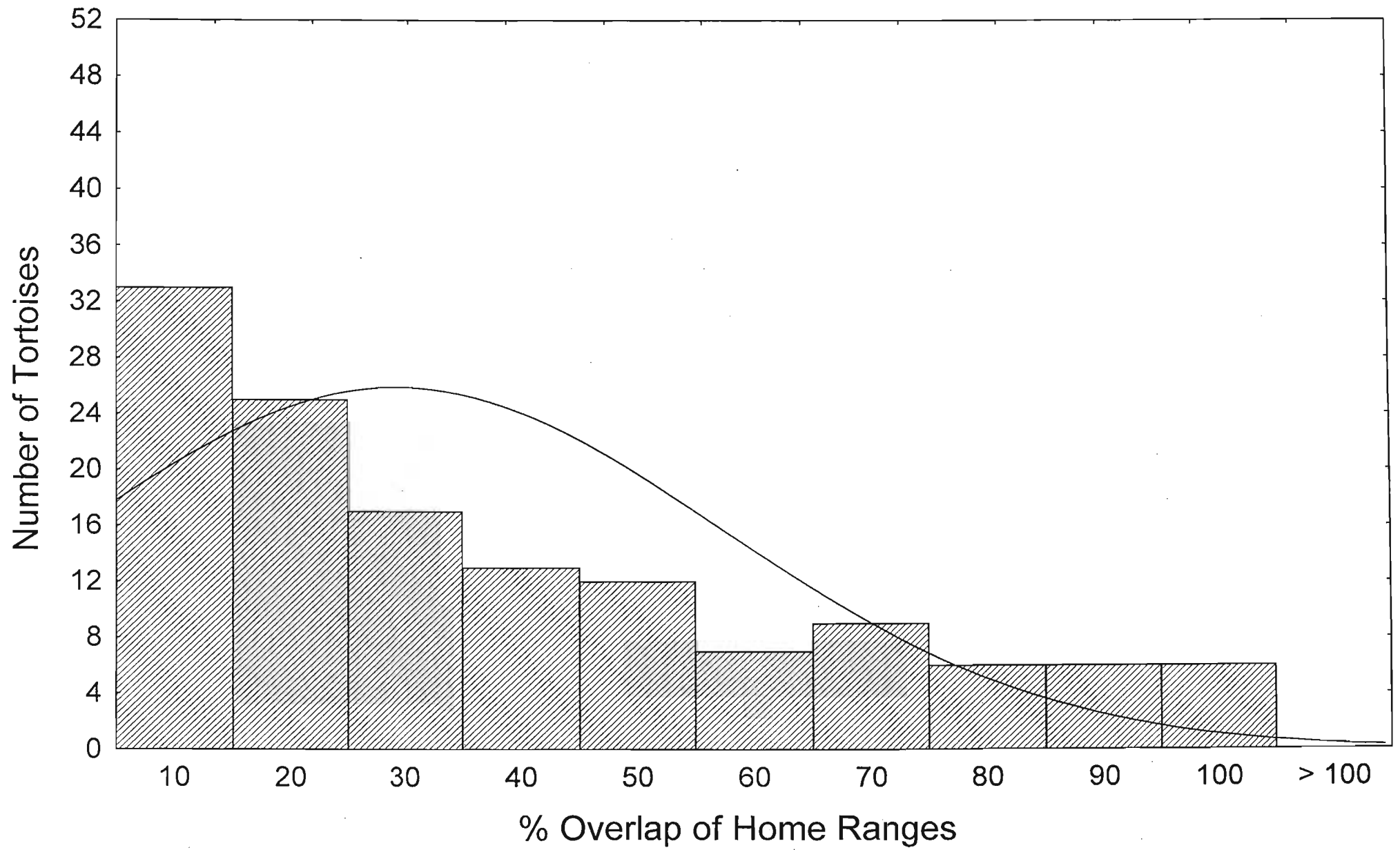
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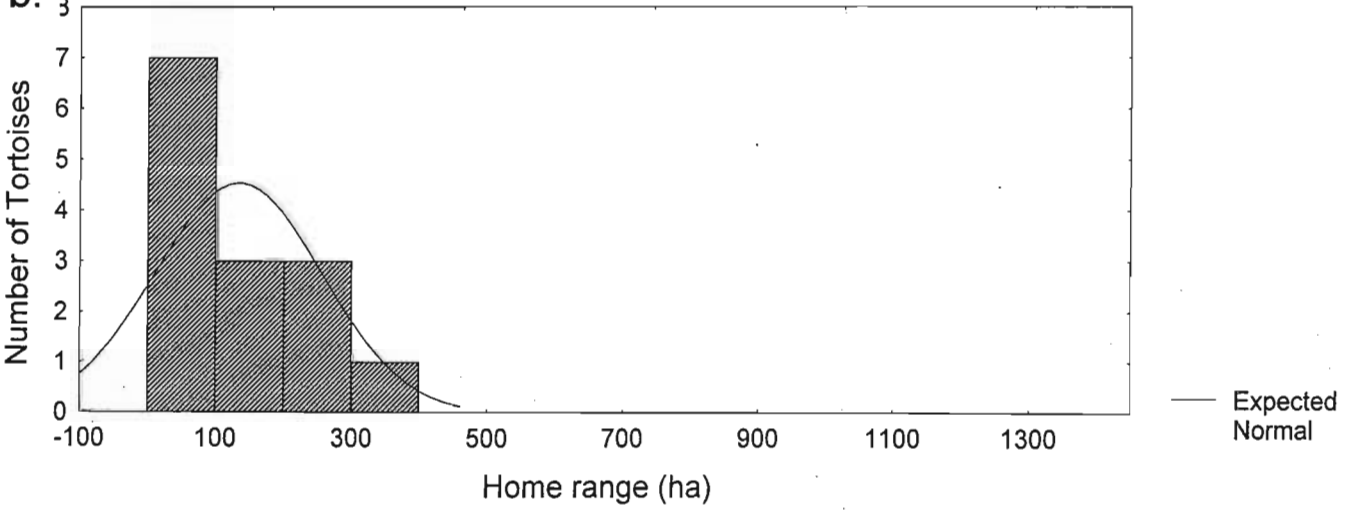
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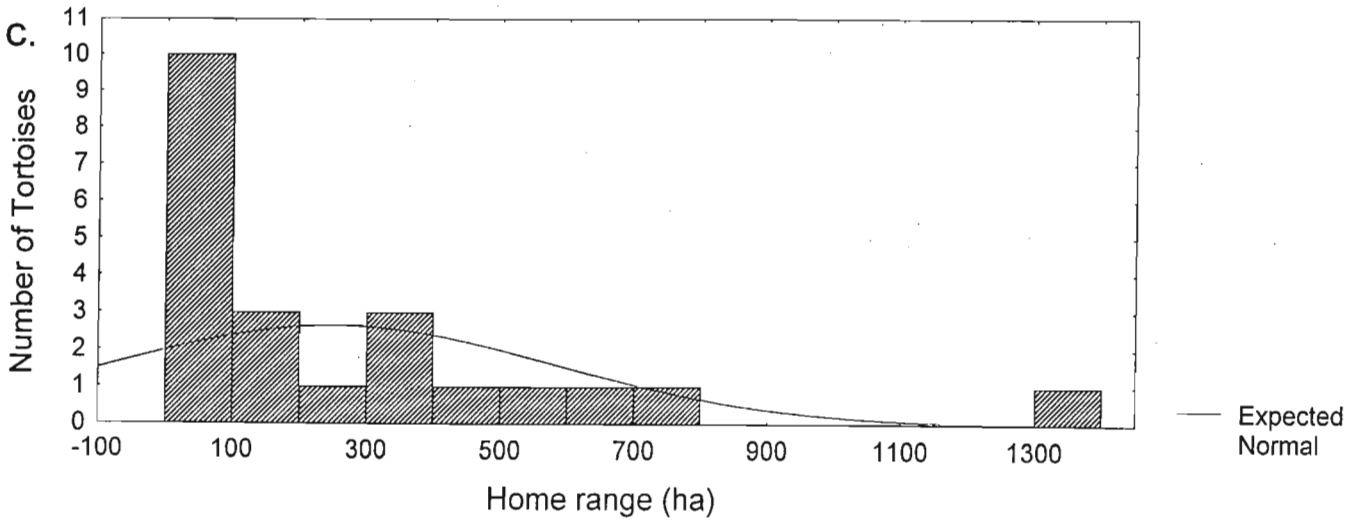
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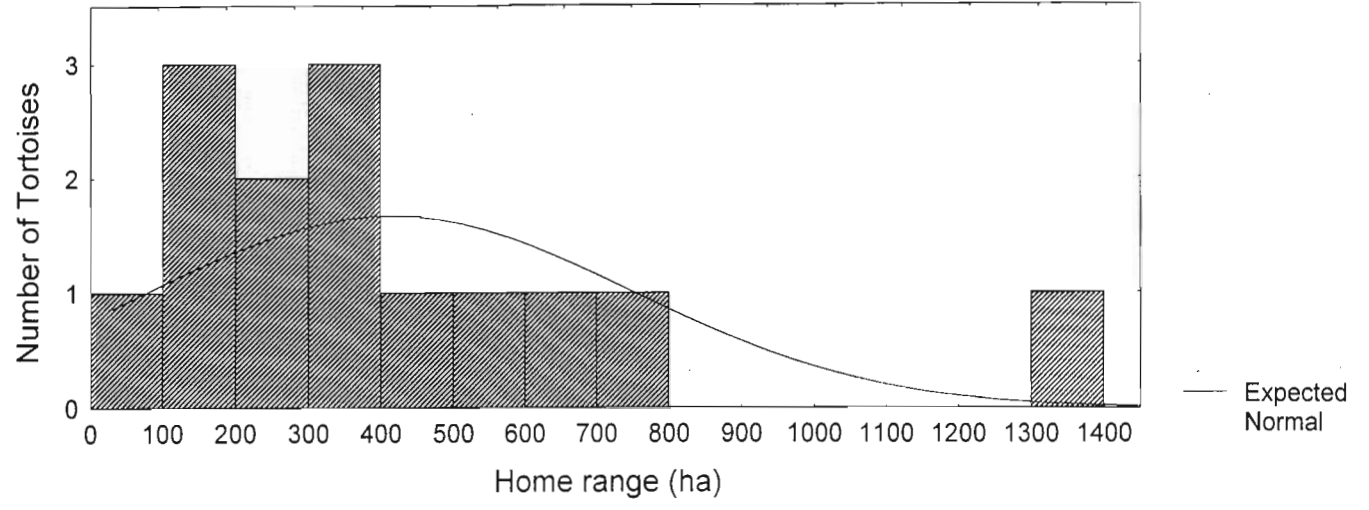
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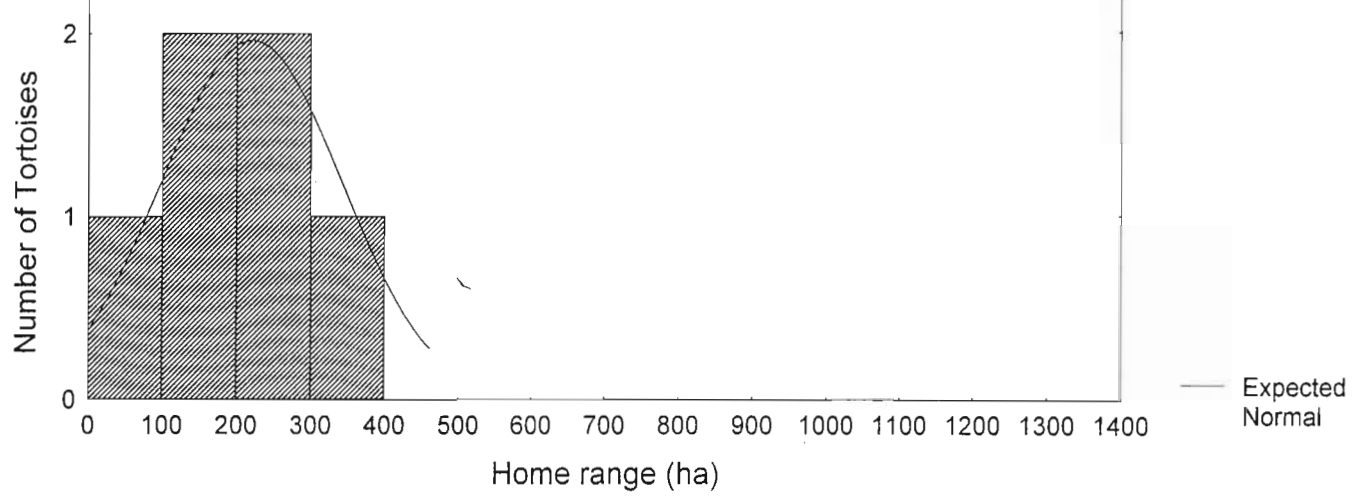
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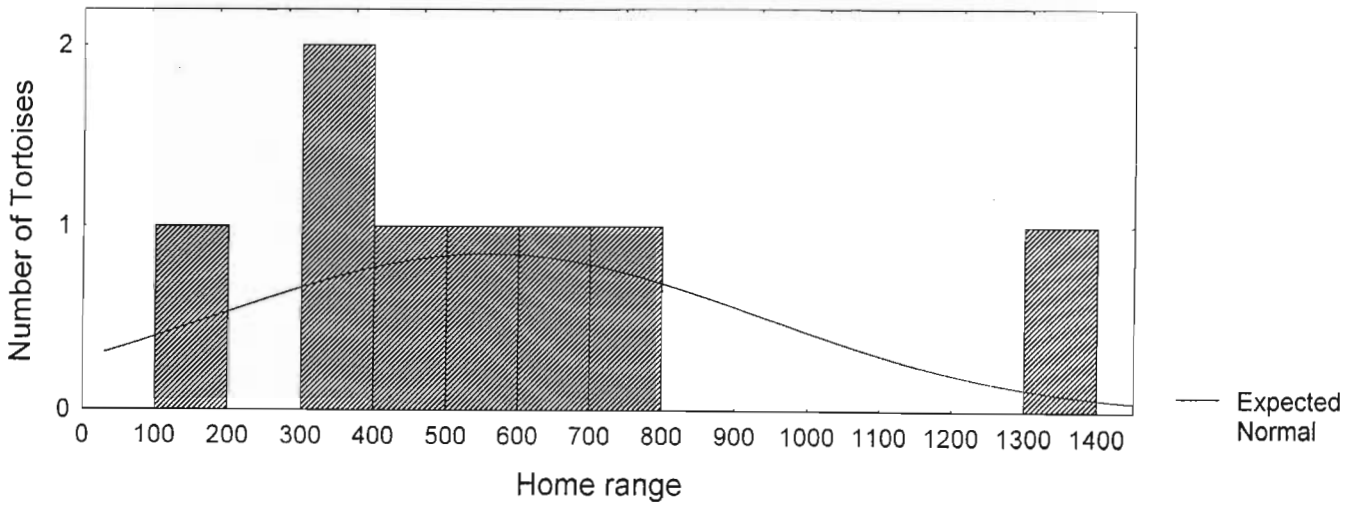
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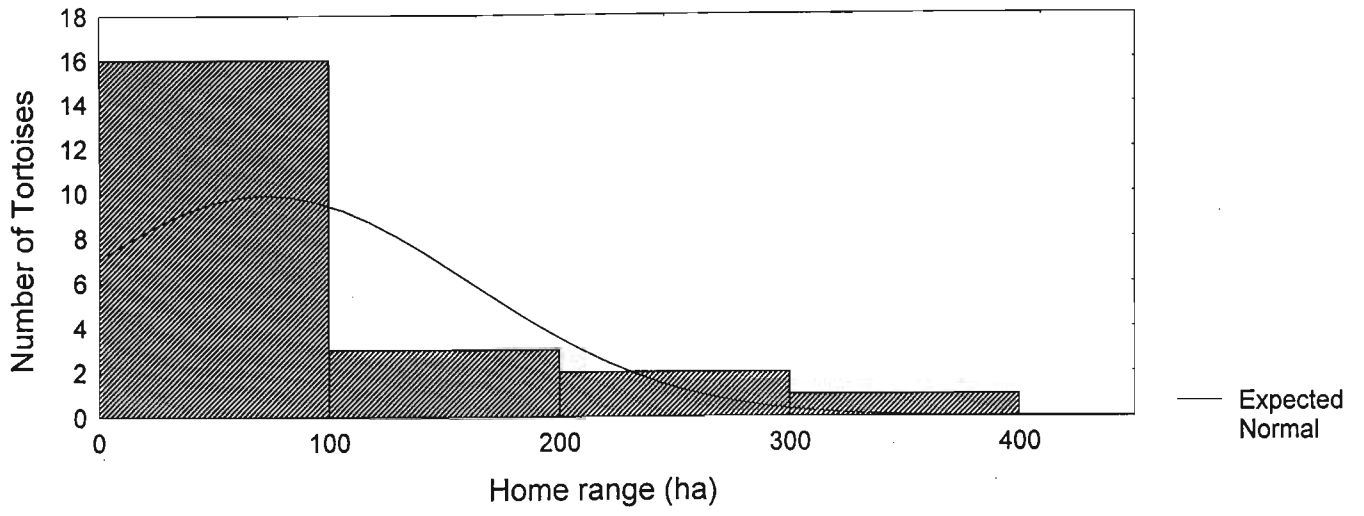
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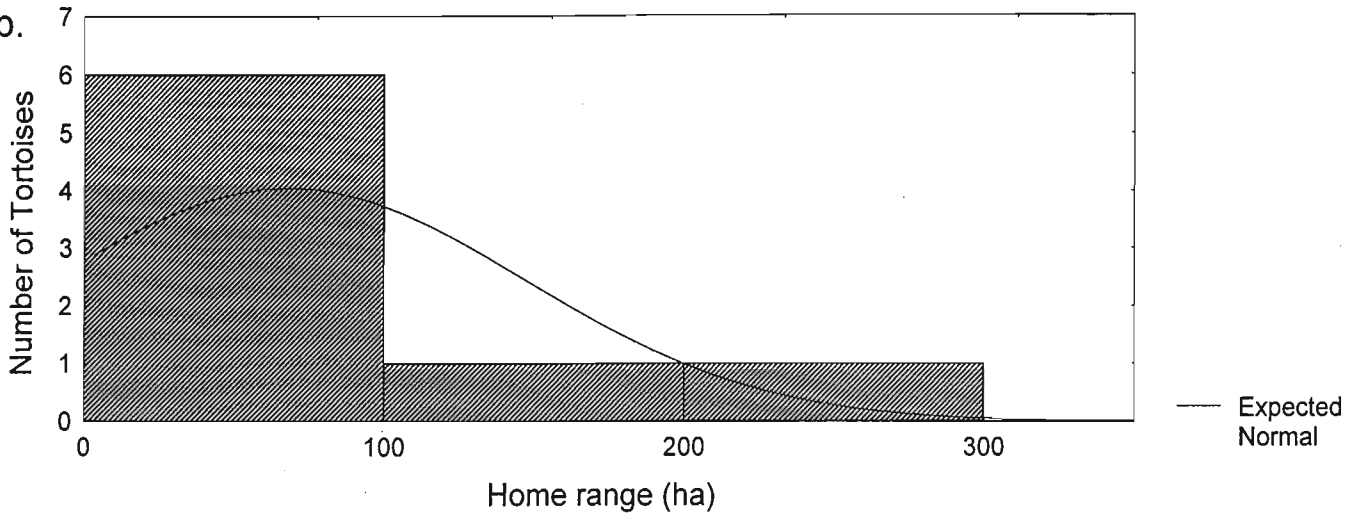
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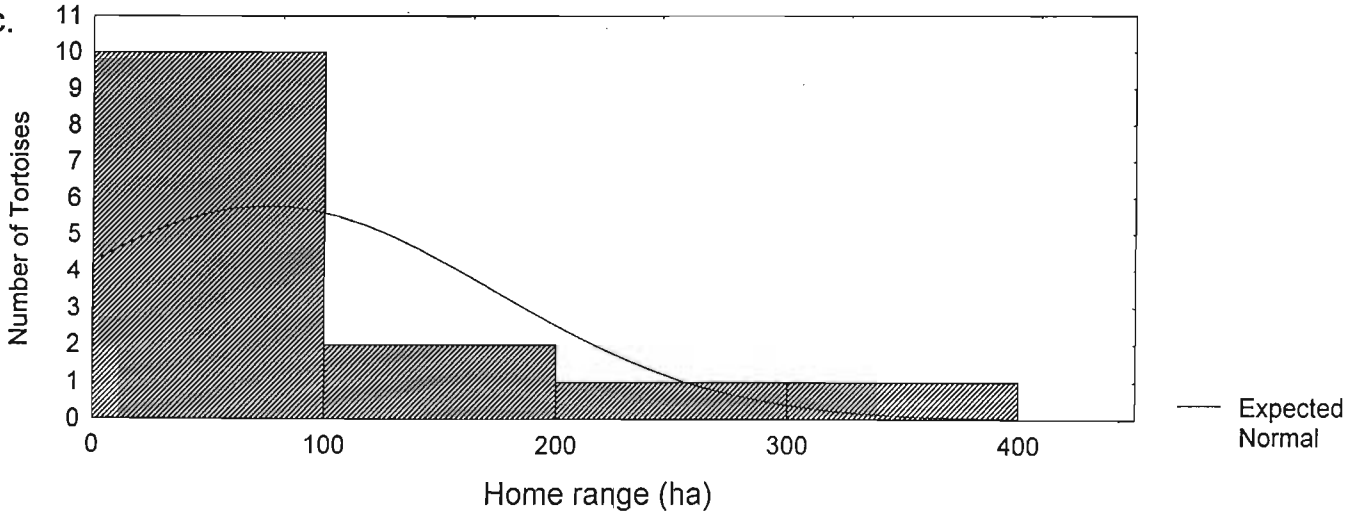
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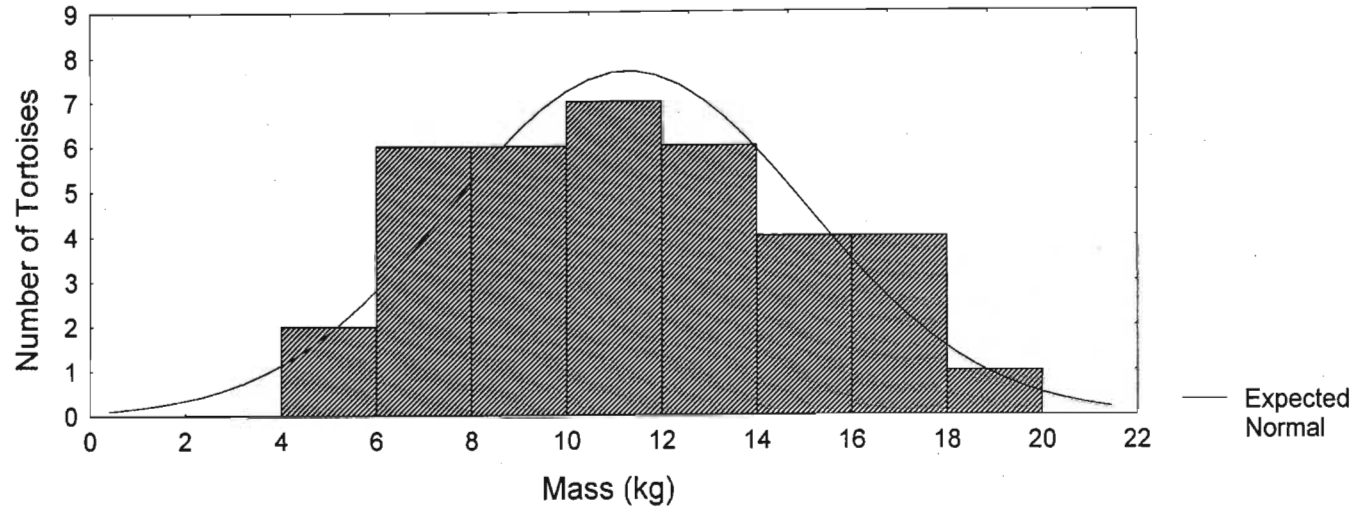
Appendix 1: Details of individual telemetered Leopard Tortoises (*Geochelone pardalis*)

