THE ECOLOGY AND PHYSIOLOGY OF THE SPRINGHARE (*PEDETES CAPENSIS*) IN THE EASTERN CAPE PROVINCE OF SOUTH AFRICA

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by

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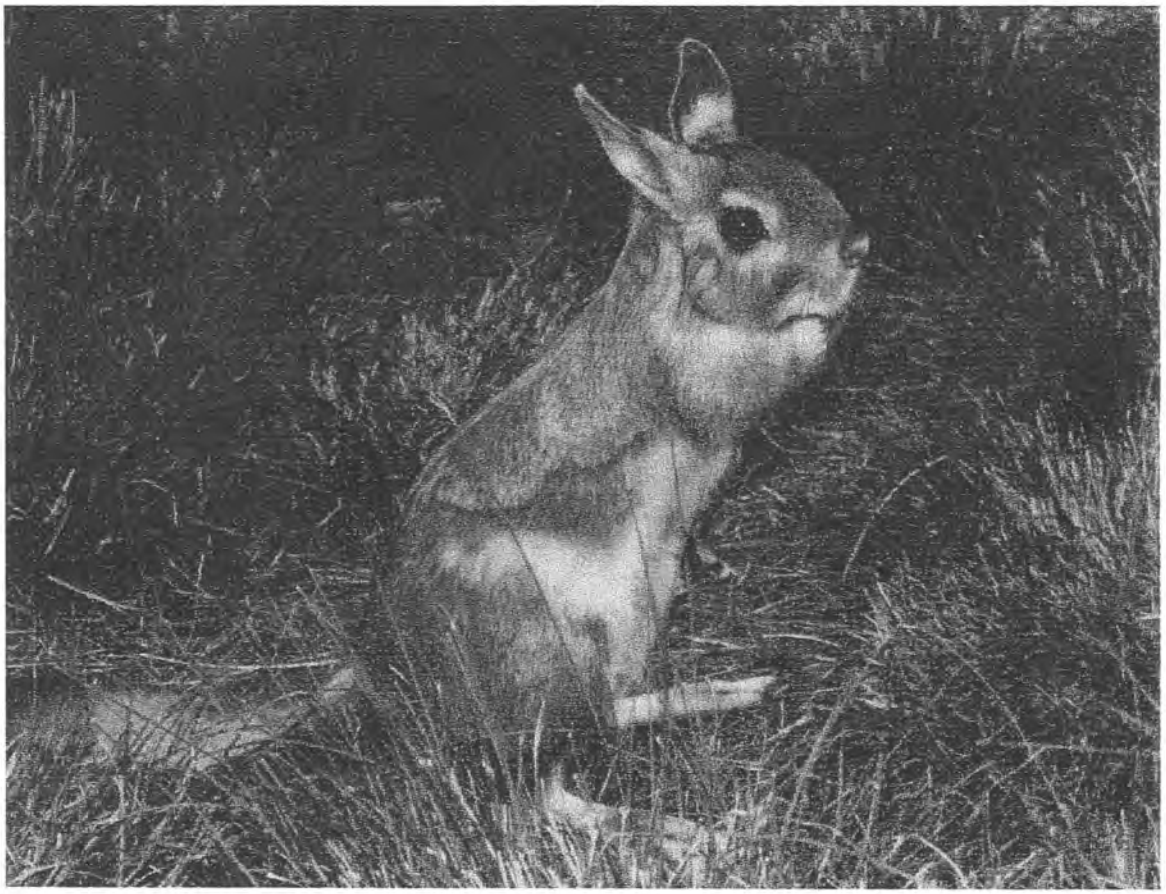

The springhare, *Pedetes capensis*

ABSTRACT

Springhare are large, bipedal, nocturnal, herbivorous, burrowing rodents that are found in arid and semi-arid parts of southern and eastern Africa. In this thesis I examine the general ecology, biology and physiology of these animals in the Eastern Cape Province of South Africa. An investigation of their distribution and activity in the study site showed that springhare exhibit a preference for flat, open, recently disturbed habitat that is dominated by the grass *Cynodon dactylon* and the sedge *Cyperus esculentus*. These two species constitute a major proportion of their diet. The impact of springhare on chicory and grazing is also discussed. Nightly activity generally peaks soon after dark and decreases in the 2-4 hour period before sunrise. This pattern is, however, modified by moonlight. Springhare typically respond to moonlight by reducing aboveground activity, shifting their activity to dark moonless periods of the night, and by reducing their use of open space. Contrary to earlier reports, springhare utilise several different burrow systems spread over large areas. They regularly change burrow systems and seldom spend more than a few consecutive days in each. Springhare do not appear to defend territories but recently used burrows appear to be avoided by conspecifics. Males and females on average use a similar number of burrows, scattered over similar sized areas. Burrows are shown to provide a stable microclimate of moderate temperature and high humidity throughout the year. Reproduction is continuous and there is no synchronised breeding season. The ability to reproduce throughout the year is attributed primarily to their ability to utilise subterranean food stores. The overall reproductive strategy of springhare (a single young with long gestation and weaning) is unusual for a mammal of this size but may be linked to low levels of adult and juvenile mortality. Physiologically, springhare are reasonably well adapted to life in hot, arid environments. They produce a concentrated urine, exhibit a high tolerance to dehydration, are good osmoregulators capable of maintaining plasma volume, osmolality and ion balance over long periods of water deprivation, and are able to produce dry faeces. They are also good thermoregulators at low ambient temperatures, which are usually encountered at night, but are poor thermoregulators at high ambient temperatures, which they avoid behaviourally.

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CHAPTER 1

INTRODUCTION

Despite their name, springhare are not hares at all, but are in fact large (3-4 kg) rodents that are rather unusual in that they are bipedal and saltatorial. They are entirely nocturnal and during the day they lie up in deep (≈ 78 cm), complex burrows from which they emerge at night to feed on the roots, rhizomes, leaves, stems and tubers of a variety of plants. They are a dark, reddish brown to sandy colour with white underparts and a long black-tipped tail. Their very short front limbs and well-developed hind limbs give them a distinct kangaroo-like appearance (see frontispiece).

Springhare are common and widespread over large parts of southern and eastern Africa (Fig. 1.1). They are particularly abundant in sandy, relatively flat, arid and semi-arid areas but are absent from areas where the substratum is not suitable for burrowing. They appear not to be dependent on free-standing water (Butynski & Mattingly 1979; Rautenbach 1982) and frequently come into conflict with agriculture (FitzSimons 1920; Shortridge 1934; Butynski 1973; Kingdon 1974; Coetzee 1979; De Graaff 1981; Rautenbach 1982; Willan 1992). In some parts of southern Africa springhare are highly sought after and of considerable value to the indigenous peoples as a source of protein (Butynski 1973; De Graaff 1981; Anderson 1996). According to Butynski (1973) in excess of 2.5 million springhare are killed for food each year in Botswana.

Ever since springhare were first described by Forster (1778), the placement of the family (Pedetidae) within the order Rodentia has baffled mammalian taxonomists. Springhare have constantly been classified and reclassified into a variety of suborders and superfamilies (for a detailed summary see De Graaff 1981). More recently, however, Carleton (1984) divided the Rodentia into two suborders, the Sciurognathi (squirrels, gophers, beavers, mice) and the Hystricognathi (porcupines, molerats, canerats). Although springhare exhibit characteristics of

both these groups, recent phylogenetic analysis of mitochondrial DNA sequences indicates that they are more closely associated with the Sciurognathi than with the Hystricognathi (Matthee & Robinson 1997a). This observation is supported by studies of rodent fetal membranes as well as reproductive and other morphological features (Luckett 1985).

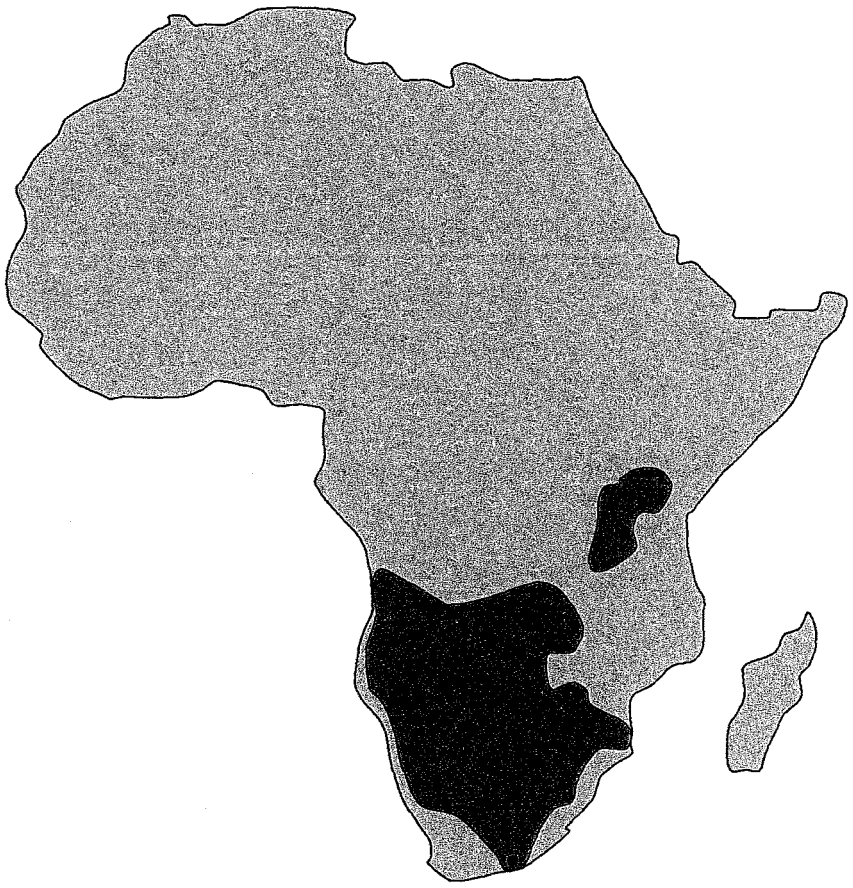

Fig. 1.1: Springhare distribution and the location (•) of the present study site (modified after Skinner & Smithers 1990).

Until recently the family Pedetidae was also widely regarded as being monotypic. The only species being *Pedetes capensis* (Misonne 1974; De Graaff 1981; Meester *et al.* 1986; Skinner & Smithers 1990; Dieterlen 1993). Recent evidence presented by Matthee & Robinson (1997b), however, suggests that the two geographical isolates, i.e. the southern African

springhare and the East African springhare can best be regarded as two separate species *P. capensis* (southern Africa) and *P. surdaster* (East Africa).

At present our knowledge of the general ecology and biology of springhare is largely due to the detailed work of Butynski (1973, 1979, 1984), Butynski & Hanks (1979) and Butynski & Mattingly (1979) in Botswana, and Anderson (1996) in the Northern Cape Province of South Africa. This information is well supplemented by a number of natural history studies (FitzSimons 1920; Shortridge 1934; Smithers 1971; Kingdon 1974; De Graaff 1981), numerous anecdotal accounts, and some additional studies on the reproductive ecology of springhare (Coe 1969; Van der Merwe *et al.* 1980; Kofron 1987) and their habitat selection and foraging behaviour (Augustine *et al.* 1995). The vast majority of this information, i.e. that of Smithers (1971), Butynski (1973, 1979, 1984), Butynski & Hanks (1979), Butynski & Mattingly (1979) and Anderson (1996) is all from very similar arid to semi-arid habitat in or bordering the Kalahari desert. The remaining studies refer to springhare in East Africa (Coe 1969; Kingdon 1974; Augustine *et al.* 1995), Namibia (Shortridge 1934), Zimbabwe (Kofron 1987) and the Orange Free State Province of South Africa (Van der Merwe *et al.* 1980), while FitzSimons (1920) and De Graaff (1981) refer to southern Africa in general. Nothing is known about the general ecology and biology of springhare from the more mesic habitats in the extreme south of their distributional range, i.e. the Eastern Cape Province of South Africa.

Physiologically, our knowledge of springhare and how they cope with the temperature extremes and lack of water encountered in the environments that they frequent can at best be described as poor. In the only previous study of this nature Müller *et al.* (1979) examined the metabolism and thermoregulatory abilities of two individuals from equatorial East Africa. They concluded that springhare are better adapted to fossorial habits than to life in arid areas and that they exhibit no special physiological adaptations to life in arid environments. This is somewhat surprising considering that springhare apparently thrive in arid areas such as the Kalahari desert (Smithers 1971; Butynski 1973, 1979, 1984; Butynski & Hanks 1979; Butynski & Mattingly 1979) and are not known to drink free water.

In this thesis I attempt to fill some of the gaps in our current knowledge of the biology, ecology and physiology of springhare. The primary objectives of the thesis can be summarised as follows:

- To examine and describe the general ecology and population biology of springhare in the Eastern Cape Province of South Africa and
- to determine what behavioural and physiological adaptations enable springhare to flourish in arid and semi-arid areas, which are characterised by the absence of free-standing water and by high diurnal and low nocturnal temperatures.

In order to achieve these objectives I start by giving a general description of the study site, i.e. location, climate, vegetation, topography and soil (Chapter 2). This is followed by detailed examinations of springhare habitat use and diet (Chapter 3), activity patterns (Chapter 4), burrow utilisation and microclimate (Chapter 5), reproduction (Chapter 6), osmoregulation and water balance (Chapter 7) and finally, metabolism and thermoregulation (Chapter 8). The most important observations and conclusions are subsequently summarised in Chapter 9.

CHAPTER 2

GENERAL DESCRIPTION OF THE STUDY SITE

2.1 LOCATION

This study was conducted near Grahamstown in the Eastern Cape Province of South Africa. A portion of the farm Marlu (33°26'S, 026°19'E), which lies approximately 30 km south-west of Grahamstown along the N2 national road to Port Elizabeth was chosen as a convenient study site. Animals for the reproductive study and for the laboratory-based physiology experiments were, however, also collected on two nearby farms, namely Thorneycroft (33°28'S, 026°15'E) and Fairfield (33°25'S, 026°19'E). Thorneycroft and Fairfield resemble Marlu in all aspects of climate, topography, soil type and vegetation.

2.2 GENERAL DESCRIPTION AND HISTORY

The main study site comprised a 226 ha area of flat grassland on the south side of the N2. It is bounded in the north-west by the N2, in the south-east and north-east by the Seven Fountains secondary road and in the south-west by a fence (Fig. 2.1). The study site is typical of the greater area inhabited by springhare in this region and was selected because it was large enough to incorporate a variety of habitat types, but small enough to allow for a detailed study of the area in the allotted time.

In the past, large sections of the natural grassland in the study site were ploughed up. Chicory is still cultivated in some of these areas (recently disturbed) but the majority of fields have been lying fallow for at least 15 years (old disturbed) and are in various successional stages of reverting back to the natural vegetation (Fig. 2.1). The sizes of individual camps, or portions

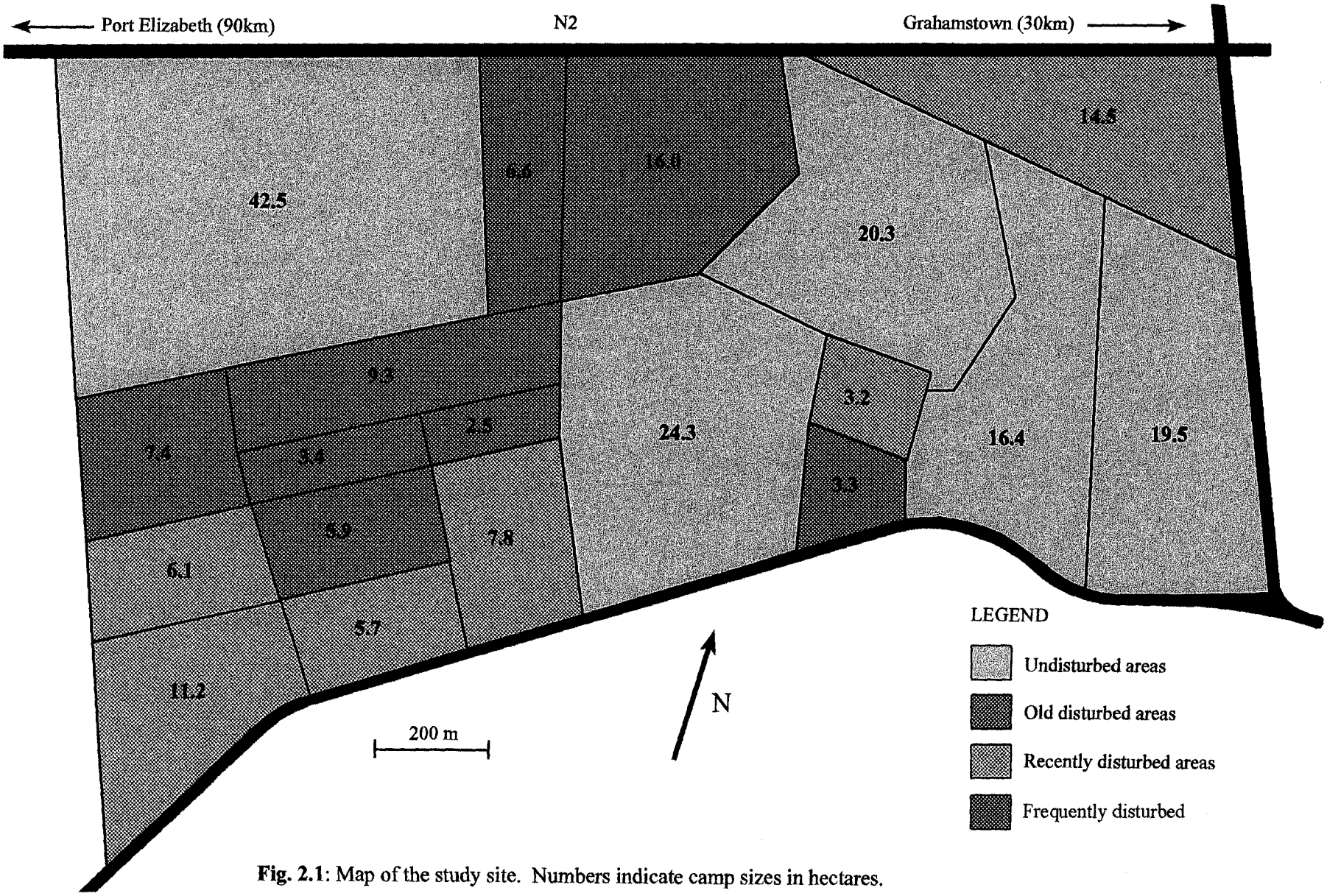

Fig. 2.1: Map of the study site. Numbers indicate camp sizes in hectares.

of camps where deemed necessary, are illustrated in Fig. 2.1. During the course of this study all camps were periodically grazed by both sheep and cattle.

2.3 CLIMATE

According to the Köppen classification the study site falls within the Cfbl climatic region which can be described as a humid, temperate (warm) climate with sufficient rainfall in all seasons (Schulze 1947).

2.3.1 Rainfall

The annual precipitation, as measured in Grahamstown, for the 23 year period 1975-1997 by the Rhodes University Department of Geography weather station, is illustrated in Fig. 2.2. Mean annual precipitation during this period was 631 ± 153 mm. Fig. 2.2 also illustrates that the annual rainfall during each of the four years of the study (1994-1997) was only slightly lower than the mean annual precipitation over the 23 year period.

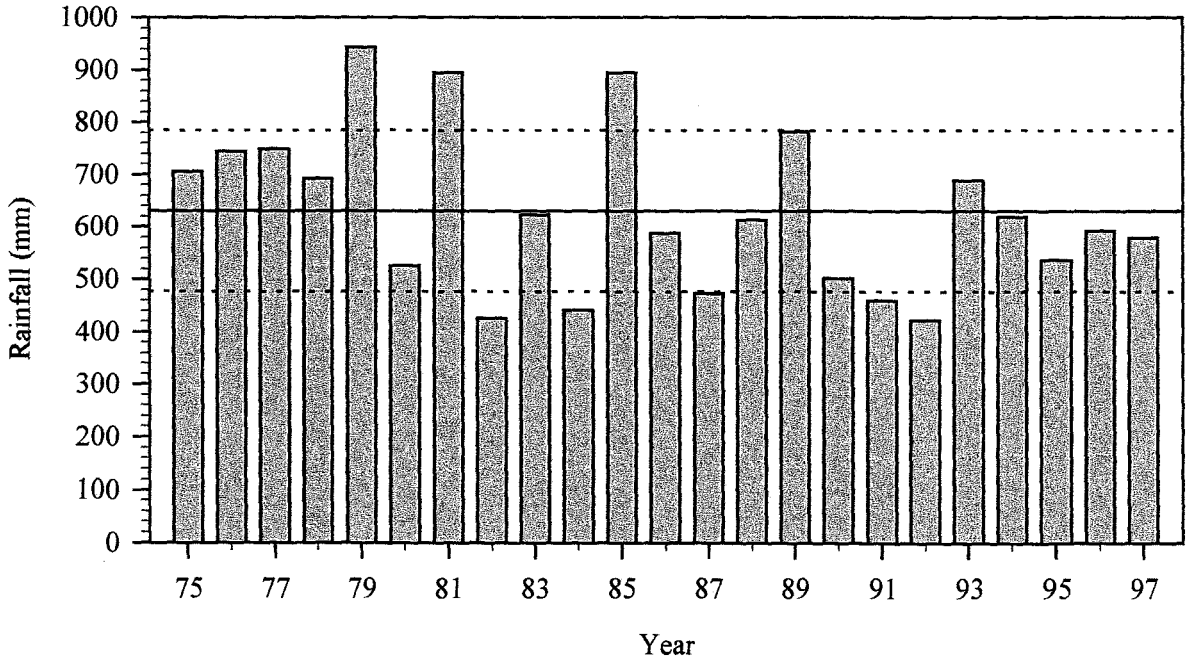

Fig. 2.2: Mean annual rainfall (solid line) ± 1 SD (dotted lines) in Grahamstown over the 23 year period 1975-1997.

The Eastern Cape is largely a transition zone of climatic types and rainfall is not as seasonal as in other parts of the country (Stone 1988; Schulze 1986). According to Schulze (1997) Grahamstown and the study site fall within an all-year rainfall region. This is illustrated in Fig. 2.3, which shows the mean monthly rainfall ± 1 SD in Grahamstown, for the period 1975-1997. From this it is apparent that on average the region obtains sufficient rain throughout the year. Rainfall, however, peaks in October and November followed by a second slightly smaller peak in February and March with the least rainfall occurring in May, June and July, the austral winter months.

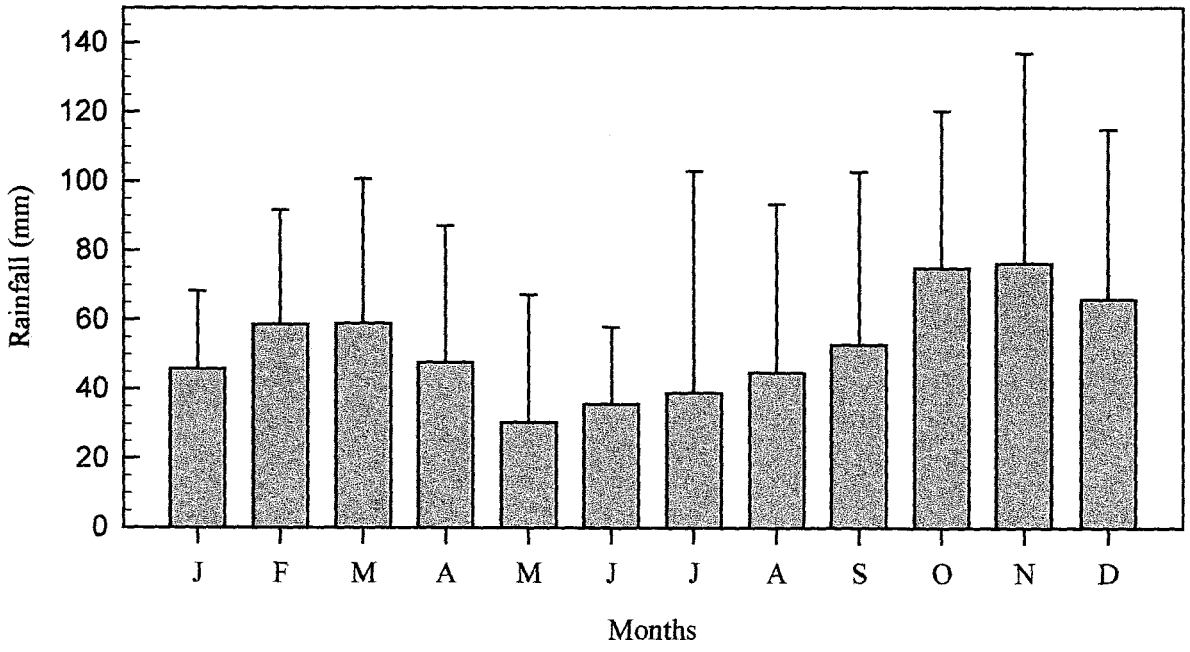

Fig. 2.3: Mean monthly rainfall ± 1 SD in Grahamstown for the period 1975-1997 (n = 23).

During the study period (1994-1997) monthly rainfall data show that winters were very dry (below average) and summers generally wet (Fig. 2.4). There were also two months of exceptional rainfall in December 1994 and November 1996. On average, the Grahamstown region experiences rain events of greater than 0.2 mm on 92-100 days per year (Stone 1988; Schulze 1986).

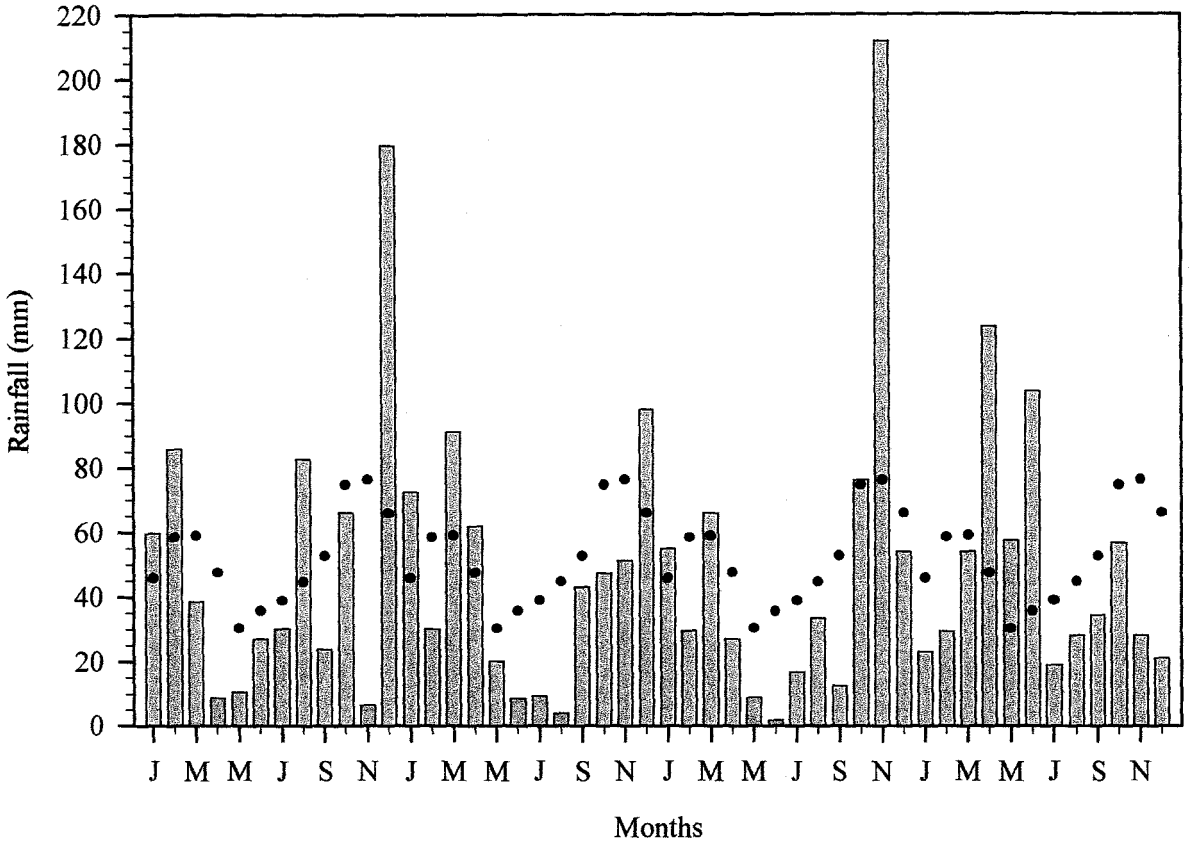

Fig. 2.4: Monthly rainfall as recorded in Grahamstown, for the study period 1994-1997. Dots indicate the mean monthly rainfall for the period 1975-1997.

2.3.2 Temperature

The mean monthly maximum and minimum temperatures as recorded in Grahamstown for the period 1985-1997 are given in Fig. 2.5. This illustrates that the climate is generally temperate and, as expected, June July and August are the coldest months whereas December, January and February are the hottest months. The mean monthly maximum and minimum temperatures for the study period (1994-1997) are also given in Fig. 2.6. Minimum temperatures generally occur at night, when springhare are active and are therefore more relevant to this study than maximum temperatures.

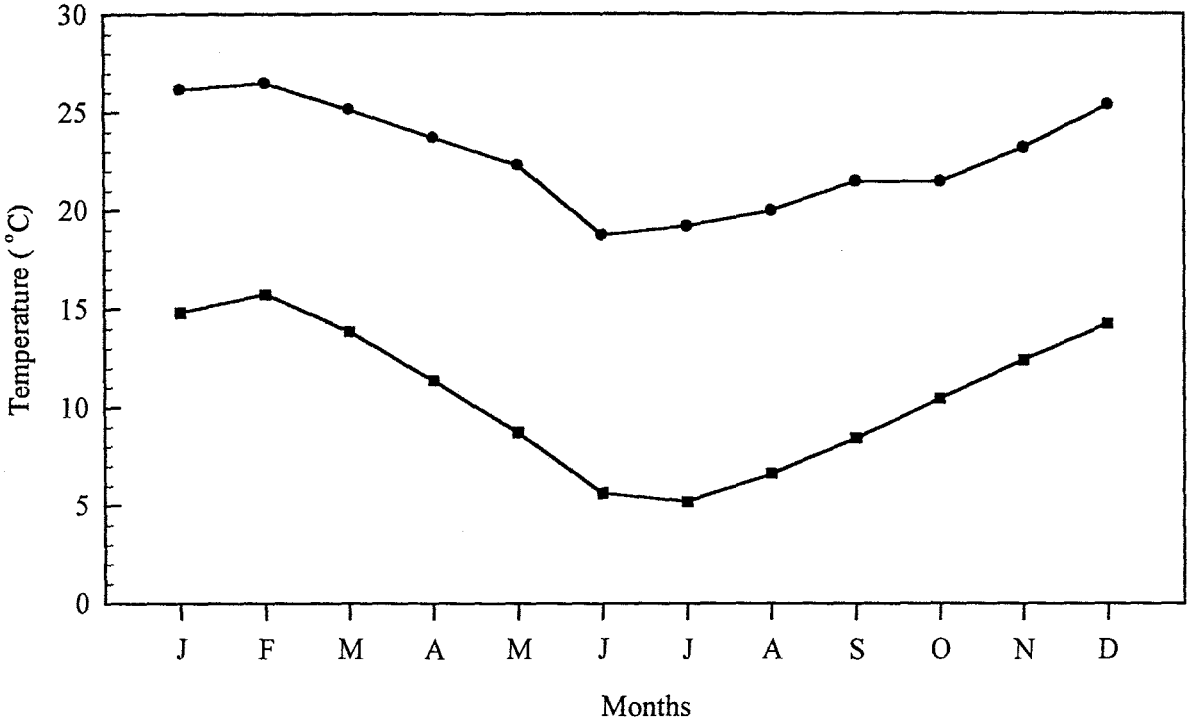

Fig. 2.5: Mean monthly maximum (●) and minimum (■) temperatures, in Grahamstown, for the period 1985-1997.

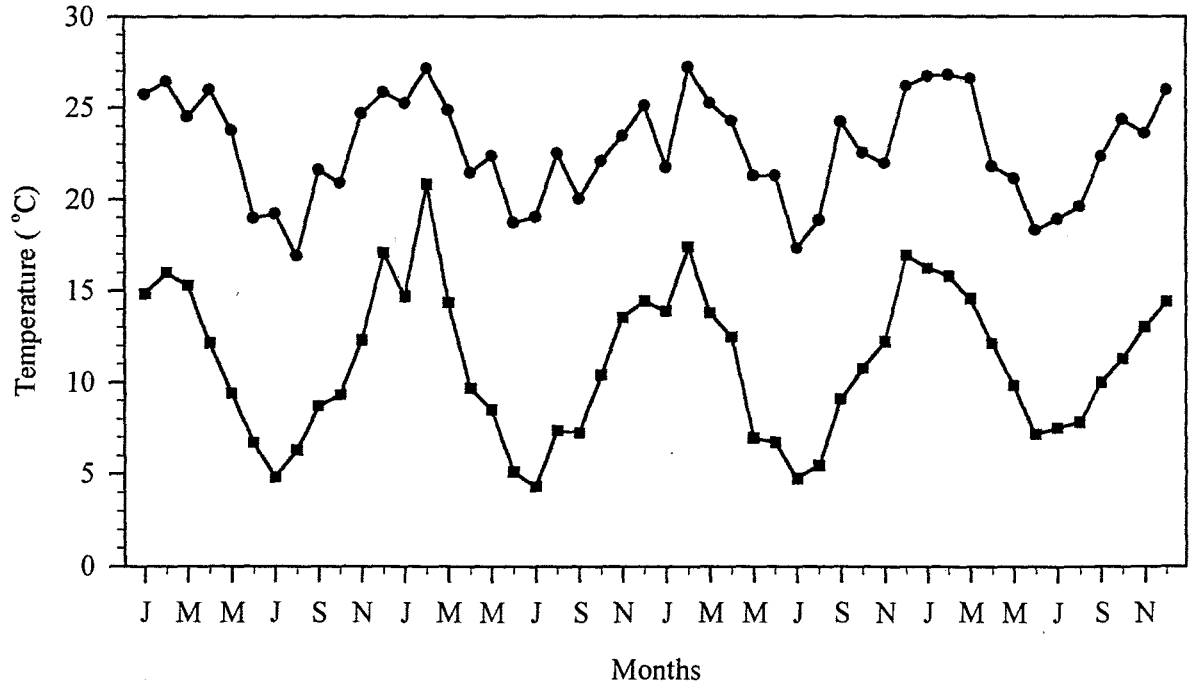

Fig. 2.6: Mean monthly maximum (●) and minimum (■) temperature, in Grahamstown, for the study period 1994-1997.

According to Schulze (1986) the hottest day likely to be encountered in this region is 45°C and the coldest night between 0 and -5°C. The coldest day likely to be experienced is 7.5°C and the warmest night 25°C. On average, 5-10 days with a temperature exceeding 35°C are experienced each year. What happens at night is, however, what is important to springhare and, on average, five nights a year are experienced where the minimum temperature exceeds 20°C and 60 nights a year where the minimum temperature exceeds 16.7°C. The average annual frequency of frosty days with a minimum temperature below 0°C is five and these five days generally occur between the 1st July and the 1st August (Schulze 1997; Schulze 1986). The mean annual temperature varies between 16 and 20°C (Schulze 1997).

2.4 VEGETATION

The study site falls virtually on the border of Acocks's False Fynbos biome and the southern form of Eastern Province Thornveld (Acocks 1988). Elements of both these veld types are apparent in the study site, although Eastern Province Thornveld appears to predominate. According to Acocks (1988) the study site falls in an area where the process of conversion of a sour grassveld into fynbos is taking place.

The natural veld is dominated by grass species such as *Eragrostis plana*, *Heteropogon contortus*, *Diheteropogon filifolius*, *Elionurus muticus*, *Sporobolus africanus*, *Tristachya leucothrix*, *Brachiaria serrata*, *Themeda triandra*, *Cynodon dactylon*, *Trachypogon spicatus*, *Ehrharta calycina* and by forbs such as *Ficinia*, *Restio*, *Senecio*, *Tephrosia*, *Helichrysum* and *Selago*. Where this has, however, been disturbed (for example in the old cultivated lands) it is dominated mainly by the grasses *Cynodon dactylon*, *Eragrostis curvula*, *Sporobolus africanus* and *Eragrostis plana*. A detailed description of the vegetation and species composition within the study site is given in Chapter 3.

2.5 TOPOGRAPHY AND SOIL

Finally, the study site is generally flat but slopes gradually downwards towards the south and east. There is a difference of only 35 m between the highest point (450 m above sea level) and the lowest point (415 m above sea level) (Fig. 2.7). The entire study site is covered by very sandy soil which is underlaid by hard clay. The depth of the soft sandy soil varies across the study site. Springhare burrows are, however, particularly abundant in areas where this sandy soil is very soft and deep (up to 1.5 m). During very wet periods water accumulates on top of the clay and the study site becomes very waterlogged. This was evident, for example, in November 1996. The lower portion of the sandy soil has distinct reddish brown and yellowish brown mottles, which are characteristic of a zone subject to periodic saturation with water (Macvicar 1991).

2.6 PREVIOUS STUDIES

Most of the previous research done on springhare has been done in more arid and seasonal environments than the present study. Smithers (1971), Butynski (1973, 1979, 1984), Butynski & Hanks (1979), and Butynski & Mattingly's (1979) work was all done in the Kalahari desert while that of Anderson (1996) was done in the neighbouring semi-arid Northern Cape Province of South Africa. These areas are climatologically very similar and are typified by a mean annual rainfall of ≈400 mm per year. Summers are typically hot (mean monthly maximum = 37°C and minimum = 11°C) and winters cold (mean monthly maximum = 27°C and minimum = -3°C) and dry with severe frost. Both of these areas are also characterised by relatively flat, sandy, semi-arid savannas and circular, flat bottomed, seasonally flooded depressions called pans.

In contrast to this, the animals used by Müller *et al.* (1979), in their examination of the metabolic and thermoregulatory abilities of springhare, were from equatorial East Africa. These animals were caught near Nairobi, Kenya which is located almost on the equator. Although annual rainfall (250-600 mm) here is very similar to that in the Kalahari desert and the Northern Cape Province, this area differs from the two aforementioned areas and the present study site

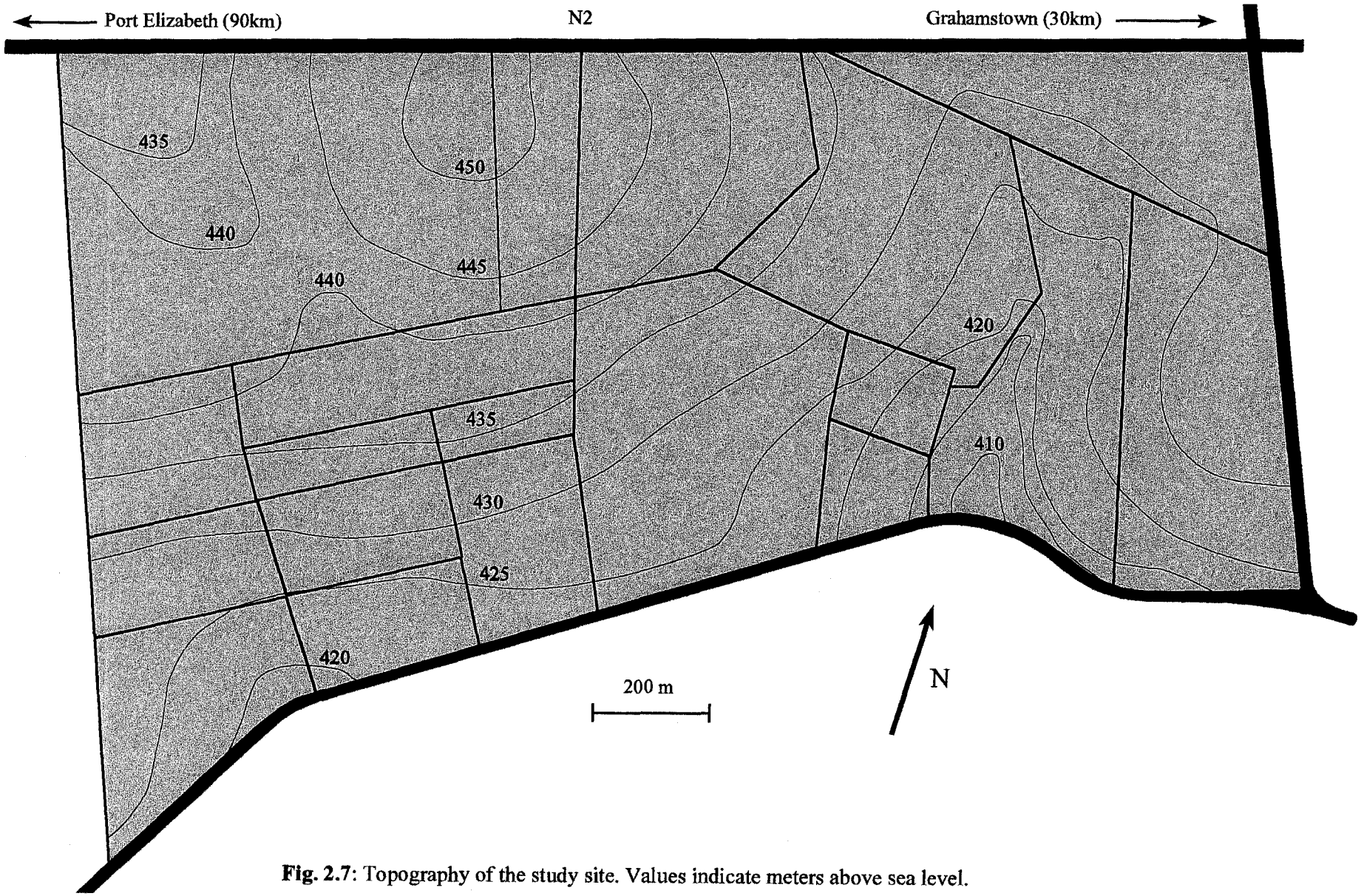

Fig. 2.7: Topography of the study site. Values indicate meters above sea level.

in that temperatures here are moderate to high throughout the year and exhibit only very slight seasonal changes.

CHAPTER 3

HABITAT USE AND DIET

3.1 INTRODUCTION

Springhare can only burrow in sandy or other soft soils. The physical nature of the substratum is consequently probably the most limiting factor in their natural distribution. Within those areas which do have a suitable substrate, springhare have been shown to exhibit a distinct preference for flat, open, short grasslands or sparsely vegetated habitats (FitzSimons 1920; Smithers 1971; Kingdon 1974; Butynski & Mattingly 1979; Coetzee 1979; Rautenbach 1982; Butynski 1984; Skinner & Smithers 1990; Augustine *et al.* 1995; Anderson 1996). According to Butynski (1984) the flood plains of rivers and swamps in northern and eastern Botswana provide the ideal habitat, whereas he has shown that springhare in the Kalahari preferentially utilise the flat, short grass areas associated with geological features known as pans, particularly the edges of these pans. Springhare in the semi-arid Northern Cape Province also show a distinct preference for this pan environment (Anderson 1996). In southern Kenya, however, where there are no pans, springhare preferentially utilise short *Cynodon* and *Cynodon/Themeda* grasslands while avoiding tall grass habitats (Augustine *et al.* 1995). Springhare also have a distinct preference for areas which have been intensively grazed by cattle and/or ungulates such as areas surrounding boreholes that provide perennial water sources, and cattle bomas (Smithers 1971; Skinner & Smithers 1990; Augustine *et al.* 1995).