Total Period Monitored: 290 days

Allocated Tortoise #	Sex 1 = Male 2 = Female	Mass (kg)	Straight Carapace Length (cm)	Total Period Monitored	Number of Relocations
7	2	13.4	43.7	280	225
9	1	6.6	35.4	279	287
11	2	10.2	42.1	276	205
13	1	7.6	39.8	274	265
14	1	8.4	40.1	274	60
15	2	17.2	48.7	274	343
17	1	7.5	44.5	271	175
18	1	8.2	41.8	271	300
22	2	14.1	43.6	268	288
23	2	10.4	27.2	268	160
50	2	9.3	40.1	247	314
57	2	15.7	45.3	232	179
62	1	6.3	35.8	219	219
70	2	13.5	41.4	202	104

Appendix 2: Details of individual non-telemetered Leopard Tortoises (*Geochelone pardalis*) recaptured >10x.

Total Period Monitored: 290 days

Allocated Tortoise #	Sex 1 = Male 2 = Female	Mass (kg)	Straight Carapace Length (cm)	Total Period Monitored	Number of Relocations
2	2	10.5	44	283	11
3	2	10	45	283	37
5	2	11.2	48	283	20
6	1	5.6	35	282	25
8	2	9.8	42	279	18
12	1	13.8	49	275	42
16	1	11	45	273	24
19	1	8.6	34	269	39
21	1	6.2	36	268	13
28	2	15.8	49.5	266	20
29	1	5.8	36	264	17
35	2	16.4	47	260	22
37	2	13.8	45	255	14
39	2	15.8	44.5	255	18
41	2	18.5	45	252	42
49	2	11.5	43	246	12
51	2	12.5	44	245	21
58	2	12.4	46	238	11
64	1	9.2	37	127	13
79	1	7.8	39	97	11
100	2	16.3	44	246	12
120	2	17.7	48	260	13

Chapter Four

Seasonal and daily activity patterns of the leopard tortoise (*Geochelone pardalis*) on farmland in the Nama-Karoo biome.

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Abstract

The Leopard Tortoise (*Geochelone pardalis*) is the largest of southern Africa's 14 tortoise species, and occurs in a variety of habitats from arid and semi-arid areas to mesic grassveld, savannah and bushveld. As part of a broader investigation into the ecology of *G. pardalis* on farmland in the Nama-Karoo biome, seasonal activity patterns of *G. pardalis* were investigated as a function of rainfall, sex, time of day, temperature and time after sunrise. It was predicted that due to seasonal rainfall, and the subsequent increase in the food available, the activity patterns of Leopard Tortoises would vary greatly between seasons, but that the primary constraint on activity levels within a season, would be ambient temperature. The type of activity, the time of day that the activity was performed, and the amount of time spent performing each activity, differed significantly between the seasons. There was no overall seasonal significant difference between the sexes in the level of activity, however, in certain seasons and with regard to specific activities, there were significant differences between the sexes. Diel activity was primarily bimodal in summer and autumn, and unimodal in winter and spring, with non-thermoregulatory activities being performed primarily in the afternoon. There was a significant positive correlation between the number of tortoises caught and rainfall per season, but activity levels and the number of tortoises walking and feeding was not correlated to seasonal rainfall. Leopard Tortoise activity behaviours responded to ambient temperature, however, results indicate that a certain activity is initiated by the time after sunrise. The response of *G. pardalis* activity to rainfall, time of day, temperature and time after sunrise, is discussed.

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Introduction

18 The Leopard Tortoise (*Geochelone pardalis*) is found in parts of central and southern Africa

in a variety of habitats including arid Karoo, Kalahari thornveld, grassveld, savanna and

20 tropical bushveld (Boycott & Bourquin, 1988). Despite the wide distribution of the Leopard

Tortoise, there is a paucity of published information regarding its ecology, physiology and

22 behaviour, with most of the studies being taxonomic, anecdotal or relating to captive

individuals (Boycott & Bourquin, 1988; Branch, 1988; Lombard, 1995).

24   Preliminary observations of field activity behaviour of *G. pardalis* during the day

(Bertram, 1979a; Rall, 1985) and over seasons (Jacobsen, 1978; Grobler, 1982; Patterson, Boycott & Morgan, 1987; Hailey & Coulson, 1996a) have been made, with one investigation of thermoregulatory behaviour in this species by Perrin & Campbell (1981).

Tortoises (Family: Testudinidae) are ectothermic and therefore their temporal and spatial activity and behavioural patterns are dependent on environmental constraints (Rose & Judd, 1975; Meek, 1984; Hailey & Coulson, 1996b). The relative importance of each of these environmental factors in determining the activity patterns of tortoises varies between species and between areas. Ambient temperature is the most well documented environmental factor influencing both the period and type of activity of tortoises, for example, the Mediterranean *Testudo spp.* (Lambert, 1981; Meek, 1984; Meek, 1988; Geffen & Mendelssohn, 1989) and *Gopherus berlandieri* in Texas (Rose & Judd, 1975). However, rainfall was the primary influence on the activity of *G. pardalis* in the Serengeti (Bertram, 1979b), and was significantly correlated with the activity of *Kinixys spekii* in Zimbabwe (Bertram, 1979a). Reduced activity during the dry season or drought may be correlated with the availability of food and water, rather than directly to rainfall or temperature (Hailey, 1989; Lambiris, Lambiris & Mather, 1989; Peterson, 1996). Cloudsley-Thompson (1970) showed a distinct "temperature-independent circadian rhythm of activity" in *Testudo sulcata* that was unaffected by photoperiod, while the primary influence on daily activity in *Testudo hermanni* was found to be habitat type (Wright, Steer & Hailey, 1988).

Hailey & Coulson (1996b) concluded that for *K. spekii* in Zimbabwe, seasonal activity was positively correlated with rainfall, but during a specific season, the level and pattern of activity was positively correlated with temperature (see also Nagy & Medica, 1986). Further influences on the type of activity and activity pattern are wind speed, cloud cover, humidity, age and sex (see Lambert, 1981; Meek, 1984; Els, 1989; Diemer, 1992).

As part of a broader ecological investigation of *G. pardalis* on farmland in the Nama-

2   Karoo biome, the aim of this study was to investigate activity behaviour as a function of

temperature, time of day, season and sex. It was predicted that due to seasonal rainfall, and

4   the subsequent increase in the food available, the activity patterns of Leopard Tortoises would

vary greatly between seasons, but that the primary environmental constraint on activity levels

6   within a season would be ambient temperature.

8   **Methods**

10   *Geochelone pardalis* was studied on a 5500 ha mixed commercial sheep and game farm of

26000 ha in the De Aar District, Nama-Karoo biome, South Africa ($31°04'S$, $23°41'E$). The

12   vegetation type is classified as grassy dwarf shrubland (Palmer & Hoffman, 1997). Dominant

shrubs include *Eriocephalus ericoides*, *Lycium spp.*, *Pentzia spp.*, and *Chrysoma ciliata*, with

14   annual grasses including *Eragrotis obtusa*, *Sporobolus spp.* and *Stipagrostis ciliata* (Palmer

& Hoffman, 1997). Seasonal mean, minimum and maximum ambient temperatures (±SE) and

16   total rainfall per season at the study site from summer 1997 to autumn 1999 are shown in

Figure 1. Although the area has its highest rainfall in late summer and autumn, the average

18   annual rainfall is low (200 - 400 mm). Temperatures range from $5°$ to $39°C$ in spring and

summer, and from $-5°$ to $26°C$ in autumn and winter. The seasons were classified as follows:

20   spring months were September to November; summer from December to February; autumn

from March to May; winter from June to August.

22   Leopard Tortoises were located by riding transects on horseback in the study area

twice daily. Date, time, individual marking, body mass, sex and type of activity were recorded

24   for all tortoises sighted. The geographical position of all tortoises was recorded using a

handheld Trimble Navigation GeoExplorer II GPS unit. In addition to spontaneous sightings,

2   eight females and six males were fitted with unique-frequency radio transmitters (see Chapter

3). Telemetered Leopard Tortoises were located twice daily for three month periods from

4   October 1997 to April 1999. The GPS position and behaviour of the tortoises were recorded

on every occasion. In addition, each individual was followed for a continuous eighteen hour

6   period once every three months, and its behaviour and GPS position recorded every 15

minutes.

8   Leopard Tortoises were classified either as inactive or active. Inactive tortoises were

those found in a refuge with their head and legs retracted into their shells. Refuges were used

10   overnight or for protection from cold weather or sun. Those tortoises that were active were

performing one of seven types of activity (following Els, 1989): i) alert: tortoise was in, or

12   just out of its form, with its head and/or legs out of its shell; ii) basking: a tortoise orientated

to expose the maximum shell surface area to the sun, often with limbs and neck extended; iii)

14   walking: tortoise actively walking in the open; v) feeding; vi) drinking; vii) shading: tortoise

is in the shade of a bush or other shelter, often with head and limbs extended; and vii)

16   courtship and mating. All ambient temperatures (T_a) are expressed as means (±SE) and were

measured to the nearest 0.5°C using a handheld thermometer in the shade 1 m above the

18   ground. All statistical tests were calculated using STATISTICA software (Statsoft, Tulsa,

USA).

20

Results

22

Daily cycles of activity and inactivity

24   Observations of Leopard Tortoise activity were made on 3955 occasions over the total search

time of 2615 man-hours. There was a significant correlation between the number of tortoises

caught per season and the total rainfall for that season ($R^2 = 0.98$, $p = 0.01$). However, there

was no significant correlation between the number of tortoises observed per month and a)

total rainfall per month ($R^2 = 0.05$, $p = 0.37$), b) mean maximum daily temperature per month

($R^2 = 0.07$, $p = 0.29$) or c) mean minimum temperature per month ($R^2 = 0.14$, $p = 0.12$).

There was also no correlation between the total rainfall per season and a) the number of

active tortoises caught per season ($R^2 = 0.52$, $p = 0.27$) or b) the number of inactive tortoises

caught per season ($R^2 = 0.59$, $p = 0.23$).

Throughout the year, Leopard Tortoises were inactive overnight, became active

following sunrise for the duration of the day, and became inactive in the late afternoon. In

autumn and winter, Leopard Tortoises became active later in the day and remained active for

shorter periods, than in spring and summer (Figure 2 & Appendix I).

There was a significant difference in the overall and the seasonal frequency of active

to inactive tortoises ($F = 22.48$, $p = 0.0004$; $F = 5.16$, $p = 0.004$, respectively). In addition, a

post-hoc Sheffe test showed there was a significant difference within each of the seasons of

spring, summer and autumn in the frequency of inactive to active tortoises (Sheffe Test: $p <$

0.001).

There was a significant difference between the sexes in the frequency of inactive to

active tortoises in spring ($t = -2.67$, $p = 0.026$), with males more active than females, but not

for any other season.

The earliest time of day that at least 75% of the tortoises observed were active

(usually alert), was 08h00 in spring (2.5 hours after mean sunrise), 06h00 in summer (57

minutes after mean sunrise), 07h00 in autumn (46 minutes after mean sunrise) and 10h00 in

winter (3.3 hours after mean sunrise) (Figure 2). The mean ambient temperatures (T_a) for

summer and autumn at these hours were $19.7 \pm 1.3°$ C and $19.5 \pm 1.3°$ C respectively, and for

winter and spring were $13.6 \pm 0.4°$ C and $15.5 \pm 0.7°C$, respectively (Appendix I). This

indicates that temperature is a primary factor influencing the onset of activity. The minimum

temperature required to initiate activity was lower in spring and winter, despite a longer time

interval (1 -2 hours) that passed after sunrise before activity was initiated.

All Leopard Tortoises observed on any day in summer were active by 08h00 (T_a =

$25.8 \pm 0.3°C$), in spring, autumn and winter by 12h00 (T_a =$24.2 \pm 0.5°C$, $T_a = 30.6 \pm 1.1°C$

and $T_a = 18.8 \pm 0.3°C$, respectively) (Figure 2; Appendix I). In autumn, 92 - 98% of Leopard

Tortoises were active from 08h00 ($T_a = 23.6 \pm 0.6°C$), until all were found active at 12h00

(Figure 2c). Thus the temperature range at which all tortoises were active was a narrow 23 -

26°C in spring summer and autumn, with winter at a slightly lower temperature.

The time and temperatures at which Leopard Tortoises returned to an inactive state

showed great seasonal variation (Figure 2). While Leopard Tortoises first became inactive at

15h00 in spring, autumn and winter and only at 19h00 in summer, the temperatures at these

times were similar for spring, summer and autumn ($T_a = 26.2 \pm 0.4°C$, $30.1 \pm 0.7°C$ & $27.8 \pm$

$1.2°C$, respectively), but were much lower for winter ($T_a = 20.2 \pm 0.4°C$) (Figure 2). All

tortoises were inactive in winter by 18h00 at a low temperature of $11.0 \pm 0.7°C$, an hour later

at 19h00 in spring and autumn at the similar temperatures of $19.0 \pm 0.8°C$ and $21.5 \pm 0.7°C$,

respectively, and at 20h00 in summer ($T_a = 26.1 \pm 0.7°C$) (Figure 2). These times

corresponded with 30 minutes, 1.5 hours, 45 minutes and 1 hour after mean sunset in spring,

autumn, winter and summer, respectively. Therefore, Leopard Tortoises seemed to respond to

a combination of decreasing ambient temperatures and decreasing light, rather than

exclusively to one or the other.

Activity Behaviour

2   The percentage of tortoises performing different activities varied both daily and seasonally. The percentage of Leopard Tortoises observed in each season as inactive or performing one

4   of seven other behaviours are shown in Table 1. Frequencies of activity behaviours performed by Leopard Tortoises per hour per season are shown in Figure 3. Percentage

6   frequency was calculated for each activity behaviour as the number of observations per hour over the total observations for the season.

8   There was a significant difference between the seasons in the frequency of tortoises performing certain activity behaviours, namely feeding (F = 8.06, p = 0.0002), drinking (F =

10   8.48, p = 0.0002), walking (F = 3.37, p = 0.028), mating (F = 11.36, p = 0.00002), alert (F = 4.84, p = 0.006), shading (F = 9.89, p = 0.00006), and inactive (F = 12.30, p = 0.000008).

12   There was no significant difference across the seasons in the frequency of tortoises found basking (F = 2.46, p = 0.07).

14   In spring, there was a significant difference between the sexes in the frequency of tortoises that were walking (t = 3.23, p = 0.008), alert (t = -3.07, p = 0.009), performing

16   thermoregulatory activities (basking and shade) (t = -2.76, p = 0.008), and non-thermoregulatory activities (walking, feeding, mating, drinking) (t = 3.066, p = 0.005).

18   In summer, there was a significant difference between the sexes in the frequency of tortoises observed alert (t = 2.70, p = 0.018), and in winter, in the frequency of tortoises observed

20   basking (t = -8.49, p = 0.000028), while there were no significant differences between the sexes in autumn activity behaviour.

22   In spring, most of the Leopard Tortoises were alert (31.5%), walking (17.8%), basking (15.8%) or inactive (14.2%) (Table 1). An unimodal pattern of activity was observed,

24   with Leopard Tortoises basking in the morning, walking from late morning through into the

late afternoon, and feeding, drinking and mating throughout the day (Figure 3a). Although

2 mating was observed in only 4.1% of all observed tortoise activity in all seasons, the highest

frequency of mating was observed in spring (Table 1).

4 After rain in late summer and autumn, a greater percentage of Leopard Tortoises were

observed feeding (28.7% and 19% respectively) and walking (15.1% and 13.2% respectively)

6 (Table 1). However, there was no significant correlation between total rainfall per season and

the frequency of tortoises observed walking ($R^2 = 0.16$, $p = 0.59$) or feeding ($R^2 = 0.46$, $p =$

8 0.32). Tortoises may therefore have increased walking and feeding activity due to the higher

food availability or simply the higher temperatures, rather then as a response to rain itself.

10 High ambient temperatures in summer resulted in a low occurrence of basking activity

(5.7%) compared with autumn (12.6%), and a large occurrence of tortoises seeking shade

12 (25.2%) compared with 19.2% in autumn (Table 1). With lower autumn temperatures,

tortoises were found alert (27%) and inactive (5.7%) more frequently than in summer (17%

14 alert and 0.7% inactive) (Table 1).

There was a distinct bimodal pattern of non - thermoregulatory activity during the day

16 in summer and autumn (Figure 3b and 3c). In summer, Leopard Tortoises were observed

feeding and walking for a limited period in the morning, sought shade from as early as 08h00

18 until as late as 18h00, and would usually resume feeding and walking only after 15h00

(Figure 3b). The majority of walking and feeding activity took place in the afternoon.

20 Similarly, in autumn, Leopard Tortoises were primarily found alert or basking in the

morning, were observed walking and feeding in the late morning, sought shade from 09h00

22 over midday (some staying in the shade until as late as 17h00), with most walking and

feeding to a greater extent after 15h00 (Figure 3c). Drinking was observed primarily in

24 summer, occurring throughout the day and increasing from midday into the late afternoon,

while mating was observed in the morning and late afternoon (Figure 3b).

In winter, the majority of tortoises were found either inactive (33.8%) or alert (46.6%), while basking was displayed by 15.6 % of the tortoises and walking by 3.2% (Table 1). Tortoises were unimodal in activity and mainly performed thermoregulatory activity, being found inactive until midday, and alert or basking throughout the day (Figure 3d). No tortoises in winter were observed mating, drinking or seeking shade.

Initiation of Activity Behaviours

To determine what initiates the onset of an activity, the time of day, temperature and time after sunrise at which Leopard tortoises were first observed performing an activity, were compared over the seasons.

The time of day appeared to have an influence on the initiation of activity (Figure 4). Leopard Tortoises in spring and summer initiated their activities at the same times, except tortoises in summer started basking and drinking before those in spring (Figure 4). Leopard tortoises in winter and autumn were initially alert at the same time (07h00), but other activity behaviours in autumn were initiated an hour earlier than those in winter (Figure 4).

Within a season, tortoises progressively changed their activity behaviour with each passing hour, becoming alert first, then basking until body temperatures were sufficiently high to allow for non-thermoregulatory activities (Figure 4). Once temperatures were too warm, shade was sought. In winter, for example, tortoises showed a strong correlation of activity with time, becoming alert at 07h00, basking by 08h00, walking by 09h00 and feeding by 11h00 (Figure 4). This progressive change in activity types at hourly intervals may be related to temperature or it may be a response to light intensity measurable by taking the number of hours after sunrise.

The temperature corresponding to the first time an activity was observed was plotted

against each activity for each season (Figure 5a). In summer and autumn, tortoises initially

performed all their activities at the same ambient temperatures except for drinking (tortoises

in summer drank at slightly lower temperatures) (Figure 5a). Some Leopard Tortoises

commenced being alert and basking from 19.5°C, started walking and feeding from 24°C,

sought shade and mated from 26°C, and then drank from 24°C and 26°C in summer and

autumn respectively (Figure 5a). This indicates a relationship between the onset of different

activity behaviours and ambient temperature, irrespective of seasonal temperatures.

However, in winter and spring, Leopard Tortoises initiated all their activity behaviours at

temperatures below 20°C, becoming alert at temperatures just above 5°C (Figure 5a).

Tortoises in winter started to bask at just below, and walk at just above, 10°C, while initially

feeding at 15°C (Figure 5a). Tortoises in spring started basking, walking and feeding by

13°C, sought shade and mated by 15.5°C, and were first found drinking at 19°C (Figure 5a).

Therefore, although activity was initiated at similar temperatures in summer and

autumn, and at similar temperatures in winter and spring, the ambient temperatures at which

activity commenced were lower in winter and spring than those in summer and autumn.

Examination of Figure 4 & 5a together, shows that the time of day at which activity

was initiated in spring was the same in summer, despite the much lower temperatures in

spring. Similarly, although the temperatures for activity initiation in autumn were the same as

summer (Figure 5a), the time of day at which these temperatures were reached in autumn was

an hour after that in summer (Figure 4). Therefore it was not exclusively time nor

temperature which initiated activity behaviours.

The majority of Leopard Tortoises (70% or more) were active at higher temperatures,

and showed greater seasonal variation in their behavioural response to ambient temperature

(Figure 5b). The majority of tortoises in spring, summer and autumn were active between ambient temperatures of 19-34°C, and in winter at a much lower range of 15-21°C (Figure 5b). Tortoises in summer sought shade, mated and drank at lower ambient temperatures than those in autumn (Figure 5b). A general variation of ± 3° C is found between the seasons for each activity (Figure 5b). Spring and summer differed consistently by 5°C in the ambient temperatures to which Leopard Tortoises responded (Figure 5b).

The time between the mean sunrise and the onset of each activity of Leopard Tortoises was compared for all seasons as an indication of whether tortoises were responding to photoperiod (Figure 6). For most of the activity behaviours (alert, basking, walking, shading), the time after sunrise before the activity was first observed, showed a variation of less than half an hour irrespective of the season involved (Figure 6). In addition, the progression from one activity to the next was consistently in hourly periods for all the seasons (Figure 6). Some variation from this trend occurred in winter, when tortoises initiated walking four hours after sunrise, compared to 1-2 hours in spring, summer and autumn, and with the onset of mating and drinking in spring, summer and autumn which varied over a 2 hour period (Figure 6). The low seasonal variation between the onset of activity behaviours and the time after sunrise, suggests that Leopard Tortoises were responding to photoperiod, triggered by the time after sunrise, to initiate activity.

Discussion

Daily cycles of activity and inactivity

In the present study, the number of Leopard Tortoises caught per season showed a significant positive correlation with total seasonal rainfall. However, in the Serengeti, 91% of all

Leopard Tortoises were caught during the wet season, although this was partly due to tortoises being more visible and easier to find when walking (Bertram, 1979b).

There was no correlation between the number of Leopard tortoises caught per month and the monthly rainfall, monthly minimum or monthly maximum temperatures. Similarly, Geffen & Mendelssohn (1989) found no correlation existed between the number of Egyptian Tortoises (*Testudo kleinmanni*) caught per month and either monthly rainfall, rainfall from the previous month or humidity (Geffen & Mendelssohn, 1989). In addition, Bertram (1979a), found no correlation between the mean daily distance traveled per month (a measure of activity) by *Kinixys belliana,* and total rainfall in that month, mean maximum temperatures, humidity levels, number of rainy days or rainfall from previous months. Monthly sightings of *K. spekii* were correlated with rainfall, but not temperature or humidity (Hailey & Coulson, 1996b).

Leopard tortoises showed no correlation between seasonal rainfall and either activity or inactivity respectively. Increased activity at the actual time of rainfall and within the same month of rainfall, has been recorded in many tortoise species, for example, *T. kleinmanni* (Geffen & Mendelssohn, 1989), *Gopherus agassizii* (Nagy & Medica, 1986), *K. spekii* (Lambiris, Lambiris & Mather, 1989) and Leopard Tortoises (Patterson, Boycott & Morgan, 1989). However, Hailey & Coulson (1996b) proposed that changes in activity associated with rainfall may also be accounted for by the lower maximum temperatures occurring during rain.

The duration and intensity of daily activity of Leopard Tortoises increased in summer and autumn, and there was a significant increase in summer and autumn in the frequency that they were active. Many tortoise species, for example, *K. belliana, G. berlandieri* and *T. kleinmanni*, alter their daily activity periods in response to seasonal changes, becoming active earlier and staying active later in the day under hot conditions (Rose & Judd, 1975; Bertram,

1979a; Meek, 1988; Geffen & Mendelssohn, 1989), and show a reduction in activity during winter months (Hailey, Pulford & Stubbs, 1984; Els, 1989; Diemer, 1992, Hailey & Coulson, 1996b). *Testudo hermanni* has a highly significant variation in activity between months (Hailey, 1989), while *K. spekii* used changes in daily activity patterns as a primary thermoregulatory mechanism (Hailey & Coulson, 1996c).

Only in spring was there a significant difference between the sexes of Leopard Tortoises in the frequency of activity compared with inactivity. *Testudo hermanni* showed no significant differences between the activity levels of the sexes in any month (Hailey, 1989), however sex ratios at two different study sites varied seasonally, suggesting that seasonal differences in activity of the sexes may occur (Hailey, Pulford & Stubbs, 1984).

Leopard Tortoise activity was initiated when ambient temperatures reached 19.5 - 20°C in summer and autumn, and 13.5 - 15.5°C in spring and winter. Thus, the initiation of activity responds to two narrow ranges of temperatures, these being much lower in winter and spring. As a comparison, in spring and summer, *Testudo graeca* were found active at ambient temperatures of 18° - 32°C, primarily between 12h00 - 16h00, with activity being initiated below 23°C and before 12h00 (Lambert, 1981). Despite differences in the actual time (before 12h00) at which all the Leopard Tortoises were active, the ambient temperatures were between 18 - 26°C. Similarly, *T. kleinmanni* were found active at a wide range of temperatures from 17 - 45°C, but 52% were active between 21 - 24°C (Geffen & Mendelssohn, 1989).

The environmental cues that initiated inactivity are clearly complex, as Leopard Tortoises did not seem to respond exclusively to either decreasing temperature or decreasing light, but rather the combination of both. Similarly, *T. graeca* were active at ambient temperatures of 18-32°C between 08h34 and 18h31, however, few tortoises were still active

during the 1.5 hours before sunset, and their activity depended not only on the ambient

2   temperature, but also the time of day at which that ambient temperature was reached

(Lambert, 1981).

4

Activity Behaviour

6   There were notable differences between seasons in the type, duration and time of day that

activity behaviours were performed by Leopard Tortoises. The frequency of Leopard

8   Tortoises performing all activities (except basking) were significantly different between

seasons. Tortoises have been widely reported to show a high seasonal variation in activity

10   patterns (Geffen & Mendelssohn 1989; Hailey, 1989; Lambiris, Lambiris & Mather, 1989).

Basking was performed by Leopard Tortoises at a similar frequency in spring, autumn

12   and winter, but at a much lower frequency in summer. High summer ambient temperatures

reduced the basking activity of *T. hermanni*, allowing for increased time available for

14   locomotory activity and feeding (Meek, 1984; Meek, 1988).

The sexes of Leopard Tortoises showed a significant difference in the frequency of

16   those in a) spring: found walking, alert, performing thermoregulatory activities (basking and

shade), and performing non-thermoregulatory activities (walking, feeding, mating), b)

18   summer: found alert, and c) winter: found basking. Female Leopard Tortoises are much larger

in size and weight than males (see Chapter 2), implying a smaller surface to volume ratio in

20   females, which would result in differences between the sexes in both thermoregulatory and

non-thermoregulatory activity patterns. In particular, Perrin & Campbell (1981) found that

22   with increasing size, *G. pardalis* has less physiological control of heat flux. *Testudo*

hermanni displayed seasonal differences in body temperatures between the sexes, with

24   females having lower body temperatures than males or juveniles (Meek, 1988). Meek (1988)

suggested that this was due to a thermal lag caused by the large body size of *T. hermanni*

2 females. Female Leopard Tortoises may therefore have an increased basking time, especially

in winter, due to their larger size. In addition to the thermal implications of differing size

4 between the sexes, activity patterns can also be affected by reproductive behaviour, for

example, males searching for females (Lambert, 1981), females searching for nesting sites

6 (Diemer, 1992) or females having increased feeding rates to increase energy uptake for egg

production (Meek, 1988).

8   Differences in activity patterns of Leopard Tortoises across the seasons were found on

a daily basis in the types and frequency of behaviours that were performed. In spring and

10 winter, a unimodal pattern of activity emerged as Leopard Tortoises became active late in the

morning, basked throughout the morning, and performed non-thermoregulatory activities,

12 such as walking and mating, over midday and into the late afternoon. Similarly, *T. hermanni*

adopted a unimodal activity pattern in spring, basking for most of the morning, walking from

14 midday and feeding in the afternoon (Meek, 1984). If temperatures were too low, Leopard

Tortoises remained alert in a refuge throughout the day, or basked for extended periods.

16 Similarly, when temperatures dropped too low, *Chersina angulata* returned to an inactive

state within a refuge (Craig, 1973).

18   While Leopard Tortoises remained active throughout the day in summer and autumn,

a bimodal pattern of non-thermoregulatory activity was followed. In these warmer seasons,

20 basking was limited to a small period of time early in the morning, and Leopard Tortoises

were observed walking and feeding early in the day, and again, to a greater degree, in the late

22 afternoon. Leopard Tortoises sought shade from midmorning until late afternoon, to prevent

overheating. Mating and drinking also followed a bimodal pattern, but were more common in

24 the afternoon. *Testudo hermanni* followed a similar activity pattern in summer, basking in the

early morning, feeding and mating both in the morning and the afternoon, and seeking shade over midday (Meek, 1988). In contrast, however, *T. hermanni* showed a unimodal pattern of activity in autumn, spending most of the day basking and only feeding in the afternoon (Meek, 1988).

A bimodal pattern of activity under warm conditions, and a switch to a unimodal activity pattern in cooler seasons, is well documented for tortoises (Rose & Judd, 1975; Hailey, Pulford & Stubbs, 1984; Hailey & Coulson, 1996b; Cloudsley-Thompson, 1970). Meek (1988) found that high summer temperatures reduced the basking frequency of *T. hermanni* and increased the time available for foraging, however, high temperatures restricted the activity period of *T. kleinmanni* before shade had to be sought (Geffen & Mendelssohn, 1989). Meek (1984) noted that the temperature range over which locomotion, feeding and mating can occur is very narrow compared to the temperature window over which basking, shading and other thermoregulatory activities can be performed. Thus while Leopard Tortoises may be alert or basking at low temperatures, they cannot become active until a certain temperature range has been reached, and ambient temperatures above that range will cause tortoises to seek shade to avoid overheating.

The higher frequency of Leopard Tortoises performing non-thermoregulatory activities in the afternoon, was also found in *G. berlandieri,* and was thought by Rose & Judd (1975) to prevent overheating. Similarly, *Testudo* spp. spent more time avoiding the midday heat than they do basking to raise their temperature in the morning (Wright, Steer & Hailey, 1988).

Generally, it appears that tortoises are more active in the late afternoon where temperatures are still high enough to allow for activity, but are decreasing as time passes, thus allowing them to be safely out walking and feeding without the threat of overheating. In

contrast though, *K. belliana* and the Giant Tortoise *Geochelone gigantea* were more active early in the morning than late in the afternoon (Bertram, 1979a; Gibson & Hamilton, 1983).

When daily ambient temperatures are consistently high for the whole season, for example in the Nevada and Negev deserts, tortoises *G. agassizii* and *Testudo* spp. completely reverse their seasonal activity patterns and have their main activity period during winter and spring, while aestivating through summer (Nagy & Medica, 1986; Geffen & Mendelssohn, 1989). This seasonal change in activity is in direct response to temperature. However, following out-of-season rainfall in summer, *G. agassizii* emerge from aestivation and become active despite high ambient temperatures (Nagy & Medica, 1986). Aestivation was initiated in *K. belliana* during dry conditions and in *T. hermanni* due to a digestive bottleneck (Hailey, 1989). Tortoises will thus respond to a combination of environmental and physiological stimuli and show plasticity in their behaviour and activity patterns. Leopard Tortoises seem to follow a similar pattern.

A high percentage of Leopard Tortoises in summer and autumn were found walking and feeding. However, there was no significant correlation with these activities and seasonal rainfall. The effect of rainfall on general activity was discussed above, however Leopard Tortoise activity was thought by Hailey & Coulson (1996b) to be significantly related to both rainfall and temperature, and Bertram (1979b) found that 91% of all movements by Leopard Tortoises in the Serengeti were made after rain. Similarly, *G. agassizii* showed dramatic seasonal changes in activity, influenced by rainfall and temperature (Nagy & Medica, 1986). Lambiris, Lambiris & Mather (1989) reported that while rain had caused an increase in the activity of *K. spekii*, it was the plant growth following rainfall that was the primary cause of increased tortoise activity. Similarly, *G. gigantea* showed seasonal changes in activity in response to changes in food availability (Gibson & Hamilton 1983).