Within these preferred habitats springhare have been reported to feed on the roots, stems, leaves, leaf bases, corms, rhizomes, fruits and seeds of various species, but particularly grasses (Shortridge 1934; Kingdon 1974; Smithers 1971; Jacobsen 1977; Temby 1977; Butynski & Mattingly 1979; Williamson 1987; Skinner & Smithers 1990; Watson 1992; Augustine *et al.* 1995; Anderson 1996). They are typically herbivorous, although there have also been isolated reports of springhare feeding on locusts and beetles (Woosnan quoted in Shortridge 1934;

Kingdon 1974; De Graaff 1981) as well as on carrion (O'Brien 1982). The principle food of springhare throughout their distributional range, however, appears to be couch grass (*Cynodon dactylon*) with the leaves and particularly the rhizomes being eaten (Shortridge 1934; Smithers 1971; Jacobsen 1977; Skinner & Smithers 1990; Watson 1992; Augustine *et al.* 1995; Anderson 1996). Of interest is that in the Eastern Cape springhare are also said to assist in the control and eradication of the common tulip, *Moraea polystachya* (Coetzee 1979) which is poisonous to domestic livestock (Mönnig & Veldman 1982). In the Northern Cape springhare have similarly been reported to feed on noxious *Salsola* species (Anderson 1996).

To date the most detailed study of the diet of springhare is that of Anderson (1996) in the Northern Cape Province. He found that a minimum of 20 plant species were utilised (eight grass species, five dwarf shrubs, one geophyte, five trees and shrubs and one herb). The eight grass species contributed approximately 76% of the springhare diet. Of the 20 species utilised only four each contributed more than 5% of the total diet. These were the grass species *Cynodon dactylon*, *Schmidtia pappophoroides* and *Eragrostis lehmanniana* as well as the geophyte *Gladiolus permeabilis*. These four species together accounted for approximately 74% of the total dietary selection.

Springhare can have a significant impact on preferred habitats and feeding grounds. They frequently congregate in large numbers in these areas, returning night after night to the same places (Kingdon 1971; Skinner & Smithers 1990; Augustine *et al.* 1995). In the process of feeding on roots and rhizomes they systematically dig over extensive patches totally denuding them of vegetation. Furthermore, they are highly selective and wasteful feeders often eating only the choicest parts and discarding the remainder (Shortridge 1934; Kingdon 1974; Skinner & Smithers 1990; Watson 1992; Augustine *et al.* 1995; Anderson 1996). This destructive and wasteful nature of springhare feeding, coupled with high population densities, regularly brings them into conflict with farmers in areas where springhare habitat overlaps with agriculture (Chapter 1).

In the Eastern Cape springhare are often regarded as pests of chicory, one of the most important crops grown in this region. Nevertheless nothing is known about their habitat preference, diet or impact on both natural veld and crops in this area. Both the biotic and abiotic factors in this region are vastly different to those where previous studies on springhare have been conducted. Rainfall, for example, is typically much higher, the climate less seasonal, agriculture is practised more intensely, and the natural vegetation is very different. The objectives of this chapter are, consequently, to examine springhare habitat preference and, to a lesser extent, diet composition and impact in the Eastern Cape Province. A better understanding of these factors may lead to a better understanding of the role of springhare populations and their management and control in problem areas.

3.2 MATERIALS AND METHODS

3.2.1 Springhare Numbers

To determine the habitat preference of springhare within the study site, the site was divided into 15 camps, each encompassing an area of relatively uniform vegetation type (Fig. 3.1). These divisions were based primarily on existing camps and fences. In some cases it was, however, necessary to subdivide existing camps because sections had been ploughed and cultivated and consequently had different species compositions. Information on the prior cultivation of the various camps was obtained from the farm owner and from orthophoto maps.

The number of springhare in each camp was determined by doing counts along a route which traversed the entire study site (Fig. 3.1). This route was selected in such a way as to ensure that practically the entire study site was covered with as little overlap as possible. Although this method may result in double counting this is unlikely to have occurred as the study site was divided into a number of clearly distinguishable camps and springhare seldom, if ever, move much when disturbed in this fashion. The method used was similar to that employed by Butynski (1984), Augustine (1995) and Anderson (1996). Sizes of those areas not covered by the drives due to dense high vegetation, or which were out of range of the spotlight were subtracted from the sizes of the respective camps and the number of springhare per hectare

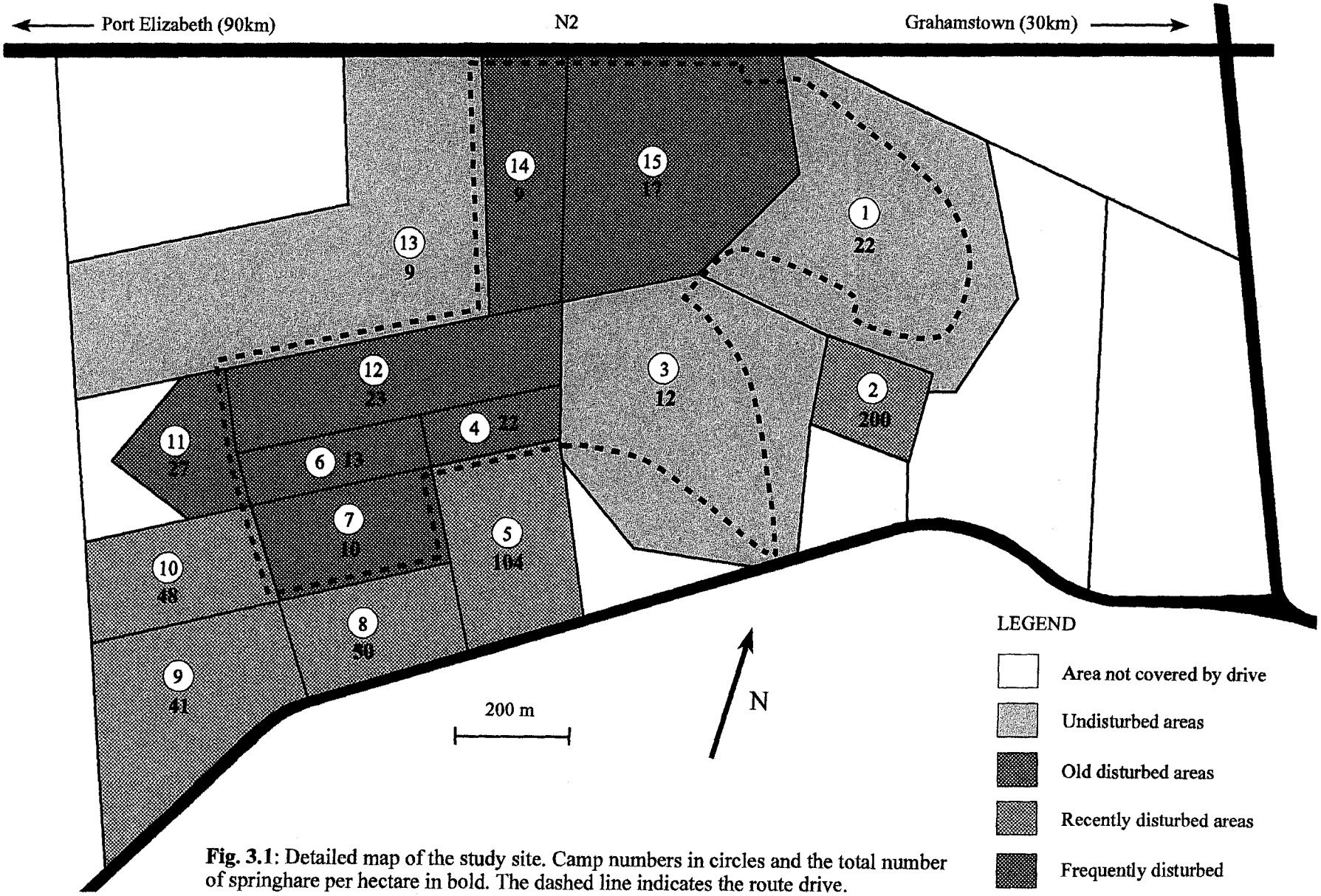

Fig. 3.1: Detailed map of the study site. Camp numbers in circles and the total number of springhare per hectare in bold. The dashed line indicates the route drive.

calculated accordingly. In total, an area encompassing 149 hectares of cultivated, old cultivated and uncultivated land was covered. This is approximately ⅔ of the total study site. The route was approximately 5 km long and took 30-40 min to complete (Fig. 3.1).

Springhare counts and observations were made from a seat mounted on top (2 m above ground) of a slow moving vehicle. A 12 volt one-million candlepower, hand-held quartz-halogen spotlight was used to detect springhare. The bright eye reflection of springhare and their habit of bobbing up and down on their hind legs when disturbed, along with the flat nature of the terrain and the height of the observer above the ground ensured that they could readily be detected at distances of up to 300 m. In places, however, a night vision telescope was also used. The number of springhare in each habitat type was recorded on a dictaphone and the data subsequently transferred to 1:10000 orthophoto maps. Counts were conducted four (Summer) or five (Winter) times a night, at about two hour intervals on 45 nights between June 1996 and September 1997. Whenever possible drives were done every Thursday night irrespective of weather or phase of the moon. Counts were, however, not conducted in thick mist due to severely impaired visibility. In total 204 drives were conducted over 45 nights. Springhare numbers were corrected for camp size and the number of springhare observed in each camp expressed as both the total number of springhare encountered (on 204 drives) per hectare and as the mean (± 1 SD) number of springhare encountered per drive per night per ten hectares.

3.2.2 Vegetation Sampling

A modified point-intercept method (Levy & Madden 1933; Goodall 1952; Cain & De Oliveira Castro 1959; Kershaw & Looney 1985; Kent & Coker 1992) of vegetation analysis was used to assess the species composition and cover in each of the camps. This survey was conducted in April and May 1997. Three points were randomly selected in each camp by starting at the approximate location of a point made on a map when blindfolded, looking down at a wristwatch and walking 30 paces in the direction of the second hand, looking down at the wristwatch again and throwing the sampling rod as far as possible in the direction of the second hand. If the point selected in this manner fell outside or within 25 m of the edge of the camp or within 50 m of a previously selected point in that camp the procedure was repeated and a

new point selected. Fifty points, at 0.5 m intervals, were subsequently sampled, in a straight line, to the North, South, East and West of each of these three central points thus giving a sample size of 3 x 201 points = 603 points per camp. Two hundred to five hundred points are generally considered to be sufficient for a detailed vegetation analysis of this type (Levy & Madden 1933; Tiver & Crocker 1951; Mueller-Dombois & Ellenberg 1974).

At each point a narrow rod, 3.9 mm in diameter, was inserted perpendicularly into the vegetation and all the species contacted recorded. All sampling was done in the complete absence of wind as this can significantly effect the results. If no vegetation was contacted bare ground was recorded. The number of points at which a given species was contacted was expressed as a percentage of the total number of points sampled, which is in turn equal to the percentage cover of that species. It is important to note that the method is a species cover method and in dense grassland the sum of the percentages of ground covered by each species plus the percentage of bare ground will exceed 100% as more than one species is covering the same unit of ground. Voucher specimens of all the species encountered during this survey are housed at the Selmar Schonland Herbarium in the Albany Museum in Grahamstown. During this survey all bare ground contacts which could be directly attributed to springhare feeding activity were also recorded.

Samples (one per species and from at least five separate plants) of some of the more common grass species within the study site were also collected each month from January-December 1997. These samples were always collected in approximately the same place and were analysed for water and energy content. Water content was determined by drying plants to constant mass at 65°C in a force-draught oven and energy content by grinding the dried plant material to a powder and bombing it in an MC-1000 Modular calorimeter (Energy Instrumentation, Pretoria). Seasonal changes in water and energy content were examined by pooling data from the winter months (March - August) and the summer months (September - February).

Springhare feeding patches encountered were also examined throughout the study period and general observations made on species, and components thereof that were eaten or discarded.

An assessment of the impact of the springhare population on the study site was also conducted. This was based on a mean population size obtained by selecting one drive, the one on which the most number of springhare were encountered, from each night i.e. a total of 45 drives and secondly, on an average ingestion capacity of 162 g of wet plant material per springhare per night (Anderson 1996). Although the average ingestion capacity of 162 g of wet plant material per springhare per night is based on measurements made in the Northern Cape Province, it is assumed to be a realistic estimate for springhare in the Eastern Cape Province as their diets are very similar.

3.2.3 Statistical Analysis

Cluster analysis was used to evaluate the grouping of the 15 camps into four main vegetation types. A Chi square test was used to determine whether or not springhare distribution within the study site was random and correlation analyses were performed to determine if springhare numbers were related to any specific plant species. Changes in the mean number of springhare observed per drive per night prior to and after various disturbances, which occurred in some camps during the study period, were examined for significance by means of t-tests. Seasonal changes in percentage water (arcsine transformed) and energy content of vegetation were similarly examined for significance by means of t-tests. Statgraphics (Version 7.0, Statistical Graphics Corporation) was used for all statistical tests and in all cases the 0.05 level of probability was accepted as indicating statistical significance.

3.3 RESULTS

The study site was composed of a mosaic of natural grassland (camps 1,3 and 13), old fallow fields in various successional stages (camps 4, 6, 7, 11, 12 and 15), recently disturbed i.e. ploughed fields (camps 2, 5, 8, 9, and 10) comprising short grasses and a frequently disturbed area (camp 14) that was devoid of all natural vegetation (Fig. 3.1). Grouping the 15 camps into these four main vegetation types was supported by a cluster analysis of species cover. All of the old fallow fields were last ploughed at least 15 years prior to this study, whereas the recently disturbed fields were all ploughed, on one or more occasion, during the course of this

study or in the three years preceding it (A. Page, pers. comm.). Of the recently disturbed camps, camps 2, 9, and 10 were all ploughed during the course of the study but had also been ploughed in the 2-3 year period prior to the study. Camp 2 was ploughed in October 1996 and subsequently left lying fallow. Camps 9 and 10 were ploughed shortly before the start of the study, again in July 1996, and subsequently planted to chicory early in September. This chicory was subsequently lifted in early April 1997 in camp 9 and in late April 1997 in camp 10, after which these camps were left lying fallow. When ploughed, recently disturbed camps rapidly returned to their former states. Even during the period when chicory was cultivated in camps 9 and 10 the pre-cultivation species were extremely abundant. Camp 14, the frequently disturbed area, was devoid of all natural vegetation because it was repeatedly ploughed from shortly before the start of this study until the end of March 1997 in an attempt to eradicate all vegetation prior to planting chicory. After chicory was planted in late March 1997 it was regularly weeded until the end of the study.

Springhare were not randomly distributed within this grassland mosaic but showed a distinct preference for specific camps ($\chi^2 = 5962$, d.f. = 14, $P < 0.001$). More springhare per hectare, than expected from a random distribution (28 per hectare) were observed in camps 2, 5, 8, 9 and 10 (Table 3.1; Fig. 3.1), with camps 2 (200 per hectare) and 5 (104 per hectare) being particularly favoured. These camps had all been disturbed during the study period or in the three years preceding it (Table 3.1) and comprised short grass. Camp 14, the frequently disturbed camp was one of the least preferred camps (Table 3.1).

A detailed vegetation composition of each camp is given in Table 3.2 for all species with a percentage cover ≥ 5%. All recently disturbed or preferred camps were dominated and characterised by a high percentage of couch grass (*Cynodon dactylon*) and the yellow nut sedge (*Cyperus esculentus*) with very few other grass species (Table 3.2). It should, however, be noted that chicory was cultivated in camps 9 and 10 for a large portion of the study period and that the vegetation survey was conducted only shortly after the chicory was harvested. Nevertheless, prior to the planting of chicory and after its harvesting these two species

Table 3.1: Camp utilization by springhare. Camps listed in order of springhare preference with those camps utilised more than expected from a random distribution (i.e. >28 springhare per hectare) in shaded portion. (RD = Recently disturbed, OD = Old disturbed, UD = Undisturbed and FD = Frequently disturbed).

Camp number	Springhare per hectare	Springhare per drive per night per ten hectares ($n = 45$)		Percentage of camp dug over by springhare	History
		Mean ± 1 SD	Range		
2	200	9.9 ± 5.7	1.0 - 30.0	6%	RD
5	104	5.0 ± 3.4	0.3 - 13.3	4%	RD
8	50	2.3 ± 2.6	0.0 - 9.8	0.5%	RD
10	48	2.4 ± 3.4	0.0 - 13.4	2%	RD
9	41	2.0 ± 2.5	0.0 - 8.8	0.3%	RD
11	27	1.3 ± 1.8	0.0 - 6.3	0%	OD
12	23	1.1 ± 1.1	0.0 - 3.7	0%	OD
1	22	1.1 ± 0.6	0.2 - 2.9	0%	UD
4	22	1.1 ± 1.3	0.0 - 5.6	0.3%	OD
15	17	0.8 ± 0.6	0.0 - 2.8	0%	OD
6	13	0.6 ± 1.0	0.0 - 4.7	0%	OD
3	12	0.6 ± 0.5	0.0 - 2.1	0%	UD
7	10	0.5 ± 1.0	0.0 - 3.4	0%	OD
13	9	0.5 ± 0.4	0.0 - 1.9	0%	UD
14	9	0.5 ± 0.8	0.0 - 3.8	0%	FD

Table 3.2: List of all species with a percentage cover of 5% or greater in each of the camps.

Species	Camp Number														
	Recently Disturbed					Old Disturbed						Undisturbed			Frequently Disturbed
	2	5	8	9	10	4	6	7	11	12	15	1	3	13	14
Arctotheca calendula	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-
Bare ground	6	6	-	20	26	-	-	-	-	-	-	-	-	9	100
Brachiaria serrata	-	-	-	-	-	-	-	-	-	-	-	5	26	9	-
Chenopodium album	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-
Conyza albida	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-
Cynodon dactylon	78	83	82	50	56	78	75	77	77	65	65	22	7	-	-
Cyperus esculentus	73	43	62	58	65	7	9	-	13	-	-	-	-	-	-
Digitaria natalensis	-	-	-	-	-	-	-	-	-	11	-	20	-	-	-
Diheteropogon filifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-
Ehrharta calycina	-	-	-	-	-	-	7	-	9	10	-	-	-	-	-
Elionurus muticus	-	-	-	-	-	-	-	-	-	-	-	5	7	6	-
Eragrostis chloromelas	-	-	-	-	-	-	-	-	-	-	8	7	7	13	-
Eragrostis curvula	-	6	-	-	-	22	9	8	34	13	71	21	30	11	-
Eragrostis plana	-	-	-	-	-	28	30	33	25	24	6	17	9	-	-

Continued on next page

Table 3.2 continued

Species	Camp Number														
	Recently Disturbed					Old Disturbed						Undisturbed			Frequently Disturbed
	2	5	8	9	10	4	6	7	11	12	15	1	3	13	14
Harpochloa falx	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-
Heteropogon contortus	-	-	-	-	-	-	-	-	-	-	-	5	6	26	-
Restio triticeus	-	-	-	-	-	-	-	-	-	-	-	22	-	-	-
Rumex acetosella	-	-	14	-	-	-	-	-	-	-	-	-	-	-	-
Senecio inaequidens	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-
Setaria sphacelata	-	-	-	-	-	-	-	-	-	18	6	-	-	-	-
Sporobolus africanus	-	-	6	-	-	35	42	45	33	33	7	23	20	8	-
Themeda triandra	-	-	-	-	-	-	-	-	-	-	-	-	39	7	-
Tristachya leucothrix	-	-	-	-	-	-	-	-	-	-	-	5	23	9	-

appeared to predominate. During the period of chicory cultivation the chicory was also heavily infested by both *Cynodon dactylon* and *Cyperus esculentus*.

In contrast to recently disturbed camps, old disturbed camps were all dominated by the grasses *Cynodon dactylon*, *Sporobolus africanus*, *Eragrostis curvula* and *Eragrostis plana* (Table 3.2). The undisturbed camps (1, 3 and 13) were more diverse than recently disturbed and old disturbed camps and were characterised by very little *Cynodon dactylon*, the absence of *Cyperus esculentus* and the presence in addition to *S. africanus*, *E. curvula* and *E. plana* of the grasses *Themeda triandra*, *Brachiaria serrata*, *Heteropogon contortus*, *Tristachia leucothrix*, *Harpochloa falx*, *Eragrostis chloromelas* and *Elionurus muticus* (Table 3.2). As previously mentioned the frequently disturbed camp 14 was characterised by the complete absence of any natural vegetation.

Springhare feeding patches were predominantly encountered in recently disturbed camps (Table 3.1). These feeding patches also occur in all other camps but because they occur at much lower densities and are much smaller they were not contacted during the point intercept survey. In the two most preferred camps (2 and 5) these feeding patches accounted for 6% and 4% of the camps cover respectively. Examination of these feeding patches indicated that springhare fed predominantly on three species, namely, *Cynodon dactylon* rhizomes, *Cyperus esculentus* tubers and, to a lesser extent on *E. curvula* leaf bases. Gross examination of the stomach contents of some animals shot for the reproductive study (Chapter 6), revealed, however, that a considerable portion of green leafy material was also consumed. Of all the plant species encountered in the study site *Cyperus esculentus* was the only species that was significantly positively correlated with springhare numbers ($r = 0.85$, $P = 0.0001$).

Surprisingly, significantly more springhare per drive per night were encountered in camps 9 and 10 when chicory was not cultivated i.e. before planting and after harvesting (Table 3.3). The same did not, however, apply to camp 14 where there was no significant difference in the number of springhare seen per drive per night prior to and after planting (Table 3.3). There was also no significant difference ($t = -1.47$, $P = 0.149$) in the number of springhare seen per drive

per night in camp 2 before (2.7 ± 0.9, $n = 17$) and after (3.5 ± 2.1, $n = 28$) it was ploughed. The mean number of springhare seen per drive per night in camp 13 did, however, increase significantly ($t = -5.72$, $P < 0.001$) from 0.33 ± 0.37 ($n = 18$) to 1.83 ± 1.07 ($n = 27$) after it was burned.