The high frequency of walking by Leopard Tortoises in spring (with a low frequency

2   of feeding) was linked to tortoises responding to higher ambient temperatures after winter,

and moving to drink and to find mates. Walking activity in *T. graeca* is associated with

4   feeding, but is also associated with males searching for females for mating purposes

(Lambert, 1981) or females searching for nesting sites (Diemer, 1992). However, Nagy and

6   Medica (1986), found that many Desert Tortoises *(G. agassizii)* did not feed at all for several

weeks after emergence from hibernation in spring. This may be the case in the present study.

8

Initiation of activity behaviours

10   Leopard tortoises in spring and summer initiated their activity behaviours at the same time of

day, with tortoises in autumn and winter initiating most activities an hour and two hours later,

12   respectively. For all seasons, usually on an hourly basis, activities progressed from alert to

basking to walking to other activity behaviours. Actual time of day has been widely recorded

14   in association with tortoise activity as an indication of daily activity patterns (Lambert, 1981;

Gibson & Hamilton, 1983; Hailey, Pulford & Stubbs, 1984; Meek, 1984; Samour, *et al.*,

16   1987). While time of day can prove useful as a measure of daily activity change, other factors

that are correlated with the time of day, such as ambient temperature and light intensity, may

18   be the primary factors that are initiating tortoise behaviour.

Leopard tortoises initiated their various activity behaviours at similar temperatures in

20   summer and autumn, and in winter and spring, respectively. Temperatures at which all

activities were initiated in winter and spring were very low. However, the majority of

22   tortoises initiated their activities at temperature ranges specific to the season. Most tortoises

performed their activities between 16°-21°C in winter, 19°-30°C in spring, 22°-34°C in

24   autumn and 25°-33°C in summer. Therefore, the temperature range at which Leopard

Tortoises were active varied seasonally and differed by ± 3°C per season. Other studies found *T. kleinmanni* were active between 17°-28°C, with 52% active within a range of 21°-24°C (Geffen & Mendelssohn, 1989). Hailey & Coulson (1996b) found the daily activity pattern of *K. spekii* differed if the maximum air temperature was above or below 29°C. When temperatures were below 29°C, *K. spekii* showed a unimodal activity pattern and above it, a bimodal. Similarly, in spring and summer, *T. graeca* were active between 18°-32°C, with a switch from unimodal to bimodal activity patterns occurring at 28°C, and tortoises becoming inactive below 18°C (Lambert, 1981). Activity in these cases were clearly temperature dependant.

The greatest correlation across the seasons in the initiation of most activity behaviours in Leopard Tortoises was time after sunrise. Each activity was initiated within a half-hour across the seasons, with the first activity (alert) being performed within the first hour after sunrise, irrespective of the actual time of sunrise or ambient temperature at sunrise in each season. This indicates that the primary factor in initiating activity behaviours in this study was photoperiod, with the trigger mechanism being time after sunrise. Cloudsley-Thompson (1970) experimentally proved that *Testudo sulcata* had a well-marked circadian rhythm which was neither accelerated nor retarded by constant light or darkness, nor reset by three-hour periods of light. *Testudo sulcata* locomotion was stimulated by light and inhibited by darkness, but Cloudsley-Thompson (1970) concluded that behaviour was in direct response to temperature and not mediated through reactions to light intensity.

If one looks holistically at the effect of time of day, temperature and time after sunrise, the following summary can be drawn as to the initiation of particular activities in Leopard Tortoises.

Leopard Tortoises showed a response to temperature with regard to activity. Activities

in summer and autumn were performed at the same temperatures, despite the difference in the time of day at which these temperatures were reached. Tortoises were found commencing the various activities at lower ambient temperatures in winter and spring, however, the time of day in spring at which these were observed, were the same as in summer. The low seasonal variation in the time after sunrise at which activity behaviours were commenced, indicated that after a certain time after sunrise, Leopard Tortoises became alert, basked, walked and fed, irrespective of the ambient temperature at that time (which in spring and winter, was still very low). While tortoises are generally reported to stay inactive until temperatures rise above a certain limit, for example 18°C (Lambert, 1981), tortoises in winter and spring in this study were walking and feeding below 18°C. This may be a consequence of the tortoises having to make up energy deficits caused by hibernation through cold periods or it may be that tortoises have a limited time in the day to perform non-thermoregulatory activities, and the actual time of the day is already late morning.

In conclusion, while temperature does have an influence on activity and activity behaviours, the time after sunrise appears to initiate tortoise activity.

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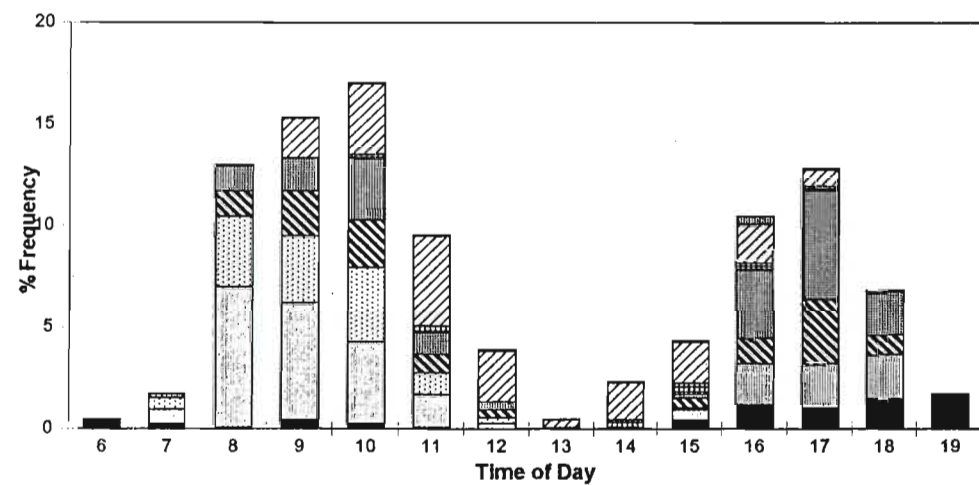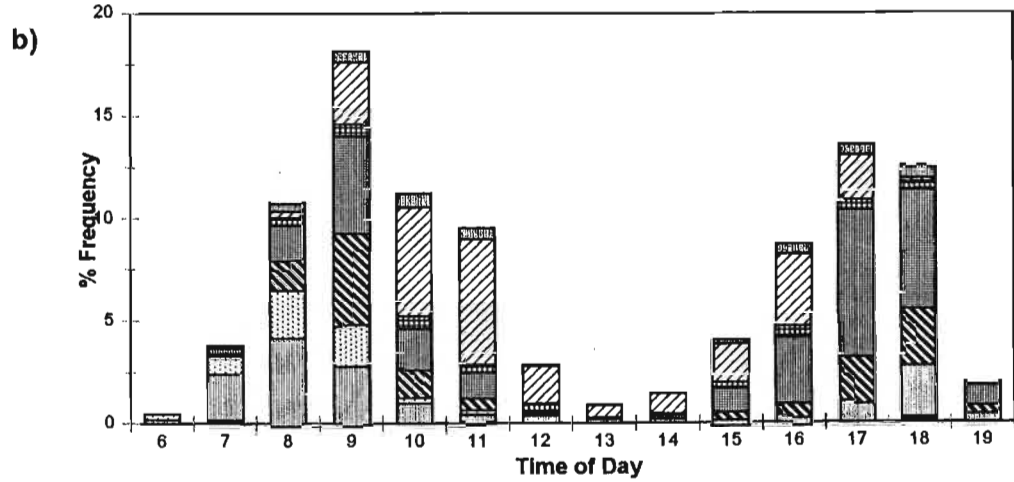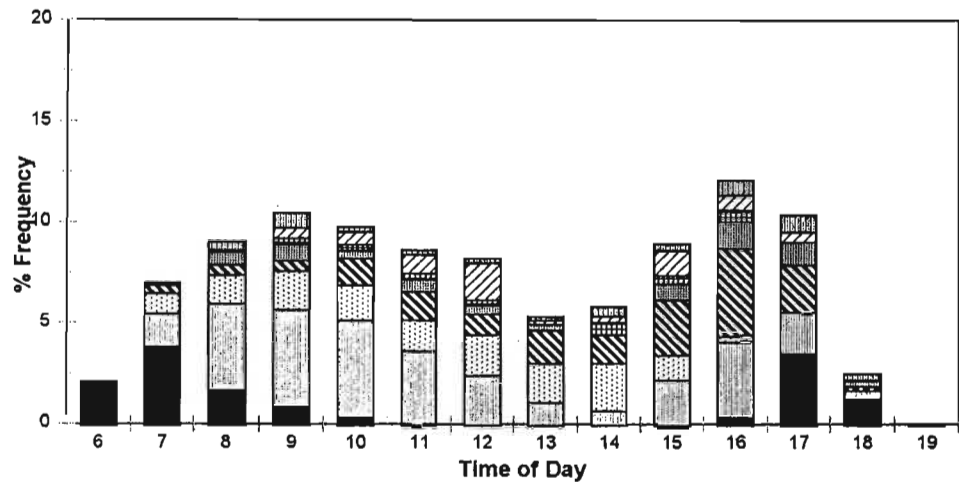
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List of Tables and Figures

Table 1: Percentage of Leopard Tortoises observed per season as inactive or

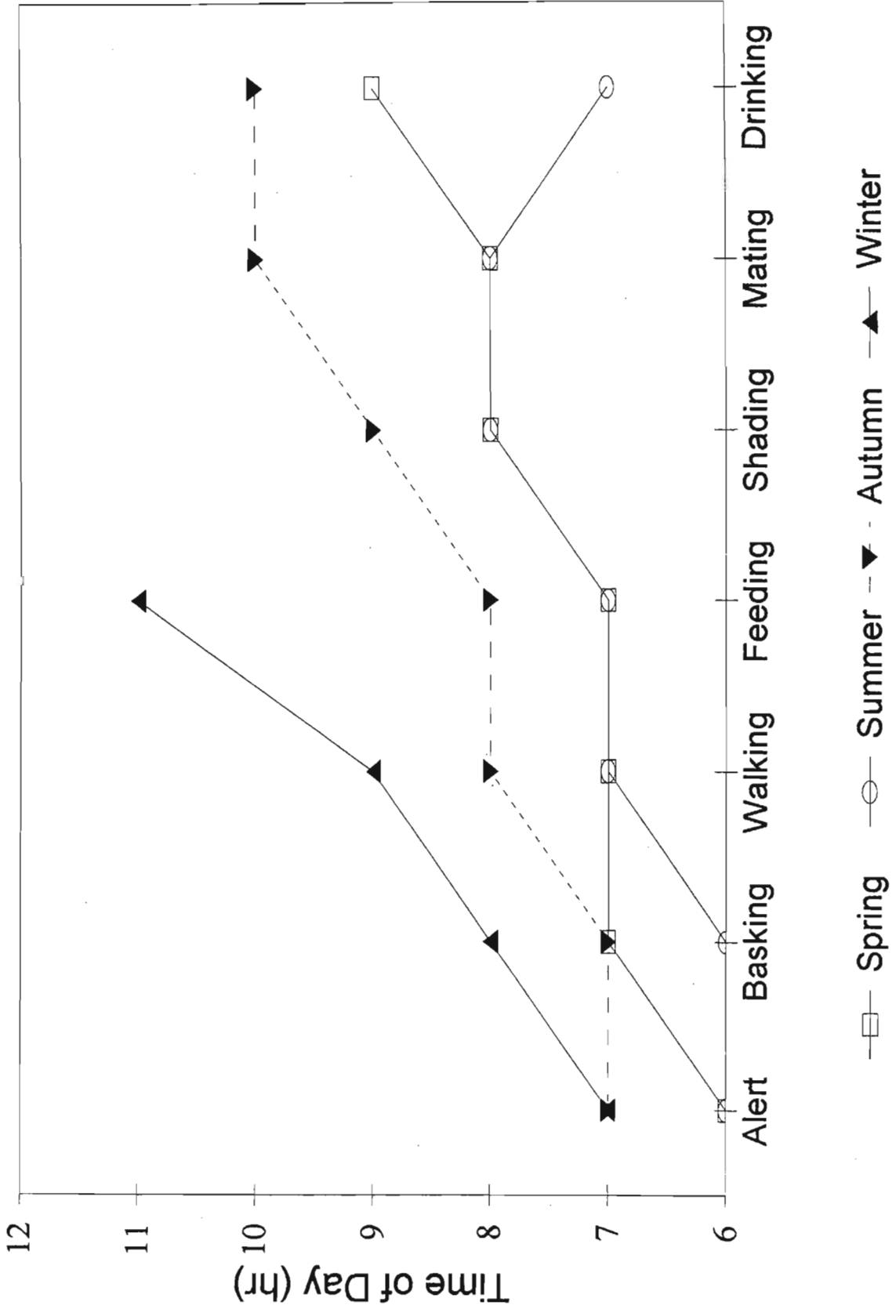performing one of the seven activity behaviours when initially encountered.

Figure 1: Seasonal mean minimum and maximum temperatures and total rainfall

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Figure 2: Percentage of inactive and active Leopard Tortoises of total observed over

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Figure 6: The hour after mean sunrise that a particular activity behaviour was first

observed in Leopard Tortoises during each season.

Table 1: Percentage of Leopard tortoises per season observed as inactive or performing one of the seven activity behaviours when initially encountered.

Activity		Spring (%)	Summer (%)	Autumn (%)	Winter (%)
n		1208	1240	637	814
Active:	Feeding	7.1	28.7	19.0	0.9
	Drinking	2.5	4.0	1.9	0.0
	Basking	15.8	5.7	12.6	15.6
	Walking	17.8	15.0	13.2	3.2
	Mating	4.1	3.6	1.7	0.0
	Alert	31.5	17.0	26.8	46.6
	Shade	7.0	25.2	19.2	0.0
Inactive		14.1	0.7	5.7	33.8

a)

mean sunrise:
05h30

mean sunset:
18h29

Inactive   Active

b)

mean sunrise:
05h03

mean sunset:
18h56

Inactive   Active

c)

mean sunrise:
06h13

mean sunset:
17h46

Inactive   Active

d)

mean sunrise:
06h41

mean sunset:
17h18

Inactive   Active

b)

d

Ambient Temperature (°C)

Alert   Basking   Walking   Feeding   Shading   Mating   Drinking

□ Spring   ○ Summer   ▼ Autumn   ▲ Winter
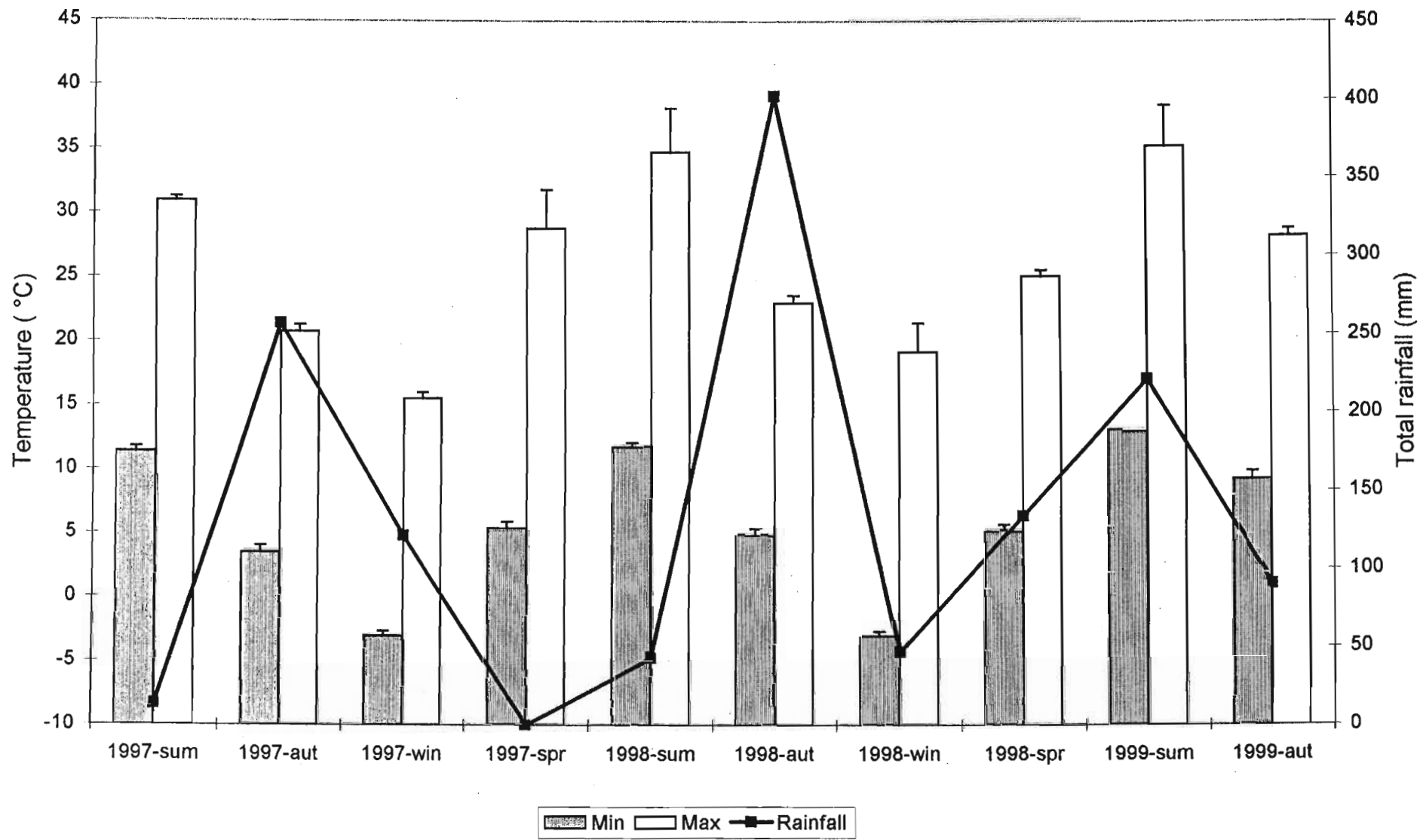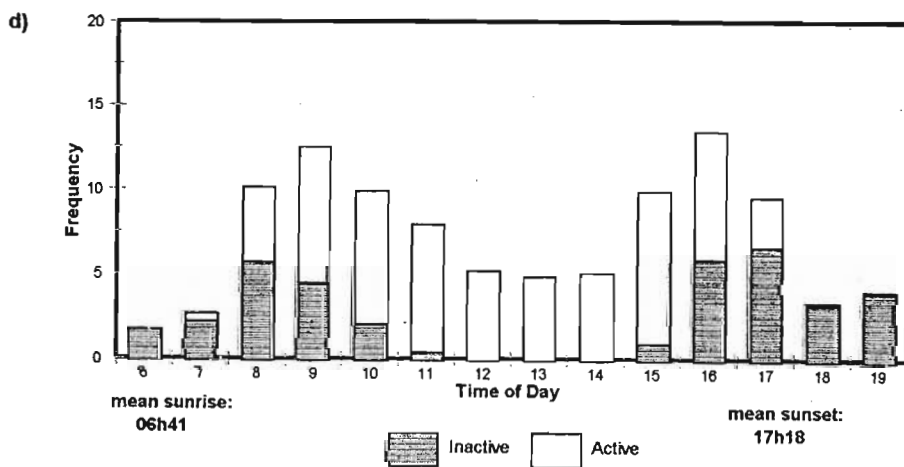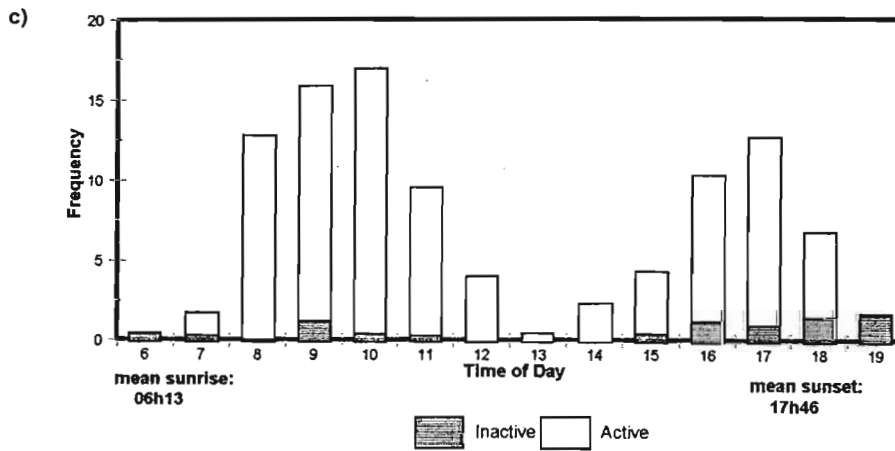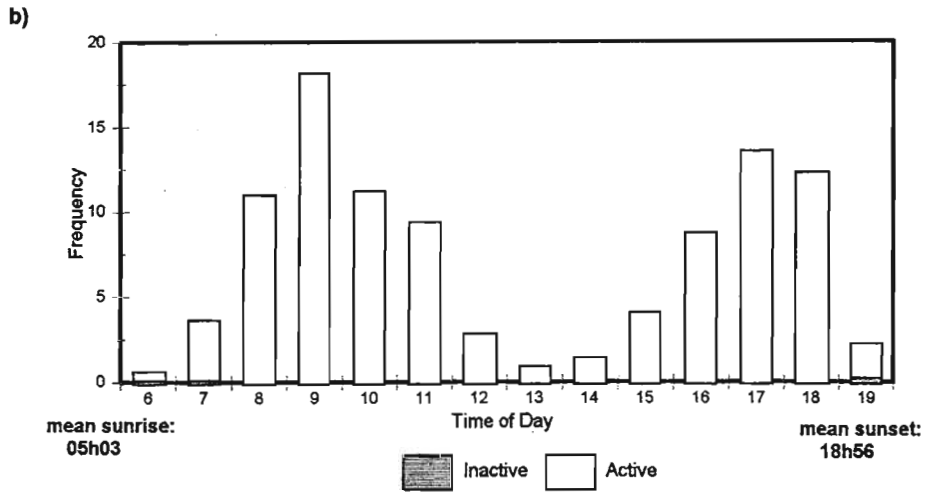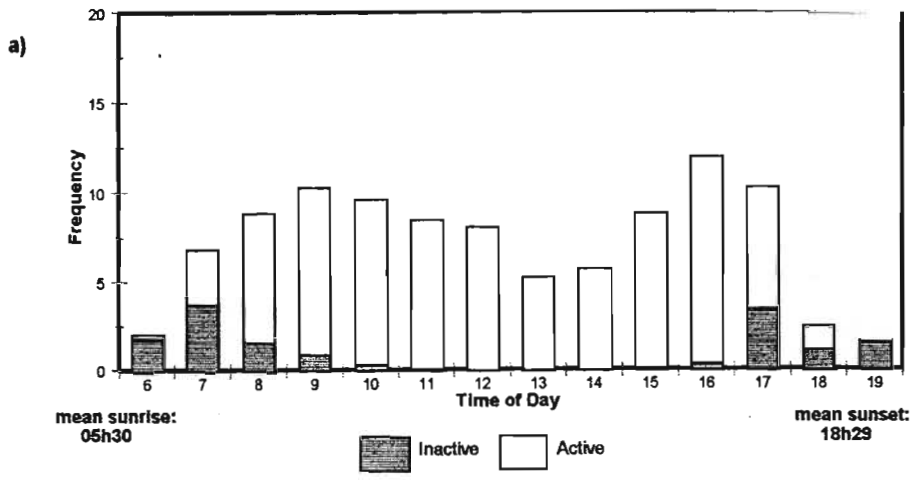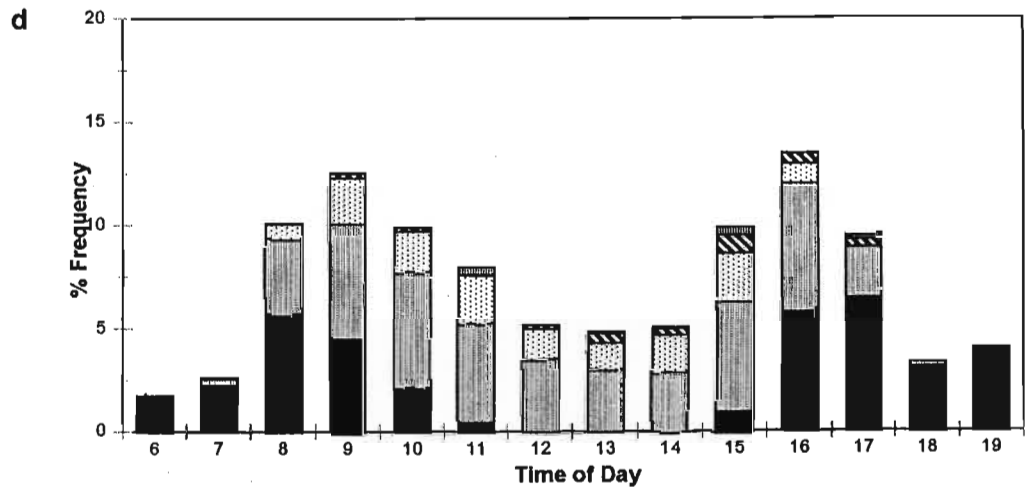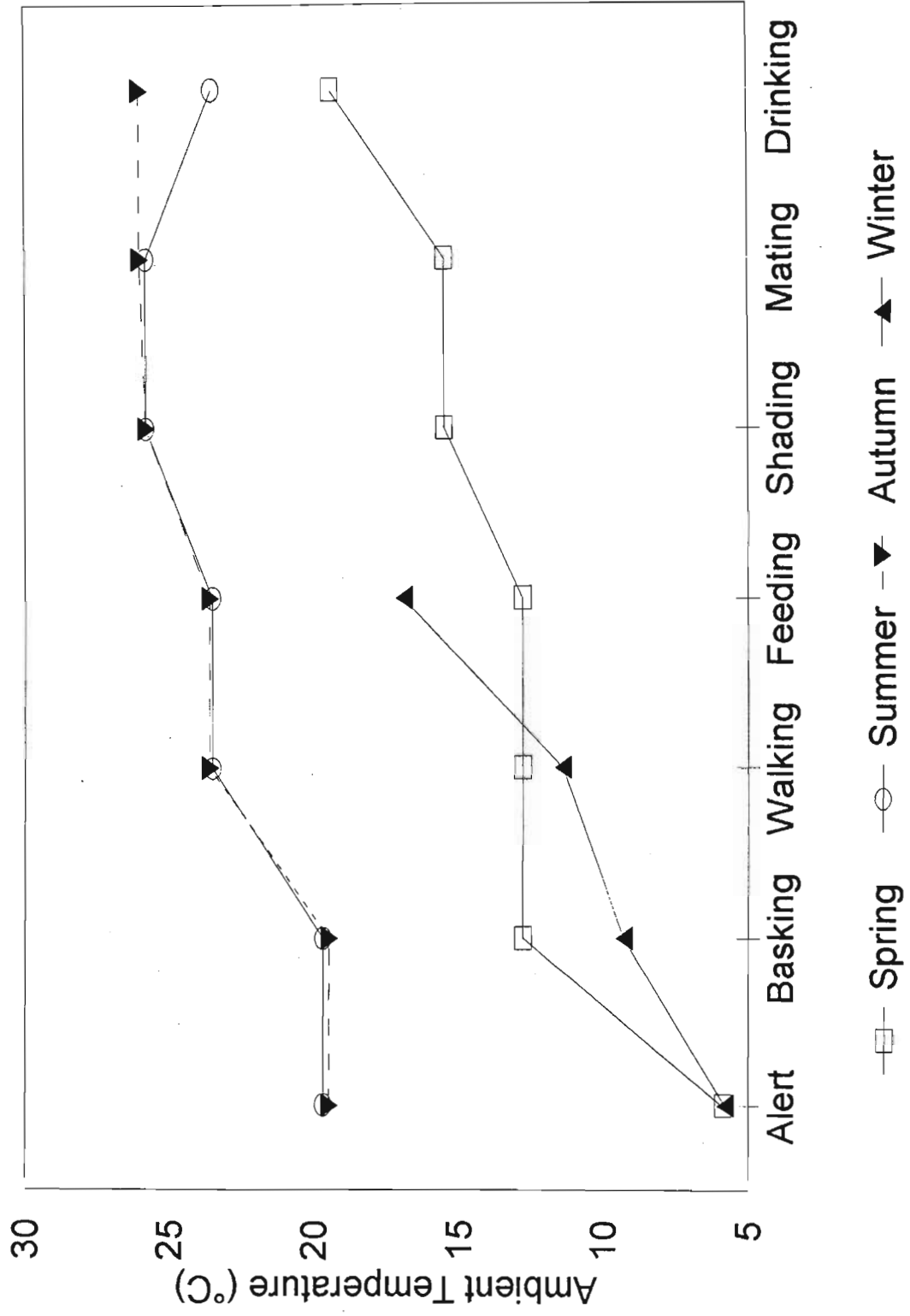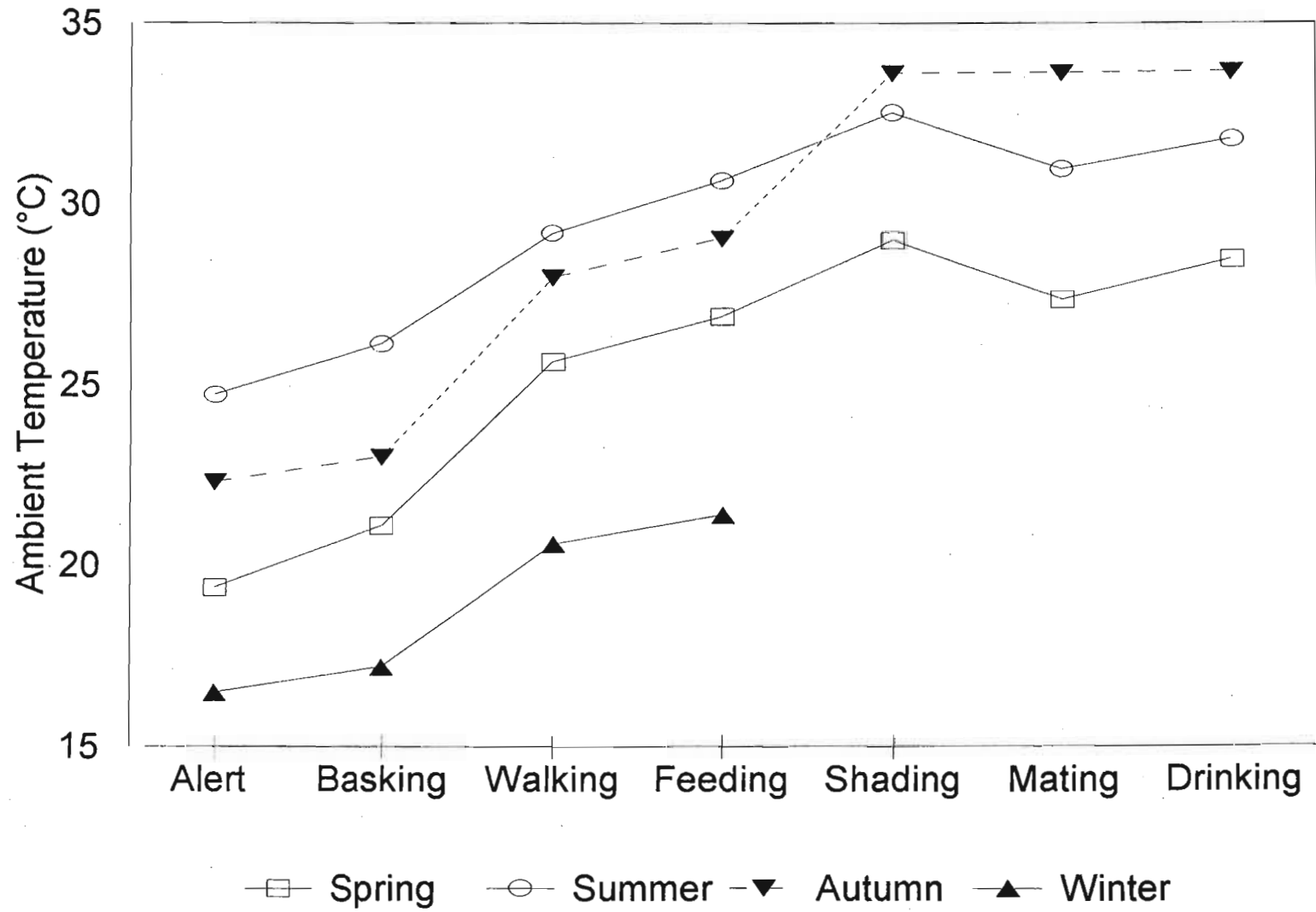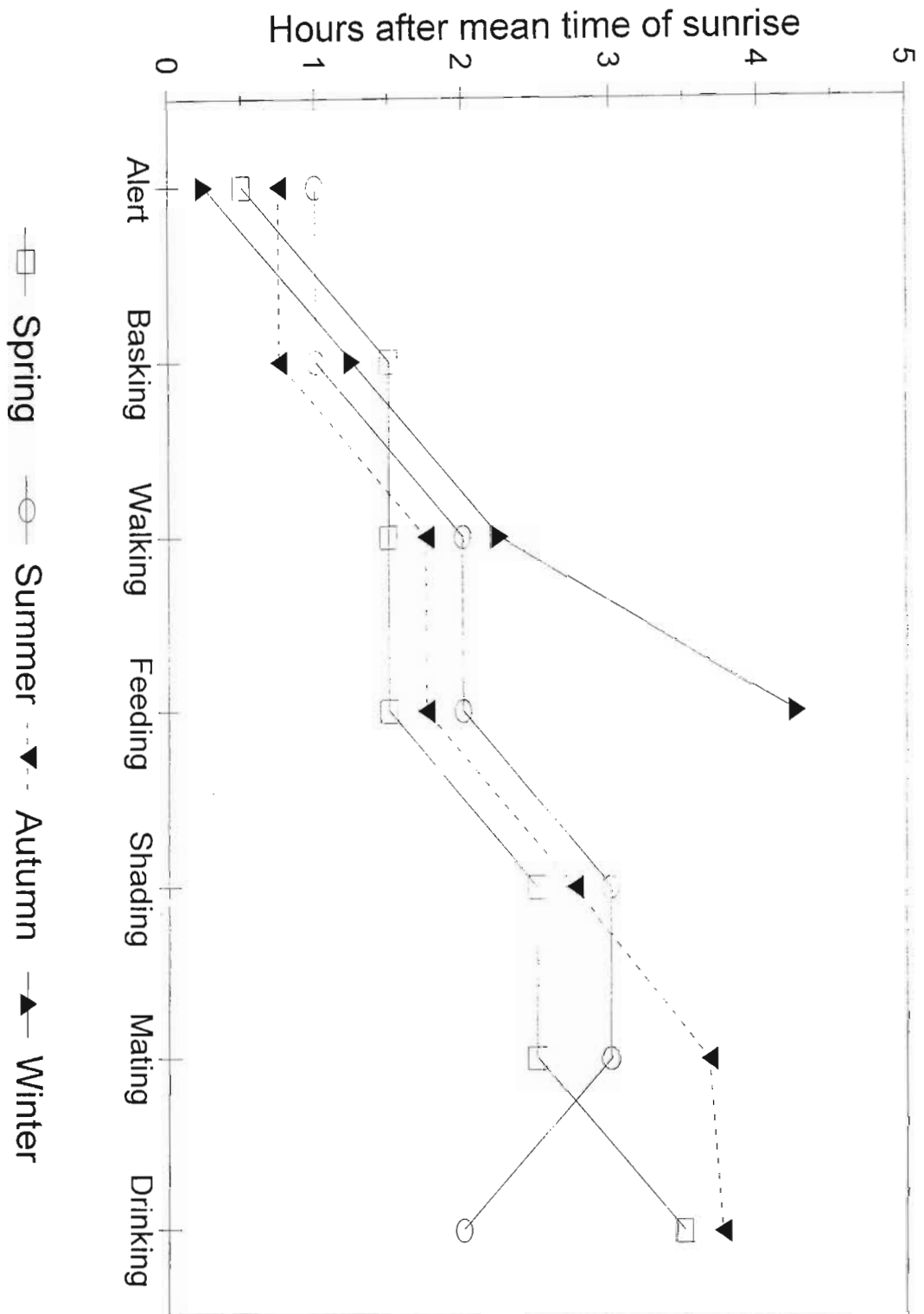
Appendix 1: Mean ± SE ambient temperatures for each hour of day for all the seasons.