Table 3.3: Mean (± 1 SD) number of springhare per drive per night encountered in camps 9, 10 and 14 in the presence and absence of chicory. Asterisk indicates a significant difference.

Camp	Springhare per drive per night		Significance
	Without chicory	With chicory	
9	3.57 ± 2.93 ($n = 27$)	0.35 ± 0.35 ($n = 18$)	$t = 4.63$, $P < 0.001$*
10	2.54 ± 2.33 ($n = 25$)	0.15 ± 0.23 ($n = 20$)	$t = 4.57$, $P < 0.001$*
14	0.39 ± 0.63 ($n = 31$)	0.09 ± 0.00 ($n = 14$)	$t = 1.73$, $P = 0.091$

Analyses of vegetation samples of the more common grasses revealed that energy content changed very little during the course of the year. There was no significant difference in the mean energy content of plants, of the same species, collected in summer and winter. There was also very little difference between the different species (Table 3.4). Water content, however, varied considerably, both during the course of the year as well as between species and components thereof (Table 3.4). Leaves of all the species examined showed a decrease in water content during the winter months, but only in the case of *Themeda triandra* and *Tristachia leucothrix* was the change significant (Table 3.5). *Cyperus esculentus* tubers and the leaf bases of those grasses examined showed a slight, but not significant, increase in water content during the winter months whereas *Cynodon dactylon* rhizomes maintained a relatively constant water content throughout the year (Table 3.5).

Springhare population size in the area covered by the survey was conservatively estimated to be 31 ± 11 springhare ($n = 45$), or 2.1 springhare per ten hectares. Considering that each animal consumes approximately 162 g of wet plant material per night, this is an overall consumption

Table 3.4: Percentage water, in parentheses, and energy content (J/g dry weight) of some of the more common grasses encountered in the study site.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cyperus esculentus nodules	(46)	(56)	(51)	-	(61)	(61)	(61)	(59)	(59)	(60)	(63)	(56)
	10.9	16.3	18.0	-	18.7	17.5	18.5	18.8	19.3	19.3	18.9	16.9
Cynodon dactylon leaves	(59)	(61)	(51)	(42)	(38)	(39)	(38)	(38)	(38)	(43)	(50)	(46)
	17.1	13.4	16.6	17.2	16.7	16.6	16.1	17.2	16.4	16.6	16.5	16.7
Cynodon dactylon rhizomes	(55)	(57)	(63)	(56)	(55)	(55)	(52)	(47)	(50)	(54)	(58)	(57)
	21.6	17.3	17.3	16.2	15.9	16.8	15.1	16.8	16.7	16.3	17.6	16.3
Sporobolus africanus leaf bases	(68)	(66)	(66)	(66)	(64)	(63)	(63)	(63)	(63)	(61)	(44)	(54)
	19.3	16.0	16.2	15.7	16.9	14.6	16.1	16.0	16.1	16.7	16.1	16.2
Sporobolus africanus leaves	(63)	(62)	(61)	(60)	(57)	(53)	(48)	(49)	(58)	(57)	(56)	(61)
	12.4	18.4	17.2	17.6	17.0	17.2	17.4	17.0	16.7	16.6	16.7	17.3
Eragrostis curvula leaf bases	(68)	(62)	(66)	(64)	(64)	(51)	(60)	(59)	(58)	(59)	(45)	(46)
	23.1	16.8	17.1	16.1	16.0	15.1	15.7	16.5	16.4	16.7	16.9	16.3
Eragrostis curvula leaves	(62)	(60)	(58)	(54)	(59)	(45)	(49)	(45)	(54)	(53)	(53)	(57)
	14.3	17.2	16.8	17.9	16.8	17.6	17.7	17.3	17.9	17.2	17.9	17.3
Themeda triandra leaves	-	-	-	(33)	(34)	(31)	(36)	(45)	(53)	-	(60)	(51)
	-	-	-	-	-	-	-	17.2	17.0	-	17.1	16.8
Tristachya leucothrix leaves	(65)	(60)	(60)	(57)	(47)	(32)	(53)	(61)	(73)	(62)	(65)	(62)
	14.5	21.5	16.8	17.3	16.9	16.8	17.0	17.3	17.6	17.4	17.6	17.5

Table 3.5: Mean percentage water content, of some of the more common species, in summer and winter. Asterisk indicates a significant difference.

Species	Mean (± 1 SD) % water content		Significant difference
	Summer	Winter	
Cyperus esculentus nodules	57 ± 6 (n = 6)	59 ± 4 (n = 5)	t = -0.544, P = 0.600
Cynodon dactylon leaves	50 ± 9 (n = 6)	41 ± 5 (n = 6)	t = 1.983, P = 0.076
Cynodon dactylon rhizomes	55 ± 3 (n = 6)	55 ± 5 (n = 6)	t = 0.219, P = 0.831
Sporobolus africanus leaf bases	59 ± 9 (n = 6)	64 ± 2 (n = 6)	t = -1.337, P = 0.211
Sporobolus africanus leaves	60 ± 3 (n = 6)	55 ± 6 (n = 6)	t = 1.871, P = 0.091
Eragrostis curvula leaf bases	56 ± 9 (n = 6)	61 ± 5 (n = 6)	t = -0.933, P = 0.373
Eragrostis curvula leaves	57 ± 4 (n = 6)	52 ± 6 (n = 6)	t = 1.698, P = 0.120
Themeda triandra leaves	55 ± 5 (n = 3)	36 ± 6 (n = 5)	t = 5.170, P = 0.002*
Tristachya leucothrix leaves	65 ± 5 (n = 6)	52 ± 11 (n = 6)	t = 2.691, P = 0.023*

of approximately 5022 g or 34 g per hectare of wet plant material each night. As many as 64 springhare were, however, encountered on a single drive.

3.4 DISCUSSION

Springhare within the study site showed a distinct preference for recently disturbed camps or those dominated by *Cynodon dactylon* and *Cyperus esculentus*. The two dominant plant species in these preferred or recently disturbed camps, *Cyperus esculentus* and *Cynodon dactylon*, are both serious weeds of cultivated lands and disturbed ground. *Cynodon dactylon* is a hardy and important pioneer grass. It is a rhizomatous and stoloniferous mat forming perennial species, which spreads rapidly to cover any bare ground. It is a relatively good pasture grass, capable of withstanding intensive grazing, and has an average grazing value under natural conditions (Georgia 1914; Bews 1929; Martin & Noel 1960; Tainton *et al.* 1976; Müller 1984; Grabrandt 1985; Gibbs Russell *et al.* 1991; Van Oudtshoorn 1992). Although the leaves are eaten, it is the rhizomes of this grass which are particularly favoured by springhare (Shortridge 1934; Smithers 1971; Skinner & Smithers 1990; Augustine *et al.* 1995; Anderson 1996; pers. obs.). *Cyperus esculentus*, like *Cynodon dactylon,* develops lateral rhizomes. These, however, terminate in edible tubers. The plant is very competitive and reproduces by seeds, rhizomes and tubers, hence its high density in recently disturbed areas. A single plant is capable of producing over 45 000 viable seeds while one tuber can produce 1900 plants and nearly 7000 tubers covering an area of approximately 3 m^2 in diameter in one year (Grabrandt 1985; Fox & Norwood Young 1988; Gordon-Gray 1995). The tubers initially develop slowly during spring and early summer, followed by massive tuber production during late summer and autumn. Although there are no previous reports of springhare feeding on *Cyperus esculentus* it was the only species that was significantly correlated with springhare numbers. In the southern USA this plant is frequently cultivated for pasturing and for fattening pigs in autumn, these animals being very fond of its fleshy tubers (Georgia 1914).

In contrast to recently disturbed lands, springhare tended to avoid old disturbed, undisturbed and frequently disturbed camps. Old disturbed camps were characterised by the grasses

Cynodon dactylon, *S. africanus*, *E. curvula* and *E. plana* which are all good indicators of veld disturbance or mismanagement and have an average to low grazing value (Tainton *et al.* 1976; Van Oudtshoorn 1992). Undisturbed camps on the other hand contained, in addition to those species mentioned above, a high proportion of more desirable good quality grasses such as *Themeda triandra*, *Brachiaria serrata*, *Heteropogon contortus* and *Tristachia leucothrix*. The grazing value of these grasses ranges from average to very high (Tainton *et al.* 1976; Van Oudtshoorn 1992). *Themeda triandra* is widely regarded as one of the best grazing grasses and along with *B. serrata* are generally regarded as indicators of veld in good condition. That springhare largely avoided these camps is consequently quite surprising, however, the reasons for this will progressively become apparent. The very low utilisation of the frequently disturbed camp 14 is not surprising as this camp was completely devoid of all vegetation, except for a short period during which chicory was cultivated.

General examination of springhare feeding patches in the field not only confirmed that springhare were feeding predominantly on *Cynodon dactylon* rhizomes and *Cyperus esculentus* tubers, but also that they are highly selective feeders eating only the choicest parts of plants and discarding the remainder. The absence of *Cyperus esculentus* and the near absence of *Cynodon dactylon* in the undisturbed and frequently disturbed camps may consequently explain the low springhare densities in these camps. Considerable evidence of springhare feeding on *E. curvula* leaf bases was also found, substantiating previous observations by Maritz (quoted in Anderson 1996) and Temby (1977). Despite the fact that springhare are often considered to be pests of chicory and that two of the three camps in which chicory was cultivated were among the preferred camps, no physical evidence of springhare feeding on chicory was found.

Stomach content analyses revealed that in addition to *Cynodon dactylon* rhizomes and *Cyperus esculentus* tubers, considerable amounts of green leaf material are also consumed. This general grazing of leaf material was, however, practically impossible to distinguish from that of native ungulates and domestic livestock in the field. In diet studies, this green leafy material is generally identified by macroscopic and microscopic examination of the stomach contents. Springhare, however, masticate their food extremely thoroughly making the macroscopic

identification of plants or components thereof virtually impossible (Anderson 1996; pers. obs.). Individual species can be identified by microscopic examination of the epidermal structures but this is extremely time consuming and was not attempted in this study. *Cynodon dactylon* rhizomes and *Cyperus esculentus* tubers could, however, be identified on the basis of their characteristic colours and textures and stomach content analyses consequently confirmed that they are heavily utilised. Grass seeds were also occasionally found in the stomachs thus confirming earlier reports by Butynski and Mattingly (1979) that springhare feed on grass seeds when they are available even though Anderson (1996) found no evidence of this in the Northern Cape Province. Out of 120 stomachs examined no evidence of springhare feeding on insects was found.

The nutritional value of springhare food plants within preferred habitats may also explain springhare's preference for specific habitats. According to Butynski (1984), springhare food plants on the pans or preferred habitat in the Kalahari had a much higher protein, mineral and water content than those on less preferred habitats. Similarly, in East Africa the preferred habitat of springhare coincided with areas where the vegetation had markedly higher levels of crude protein and lower fibre levels (Augustine *et al.* 1995). In America, bison (*Bison bison*), elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) have been shown to preferentially select for grazing areas inhabited by prairie dogs (*Cynomys ludovicianus*) (Coppock *et al.* 1983b; Wydeven & Dahlgren 1985; Krueger 1986). This preference has largely been attributed to the improved digestibility of the plant material, higher shoot-nitrogen concentration and higher plant live:dead ratios within these areas. This, in turn, has been ascribed to the continual and intense clipping and grazing of vegetation by the prairie dogs (Coppock *et al.* 1983a, 1983b; Krueger 1986; Whicker & Detling 1988). Although the energy and water content of some of the more common grasses in the study site were examined, variation between habitat types was not and neither was protein and fibre content. It is, however, possible that species in the recently disturbed camps might have a greater nutritional value than their counterparts growing in the old disturbed and undisturbed camps due to continuous grazing by springhare, severe disturbances such as ploughing, artificial fertilization during previous cultivation and the mixing back into the soil of nutrients in the form of organic

material. Soil in the recently disturbed camps is also much softer and not as compact as that in old disturbed and undisturbed camps, presumably making it energetically cheaper to forage for rhizomes and tubers in these camps.

The study site falls in the sourveld region which is characterised by constituent grasses becoming unpalatable at a relatively early stage in growth, usually as soon as they have flowered and set seed (Scott 1955; Comins 1962; Van Oudtshoorn 1992). This is believed to be linked to a high fibre content which makes the grass both unpalatable and indigestible, although the protein content may be relatively high (Scott 1955). Grasses in this region are consequently seldom of nutritional value for more than four or five months of the year. Thus, although food might appear to be plentiful, it often is not. As autumn sets in grasses translocate reserve nutrients to the roots and leaf bases where they are stored until they are needed for spring growth (Scott 1955; Van Oudtshoorn 1992). This may explain why the water content of *Cyperus esculentus* tubers, *Cynodon dactylon* rhizomes and the stem bases of the grasses examined increased slightly or remained unchanged through winter. The ability of springhare to dig up and feed on these underground food reserves ensures that they have a plentiful and relatively stable food and water supply throughout the year even when the vegetation cannot support other herbivores (Williamson 1987). Support for this is found in the fact that Anderson (1996) measured no significant seasonal fluctuations of nitrogen, crude protein and percentage *in vitro* digestibility of springhare stomach samples. This not only suggests that springhare were on a relatively stable quality diet throughout the year but also supports the view that springhare are highly selective feeders.

Recently disturbed or *Cynodon dactylon/Cyperus esculentus* dominated camps not only provide an abundant food source but also flat open terrain which is typically preferred by springhare. *Cynodon dactylon* typically grows to a height of between 50 and 350 mm tall (Gibbs-Russell *et al.* 1991; Van Oudtshoorn 1992), while *Cyperus esculentus*, though capable of reaching a maximum height of 800 mm (Grabrandt 1985), seldom exceeded a height of 300 mm in the study site. Old disturbed and undisturbed camps on the other hand were typically characterised by an abundance of tall grass species ≈ 1000 mm in height (Gibbs-Russell *et al.* 1991; Van

Oudtshoorn 1992). Grass height on the study site did vary depending on season, rainfall and grazing by domestic livestock. This did not, however, alter the overall pattern of short and tall grass camps. It may be argued that less springhare were encountered in long grass camps due to decreased visibility of springhare in these habitats but this seems unlikely because when springhare are disturbed they immediately stand up on their hind legs, which brings their eyes to approximately 400-500 mm above ground level. This, along with the very bright eye reflection and the height of the observer above ground level, ensured that very few if any springhare were missed. The fact that no or very little evidence of springhare feeding was found in these camps supports this.

Flat open terrain not only facilitates social behaviours such as mate-finding but also provides ideal conditions for predator detection and avoidance by springhare (Kingdon 1974; Butynski 1984; Augustine *et al.* 1995; Anderson 1996). Rabbits (*Oryctolagus cuniculus*) in southern Spain, which typically use well vegetated patches during the day have similarly been shown to avoid these patches and preferentially utilise open grassland at night (Moreno *et al.* 1996). This has been attributed to the fact that they are hunted by carnivorous mammals that need cover to stalk them. Moreover springhare's bipedal hopping mode of locomotion relies heavily on balance and is most unsuitable for high speed movement across broken, irregular or densely vegetated terrain (Kingdon 1974). This is substantiated by the relative ease with which animals are captured under these conditions. Initially it was thought that bipedal hopping had evolved amongst desert and plains-dwelling mammals due to the lower energetic cost of this form of locomotion in these environments; this was subsequently refuted (Thompson *et al.* 1980). Consequently bipedality must have benefits other than those related to the energetic costs of locomotion and it is now thought that this form of locomotion has evolved as a result of its advantages for avoiding attacks by predators in flat open terrain (Thompson *et al.* 1980).

The fact that camps 9 and 10, in which chicory was cultivated for a large part of the study period, were amongst the preferred camps creates the impression that springhare might have been attracted to these camps by the chicory. This was, however, not the case and significantly less springhare were found in these camps during the periods when chicory was cultivated than

when the camps were fallow. That there was no significant difference in the number of springhare found in camp 14 prior to and during chicory cultivation can be ascribed to the already low numbers encountered in this camp prior to the planting of chicory due to continuous tilling of the soil and consequent lack of vegetation. Chicory is cultivated for its thick, very bitter, fleshy roots which are dried and used as a substitute or additive for coffee. Considering springhare's preference for underground roots and tubers and the fact that this crop is readily attacked by other grazers such as common duiker (Coetzee 1979) it is surprising that springhare appear to avoid it. The answer to this may lie either in the extremely bitter taste of the root and/or in the method in which chicory is cultivated. Chicory is typically planted in parallel raised rows with each row raised approximately 300 mm above ground level. This creates an extremely uneven surface and poses serious impediment to bipedal hopping locomotion.

Springhare are often blamed for serious damage caused to chicory crops by common duiker, which not only cause severe damage to the leaf stock but also actively dig to expose and eat the root. Results of this study indicate that springhare typically avoid cultivated chicory and no evidence of springhare feeding on chicory roots or leaves was found in this study. Damage caused to chicory by springhare is rather of an incidental nature due to the exposure of the root while feeding on *Cynodon dactylon* and *Cyperus esculentus* rhizomes and tubers and this largely occurs only around the edges of cultivated lands.

The burning of camp 13 midway through the study provided the opportunity to examine the effect of a disturbance of a different nature. After burning, significantly more springhare were encountered in this camp thus confirming earlier reports by Rautenbach (1982). Whether this increase was due to the decreased height and density of the vegetation or an improvement in the forage quality i.e. new green shoots, or a combination of these factors is, however, unknown. The ploughing of camp 2 during the study caused a temporary decrease in springhare numbers in this camp. Numbers, however, increased rapidly and there was no significant difference in the number of springhare prior to and after ploughing. Continual ploughing and

subsequent abandonment of camps, in this region resets succession and ensures the continued dominance of *Cynodon dactylon* and *Cyperus esculentus*.

Springhare themselves can also have profound effects on preferred habitat types (Butynski 1984; Anderson 1996). In the process of digging up rhizomes, roots and tubers springhare can totally denude large patches of vegetation. These patches are typically well worked over and devoid of all living vegetation. In this study small feeding patches of less than 500 mm in diameter were scattered all over preferred camps. Feeding patches of 2-3 m in diameter and greater were also common. Although only an insignificant proportion of most camps were dug over, these patches accounted for 6% and 4% of the total cover in the two most preferred camps. In the Northern Cape Province springhare feeding patches measuring in excess of 240 m^2 have been reported. These large feeding patches are subsequently used predominantly by black wildebeest (*Connochaetes gnou*) and blesbok (*Damaliscus dorcas phillipsi*), not for grazing, but rather for various territorial activities (Anderson 1996). According to Anderson (1996) these disturbed patches are rich in nitrogen due to high concentrations of discarded plant and faecal material and are quick to produce grass shoots following summer rains. Springhare in turn then preferentially selected these green areas. In the Eastern Cape springhare feeding patches are rapidly recolonised by *Cynodon dactylon* and *Cyperus esculentus*. Many of these patches, particularly the larger ones, appear to be used repeatedly. This continuous disturbance by springhare, like ploughing, appears to favour the pioneer species *Cynodon dactylon* and *Cyperus esculentus* which are in turn favoured by springhare.

Finally the organic matter consumption by springhare on the study site was estimated. If each springhare consumes approximately 162 g of wet plant material per night (Anderson 1996) then the estimated population of 31 springhare consume approximately 5022 g in total or 34 g per hectare of wet plant material each night. It is, however, important to note that most of the feeding occurs in only five camps covering 34 hectares and not over the entire study site. Consequently, in these five camps, springhare consume approximately 148 g per hectare of wet plant material each night. The 162 g of wet plant material consumed each night is based on the mass of the stomach content of the ten heaviest stomachs collected out of a sample of 243

springhare shot in the Northern Cape Province and on the assumption that springhare fill the stomach only once a night. Consequently this value is only an estimate. With regard to farming, the effect of springhare on the available grazing can perhaps best be visualised by equating springhare to sheep. If a single springhare consumes approximately 162 g of wet plant material each night and a single adult non-reproductively active sheep consumes in the vicinity of 1000 g of organic matter a day (Arnold & Dudzinski 1967; Arnold 1975) then one springhare consumes approximately 16% of the amount that one sheep does in one day.

When comparing springhare to domestic livestock, such as sheep, it is however important to keep in mind that a large amount of the organic matter consumed by springhare originates from underground sources which are generally unavailable to ungulates. In the process of foraging for these underground food sources springhare do however destroy the above ground portions which are available to other herbivores. Furthermore springhare in the study site avoided undisturbed natural vegetation which is where the grasses with the highest grazing value are found and spent a considerable amount of time feeding on *Cyperus esculentus* tubers, which are of little consequence to domestic livestock as they do not eat this plant at all. Thus although the potential for competition between springhare and domestic livestock does exist, on the study site it appears to occur only on a very limited scale.

In conclusion, the observed patterns of habitat use indicate that springhare in the Eastern Cape preferentially utilise the short grass *Cynodon dactylon/Cyperus esculentus* dominated habitats found in recently disturbed camps. These camps not only provide a suitable environment for predator detection and avoidance but also facilitate social interactions such as mate finding and provide an abundant good quality and stable food supply throughout the year. As previously suggested by Augustine *et al.* (1995) in Kenya and Rautenbach (1982) in the Transvaal, springhare habitat preferences in the Eastern Cape are compatible with modern farming and agricultural practices. Although springhare only appear to have a relatively low impact in the study site, in arid and semi-arid environments as well as in areas where preferred crops or pastures are grown their destructive feeding habits may have more severe consequences.