Hour of Day	Spring	Summer	Autumn	Winter
06h00	5.9 ± 0.8°C	19.7 ± 1.3°C	16.6 ± 1.0° C	2.7 ± 0.5° C
07h00	12.8 ± 0.7°C	23.5 ± 0.6°C	19.5 ± 1.3° C	5.8 ± 0.4° C
08h00	15.5 ± 0.7°C	25.8 ± 0.3°C	23.6 ± 0.7° C	9.3 ± 0.3° C
09h00	19.4 ± 0.6°C	28.3 ± 0.3°C	25.8 ± 0.7° C	11.4 ± 0.3° C
10h00	20.9 ± 0.4°C	30.5 ± 0.4°C	26.0 ± 0.6° C	13.6 ± 0.4° C
11h00	22.8 ± 0.5°C	32.0 ± 0.3°C	28.8 ± 0.8° C	16.9 ± 0.5° C
12h00	24.2 ± 0.5°C	32.6 ± 0.7°C	30.6 ± 1.1° C	18.8 ± 0.3° C
13h00	23.6 ± 0.4°C	34.0 ± 1.1°C	30.9 ± 0.4° C	19.4 ± 0.3° C
14h00	25.0 ± 0.4°C	34.4 ± 0.9°C	28.5 ± 0.2° C	19.8 ± 0.3° C
15h00	26.2 ± 0.4°C	34.5 ± 0.6°C	27.8 ± 1.2° C	20.2 ± 0.4° C
16h00	25.3 ± 0.4°C	32.9 ± 0.3°C	27.0 ± 0.9° C	17.0 ± 0.4° C
17h00	23.5 ± 0.6°C	31.7 ± 0.3°C	25.8 ± 0.7° C	15.6 ± 0.4° C
18h00	21.4 ± 1.3°C	30.4 ± 0.3°C	23.7 ± 0.7° C	11.0 ± 0.7° C
19h00	19.0 ± 0.8°C	30.1 ± 0.7°C	21.5 ± 0.7° C	9.1 ± 0.7° C

Chapter Five

Refuge Use and Orientation of *Geochelone pardalis* on Farmland in the Nama-Karoo

Megan K. McMaster and Colleen T. Downs

Abstract

Tortoises (Family Testudinidae), as ectotherms, rely largely on behavioural thermoregulation to moderate the effects of daily and seasonal fluctuations in ambient temperature on their body temperature. Extensive use is made of refuges to facilitate this behavioural thermoregulation. The Nama-Karoo experiences wide temperature fluctuations both daily and seasonally, and therefore the types and seasonal use of refuges by the leopard tortoise (*Geochelone pardalis*), in addition to the orientation of the exits and of the tortoises within the refuges, was investigated. A wide variety of refuges were used, but *Lycium spp., Eberlanzia ferox, Opuntia ficus* and grass clumps were preferred as refuges. There was seasonal variation in the use of these refuges that further depended on whether the refuges were used as forms or shelters. Tortoises in spring and winter often remained in the same refuge for the entire season, or returned to the same refuge on consecutive nights.

There was seasonal and behavioural variation in a) the compass direction that the tortoises were facing within a refuge, b) the compass direction that the exits of the refuges were open to, and c) the portion of the shell of each leopard tortoise within a refuge that was exposed to sun radiation. Tortoises in winter and spring used these three factors to maximise the amount of solar radiation received on their shells, while tortoises in summer and autumn used them to minimise solar radiation received. Therefore, using a combination of refuge type, exit orientation and tortoise orientation, leopard tortoises were able to passively thermoregulate and further control temperature fluctuations experienced in an extreme environment.

Introduction

All tortoises (Family Testudinidae) are ectotherms and rely largely on behavioural thermoregulation to moderate the effect of daily and seasonal fluctuations in ambient temperature on their body temperature (Perrin and Campbell, 1981; Cloudsley-Thompson, 1991). To facilitate this behavioural thermoregulation, extensive use is made of refuges to protect them from extreme temperatures, prevailing winds and solar radiation (Grobler, 1982; Hailey, 1989).

Many tortoise species use a wide range of temporary shelters, such as tunnels or scrapes under vegetation, rocks and holes (Rose and Judd, 1975; Lambert, 1981; Geffen and Mendelssohn 1988, 1989; Hailey, 1989). Els (1989) differentiated between refuges used by the angulate tortoise (*Chersina angulata*) as shelters from cold, heat or wind during the day and those refuges used overnight (termed "forms"). Gopher tortoises (*Gopherus spp.*) actively dig burrows in loose soil as shelters overnight, and for aestivation or hibernation (Nagy and Medica, 1986; Diemer, 1992; McCoy *et al.*, 1993), but most tortoise species will use existing burrows or structures for shelter (Lambiris *et al.*, 1987; Hailey and Coulson, 1996).

It has been recorded that some tortoise species orientate the exits of their shelters or burrows to face certain directions, for further protection from prevailing winds and cold temperatures (Els, 1989; McCoy *et al.*, 1993).

The largest of Southern Africa's 14 species, the leopard tortoise (*Geochelone pardalis*), has a wide distribution, ranging from arid and semi-arid areas to wetter grassveld, savannah and bushveld (Baard, 1996; Boycott and Bourquin, 2000). However, there is a paucity of information regarding the ecology and behaviour of

leopard tortoises, especially in arid and semi-arid areas. The Nama-Karoo experiences wide temperature fluctuations both daily and seasonally, and while it has been recorded that leopard tortoises use boulders and trees as refuges from heat and frost (Grobler, 1982; Milton and Dean, 1993), and sleep under bushes overnight (Rall, 1985), there is no information regarding the exact types of refuges used, whether some refuges are utilized more than others, or if there is any orientation in the exits of the refuges that may aid thermoregulation in these tortoises.

As part of a large scale study investigating the status and ecology of leopard tortoises in the Nama-Karoo, the types and seasonal use of refuges, the orientation of the exits and of the tortoises within the refuges, was investigated. It was predicted that the type of refuge used would differ seasonally and would differ according to the thermoregulatory requirements of the tortoises. In addition, it was predicted that tortoises would orientate themselves within a refuge with regard to the sun, in order to manipulate the amount of solar radiation received on the shell of the tortoise and therefore further aid in thermoregulation.

Methods

Geochelone pardalis was studied on a 5500 hectare area on a mixed commercial sheep and game farm of 26000 ha in the De Aar District, Nama-Karoo biome, South Africa (31°04'S, 23°41'E). The vegetation type is classified as grassy dwarf shrubland (Palmer and Hoffman, 1997). Dominant shrubs include *Eberlanzia ferox*, *Eriocephalus ericoides, Lycium spp., Pentzia spp.*, and *Chrysoma ciliata*, with annual grasses including *Eragrotis obtusa, Sporobolus spp.* and *Stipagrostis ciliata* (Palmer

and Hoffman, 1997).

Although the area has its highest rainfall in late summer and autumn, the average annual rainfall is low (200 - 400 mm). Temperatures range from 5° to 39°C in spring and summer, and from -5° to 26°C in autumn and winter. The seasons were classified as follows: spring months were September to November; summer from December to February; autumn from March to May; winter from June to August.

Leopard tortoises were located by riding transects on horseback in the study area twice daily. Date, time, individual marking, body mass, sex and type of activity were recorded for all tortoises sighted. The geographical position of all tortoises was recorded using a handheld Trimble Navigation GeoExplorer II Geographical Position System (GPS) unit, U.S.A.

Refuges used by tortoises were classified as "forms" or "shelters", following Els (1989) where a form is a refuge that a tortoise uses overnight, while a shelter is used as a protection from the sun, wind or cold during the day. The type of form or shelter used, the orientation of the refuge exit, the compass bearing that the tortoise was facing in the refuge and the portion of the shell that was receiving solar radiation, were recorded. The compass orientations of the exit tunnels and the compass bearings that the tortoises were facing were recorded as eight cardinal points following McCoy *et al.* (1993). The radiation exposure on the tortoise shell was assigned to either being on the right, left, front or rear half. Activity behaviours (defined in Chapter 4) were grouped into those that would be performed as activities in a form (such as inactivity, alert and basking), or those activities that would be performed during the day under shelter (for example shading and feeding).

In addition to spontaneous sightings, eight females and six males were fitted

with unique-frequency radio transmitters (see Chapter 3). Telemetered leopard

tortoises were located twice daily for three month periods from October 1997 to April

1999. The GPS position and behaviour of the tortoises were recorded on every

occasion. In addition, each individual was followed for a continuous eighteen hour

period once every three months, and its behaviour and GPS position recorded every 15

minutes. All statistical tests were calculated using STATISTICA software (Statsoft,

Tulsa, USA).

Results

Refuge use

Leopard tortoises followed a daily activity pattern that varied seasonally in the length

of time spent performing certain activities, and in some seasons, in the activity types

themselves (discussed in detail in Chapter 4). On a daily basis, leopard tortoises were

inactive in a form overnight and would become alert at some time during the morning.

Tortoises would then bask when exposed to radiation while still in, or just out of, their

forms. If ambient temperatures became high enough, tortoises would then pursue non-

thermoregulatory activities, for example, walking and feeding. If ambient

temperatures became too warm, leopard tortoises would seek shade under a bush, or if

too cold, they would remain in their forms. Thus, a distinction can be made between

those refuges used during the day for shelter from the sun or other adverse conditions,

and those refuges used overnight as forms.

Leopard tortoises used various types of refuges both as forms or as shelters

throughout the year (Table 1). Refuges termed "other" included piles of dead branches

or water tanks. The most commonly used refuges overall were *Lycium spp.*, *Eberlanzia ferox* and grass clumps, however, the preference of one refuge over another varied seasonally (Table 1). In spring, summer and autumn *Lycium spp.* were used most commonly, while in winter *Eberlanzia ferox* was preferred (Table 1).

There was a significant correlation in the types of refuges used in spring and autumn ($r_s = 0.87$; $n = 13$; $p < 0.001$), spring and winter ($r_s = 0.79$; $n = 13$; $p < 0.01$), and autumn and winter ($r_s = 0.63$; $n = 13$; $p = 0.02$). In addition, types of refuges used in spring, autumn and winter were significantly correlated to overall refuge use (spring: $r_s = 0.95$, $p << 0.001$; autumn: $r_s = 0.86$, $p < 0.001$; winter: $r_s = 0.81$, $p < 0.001$; $n = 13$ for all seasons).

Seasonal differences in refuge use was primarily due to the different activity behaviours and the resultant refuge requirements of leopard tortoises. Figure 1 shows the seasonal use of refuges as forms and shelters. Leopard tortoises in spring preferred *Lycium spp.* as both a shelter and a form (Figure 1). In summer, autumn and winter, *Lycium spp.* and *Opuntia ficus* were preferred as shelters, and *E. ferox* was primarily used as a form (Figure 1). Some forms, for example grass clumps, provided little shade, but more protection, and so were more suitable as a winter refuge.

Under cooler ambient temperatures in spring and winter, tortoises would often remain alert within their forms or bask, with temperatures not necessarily becoming warm enough for walking, feeding or mating activity. As a result, there was a significant correlation between the types of refuges used as shelters or as forms in spring ($r_s = 0.81$, $p < 0.001$) and winter ($r_s = 0.67$, $p = 0.01$). In spring, 5.3% of leopard tortoises returned to the same forms on consecutive nights, with 43% staying the entire day within a form. In winter, 71% of leopard tortoises stayed in the same

form for the entire winter season, and 43% returned to the same form the following winter. Those tortoises that did move during the day in winter, usually females, returned to the same form that afternoon, or alternated between two or three forms that were within a 20 m. radius of each other. In addition, 50% of the leopard tortoises in spring and 57% in winter (compared to 5% and 7% in summer and autumn, respectively), moved from the plains into surrounding hills, preferring the northern aspect of the slope and using the additional protection of boulders and grass clumps as refuges from cold south winds.

Temperatures in autumn and summer were high enough to allow leopard tortoises to become active and move out of their forms, seeking shade under a different refuge later on in the day (see Chapter 4). As such, there was no significant correlation between the types of refuges used as forms and those used later as shelters in summer ($r_s = 0.46$, $p = 0.11$) and autumn ($r_s = 0.29$, $p = 0.33$). Only 0.3% and 4.6% of leopard tortoises returned to the same forms on consecutive nights in summer and autumn respectively.

Orientation of refuge exits and leopard tortoises within a refuge

Leopard tortoises typically entered a refuge head-first and pushed themselves as far into the refuge as they could, often shifting and digging down into the loose sand during cold temperatures (<15°C). Exposure of leopard tortoises to the open elements in a refuge varied seasonally and occurred to varying degrees depending on the activity behaviour, size and type of refuge being used, orientation of the exit, and compass bearing that the leopard tortoises were facing. Leopard tortoises used a combination of these factors to aid in passive thermoregulation while in a refuge.

Different behaviours were indicative of different thermoregulatory requirements. To test whether leopard tortoises used a combination of the above mentioned factors to aid in thermoregulation, a distinction was made (as mentioned in Methods) between those activities performed while the tortoises were in a form, ie. still in their overnight shelter, and those activities that were performed in a shelter during the day.

When in their overnight forms, tortoises in winter preferred to orientate themselves to the face south and south-west (Figure 2d), while having the exits of their refuges open to the north-east and north (Figure 3d). This would allow solar radiation to fall on the whole shell or on the rear half (Figure 4d), maximising the amount of solar radiation reached while the leopard tortoises is still in its form. However, when found in shelters during the day, leopard tortoises in winter tended to face west (Figure 2d), preferred to have the exits of their refuges open either to the north-east or to be completely protected by their refuges (Figure 3d), and had solar radiation primarily on their whole shell or on the rear half of the shell (Figure 4d).

Similarly to those in winter, leopard tortoises in spring faced west and north-west when in their forms (Figure 2a), and had their exits facing north, north-east and east (Figure 3a). Solar radiation was thus primarily on their whole shell or on the right half (Figure 4a) which would aid in basking behaviour. When seeking shelter, tortoises in spring faced east, north-east or west (Figure 2a), had exits facing north (Figure 3a) and were most frequently found to have solar radiation on their whole shell (Figure 4a).

The prevailing cold winds in spring and winter were from the south and west, and as such these results were consistent with tortoises trying to seek protection from cold, choosing to have the exits of their shelters open to directions opposite to those of

the prevailing cold winds and by doing so, also maximising the amount of solar radiation falling on their shells.

In summer, leopard tortoises in forms tended to face east (Figure 2b), but had no distinct preference in the direction that the exit of a refuge faced (Figure 3b). Most tortoises in summer were found with no solar radiation on them when in their forms (Figure 4b). Leopard tortoises in summer seeking shelter were also primarily found facing east (Figure 2b), but had refuge exits facing south-west more frequently (Figure 3b), and were found with no solar radiation on their shells (Figure 4b).

Leopard tortoises that were found in their forms in autumn faced south and south-west (Figure 2c), had their exits facing north and north-east (Figure 3c), and had solar radiation primarily on the whole shell (Figure 4c). Those leopard tortoises seeking shelter during the day in autumn faced north and north-east (Figure 2c), had exit openings to the south-west and south-east (Figure 3c), and most commonly were found with no solar radiation on their shells (Figure 4c).

Therefore, in contrast to spring and winter, leopard tortoises in summer and autumn orientated themselves in their refuges to avoid the sun and direct solar radiation on their shells, especially when seeking shade during the day. With no openings to the north and north-east, and no exposure of the shell to sun radiation, leopard tortoises would be able to reduce the amount of heat received and aid in passive thermoregulation.

Discussion

Refuge use

Geochelone pardalis used a wide variety of refuge types, but selected certain refuges over others depending on the function that the refuge was to serve. *Lycium spp.* and *O. ficus* were better suited as shade plants as they allowed for air movement through the bush, while providing dense shade. Boulders, grass clumps and small shrubs, such as *E. ferox* and *E. ericoides*, provided shelter against wind, while still allowing radiation from the sun to fall directly on the tortoise, and were therefore preferred as forms and shelters against cold winds. Leopard tortoises in this study preferred *Lycium spp, E. ferox,* and *O. ficus* over other refuge types. Seasonal differences in refuge use occurred with tortoises preferring *Lycium* spp. as both a shelter and a form in spring, and using *Lycium spp.* and *O. ficus* for shelter, and *E. ferox* as a form, in summer, autumn and winter.

Rall (1985) reported leopard tortoises using various shrubs as refuges, while leopard tortoises in the Mountain Zebra National Park sought refuge in winter under *Lycium spp.* thickets and *R. glauca* bushes (Grobler, 1982). Angulate tortoises *(Chersina angulata)* predominantly used *Acacia karoo* as both a shelter and a form (Els, 1989), while *Testudo hermanni* distinguishes between refuges that offer substantial cover and those that provide only shade and physical concealment (Hailey, 1989). Hingeback tortoises *(Kinixys spp.)* show seasonal differences in refuge use, sheltering under rocks in hot weather (Archer, 1948) and using gaps between rocks as forms in the dry winter months (Bertram, 1979). Seasonal differences in refuge use were also documented in *Testudo hermanni* (Hailey, 1989) and *Gopherus spp.* (Nagy

and Medica, 1986; Geffen and Mendelssohn, 1988).

In spring and winter, leopard tortoises were very conservative in their use of refuges, frequently remaining in the same refuge for the entire day or in some cases, the entire season. Tortoises also returned to previously used refuges, especially in winter. The continuous use of a form throughout winter has been documented in other arid-area species, for example *Gopherus polyphemus* (Diemer, 1992), *G. berlandieri* (Rose and Judd, 1975) and *Testudo hermanni* (Hailey, 1989). Female leopard tortoises that showed limited movement in winter often returned to the same form or forms close-by. This was observed in a female *Kinixys belliana*, who regularly used four refuges, using one of these continuously throughout winter (Bertram, 1979). Hailey (1989) found that the probability of *T. hermanni* returning to a refuge was significantly correlated with the type of refuge and the availability of suitable refuges in the area.

The use of burrows by a variety of tortoise species is fairly common, especially in arid areas (Nagy and Medica, 1986; Geffen and Mendelssohn, 1989), with the primary function of the burrow being to provide species with shade and prevent the tortoises reaching their maximum critical body temperatures (Cloudsley-Thompson, 1991). However, the use of burrows in winter is extensive and burrows must provide good protection from cold temperatures and winds (Nagy and Medica, 1986; Diemer, 1992). McGinnis and Voigt (1971) found that the body temperature of a desert tortoise (*Gopherus agassizii*) that spent the night in a burrow was likely to be warmer than that of an individual that stayed overnight in a bush. *Gopherus agassizii* therefore avoided the use of burrows as overnight forms in summer, as the warmer conditions in the burrow caused the critical maximum body temperature to be reached earlier in the

day (McGinnis and Voigt, 1971). However, burrows were used for shade at midday, and as shelters in winter.

In this study, leopard tortoises used antbear (*Orycteropus afer*) holes more often in summer than in winter, but the overall utilization of antbear holes as refuges was surprisingly low. This may be due to the relative scarcity of usable antbear holes on the study site, as leopard tortoises do not dig their own burrows and were never observed widening or altering existing ones.

Orientation of refuge exits and leopard tortoises within a refuge

Tortoises need to reach a certain temperature before they can become active and perform activities such as basking, walking etc. (Cloudsley-Thompson, 1991). Active basking activity by *G. pardalis* involved tortoises being out of their forms and orientated to expose the maximum shell surface area to the sun, this being performed once a certain minimum temperature has been attained (Lambert, 1981). It would therefore be advantageous for tortoises to orientate themselves in the form itself such that they get exposure to sun radiation while still remaining sheltered from cold and wind. This would aid in the initial heating of the tortoises and they would more rapidly reach the temperatures required for active basking. While basking activity can be seen as a form of active thermoregulation, the exposure of a tortoise still in its form to sun radiation can be seen as a type of passive basking or passive thermoregulation that gives the tortoise the advantages of basking without losing the protection against cold or wind provided by the shelter.

The selection by leopard tortoises in spring and winter (in both forms and shelters) to face south, south-west and west, and remain exposed to the north, north-

east and east, maximised the amount of solar radiation falling onto the shell surface

area, while the tortoise is still protected from cold winds by the rest of the refuge.

Geffen and Mendelsohn (1989) found that 77% of the egyptian tortoises (*Testudo*

kleinmanni) found in winter and spring were on the east or south side of the bush;

15% facing north and 8% west. The authors concluded that this preference and

orientation would allow for the minimum activity temperature to be reached earlier in

the day.

In summer and autumn, there was less need for leopard tortoises to practice

passive basking, as minimum activity temperatures are reached early in the day.

Leopard tortoises spend very little time basking in summer, and overheating is more

of a threat to survival (Geffen and Mendelssohn, 1989; Cloudsley-Thompson, 1991).

Leopard tortoises in their forms in summer and autumn showed very little preference

to either the direction they faced or the direction that they were exposed to. However,

they did show a preference when under shelter to have exits facing south and south-

west, while facing east and north-east, thus reducing the exposure to the sun and using

the shelter to prevent solar radiation falling onto their shells. Leopard tortoises

therefore changed their orientation within a refuge and the orientation of the refuge

exit to manipulate the amount of solar radiation striking their shells. This then aids in

passive thermoregulation, whether exposing themselves to additional radiation in

order to raise their body temperatures or shading themselves to keep their

temperatures down.

Els (1989) found that angulate tortoises (*Chersina angulata*) orientated the

exits of their forms to protect themselves from prevailing winds, however, the

burrows of the gopher tortoise (*Gopherus polyphemus*) showed no particular

orientation to any compass direction (McCoy *et al.*, 1993). The protection offered by a burrow would preclude the necessity of orientating the exit of a form or the tortoise itself, to the sun.

In conclusion, *G. pardalis* in the Nama-Karoo used a wide variety of refuges, favouring *Lycium spp, E. ferox*, and *O. ficus*. There was a seasonal variation in refuge use that further depended on whether the refuge was being used as a form or a shelter. Tortoises in spring and winter often remained in the same refuge for the entire season, or returned to the same form on consecutive nights. However, tortoises in summer and autumn left their overnight forms to pursue non-thermoregulatory activities and usually found refuge in different form the following night. There was seasonal and behavioural variation in the compass direction that the tortoises and the refuge exits faced, allowing tortoises to manipulate and either maximise (in spring and winter) or minimise (in summer and autumn) the amount of solar radiation received by the shell. Therefore leopard tortoises could passively thermoregulate and exert a finer control over temperature fluctuations within the environment.

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2   **List of Table and Figures:**

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Table 1: Types and seasonal usage (%) of refuges used by *Geochelone pardalis* in the Nama-Karoo (name in parentheses is common name).

	Refuge Type	Spring	Summer	Autumn	Winter	Overall
		%	%	%	%	%
1.	*Eberlanzia ferox* (Doringvygie)	13.88	9.52	16.22	27.45	18.16
2.	*Eriocephalus ericoides* (Kapokbos)	8.95	4.84	10.40	11.31	9.21
3.	*Lycium cinereum* (Kriedoring)	24.75	29.33	23.08	17.43	22.81
4.	*Psilocaulon absimile* (Asbos)	1.92	5.30	2.70	0	2.00
5.	*Pentzia spp.*	0.91	3.12	1.04	0.75	1.29
6.	Boulders	7.03	1.25	8.32	12.81	8.16
7.	*Orycteropus afer* (Antbear) holes	1.19	3.12	0.83	0.42	1.23
8.	*Euryops subcarnosus* (Soet harpuis)	8.49	0.78	3.12	0.08	3.33
9.	Grass Clumps	13.33	11.86	6.24	17.89	13.66
10.	*Rhus erosa*	4.29	4.84	6.86	0.08	3.28
11.	Other	0.09	10.45	0	0	2.00
12.	*Opuntia ficus* (American Prickly Pear)	10.69	15.60	19.75	5.57	11.09
13.	*Asparagus striatus* (Bergappel)	4.47	0	1.46	6.16	3.80
	n	1095	641	481	1202	3419

b)

d)

a)

b)

c)

d)
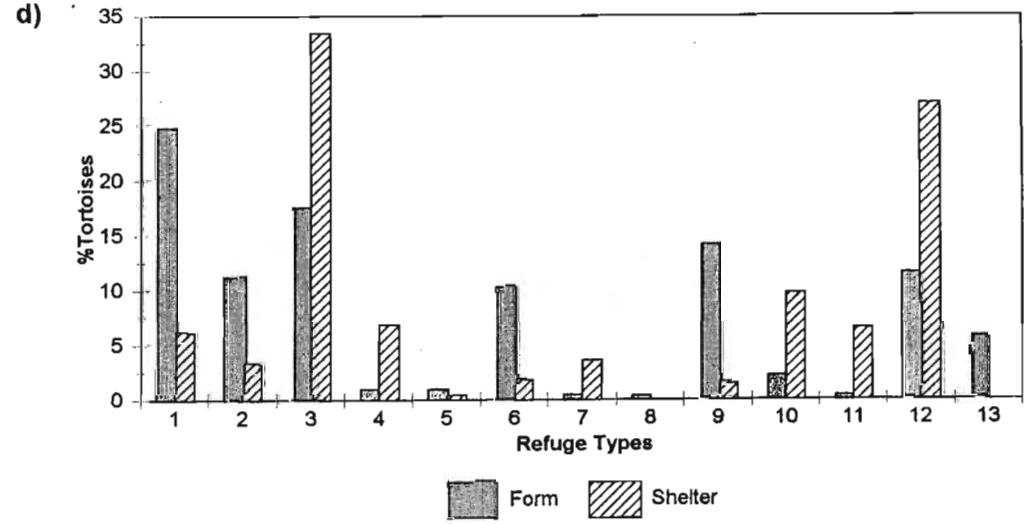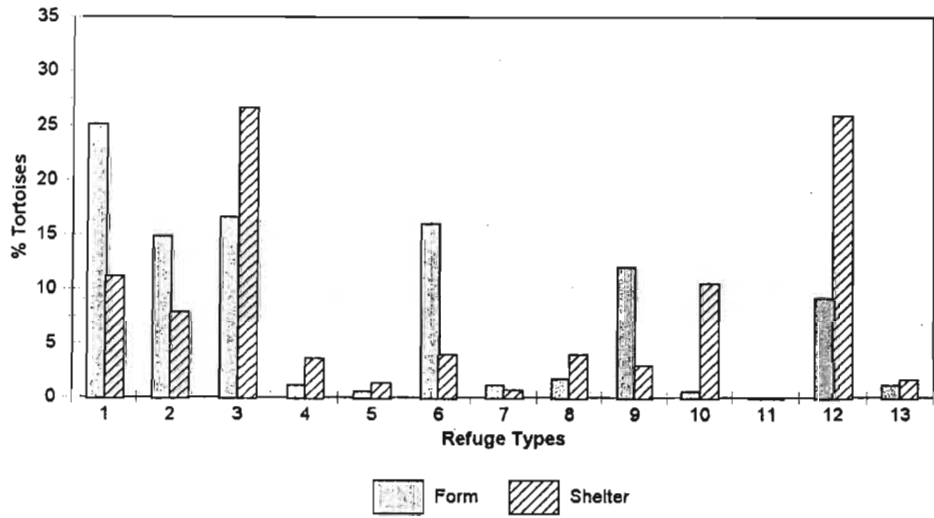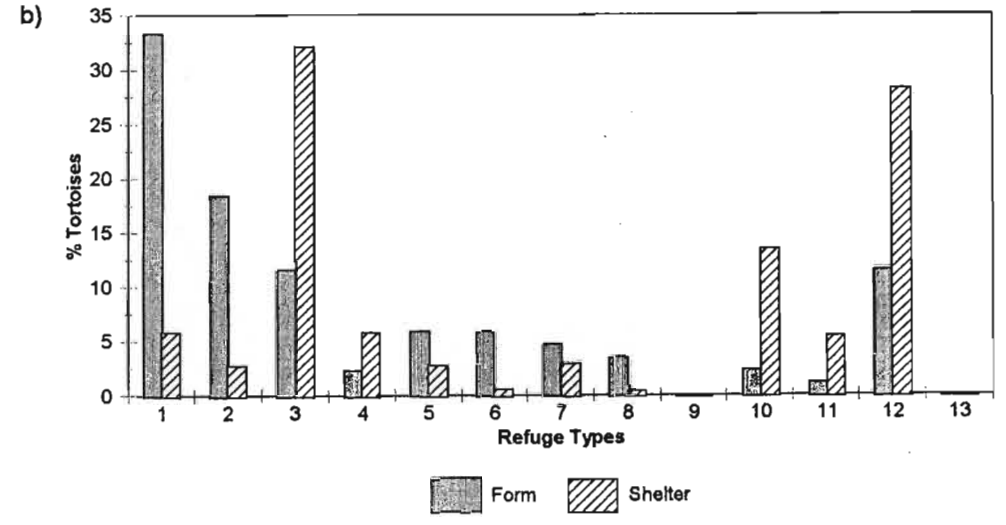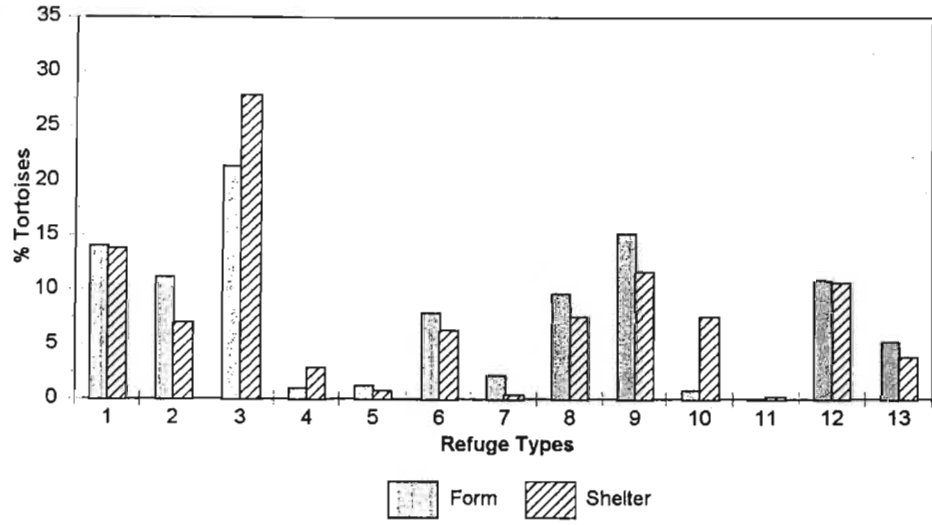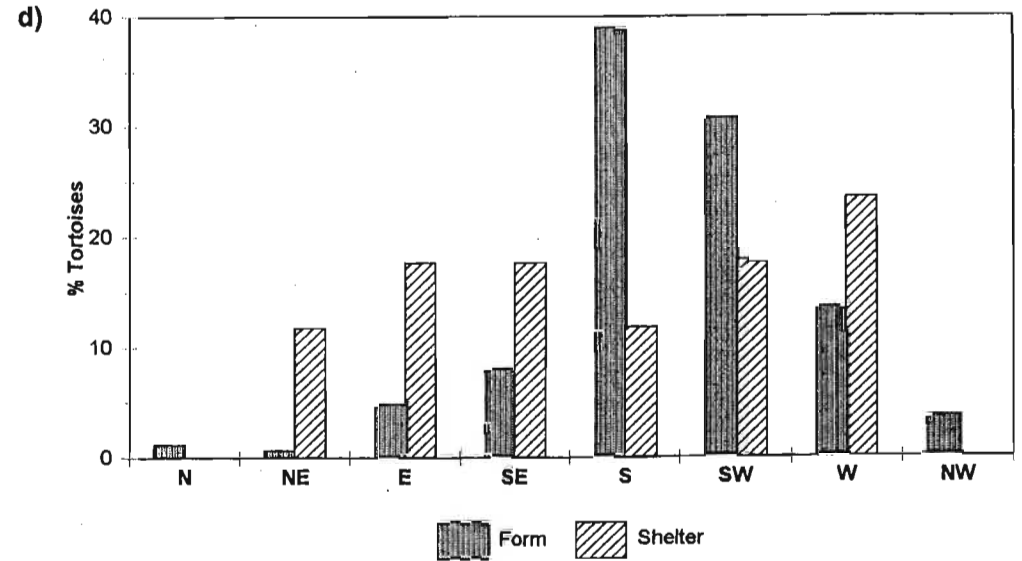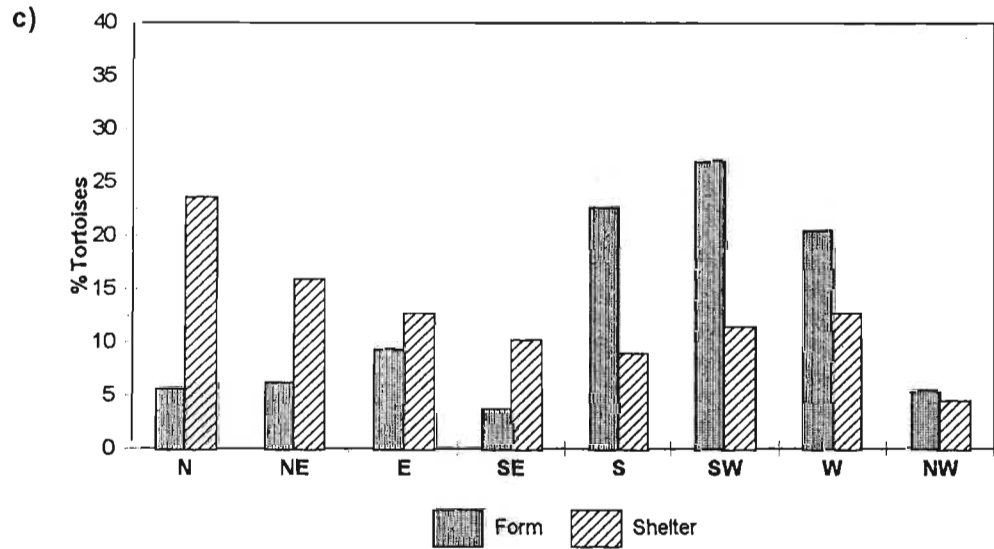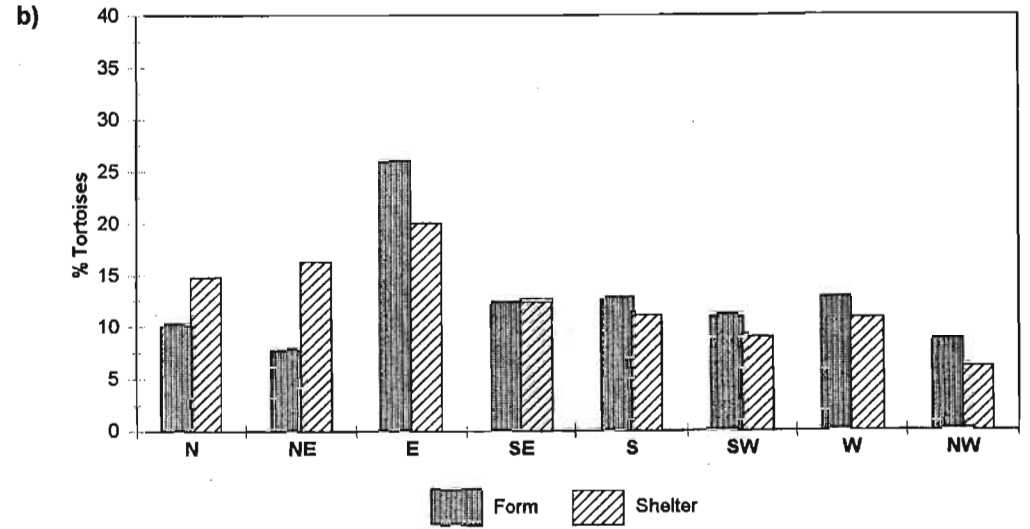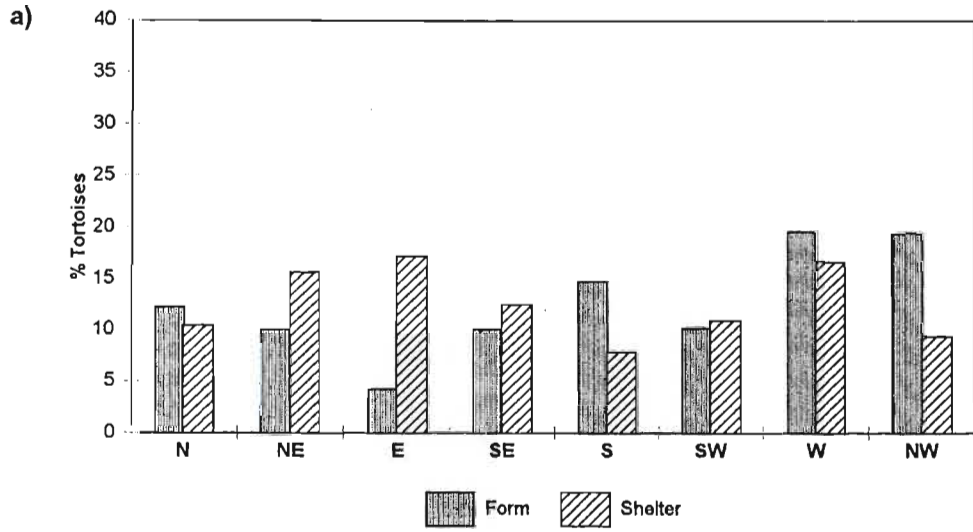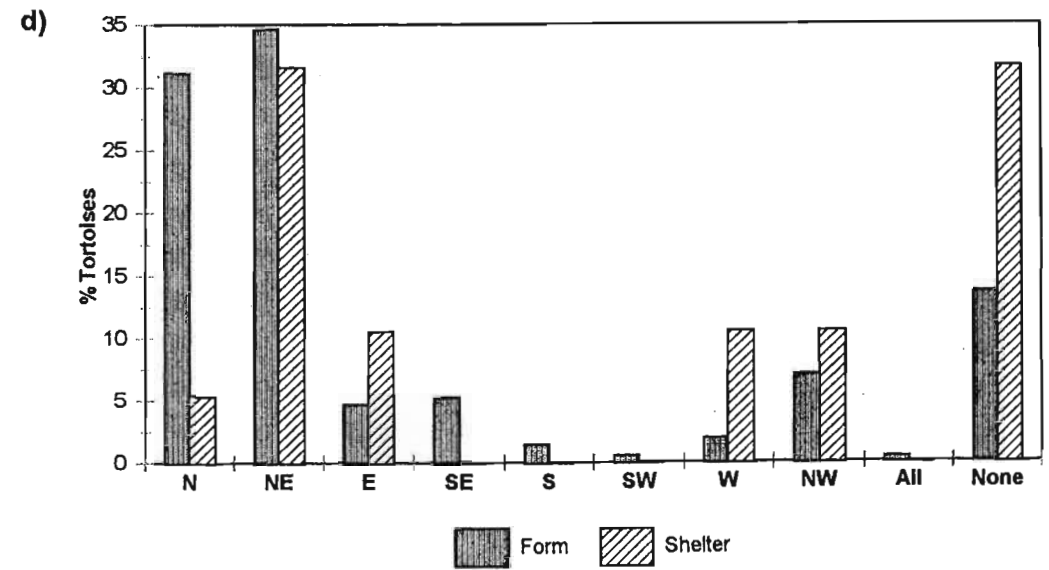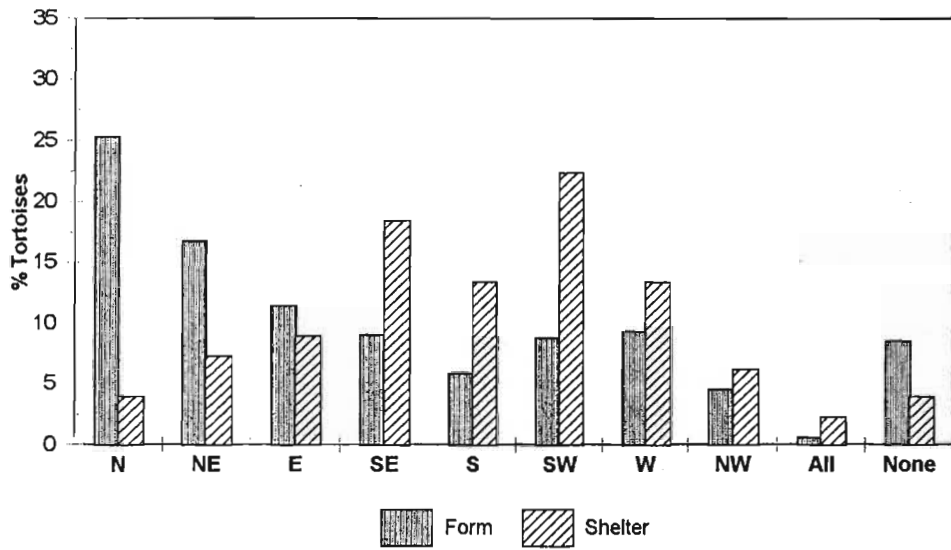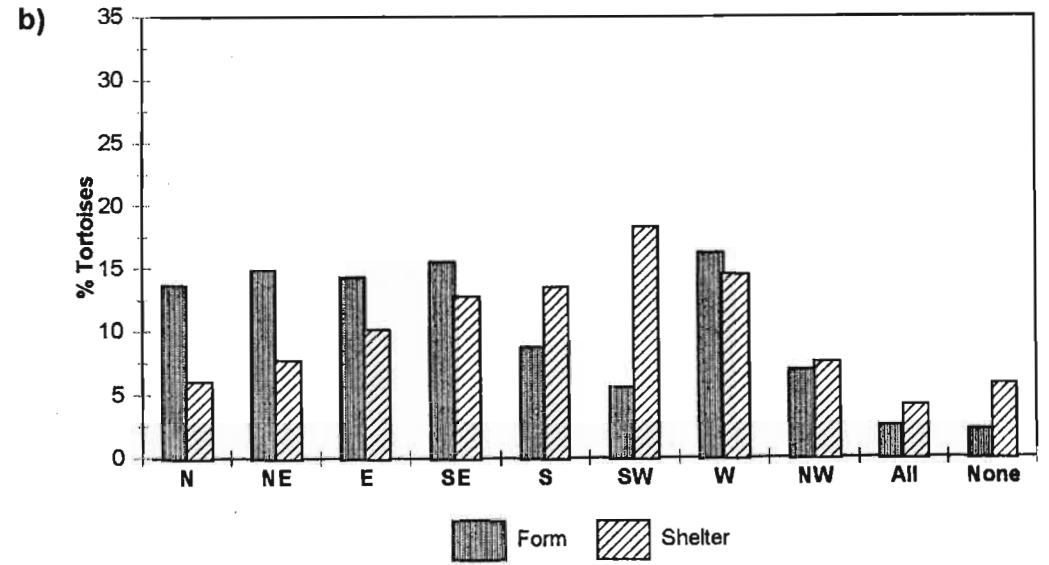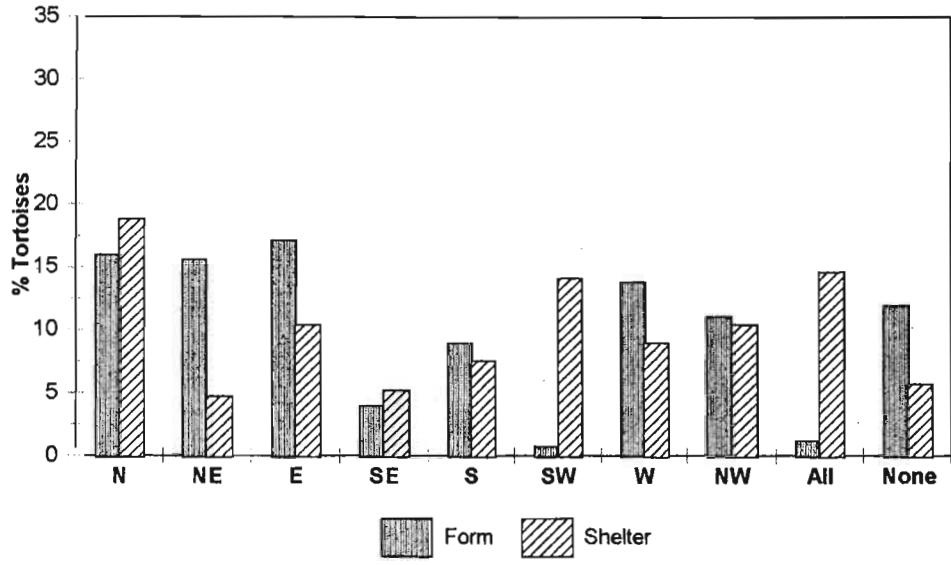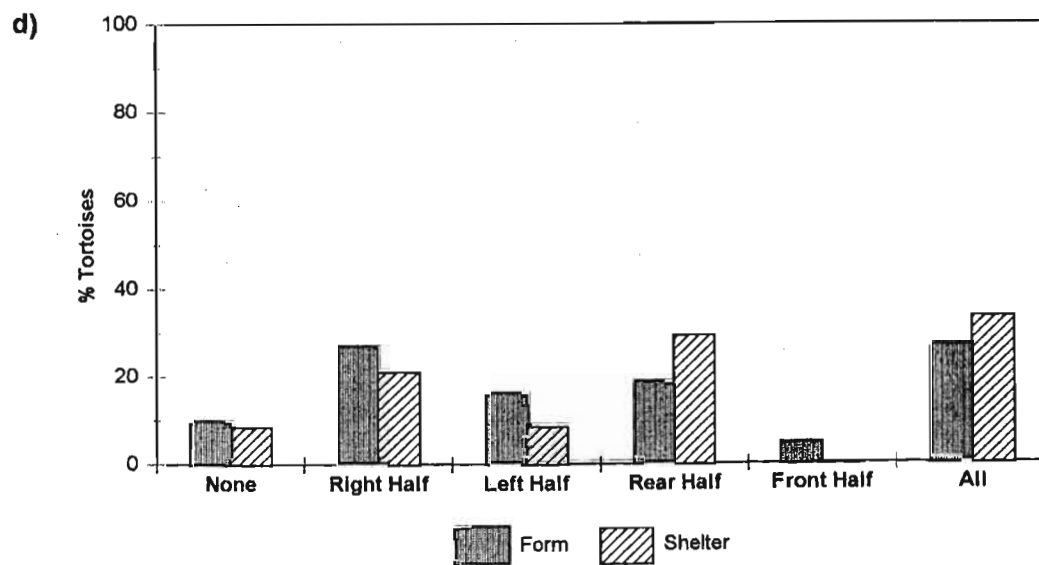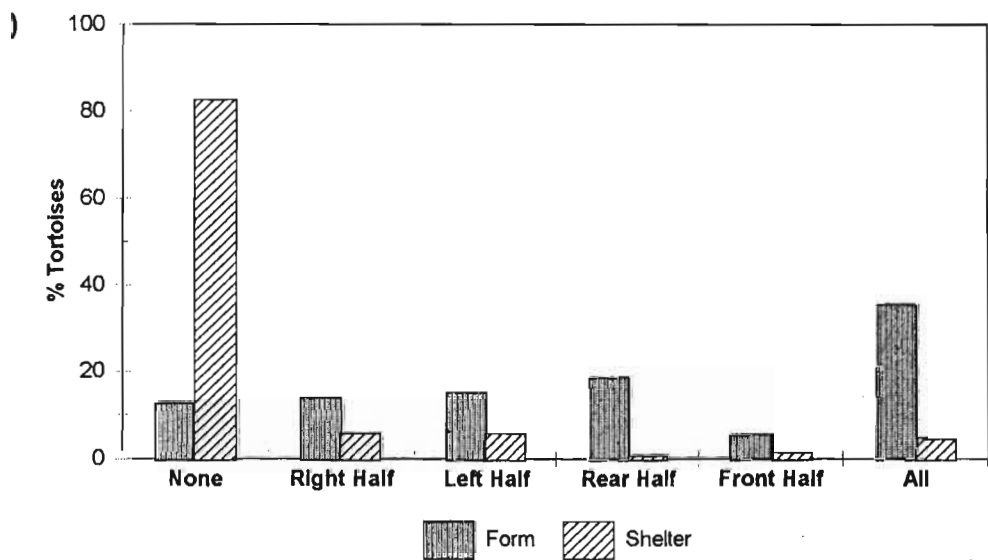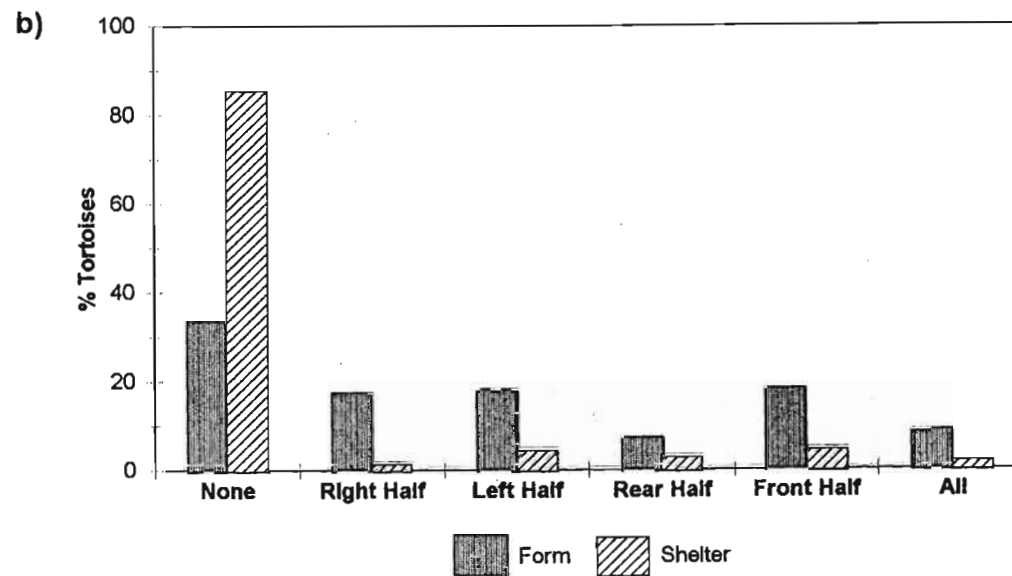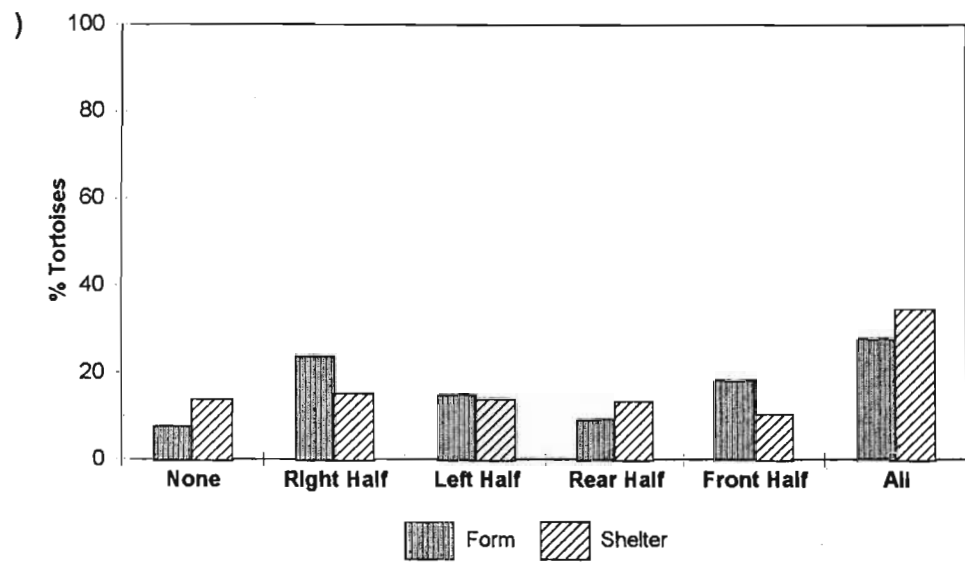
Conclusion