CHAPTER 4

ACTIVITY PATTERNS

4.1 INTRODUCTION

Activity patterns adopted by animals are generally regarded as the outcome of two conflicting demands, namely, the activity required to maximise nutritional, social and reproductive objectives, and the need to minimise the costs and risks imposed by the environment (Rosenzweig 1974). A great deal of work has been done on the activity patterns of small mammal and the factors affecting them, particularly with regard to small desert rodents. By means of a variety of different techniques such as live trapping (Price *et al.* 1984), seed removal (Bowers 1988), sand-tracking (Wolfe & Summerlin 1989), recording feeding stations (Lockard & Owings 1974), roadside surveys (Kline 1965; Kaufman & Kaufman 1982; Haspel & Calhoon 1993; Twigg *et al.* 1998) and radiotelemetry (Alkon & Saltz 1988; Cresswell & Harris 1988; Daly *et al.* 1992; Julien-Laferrière 1997; Rogowitz 1997), it has been shown that time of year, time of night, light intensity and various weather variables can significantly affect the activity of small nocturnal animals.

At present very little is known about springhare activity and the biotic and abiotic factors which affect it. Although springhare activity patterns are discussed at length by Anderson (1996), Butynski's (1984) work on springhare in Botswana provides the only quantitative data on springhare activity and the factors affecting it. Observations made by Butynski (1984) are largely supported by Anderson (1996) as well as by a number of anecdotal accounts from other springhare studies There are, however, occasional contradictions.

At present we know that springhare are strictly nocturnal and, bar the odd occasion (Kingdon 1974; Anderson 1996), are generally never encountered during daylight or twilight hours (Smithers 1971; Butynski 1984; Augustine *et al.* 1995). They have been shown to have only

a single nightly activity peak with the number of animals active generally increasing steadily during the first five hours after sunset, thereafter remaining relatively constant during the middle four hours of the night before decreasing during the four hours prior to sunrise (Butynski 1984; Anderson 1996). Moonlight, although having no significant effect on the number of springhare active (Butynski 1984), has been shown to significantly affect the distance that springhare forage from their burrows (Butynski 1984; Anderson 1996). With regard to weather, temperature has a significant positive effect on activity (Butynski 1984), wind has been suggested to have a negative effect on activity (Anderson 1996), and there are contradictory reports as to whether or not springhare are active in rain (Kingdon 1974; De Graaff 1981; Rautenbach 1982; Butynski 1984; Anderson 1996).

Preliminary observations made prior to the start of the present study suggested that many of Butynski's observations of activity patterns in Botswana might not hold true of springhare in the Eastern Cape. A detailed examination of springhare activity and the factors affecting it was consequently initiated. The objective was to determine not only the effects of time of year, time of night, level of illumination, temperature, rain, windspeed, dew and humidity on springhare activity in the Eastern Cape, but also to determine just how well these variables describe the activity patterns observed in the study site. A better understanding of springhare activity will not only clarify the present situation but may also have important implications for springhare management strategies.

4.2 MATERIALS AND METHODS

4.2.1 Surface Activity

Springhare activity was examined by counting the number of springhare active in the study site at different times of the year, times of night and under different conditions of weather and moonlight. Springhare were considered to be active when above ground and inactive when in their burrows. The method used is described in Chapter 3 and data were collected simultaneously. Counts of springhare were conducted while driving a fixed route through the study site every Thursday night irrespective of weather or phase of the moon (see Chapter 3).

Drives were conducted four times per night during the short mid-summer months (December, January and February) and five times per night for the remainder of the year. They began approximately two hours after sunset and were repeated at intervals of approximately two hours throughout the night with the last drive beginning two hours before sunrise. Prior to the start of each drive the wet and dry bulb temperature (°C), windspeed ($m.s^{-1}$), level of illumination, and the presence and intensity of dew and rain were recorded. Standard wet and dry bulb mercury thermometers were used to measure wet and dry bulb temperatures and windspeed was measured with a hand-held anemometer. The level of illumination took cloud cover and phase of moon into consideration and was subjectively categorised as 1 = new/no moon, 2 = crescent moon (less than quarter moon), 3 = gibbous moon (quarter moon to full moon) and 4 = full moon (± 2 days either side). On cloudy nights the level of illumination was subjectively adjusted to the appropriate level. Intensity of rain and dew was classified as 1 = none, 2 = mild and 3 = heavy.

4.2.2 Burrow Activity

Activity at 31 different burrow systems was monitored by means of modified passive infra-red burglar alarm sensors connected to an MC-Systems 120 data logger. Each of four sensors was placed at a different entrance to a single burrow system. Only burrow systems that showed signs of fresh springhare spoor and digging activity were monitored. Sensors were mounted on stakes at the burrow entrances and any long grass and other vegetation that might affect the sensors was cleared. Sensors were usually left at a burrow system for three to four nights and then moved to another burrow system. During an initial trial period the system was set up at burrows occupied by radio-collared animals whose presence and absence from the burrows could be monitored. The fact that these animals returned to the same burrow the following morning was taken to indicate that the sensors did not affect the use of the burrows by the animals.

Because the minimum time interval at which the data logger could record events was one minute, sensors were modified with electronic timers so that once triggered they remained activated for one minute. Each sensor could consequently only detect one trigger event per

minute. Light emitting diodes in the sensors were also disconnected to prevent unnecessary disturbance. In order to save memory and prolong operational time the data logger was programmed to sample once every minute but to record only the average voltage from each sensor every five minutes. The total voltage recorded in each five minute log period was thus proportional to the number of trigger events. A voltage of 1200 mV, for example, indicated that a specific sensor, had been triggered at least once each minute in the preceding five minutes. Similarly a voltage of 240 mV indicated that the sensor had been triggered only once in the preceding five minutes. Data were stored by the logger on an E-PROM module. After each session the module was returned to the laboratory where the data were subsequently downloaded onto a computer for analysis.

4.2.3 Statistical Analysis

To determine which of the variables measured had a significant effect on springhare activity a stepwise regression was performed. Radians were used for the cyclic variables time of year and time of night as these are circular and not linear variables (Batschelet 1981; Bell 1997). Data were subsequently linearised by taking the sin and cos thereof. Relative humidity data (%) were arcsine transformed prior to statistical testing. Parametric one way analyses of variance tests were also performed to determine whether or not there were significant changes in the mean number of springhare encountered at different times of the year, times of the night and levels of illumination. Where significant differences were detected multiple range tests were performed to determine where they lay. The mean number of springhare encountered per drive prior to and after moonrise and moonset were examined for significance by means of t-tests. All data were analysed using Statgraphics (Version 7.0, Statistical Graphics Corporation) and in all cases the 0.05 level of probability was accepted as indicating statistical significance.

4.3 RESULTS

Stepwise regression analysis revealed that time of year, time of night and level of illumination all had a significant effect on the number of springhare active (Table 4.1). Temperature, humidity, wind and dew had no significant effect (Table 4.1). Rain was excluded from the

analyses due to insufficient data. Time of year, time of night and level of illumination were found to explain 43% of the variation in the data (R^2 = 0.433) and the model was highly significant (F = 26.284, P < 0.001).

Table 4.1: Significance level of each of the independent variables time of year, time of night, temperature, humidity, level of illumination, wind and dew on the nocturnal activity of springhare.

Variable	Coefficient	Significance level
Constant	6.716	0.417
sin (time-of-year)	-5.416	< 0.001
sin (time-of-night)	-7.048	< 0.001
cos (time-of-year)	-5.434	0.002
cos (time-of-night)	16.216	< 0.001
Temperature	0.370	0.198
Humidity	0.024	0.722
Level of illumination	-3.175	< 0.001
Wind	-1.385	0.077
Dew	-0.981	0.401

The effect of time of year on the number of springhare active is largely reflected in Fig. 4.1. The number of springhare active above ground decreased significantly from a mean of 25 ± 15 and 24 ± 12 springhare per drive in winter (Jun, Jul & Aug) and spring (Sep, Oct & Nov), respectively, to a mean of 17 ± 7 and 16 ± 9 springhare per drive in summer (Dec, Jan & Feb) and autumn (Mar, Apr & May), respectively (F = 7.601, P < 0.001).

As the level of illumination had a significant effect on the number of springhare active, the effect of time of night on springhare activity is best illustrated by examining the number of springhare active throughout those nights during which the level of illumination did not change. This occurred only on new moon and clear, full moon nights i.e. the moon did not rise or set. Results indicate that during the six long (winter, spring and autumn) new moon nights

examined the mean number of springhare active at each time interval remained relatively constant at approximately 29 ± 12 for most of the night but decreased significantly ($F = 3.756$, $P = 0.016$) two hours before sunrise to 10 ± 4 (Fig. 4.2A). During this period considerably fewer springhare were active on the five full moon nights than on the new moon nights and activity decreased earlier. On these nights the mean number of springhare active remained fairly constant at approximately 20 ± 5 during the first half of the night before decreasing approximately four hours before sunrise (Fig. 4.2A). By ten hours after sunset the mean number of springhare active was significantly different to that after two, four and six hours, but not from that after eight hours ($F = 5.368$, $P = 0.005$).

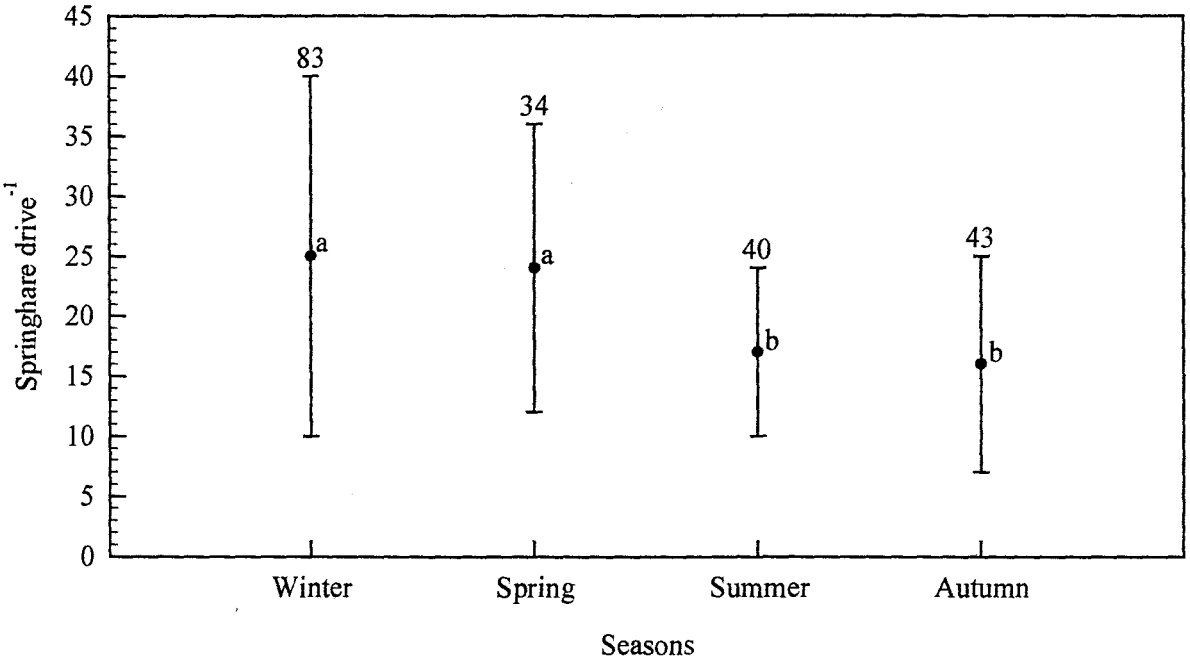

Fig. 4.1: Mean (± 1 SD) number of springhare per drive encountered in each of the four seasons. Numbers indicate sample sizes and shared letters indicate no significant difference.

During the short (summer) new moon and full moon nights the number of springhare active followed the same basic activity pattern but activity did not decrease as dramatically two hours before sunrise (Fig. 4.2B). On the three new moon nights examined the mean number of springhare active remained relatively constant at approximately 19 ± 3 for most of the night and

decreased slightly, but not significantly ($F = 1.862$, $P = 0.214$), to 13 ± 6 animals, two hours before sunrise (Fig. 4.2B). Fewer springhare were once again encountered on the full moon nights. The overall pattern of activity on these two nights was, however, the same as on new moon nights with the number of springhare active remaining constant at 14 ± 4 for most of the night and decreasing only slightly to 10 springhare, two hours before sunrise. Due to the small sample size results could, however, not be tested statistically.

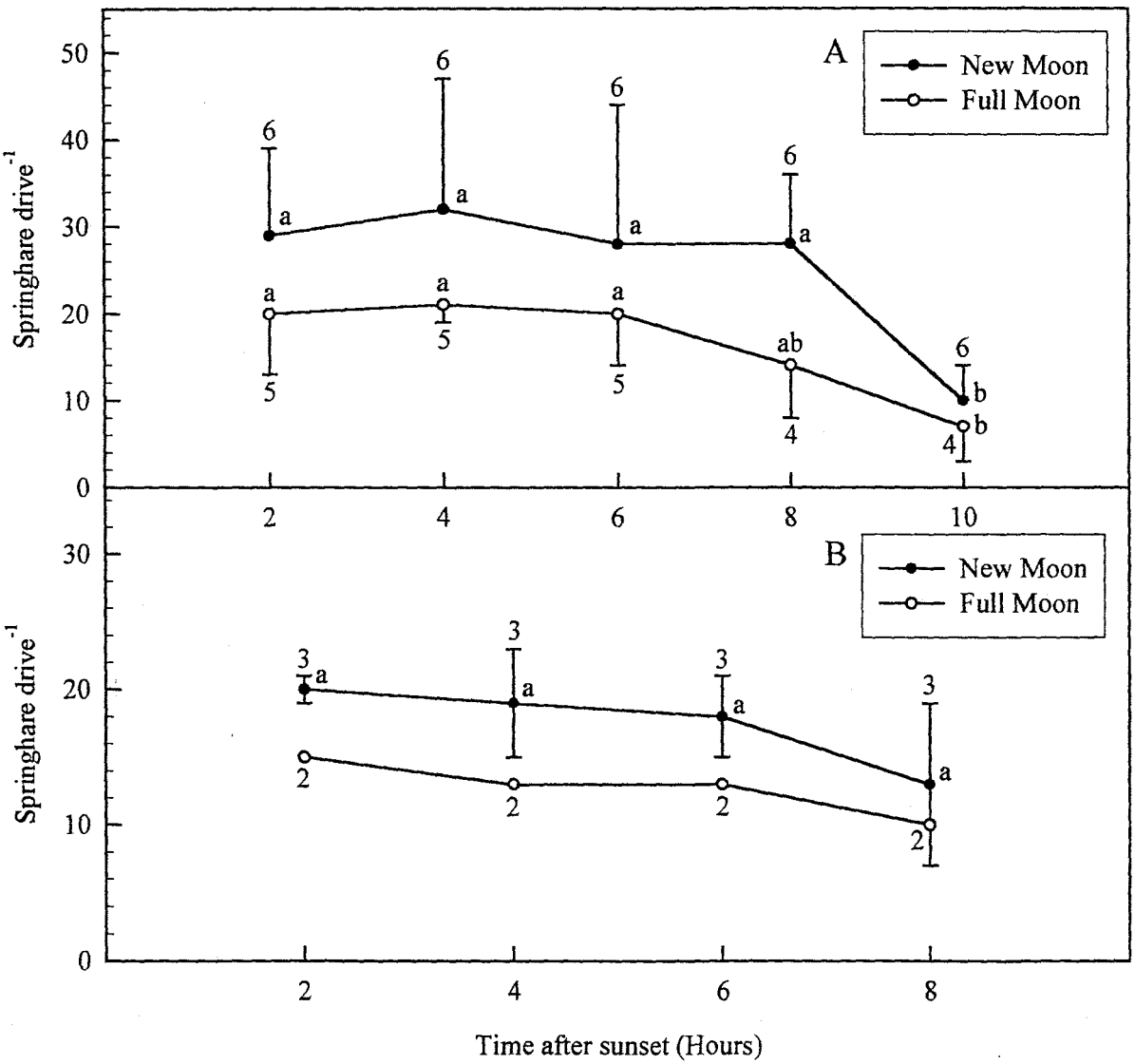

Fig. 4.2: Mean (± 1 SD) number of springhare encountered per drive at new and full moon during the long winter spring and autumn nights (A) and the short summer nights (B). Numbers indicate sample sizes and shared letters indicate no significant difference. New moon nights are, however, not statistically compared to full moon nights or short nights to long nights.

It is already apparent that fewer springhare are active at full moon than at new moon. The effects of moonlight on springhare activity are, however, best illustrated when the mean number of springhare active two hours after sunset at new/no, crescent, gibbous and full moon are compared. Two hours after sunset was chosen as springhare had reached peak activity by this time and also because all four phases of the moon were encountered during this period. The mean number of springhare encountered per drive decreased from 30 ± 13 at new/no moon through 19 ± 9 at crescent moon to 13 ± 10 at gibbous moon, after which it increased slightly to 15 ± 9 at full moon (Fig. 4.3). Significantly more springhare were encountered at new/no moon than during any of the other lunar phases ($F = 6.341$, $P = 0.001$).

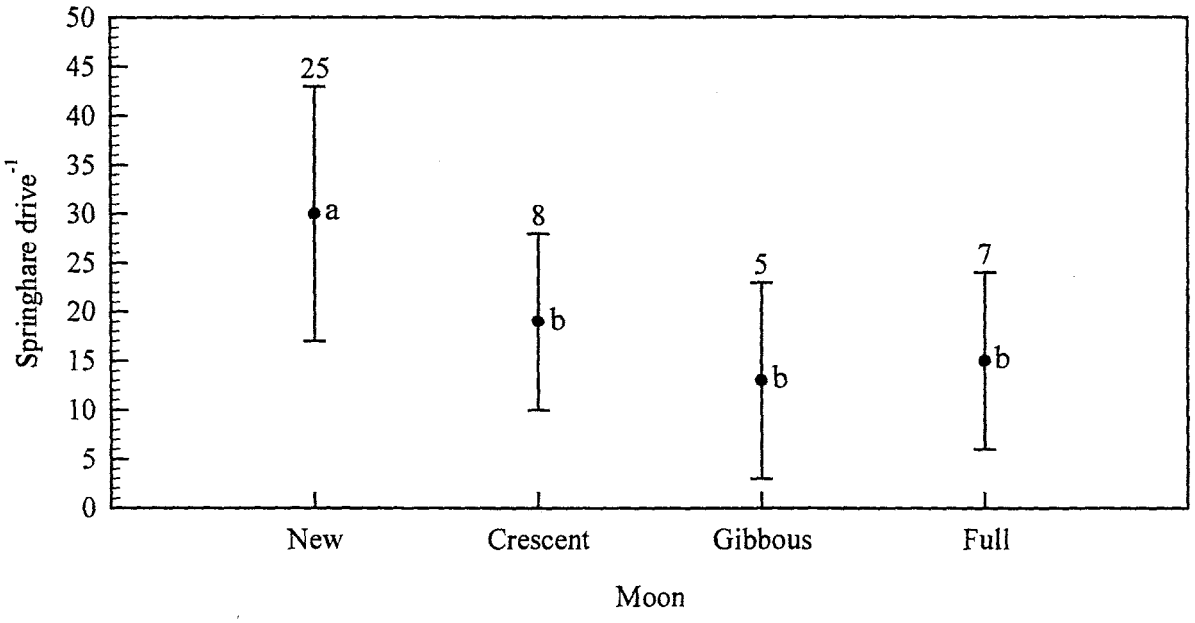

Fig. 4.3: Mean (± 1 SD) number of springhare encountered per drive, two hours after sunset, at different levels of illumination. Numbers indicate sample sizes and shared letters indicate no significant difference.

The interaction between time of night and level of illumination becomes apparent when the mean number of springhare active per drive prior to and after moonrise and moonset are compared. Between new moon and full moon the moon either rises or sets during the night depending on whether it is waning or waxing. Consequently some nights start dark and end light (waning moon) and others start light and end dark (waxing moon). The duration of the

light and dark periods as well as the level of illumination during the light period thus depends on the phase of the moon. On waning moon nights 32 ± 13 springhare per drive were encountered before the moon rose and significantly fewer ($t = 7.081$, $P < 0.001$), only 12 ± 10 springhare per drive, after it rose (Fig. 4.4A). On waxing moon nights the difference was not as pronounced and there was no significant difference ($t = -0.732$, $P = 0.467$) between the number of springhare per drive encountered before (19 ± 10) and after moonset (22 ± 11) (Fig. 4.4B).