There were seasonal influences affecting the number of Leopard Tortoises that were captured or observed caused by a decrease in activity in cooler months, with tortoises retreating into refuges and becoming harder to find. Radio telemetry allows for an unbiased sampling period across all seasons. The low number of hatchlings captured seems to indicate a high predation pressure being exerted on eggs, nests or hatchlings, which is consistent with findings elsewhere. In this study, Leopard Tortoise females were larger than males and were larger in overall size compared with other populations. In addition, on this study site, they were found at very low densities and biomass compared to Leopard Tortoises in other habitats. This may be due to a low recruitment, competition for resources with domestic stock, an inability to cope with extreme temperatures or a low carrying capacity in this habitat for tortoises. This has implications for the conservation of this species in semi-arid areas, and must be taken into account when planning a conservation area for tortoises distributed in these regions.

Leopard Tortoises have larger home range sizes and a greater daily movement distance in the semi-arid Nama-Karoo, than those Leopard Tortoises in savannah, valley bushveld or thronveld. There was a significant difference in the home range size of telemetered vs non-telemetered tortoises. This has implications for the accuracy of estimating home ranges using a low number of recaptures, especially with the influence of seasons on activity and thus recapture probability. In comparison to Leopard Tortoises in other habitats, the larger home range size used by Leopard Tortoises in the Nama-Karoo, in conjunction with the low density and population size (see Chapter 2), has great implications with regard to the conservation of Leopard Tortoises in semi-arid regions (as well as other semi-arid tortoise species). The variation in home range size both seasonally and with regard to habitat type must be taken into account when planning

conservation efforts for tortoises in semi-arid areas and when planning the size of reserves. To conserve Leopard Tortoises in these semi-arid regions, allowance must be made for their huge home ranges, their low juvenile recruitment and low densities, in addition to the distribution of the home ranges in relation to resources and seasonal variation.

Leopard Tortoises did show a response to temperature with regard to activity. Activities in summer and autumn were performed at the same temperatures, despite the difference in the time of day at which these temperatures were reached. Tortoises initially performed the various activities at lower ambient temperatures in winter and spring, however, the time of day in spring and summer at which these were observed, was the same. The low seasonal variation in the time after sunrise at which activity behaviours were commenced, indicated that after a certain time after sunrise, Leopard Tortoises became alert, basked, walked and fed, irrespective of the ambient temperature at that time (which in spring and winter, was still very low). While tortoises are generally reported to stay inactive until temperatures rise above a certain limit, for example 18°C (Lambert, 1981), tortoises in winter and spring in this study were walking and feeding below 18°C. This may be a consequence of the tortoises having to make up energy deficits caused by hibernation through cold periods or it may be that tortoises have a limited time in the day to perform non-thermoregulatory activities, and the actual time of the day is already late morning. While temperature does have an influence on activity and activity behaviours, the time after sunrise appears to initiate tortoise activity.

Leopard Tortoises used a wide variety of refuges in the Nama-Karoo, favouring *Lycium spp*, *E. ferox*, and *O. ficus*. There was a seasonal variation in refuge use that further depended on whether the refuge was being used as a form or a shelter. Tortoises in spring and winter often remained in the same refuge for the entire season, or returned to the same form on consecutive nights. In contrast, tortoises in summer and autumn left their overnight forms to pursue non-

thermoregulatory activities and usually found refuge in different form the following night. There was seasonal and behavioural variation in the compass direction that the tortoises and the refuge exits faced, allowing tortoises to manipulate and either maximise (in spring and winter) or minimise (in summer and autumn) the amount of solar radiation received by the shell. Leopard tortoises could therefore passively thermoregulate and exert a finer control over temperature fluctuations within the environment.

In summary, Leopard Tortoises on farmland in the Nama-Karoo had lower densities, larger body sizes and much larger home ranges than Leopard Tortoises in other habitat types. These are important aspects to take into account when planning for the conservation of Leopard Tortoises in semi-arid areas, and may hold further implications for other arid or semi-arid tortoise species. Conservation areas for Leopard Tortoises in these areas must be large enough to accommodate the large home range and daily distances moved by the tortoises, and their seasonal variation in relation to resources. In addition, further investigation must be made into the density that these semi-arid regions can carry. This study indicates that the tortoises only occur at low densities and in low population numbers. Therefore care must be taken not to overstock proposed conservation areas. Further investigation is also needed to determine the reason for the low recruitment of juveniles, so that any conservation measures taken can try eliminate or minimise the causes of mortality in hatchlings and juveniles.

Activity patterns and patterns of thermoregulation allows for further understanding of the interactions between tortoises and their environment, habitat, and climate in the wild. In addition, it further aids in the understanding of the methods used by ectotherms to thermoregulate and manipulate body temperatures, especially when living in regions of unpredictable rainfall and extreme temperatures.