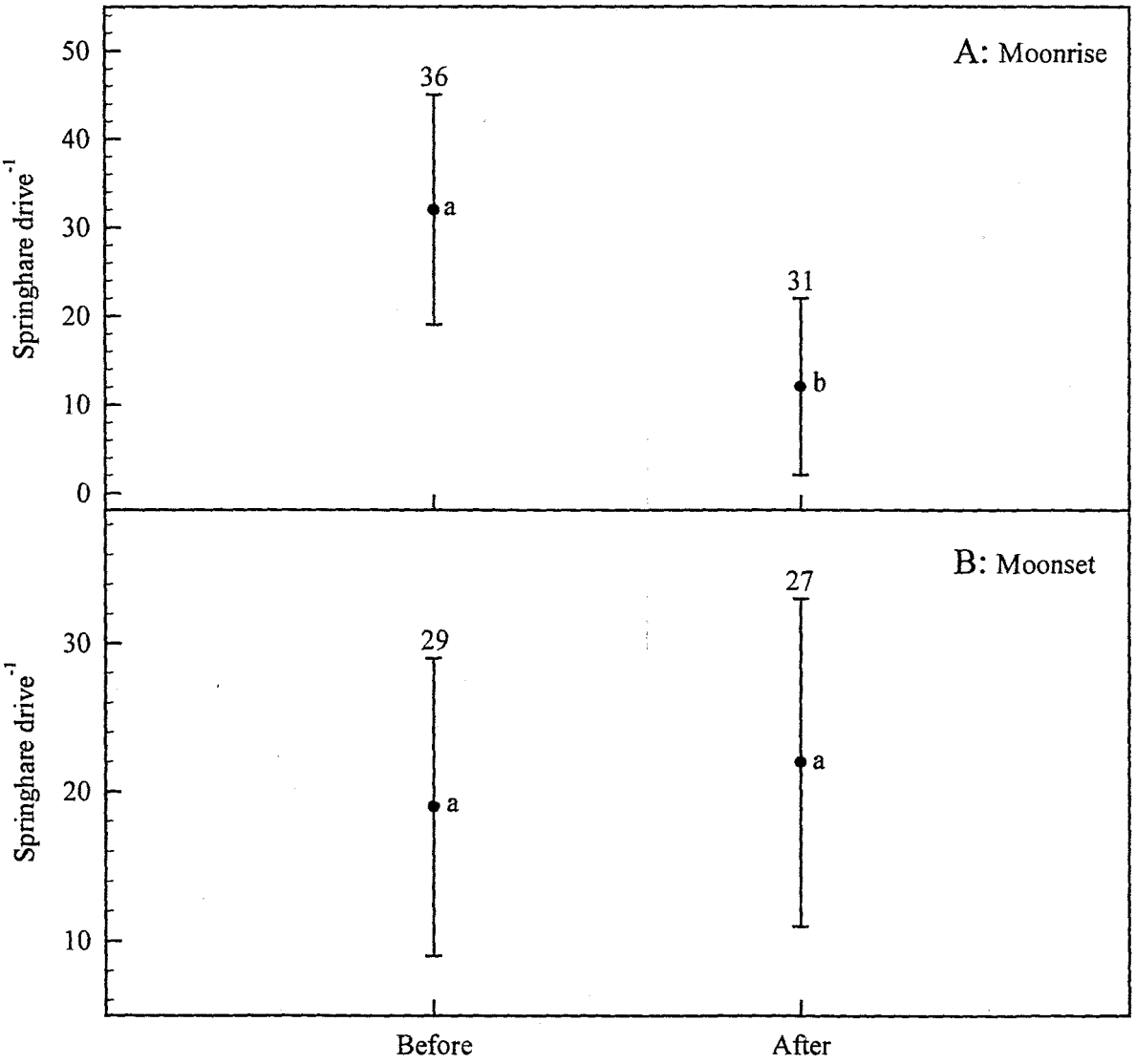

Fig. 4.4: Mean (± 1 SD) number of springhare encountered per drive, before and after moonrise (A) and moonset (B). Numbers indicate sample sizes and shared letters indicate no significant difference.

Activity sensors at burrow entrances recorded intermittent trigger events throughout the night. This is illustrated for a representative burrow over a two night period in Fig. 4.5. First trigger events occurred within one hour of sunset on at least one day at 36% of the 31 burrows monitored and by two hours after sunset trigger events had been recorded at 62% of the burrow systems monitored. The earliest trigger event recorded occurred within five minutes of sunset on a heavily overcast day. Last trigger events occurred within an hour of sunrise on at least one day at 29% of the burrows and within two hours of sunrise at 52% of the burrows. The latest trigger event recorded occurred approximately 20 minutes before sunrise. Overall, trigger events were not confined to, or concentrated in, specific parts of the night or dark periods and no clearly discernable activity patterns could be detected (Fig. 4.5).

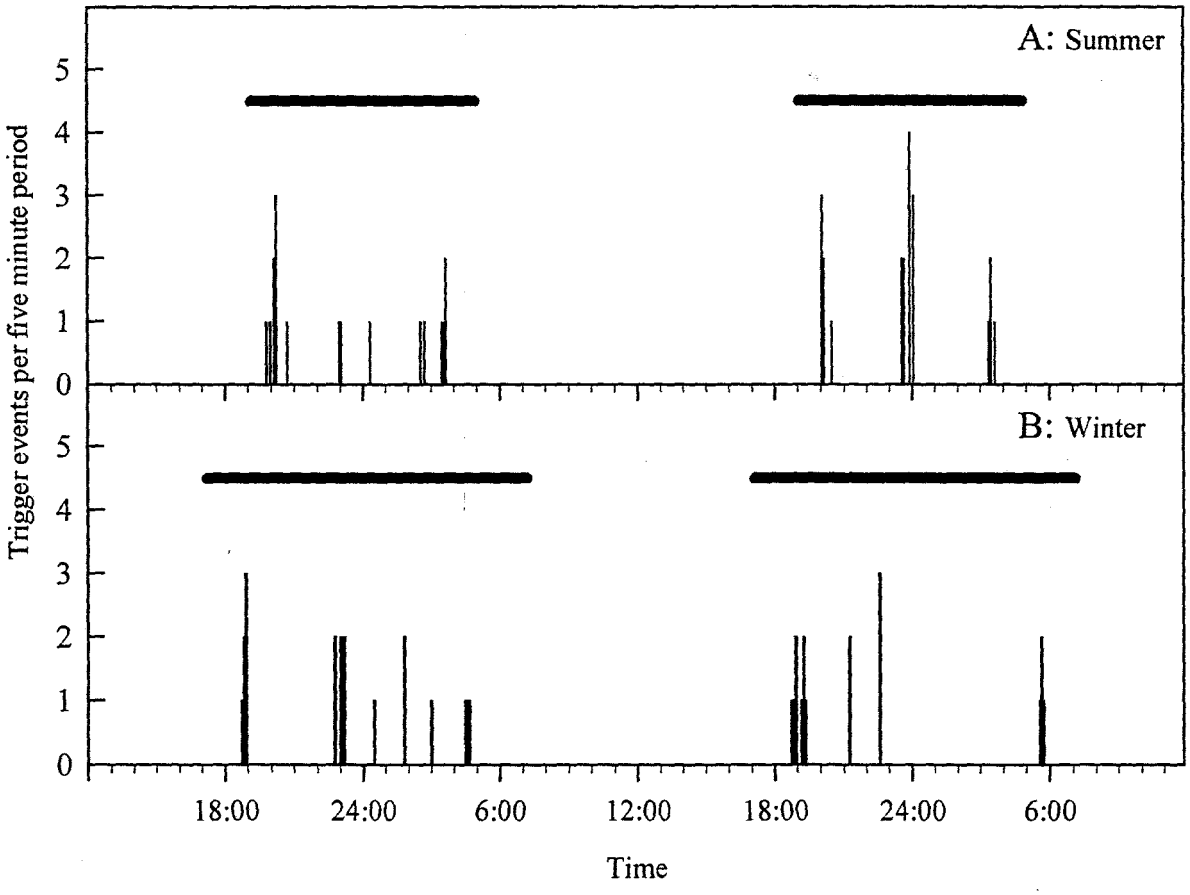

Fig. 4.5: Typical activity pattern recorded, over a two day period, at a burrow in summer (A) and another in winter (B). Data are from new moon nights and the horizontal black bar indicates night i.e. the period between sunset and sunrise.

4.4 DISCUSSION

Of the variables measured, a combination of time of year, time of night and level of illumination best described springhare activity. These three variables accounted for 43% of the variation in the data which, considering the large amount of variation in natural systems and all the other factors that may affect activity, is quite high. In a number of similar studies, combinations of various independent variables have been found to account for 33% of the variation in the activity of feral-cats (*Felis catus*) (Haspel & Calhoon 1993), less than 50% of the variation in white-tailed jackrabbit (*Lepus townsendii*) activity (Rogowitz 1997), less than 30% of the variation in badger (*Meles meles*) activity (Cresswell & Harris 1988), 38% of the variation in summer and 60 % of the variation in winter activity of cottontail rabbits (*Sylvilagus floridanus*) (Kline 1965).

Fewer springhare per drive were encountered during summer and autumn than in winter and spring. This observation was surprising as one might expect to encounter more springhare per drive during summer when foraging and other activities have to be fitted into a shorter night and when night-time temperatures are higher and impose a lower thermoregulatory cost on the animals. This apparent anomaly can, however, potentially be explained by a change in population size, which may have been brought about by unusually high rainfall in this particular year. During the last month of spring (November) a total of 212 mm of rain fell over the study site. This is approximately three times the mean monthly rainfall for November (Chapter 2). Coming on top of good rains the previous month, this heavy rain saturated areas of the study site and resulted in large scale flooding of springhare burrows. This may in turn have resulted in either a high mortality or forced springhare to migrate to higher ground, mostly outside the study site. Good follow-up rains together with heavy rain in April (124 mm) ensured that large parts of the study site remained saturated throughout summer and autumn. As the study site dried out during the subsequent winter springhare activity rapidly returned to its former levels presumably through immigration. It is, consequently, important to note that time-of-year may not normally have a significant effect on springhare activity.

As suggested by Butynski (1984) and Anderson (1996), springhare (*Pedetes capensis* from Botswana and the Northern Cape Province) exhibited only a single nightly activity peak. This is fairly common amongst rodents (Ashby 1972; Lockard & Owings 1974; Wolfe & Summerlin 1989). The period of nightly activity increased from summer to winter, closely tracking changes in day length. Springhare numbers did not, however, increase during the first half of the night as suggested by Butynski (1984) and Anderson (1996). Throughout the year, during both full moon and new moon nights, springhare numbers peaked relatively soon after sunset and thereafter remained relatively constant during the first six to eight hours of the night. Activity subsequently decreased during the two to four hour period before sunrise. During the short summer nights activity during the pre-dawn hours did not decline as dramatically as it did during the longer winter, spring and autumn nights, indicating that springhare were using a greater proportion of the night in summer. This general nightly activity pattern was, however, modified by moonlight at lunar phases between full moon and new moon i.e. when the moon rose or set during the night.

The effects of moonlight on the activity of various animals are well documented. Moonlight has been shown to inhibit activity not only in springhare but also in other smaller nocturnal rodents (Lockard & Owings 1974; Kaufman & Kaufman 1982; Kotler 1984; Price *et al.* 1984; Bowers 1988; Wolfe & Summerlin 1989; Daly *et al.* 1992), woolly opossums (*Caluromys philander*) (Julien-Laferrière 1997), adult rattlesnakes (*Crotalus viridis viridis*) (Clarke *et al.* 1996), European rabbits (*Oryctolagus cuniculus*) (Twigg *et al.* 1998), white-tailed jackrabbits (Rogowitz 1997), Badgers (Cresswell & Harris 1988), and crested porcupines (*Hystrix indica*) (Alkon & Saltz 1988). These animals all respond to increasing level of illumination by reducing above-ground activity and/or the use of open space. In all these studies the inhibitory effect of moonlight is attributed to increased predation risk by visually-hunting predators during moonlit periods. Although there is no direct evidence to show that springhare are more at risk to predation on moonlit nights, this nevertheless seems a plausible explanation. Both Cape fox (*Vulpes chama*) and domestic dogs (*Canis familiaris*), both of which are known to prey on springhare (Bothma 1966; Skinner & Smithers 1990; Anderson 1996), were regularly encountered in the study site at night.

Contrary to the conclusion of Butynski (1984) that moonlight has no effect on the number of springhare active, this study showed that level of illumination has a significant effect on the number of springhare active. Up until full moon, springhare activity, as expected, decreased with increasing level of illumination. On average though, slightly more springhare per drive were encountered at full moon than at gibbous moon. This is readily explained by the fact that at full moon the moon remains up for the entire night with the result that activity cannot be shifted to a dark period as it can during crescent and gibbous moons. Springhare consequently have no choice but to be active in this light or curtail surface activity entirely.

When active during bright moon-up periods springhare did, as suggested by Butynski (1984) and Anderson (1996), restrict their use of open space. During these periods springhare seldom moved far from their burrows and generally remained in shadows under trees and shrubs. It may be argued that fewer springhare are encountered during moonlit periods because they restricted activity to wooded areas where they are not as easily seen. I discount this explanation here because, as mentioned in Chapter 3, springhare have a very bright and distinctive eye reflection, they tend to sit up and look at any disturbance, the observer was located well above ground level and because shadows under trees and bushes did not hinder observation.

Moonlight avoidance or the shifting of activity to the dark portion of the night is clearly illustrated when one looks at the mean number of springhare encountered per drive before and after moonrise and set. A clear pattern of moonlight avoidance superimposed on a trend of decreasing activity during the later part of the night becomes apparent (Fig. 4.4). During the waning moon springhare activity was strongly concentrated in the early, dark part of the night and decreased significantly after moonrise. In contrast, when the first part of the night coincided with a moon-up period, during the waxing moon phase, springhare activity was more evenly distributed through the night with some suppression during the moon-up period.

Despite the fact that the number of springhare active was significantly correlated with temperature in Botswana (Butynski 1984), temperature was found to have no significant effect on springhare activity in the Eastern Cape. This may be because during summer, when

temperatures were high, springhare numbers were low due to high rainfall and flooding of burrows. Alternatively, it may be due to the fact that the climate in the Eastern Cape is relatively mild (Chapter 2) and temperature fluctuations not as severe as those in Botswana.

Previous attempts to link activity to temperature in small mammals have similarly met with varied results. Temperature has been found to have no significant effect on the activity of white-tailed jackrabbits (Rogowitz 1997), cottontail rabbits in winter (Kline 1965) and crested porcupines (Alkon & Saltz 1988). It has, however, been shown to have a significant effect on the activity of domestic cats (Haspel & Calhoon 1993) and adult badgers (Cresswell & Harris 1988). The fact that temperature has no significant effect on the activity of some animals may also be attributed to the fact that these animals are well insulated (Rogowitz 1997).

Although windspeed has been reported to significantly affect the time of emergence from setts and the distance travelled by badgers (Cresswell & Harris 1988) as well as the number of cottontails active at a given time (Kline 1965) it had no significant effect on the number of springhare active. Very strong wind did, however, appear to restrict the number of springhare active in the study site and this may explain why the effect of windspeed did approach significance. Observations from this study confirm Anderson's (1996) suggestion that springhare remain in close proximity to their burrows during windy conditions. This is not surprising as strong wind has a severe impact on springhare locomotory and, consequently, predator avoidance abilities. As previously mentioned (Chapter 3) bipedal hopping locomotion relies heavily on balance and this is easily upset by strong wind (pers. obs.). Excessive movement and noise caused by strong wind is also likely to have a negative effect on the ability of springhare to detect predators.

The effects of rain on springhare activity were not tested statistically. Field observations nevertheless suggest that light rain, as suggested by Butynski (1984) and Anderson (1996), had little effect on activity but that animals return to their burrows during heavy rain. In a similar study Geffen & Macdonald (1993) found that although weather conditions had no effect on the activity patterns of Blanford's foxes (*Vulpes cana*), heavy rain and strong wind caused foxes

to retreat to their dens. Badgers have similarly been reported to reduce activity during heavy rain (Cresswell & Harris 1988), while rain in general has also been shown to have a significant effect on activity of domestic cats (Haspel & Calhoon 1993).

Very little is known about the effects of dew and relative humidity on animal activity. Both had no significant effect on the activity of springhare. Kline (1965) similarly reported that these two factors had no significant effect on cottontail rabbit activity, although relative humidity has been shown to influence activity of domestic cats (Haspel & Calhoon 1993).

In addition to those factors which have already been discussed, springhare's avoidance of extreme weather conditions such as low temperature, very strong wind and heavy rain can also be attributed to the increased thermoregulatory costs associated with being active under these conditions. Initially it was thought that dew might similarly, through its wetting action, have a negative effect on activity by increasing the thermoregulatory costs. Alternatively, as springhare are not known to drink water and often inhabit areas where there is no free standing water (Chapter 7), it was thought that dew might have a positive effect on springhare activity by increasing the amount of moisture available to springhare. That dew had no significant effect on springhare activity may be because these two factors either cancel each other out or alternatively that neither has an effect on springhare activity in the Eastern Cape. As with dew it was initially thought that increasing relative humidity might positively affect springhare activity by increasing the succulence of the vegetation (Nagy 1994) and by decreasing evaporative water loss.

During the course of this study no springhare were ever encountered during daylight or twilight hours, thus confirming earlier reports by Smithers (1971), Butynski (1984) and Augustine *et al.* (1995) that springhare are strictly nocturnal. Some rodents, such as Merriam's kangaroo rat (*Dipodomys merriami*), are known to offset the suppression of nocturnal activity at full moon by increasing activity at dawn and dusk (Daly *et al.* 1992) but no such compensation was observed in springhare. Daytime activity, as reported by Kingdon (1974) and Anderson (1996), appears to be very rare and can be assumed to be due to exceptional circumstances. Data from

activity sensors at burrow entrances indicated that a large number of springhare initiated activity within one hour of sunset. Most of these trigger events occurring between 30 and 60 min after sunset. Considering that twilight at the study site generally lasts for approximately 30-40 min after sunset this suggests that springhare initiate activity as soon as it is dark. A few trigger events did occur during the twilight period. These, however, all occurred on overcast days or at burrows situated in heavily wooded areas. Similarly, activity was recorded at 29% of the burrows examined during the hour preceding sunrise but the latest trigger event recorded occurred approximately 20 min before sunrise indicating that activity ended rather abruptly at approximately dawn. These data support previous observations by both Butynski (1984) and Anderson (1996) on the onset and cessation of activity in springhare. Both red foxes (*Vulpes vulpes*) and European hares (*Lepus europaeus*) have similarly been shown to initiate activity at approximately 30 min after sunset and end on average 15 min before sunrise (Pépin & Cargnelutti 1994; Doncaster & Macdonald 1997).

That no regular springhare activity patterns could be detected from the activity sensor data may be attributed to the fact that cloud cover was not taken into consideration, or that springhare repeatedly visit the burrow entrance even during inactive or unfavourable parts of the night. Repeated trigger events throughout the night suggest that springhare either return to their burrows intermittently during active periods or that springhare regularly investigate other springhare's burrows. It is also possible, however, that the sensors aroused the curiosity of other individuals who subsequently triggered the sensors while investigating. This does not seem totally unfeasible as sensors and cables were regularly chewed and bitten off by springhare. Springhare generally appeared to leave their burrows very cautiously as a number of consecutive trigger events were often recorded shortly after the first. During the night trigger events varied from a single event to a number of consecutive trigger events at the same or different burrow entrances. Termination of activity in the early morning was also generally proceeded by a number of consecutive trigger events. Consecutive trigger events may also be due to routine burrow maintenance activities.

It is, however, important to note that any other animal entering the burrow system would also trigger the sensors. This, however, appears unlikely as only very occasionally were spoor of other animals, such as mongoose and small rodents, found in the soft sand of springhare burrow entrances. Springhare burrow systems also often have more than four entrances and, although only one or two of these are normally used, springhare did have the option of using entrances other than those at which sensors were located.

In summary it can be said that a combination of time of year, time of night and level of illumination best explain springhare activity in the Eastern Cape. The effect of time of year on the number of springhare active can, however, largely be attributed to uncharacteristically heavy rain and may consequently not have a significant effect on springhare activity in normal years. Springhare activity generally reaches its peak relatively soon after dark, thereafter it remains fairly constant throughout most of the night and only decreases in the two to four hour period prior to sunrise. On those nights when the moon either rises or sets during the night this pattern is, however, slightly modified by the level of illumination. Springhare respond to moonlight by reducing above ground activity, shifting activity to dark moonless periods and by reducing the use of open space. Except for extremes, weather has no significant effect on springhare activity.

Finally, as previously mentioned, a sound knowledge of springhare activity patterns and the factors affecting activity may have important implications for springhare management strategies. At high densities springhare can be exceedingly destructive both to crops and natural vegetation. Consequently on farms and in wildlife sanctuaries where their natural predators no longer occur, it is often necessary to manage these populations. In order to manage springhare populations effectively it is necessary to have accurate estimates of population size and these are best obtained at times (first half of the night) and under conditions (dark, no moon) when most springhare are active.

CHAPTER 5

BURROW UTILISATION AND MICROCLIMATE

5.1 INTRODUCTION

Semi-fossorial animals use burrows not only for protection from predators but also for protection from adverse environmental conditions and occasionally as a place to store food (Reichman & Smith 1990). Most of these animals spend a large part of their time within or near these burrows and as such a knowledge of their burrow utilisation behaviour, ie. how many burrows they use, how often they change burrows and how far apart their burrows are, is consequently central to understanding their overall ecology. Prior to the 1960's very little was known about burrow utilisation by semi-fossorial animals. This lack of knowledge can be attributed to the inability to locate repeatedly individual animals underground, over extended periods, without disturbing them or their burrows. The advent of radio-tracking in the early 1960's when Cochran & Lord (1963) devised the first practical radio-tracking system, however, solved this problem and since then our knowledge of burrow utilisation, particularly by nocturnal animals, has improved tremendously. Unfortunately, much of this information has accumulated almost as a by-product of studies of home-ranges and as a result is seldom thoroughly investigated and discussed. Nonetheless, we now know that burrow utilisation behaviours vary considerably amongst animals. At one extreme are those animals such as banner-tailed kangaroo rats (*Dipodomys spectabilis*) (Jones 1987), eastern chipmunks (*Tamias striatus*) (Yahner 1978; Lacher & Mares 1996), plains vizcachas (*Lagostomus maximus*) (Branch 1993), badgers (*Meles meles*) (Butler & Roper 1994) and the herbivorous jerboa (*Stylodipus telum*) (Heske *et al.* 1995), which generally inhabit only a single home burrow per home-range. Although some of these animals maintain a number of smaller contemporary burrows scattered throughout their home-ranges these are never used as home burrows and serve only as temporary shelters in emergencies. At the opposite extreme are those animals like Merriam's kangaroo rats (*Dipodomys merriami*) (Behrends *et al.* 1986; Jones 1989), giant

jumping rats (*Hypogeomys antimena*) (Cook *et al.* 1991), woodchucks (*Marmota monax*) (Swihart 1992) and Cape porcupines (*Hystrix africaeaustralis*) (Corbet & Van Aarde 1996) that use several different home burrows scattered throughout their home-ranges. These animals, however, all differ in the number of burrows they use, the frequency with which they move between them, and the amount of time they spend in each burrow.

Our knowledge of springhare burrow utilisation is largely restricted to that obtained from four animals that were radio-collared by Anderson (1996). Smithers (1971), Butynski & Mattingly (1979) and Skinner & Smithers (1990) all make no mention of burrow utilisation and are wrongly quoted by Anderson (1996) as saying that springhare utilise only a single burrow system. With the exception of Anderson (1996), the only two previous authors to have mentioned burrow utilisation by springhare are Shortridge (1934) and De Graaff (1981), both of whom suggest that springhare use several different burrows and that they may occupy these in turn, only remaining a day or so in each. The four animals radio-collared by Anderson (1996), however, exhibited a very different pattern of burrow utilisation. These animals were collared for between two and six months and during this time three of them used only two burrow systems, one main and one alternate, whereas the fourth animal used only a single burrow system. Data from these animals, however, appear to have been collected infrequently and the animals were located only 5-11 times each and at unknown intervals. Our understanding of springhare burrow utilisation can consequently at best be described as sketchy.

In this chapter I attempt to clarify the present situation with regard to burrow utilisation by springhare by providing the first detailed, quantitative information on temporal and spatial patterns of burrow occupancy. In addition to this I present data on springhare burrow microclimate and relate this to ambient conditions in a bid to show how ambient extremes are buffered by living underground. Springhare's apparent preference for burrowing under trees and bushes (Butynski & Mattingly 1979; Anderson 1996), and whether or not burrow microclimate can be used to explain this, is also examined and discussed.

5.2 MATERIALS AND METHODS

5.2.1 Burrow Utilization

Between April 1996 and April 1998, 14 adult springhare (seven males and seven females) were caught and radio-collared. The animals were caught on dark moonless nights by chasing them on foot with the assistance of a vehicle and spotlights. Ten of these animals were caught in the study site, fitted with AVM type P2 radio-collars (AVM Instrument Company Ltd, Livermore California, USA), and immediately released at the point of capture. Each radio-collar transmitted on a unique frequency in the 150.000-150.700 MHZ band. The collars had a total weight of 37-39 g (≈ 1% of adult body weight) and a potential battery life of 600 days. An AVM portable LA12-Q radiotelemetry receiver and a collapsible three element yagi antenna were subsequently used to locate animals. Springhare were easily traced to their burrows during the daytime and could be pinpointed to within 0.5 m by walking in the direction of the strongest signal until it came from directly underfoot. Effective range of collars when animals were down their burrows varied but was approximately 500 m. Due to some difficulty experienced in capturing animals in the study site, four additional animals were captured on surrounding farmland, collared, and released into apparently unused burrows in parts of the study site where they were unlikely to come into contact with other radio-collared animals. Introduced animals were allowed between one and two months to settle prior to data collection whereas data collection began approximately two days after the capture and release of animals caught in the study site. On completion of the study or when necessary for battery replacement, the transmitters were recovered from the animals by digging them out of their burrows. The animals were subsequently released into what was left of the burrow system.

Springhare were located at three to four day intervals for periods of up to a year. Each new burrow system used by an animal was marked by inserting a numbered pole into the soil directly above the animal. Any animal subsequently located within 10 m of this flag was considered to be in the same burrow system. All burrows used by animals were accurately plotted on a 1:10000 orthophoto map and whether or not the burrow was under a tree or bush recorded. The distance between the two burrows situated farthest apart as well as the area of the

minimum convex polygon (Mohr 1947; Macdonald *et al.* 1980) encompassing all the burrows used by each animal were digitised and measured using computer software (SigmaScan, Jandel Scientific).

5.2.2 Burrow Microclimate

Burrow microclimate was monitored at two different burrow systems, one under a stand of tall wattle trees (*Acacia mearnsii*) and the other in flat open grassland, for five days each month from June 1995 to May 1996. Both burrow systems appeared to be used periodically by springhare, were approximately the same size and had the same number of entrances. To determine the location of the underground tunnels the burrow systems were probed with a long metal rod. Four points at least 1.5 m from the nearest entrance were selected in each burrow system and 20 mm plastic piping inserted into the burrow to allow access to the tunnel systems from the surface. The top ends of these pipes were kept sealed and the pipes were left in position for the duration of the study. Once each month thermocouples were inserted into the burrows at three of these access points while a humidity sensor (MC Systems MCS 174) and a thermocouple were inserted at the fourth. These four thermocouples and the humidity sensor, along with another thermocouple and humidity sensor measuring ambient air temperature and humidity in shade above the burrows, were connected to an MC-Systems 120 data logger programmed to record temperature and humidity once every hour for five days. Data were stored by the logger onto an E-PROM module and were subsequently downloaded onto a computer for analysis. Unfortunately, because a second data logger was not available, burrow microclimate could not be monitored concurrently at the two different burrow systems. Consequently, after five days the thermocouples and humidity sensors were removed from the one burrow system and moved to the second burrow system.

5.2.3 Statistical Analysis

Pearson product moment correlation was used to determine whether or not the number of burrows used by springhare was significantly correlated to the number of times they were located and the length of the period over which they were tracked.

The mean number of burrows used by males and females as well as the mean maximum distance between burrows of males and females were examined for significance using t-tests. Data regarding the size of the area over which the burrows of males and females were scattered, however, failed to meet the assumptions required for t-tests and were consequently compared by means of the non-parametric Mann-Whitney U-test. Mann-Whitney U-tests were also used to test for significant differences between the mean monthly burrow temperatures recorded in the different burrow systems.

All data were analysed using SigmaStat (Jandel Scientific) and in all cases the 0.05 level of probability was accepted as indicating statistical significance.

5.3 RESULTS

5.3.1 Burrow Utilization

Due to problems experienced with transmitters, the length of time animals carried radio-collars varied from one to 12 months. Collars had to be recovered from ten of the animals due to premature battery and transmitter failures while another two animals disappeared without a trace, presumably due to transmitter failure. Of the remaining two animals one managed to break free of its collar and one died, apparently of natural causes. No predation of radio-collared animals occurred during this study, although during the pre-study survey one radio-collared animal was caught and eaten, possibly by a Cape fox (*Vulpes chama*).

Details of each animal including sex, number of days over which data were collected, number of times the animal was located, number of burrows utilised, size of the area over which burrows were distributed and the distance between the two burrows situated farthest apart are given in Table 5.1. These data clearly show that springhare utilise a number of different burrow systems which can be spread over an area of considerable size. In one year, for example, animal A used 27 different burrows scattered over an area of 28.5 ha. Two sets of data are given for

Table 5.1: Summary of the data obtained from radio-collared springhare. Two sets of data are given for animal D as this animal emigrated from the study site and established a new home-range.

Animal	Period tracked	No. of Days	Sex	No. of times animal located	No. of burrows used	Area encompassed by burrows (ha)	Max. distance between burrows used (m)
A	03/05/96 - 13/10/96	163	Female	43	15	12.0	750
B	03/05/96 - 19/06/96	47	Female	13	5	4.7	570
C	03/05/96 - 30/04/97	362	Male	97	27	28.5	900
D	07/11/96 - 05/12/96	31	Male	8	4	0.6	170
	09/12/96 - 13/02/97	66		16	5	0.7	220
E	07/11/96 - 24/12/96	47	Male	13	7	17.8	780
F	11/11/96 - 30/09/97	323	Female	100	13	11.2	670
G	13/02/97 - 25/10/97	254	Male	83	15	16.3	870
H	17/03/97 - 28/10/97	225	Female	74	12	3.0	390
I	18/04/97 - 08/12/97	234	Male	76	9	21.8	1000
J	01/07/97 - 20/09/97	82	Female	26	5	7.6	460
K	24/11/97 - 27/04/98	154	Male	35	8	2.0	420
L	24/11/97 - 24/02/98	92	Male	27	6	3.1	320
M	20/11/97 - 26/02/98	98	Female	30	5	0.4	190
N	20/11/97 - 19/12/97	29	Female	9	4	12.4	760

animal D, which was one of the four animals originally introduced into the study site. This animal left the study site and establish a new home-range to the north. As it never returned to the original burrows in the study site and the two areas utilised by it were separated by 1060 m with no other utilised burrows in-between, the two areas were considered to be distinct from each other. Of the remaining three introduced animals, two (H and N) settled and remained in the study site for the duration of the period that they carried radio-collars. The fourth animal, E, left the study site after 86 days (47 days of being tracked) and only data from the period that this animal spent in the study site are reported. None of the animals caught and released in the study site moved to new areas.

The overall pattern of burrow utilisation appears to be one whereby springhare constantly move from one burrow system to another. Only occasionally were they found in the same burrow system on more than two or three consecutive occasions. Some previously used burrows were frequently reused by the same radio-collared individual and burrows previously unused by a particular individual were periodically added to the burrows used. The number of burrows utilised by springhare was significantly and positively correlated with both the number of times the animals were located ($r = 0.772$, $P = 0.001$) and the length of the period over which they were tracked ($r = 0.845$, $P < 0.001$), suggesting that individuals continually exploited previously unused burrows. Even those animals tracked for more than 300 days were still periodically found in previously unused burrows.

Most of the burrows used by individual springhare were used only infrequently ie. they were found in them less than 10% of the total number of times they were located (Table 5.2). Nine of the 14 springhare did, however, have one or two burrow systems in which they were located more than 30% of the time (Table 5.2). The very high percentage utilisation of one burrow by animal M (> 50%) and another by animal J (41-50%) can, however, be attributed to the fact that these animals gave birth and were subsequently confined by rearing young to a single burrow system for the majority of the period for which they were tracked.

Table 5.2: Percentage burrow utilisation by springhare as determined by radiotelemetry (e.g. Animal A used 15 burrows in total. It was found in each of 13 of these on fewer than 10% of the total number of times located and in each of the two remaining burrows on 11-20% of the total number of times located).

Animal	Sex	No. of times animal located	Total No. of burrows used	Number of burrows at which springhare were found for the following percentages of the total number of times located					
				≤ 10%	11-20%	21-30%	31-40%	41-50%	> 50%
A	Female	43	15	13	2	-	-	-	-
B	Female	13	5	2	1	-	2	-	-
C	Male	97	27	24	3	-	-	-	-
D	Male	24	9	6	-	3	-	-	-
E	Male	13	7	5	1	-	-	1	-
F	Female	100	13	9	3	-	1	-	-
G	Male	83	15	11	3	1	-	-	-
H	Female	74	12	9	2	-	-	1	-
I	Male	76	9	6	1	1	1	-	-
J	Female	26	5	2	1	-	1	1	-
K	Male	35	8	6	1	-	-	1	-
L	Male	27	6	2	2	2	-	-	-
M	Female	30	5	3	-	1	-	-	1
N	Female	9	4	-	1	1	2	-	-

To compare burrow utilisation of males and females, only data obtained from the first 26 occasions that each animal was located were used. This was necessary as animals had all been tracked for different lengths of time and because the number of burrows used by springhare was found to be significantly correlated with both the number of times they were located and the length of the period over which they were tracked. Four animals (B, D, E and N) that were located fewer than 26 times were also excluded from the analysis, leaving a sample size of only ten; five males and five females. The first 26 occasions that these ten animals were located occurred over a period of 90 ± 2 days i.e. three months. During this period males and females exhibited no significant difference in the number of burrows used ($t = 0.690$, $P = 0.510$) and although burrows used by males were on average scattered over a slightly larger area and had a greater maximum distance between them, the maximum distance between burrows ($t = 1.230$, $P = 0.254$) and the size of the area over which the burrows were scattered ($U = 33.000$, $P = 0.310$) were also not significantly different from females (Table 5.3).

During the course of the study two radio-collared animals gave birth and another two are thought to have given birth. Animals A and M were both found to be lactating when they were dug up to recover faulty transmitters. Animal A had been consistently located at the burrow at which it was dug up during the preceding 36 days, and animal M was exclusively located at the burrow at which it was dug up during the preceding 32 days. Two other females, F and J, are also thought to have given birth. Animal F was consistently located at one burrow system for 45 days and animal J was consistently located at another for 43 days. Animal K, a male, was the only other animal to be consistently located at one burrow for a period in excess of 30 days being found in the same burrow for 39 days.

Despite the fact that there was considerable male/male, male/female and female/female overlap of the areas over which the burrows of different animals were distributed (Figs. 5.1 & 5.2), there was very little overlap in the use of burrows (Table 5.4). With the exception of those animals found in the same burrow on the same day, none of the burrows were used within one month of them previously having been used by another radio-collared animal. Burrows used by springhare were either scattered throughout the areas encompassed by the minimum convex

polygons or occasionally clustered in parts of these polygons. Burrow distribution within the minimum convex polygons of three different animals is illustrated in Fig. 5.3.

Table 5.3: Burrow utilisation and distribution of male and female springhare during the first 90 ± 2 days of radio-tracking. Shared letters indicate no significant difference between males and females.

	Animal	No. of burrows used	Area (ha)	Max. distance between two burrows (m)
Males	C	13	13.6	670
	G	8	9.9	750
	I	5	8.4	1000
	K	4	0.2	120
	L	6	3.1	320
		7.2 ± 3.6[a]	7.0 ± 5.4[a]	572 ± 351[a]
Females	A	12	8.5	540
	F	5	7.5	480
	H	9	2.2	290
	J	5	7.6	460
	M	5	0.4	190
		7.2 ± 3.2[a]	5.2 ± 3.7[a]	392 ± 146[a]

Table 5.4: Number of burrows used by one, two, three and four different radio-collared springhare during the course of this study.

Number of springhare	Number of burrows	Minimum time interval between use by different animals
1	70	-
2	25	29 days
3	4	34 days
4	2	33 days

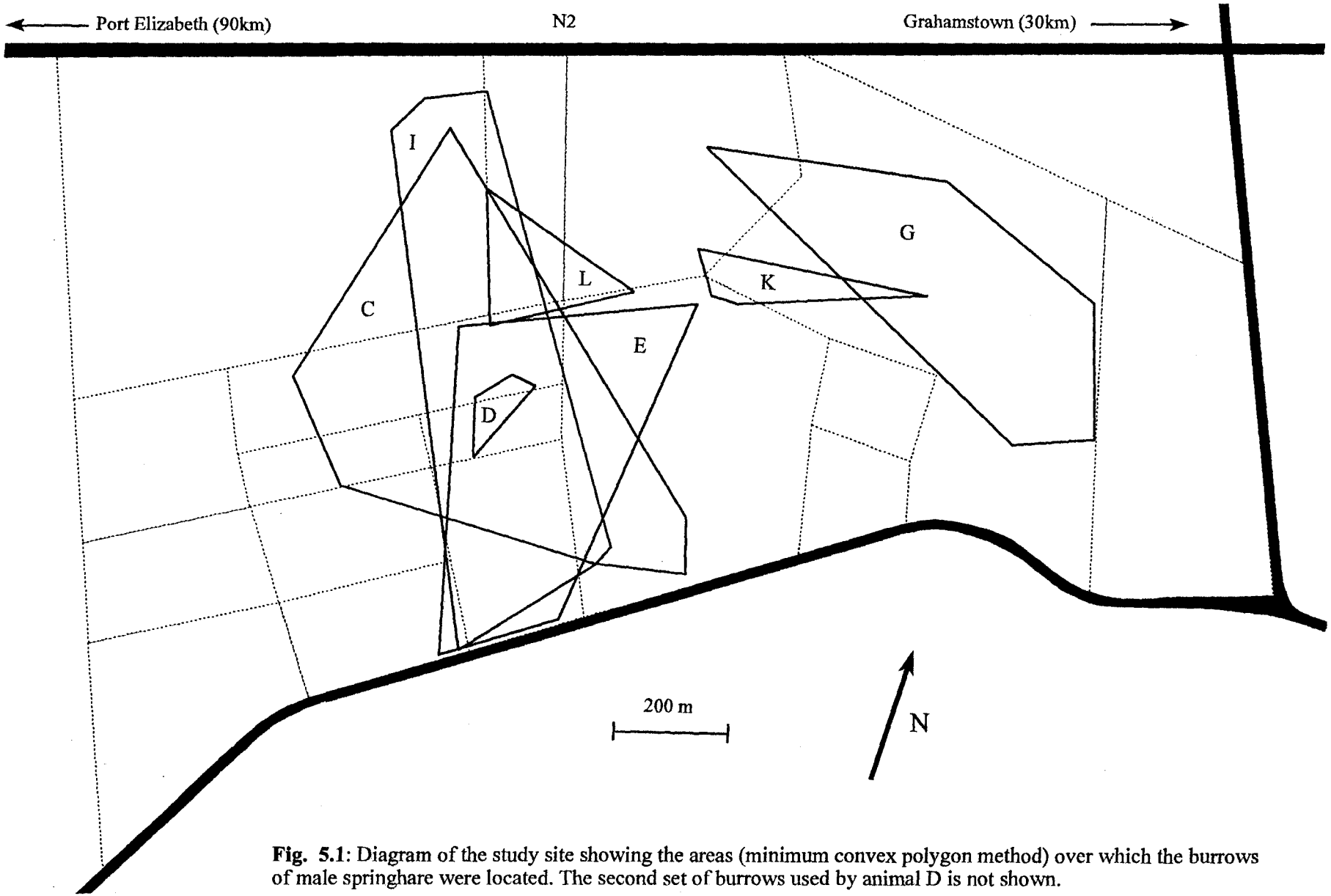

Fig. 5.1: Diagram of the study site showing the areas (minimum convex polygon method) over which the burrows of male springhare were located. The second set of burrows used by animal D is not shown.

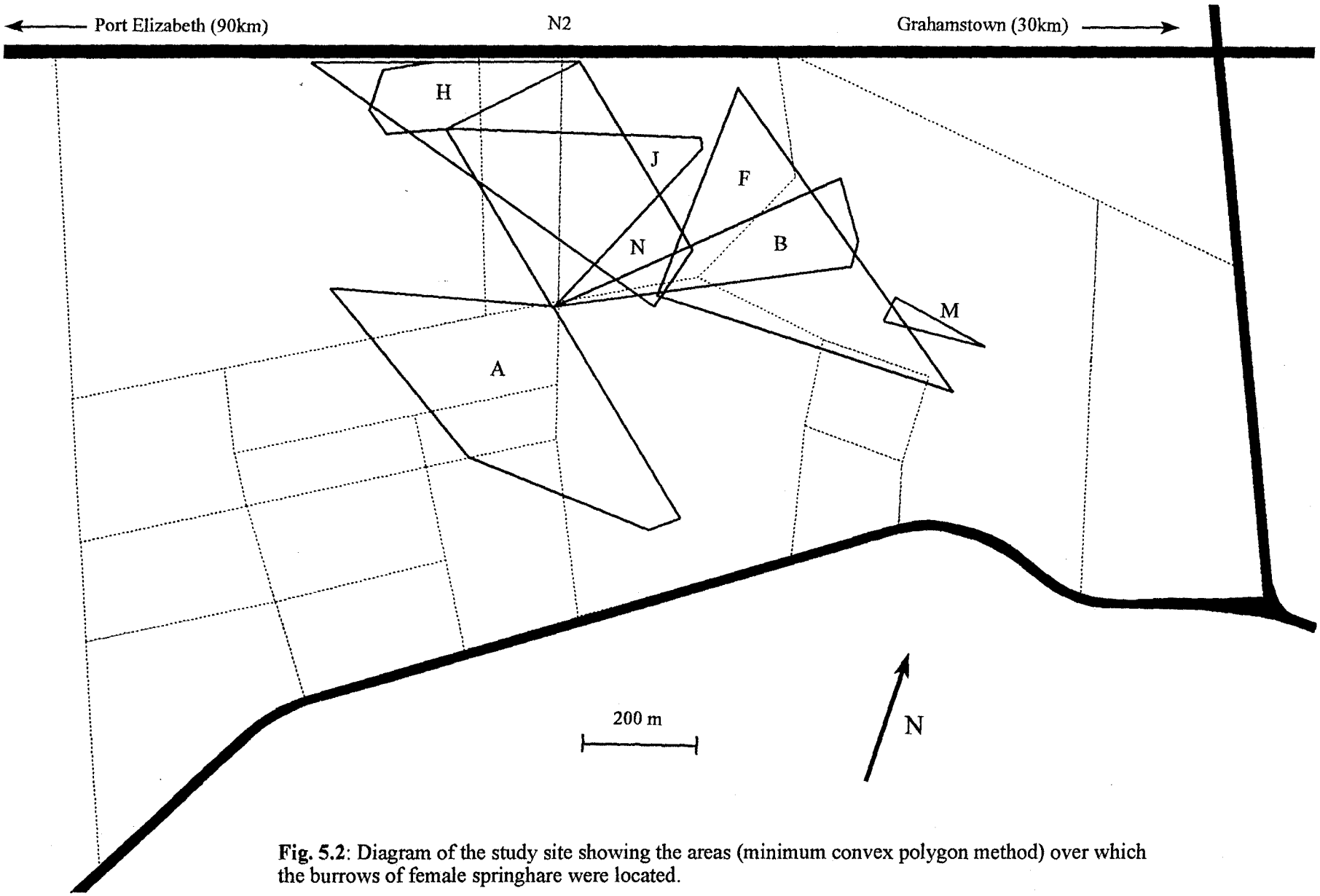

Fig. 5.2: Diagram of the study site showing the areas (minimum convex polygon method) over which the burrows of female springhare were located.

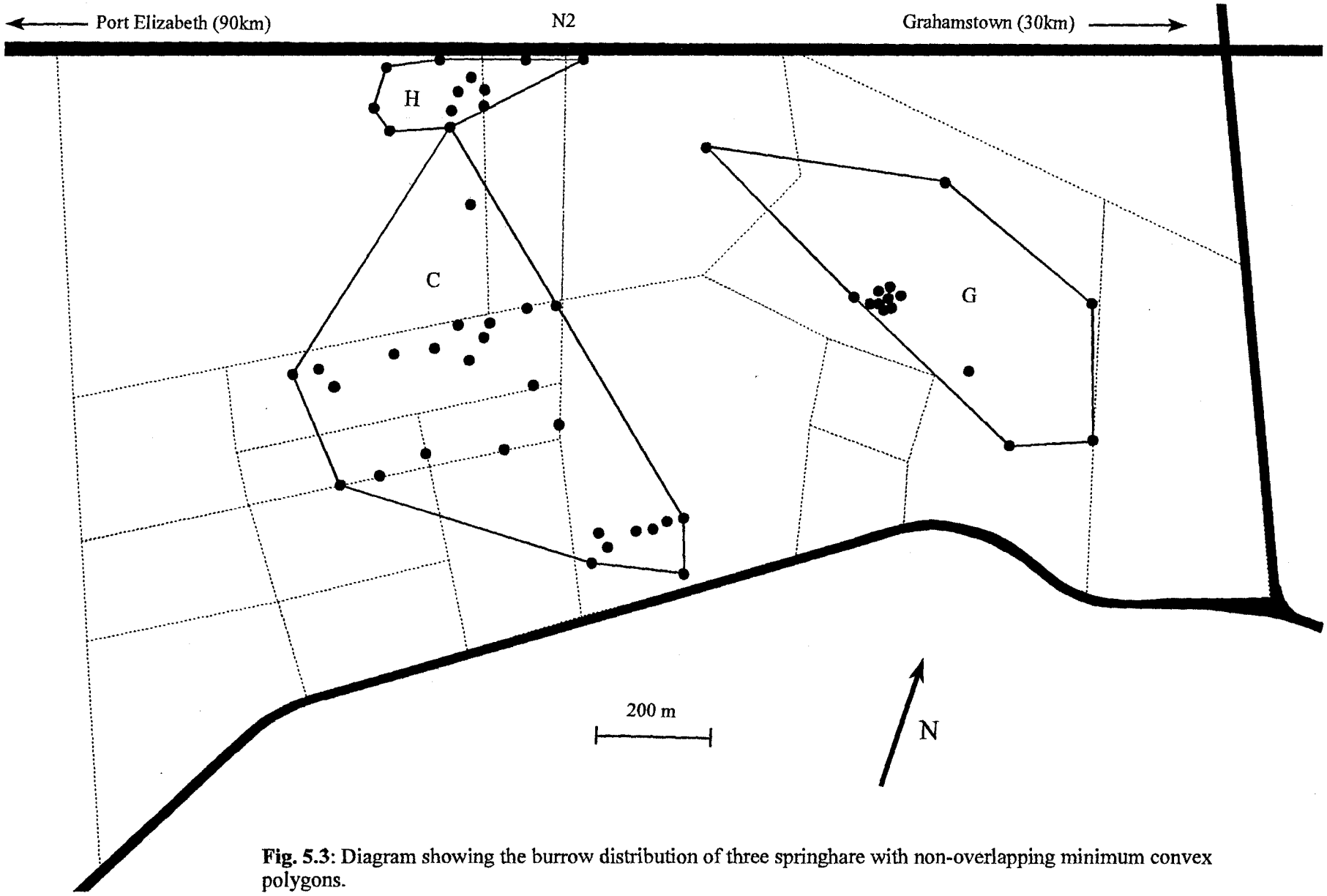

Fig. 5.3: Diagram showing the burrow distribution of three springhare with non-overlapping minimum convex polygons.

Although at most, only five radio-collared animals were ever simultaneously present in the study site, two collared animals were found down the same burrow on three occasions. The same two animals (H^{φ} and I^{σ}) were involved in all three cases and always at the same burrow system. There was no doubt that these animals were in the same burrow as it was a relatively small system with only two entrances and there were no other holes in the immediate vicinity. On all three occasions the animals were 2-3 m apart.

Only one of the burrows used by radio-collared animals was actually excavated by them during the course of this study. The remaining burrows were all excavated prior to the start of the study. The construction of the new burrow was initiated by animal H shortly after heavy rain in April 1997. Over a period of eight months this burrow was gradually extended, initially by animal H and later by I, from a system with a single entrance to one with five separate entrances.

Of the 101 burrows utilised by radio-collared springhare, 52 were in open grassland and 49 were located under large trees and bushes. If the relative proportions of these two habitat types are, however, taken into consideration this represents a considerable bias in favour of burrows being located under trees and bushes. That springhare preferentially burrow under trees and bushes is supported by the fact that there are very few if any trees and bushes which do not have burrows under them.

5.3.2 Burrow Microclimate

Throughout the year burrow temperature in both burrow systems monitored was remarkably stable and moderate in comparison to ambient temperature. The air spaces in both burrows were also saturated with water vapour at all times despite large ambient fluctuations in relative humidity. Examples from the hottest month (February) and the coldest month (July) (see Chapter 2) are given in Figs. 5.4 & 5.5, respectively. As the temperatures recorded in the four different parts of each burrow were very similar (i.e. within 1 °C) data from only one point in each burrow are presented. Although there were no differences in relative humidity between the two burrow systems, as air spaces in both were saturated with water vapour throughout the

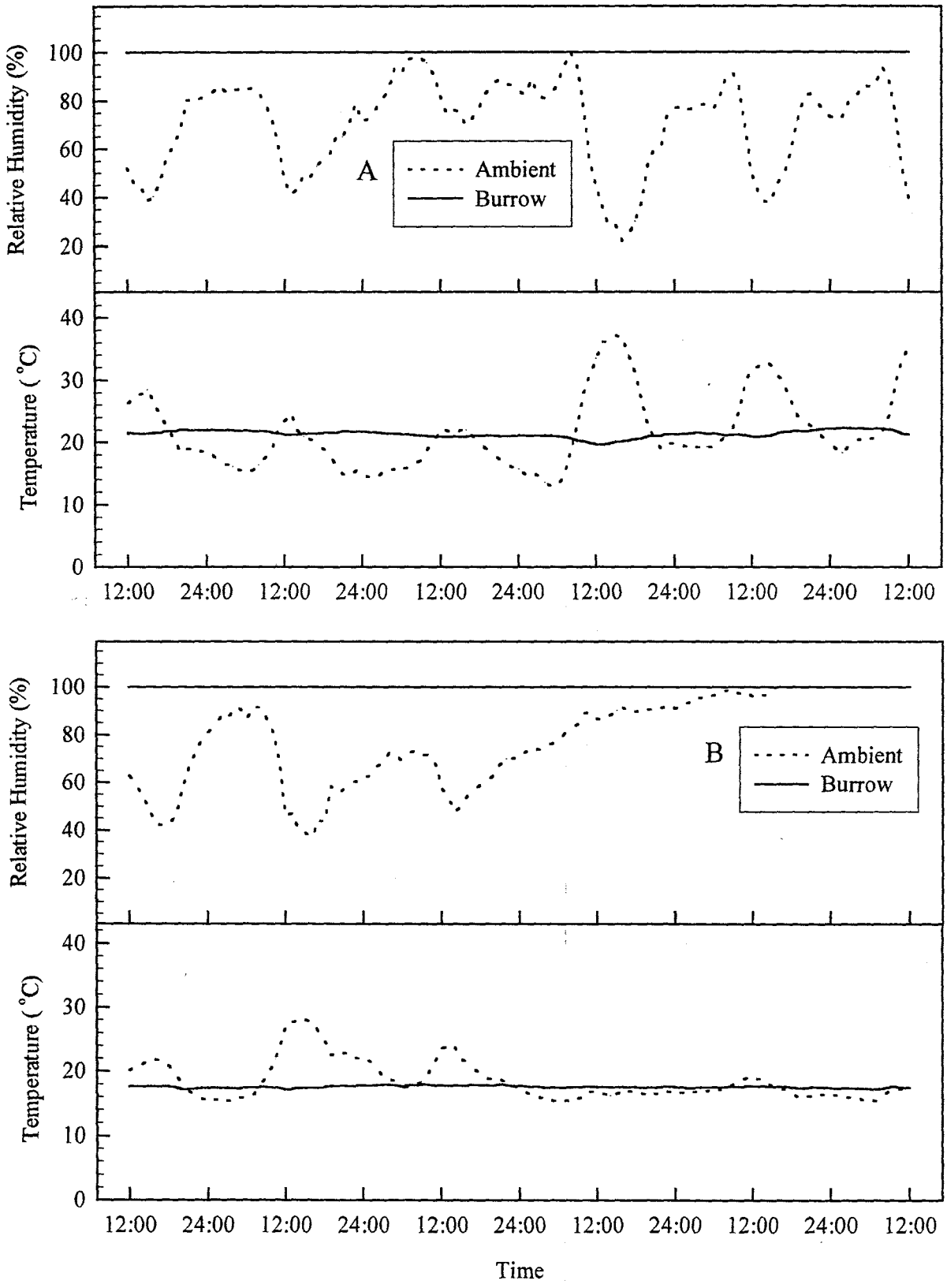

Fig. 5.4: Ambient and burrow temperature and humidity recorded in a burrow located in the open (A) and a burrow located under trees (B), during a five day period in February (summer).

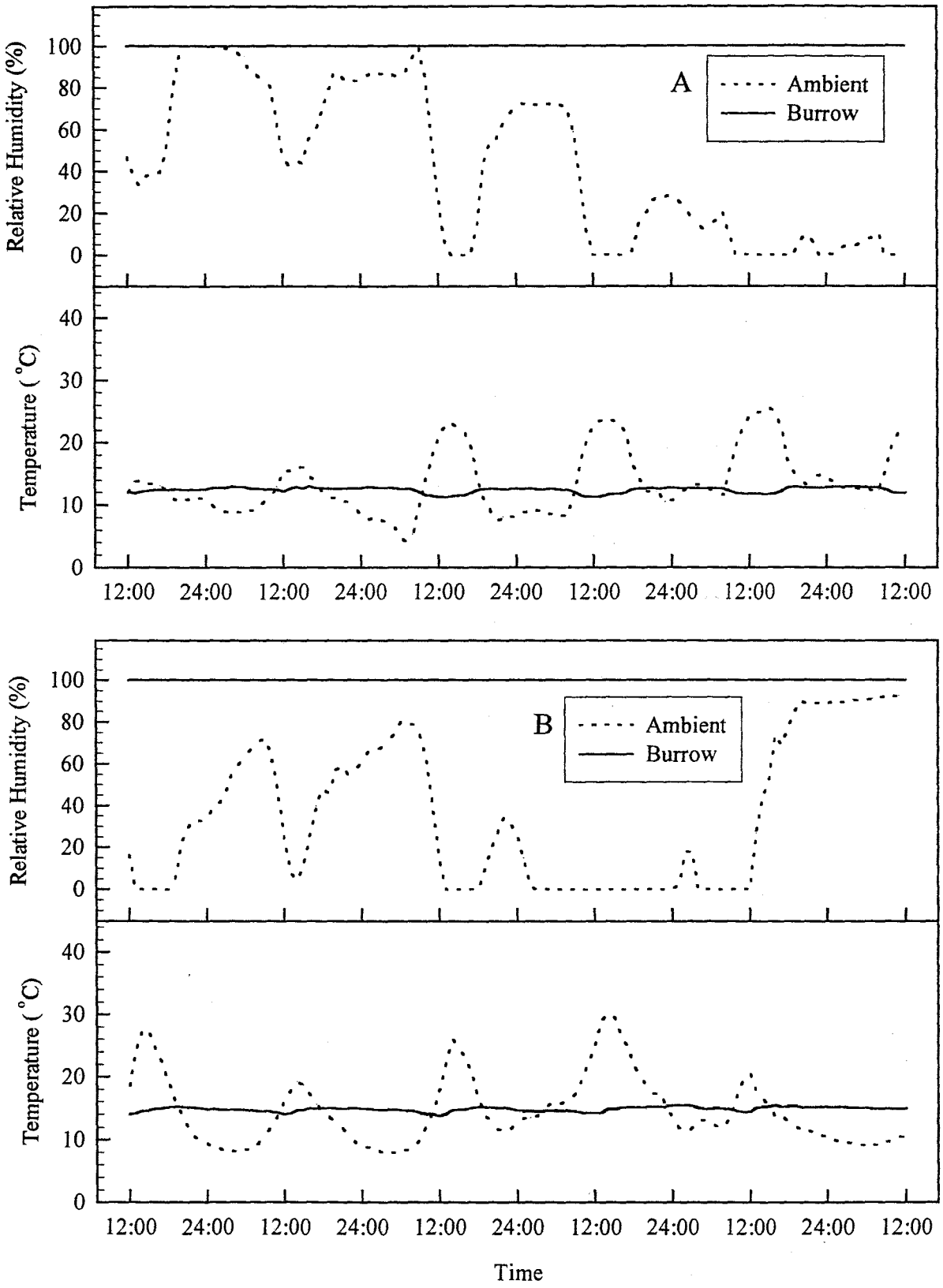

Fig. 5.5: Ambient and burrow temperature and humidity recorded in a burrow located in the open (A) and a burrow located under trees (B), during a five day period in July (winter).

year, there were temperature differences between them. During the course of the year the mean monthly temperature of the burrow located in open grassland ranged between 12.0 and 22.0°C (mean 17.6°C) while that of the burrow under trees ranged between 11.4 and 19.0°C (mean 15.8°C) (Fig. 5.6). Mann-Whitney U-tests indicated that from August to April (spring-autumn) the mean monthly temperatures recorded in the burrow under the trees were significantly lower than mean monthly temperatures recorded in the burrow in the open (mean monthly difference = 2.9°C; range = 0.9-4.5°C). During the remaining three winter months (May, June and July), however, mean monthly temperatures recorded in the burrow under trees, were significantly higher (mean monthly difference 1.5°C, range = 0.7-2.5°C) than those recorded in the burrow in the open (Fig. 5.6).

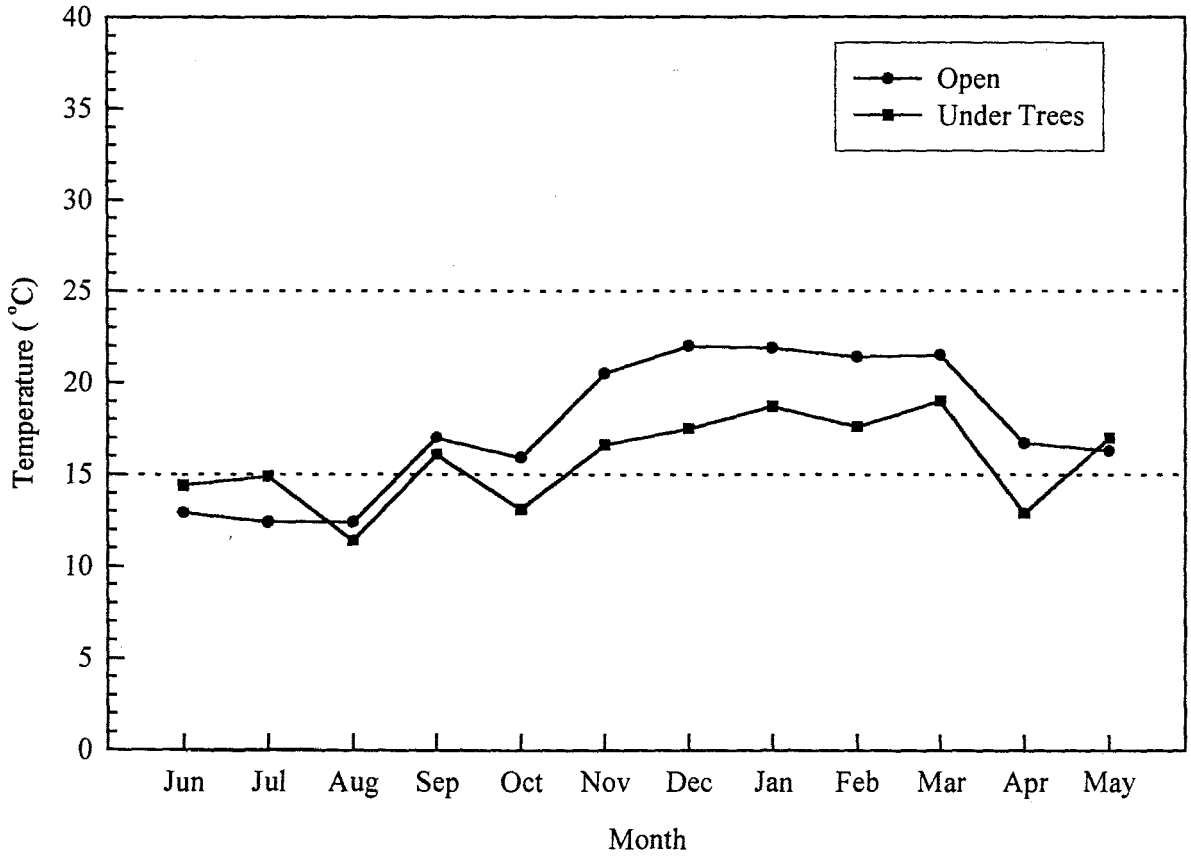

Fig. 5.6: Mean burrow temperature recorded each month from June 1995 to May 1996, in a burrow located out in the open and another located under trees. Standard deviations are not given as these are so small they cannot be distinguished from the means. Dashed lines indicate the thermal neutral zone of springhare.

5.4 DISCUSSION

Springhare in the Eastern Cape exhibited a pattern of burrow utilisation that was very similar to that previously suggested by Shortridge (1934) and De Graaff (1981) and quite unlike that described by Anderson (1996). Springhare in this study, unlike those described by Anderson (1996), were not restricted to one or two burrows but made use of a considerable number of different burrows, often scattered over an area of considerable size. Anderson (1996) does, however, point out that all four animals collared by him inhabited the very densely populated pan border area and that animals inhabiting the much less densely populated Kalahari sandveld areas appeared to use up to four different burrow systems. This suggests that differences between the number of burrows used by springhare in this study and in Anderson's (1996) study may be due to differences in population densities. As Anderson's (1996) observations are, however, based on a small sample size and very few locations per animal it cannot be said with certainty whether or not they are a true reflection of burrow utilisation by springhare in the Northern Cape Province.

Springhare in the Eastern Cape not only used more burrows than springhare in Anderson's (1996) study but the burrows were also spread over a much larger area. The distance between burrows of the animals collared by Anderson (1996) ranged from 65 to only 144 m whereas springhare in the Eastern Cape were found repeatedly to use burrows situated as far as 1000 m apart. Due largely to electromagnetic interference associated with a power line running across the centre of the study site (Sargeant 1980; Parker *et al.* 1996), the home-ranges of the springhare in this study were not determined. Electromagnetic interference causes signal bounce and deflection, which makes accurate triangulation impossible. Anderson (1996) did, however, measure the home-ranges of the four springhare he collared. Their home-ranges were apparently determined according to the minimum convex polygon method. Diagrams presented by Anderson (1996), however, suggest that they were determined simply by connecting all the locations together to form a polygon. Nevertheless the home-range sizes presented by Anderson (1996), i.e. 0.3-2.8 ha, are only a fraction of the size of the areas over which only the burrows of most of the springhare in this study were spread (Table 5.1). Springhare are known

to range up to 400 m from their burrows (Smithers 1971; Butynski 1984; Skinner & Smithers 1990) and if this is taken into consideration it becomes apparent that springhare in the Eastern Cape are capable of ranging over very large areas over time, although, the distance over which they forage from any specific burrow system may, of course, be much less.

The pattern of burrow utilisation exhibited by springhare in this study most closely resembles that of another bipedal-arid adapted rodent, Merriam's kangaroo rat. Merriam's kangaroo rats, like springhare, utilise a number of different burrows, frequently change burrows and seldom spend more than a few consecutive days in each burrow (Behrends *et al.* 1986; Jones 1989). They differ from springhare only in that they do remain relatively faithful to at least one burrow, to which they frequently return and in which they are found on average 64% of the time (Behrends *et al.* 1986). Although some springhare do utilise some burrows more frequently than others, none were used with such regularity.

Although springhare were originally described as colonial (FitzSimons 1920) and later thought to live in pairs (Shortridge 1934; De Graaff 1981), it is now generally accepted that they are solitary. According to Butynski & Mattingly (1979) and Anderson (1996) at most a mother and its young are associated with each burrow system. Radio-tracking data from this study, however, confirms earlier reports by Smithers (1971) and Kingdon (1974) that pairs are occasionally found in the same burrow. A similar situation has been reported in woodchucks (Swihart 1992). Among solitary rodents, adult males generally range more widely than females (Brown 1966; Brooks & Banks 1971; Daly & Daly 1975a, 1975b; Yahner 1978; Madison 1980). This is generally attributed to the fact that males of solitary species expend their reproductive effort in the pursuit of mating opportunities i.e. competing with other males for access to females, rather than investing in parental care. Springhare, however, exhibited no sex-related differences in the number of burrows used or in the size of the areas over which their burrows were distributed. This lack of differentiation between the sexes is, however, not entirely unusual and has also previously been reported in Merriam's kangaroo rat and the chisel-toothed kangaroo rat (*Dipodomys microps*) (Allred & Beck 1963; Chew & Butterworth 1964; Maza *et al.* 1973; Behrends *et al.* 1986).

Although four of the six radio-collared females are thought to have given birth, only two were tracked for the duration of lactation. Of these two animals, one was consistently located in the same burrow for 43 days and the other for 45 days. Springhare were, however, only located once every three to four days, consequently, these animals may have spent up to six days more than this in each of their respective burrows. Juveniles thus appear to emerge from their burrows at an age of approximately 43-51 days and because springhare are rapidly weaned once they emerge from their burrows (Butynski 1979; Anderson 1996; Chapter 6) this suggests that females lactate for at least this long. This confirms earlier estimates, made in Botswana (Butynski 1979) and in this thesis (Chapter 6), that springhare lactate for approximately 46-52 days. Although some females were tracked for up to 323 days (Table 5.1) none apparently gave birth on more than one occasion.

During the course of this study no intraspecific aggression or active defence of territorial boundaries was observed. Furthermore, springhare were often observed to feed in large groups, which individuals appeared to join and leave without any reaction from other animals. These observations, along with the fact that there was considerable overlap of the areas in which the burrows of different animals were found, confirms earlier suggestions that springhare have widely overlapping home-ranges and do not have actively defended territories (Butynski 1984; Skinner & Smithers 1990; Anderson 1996). Whether or not burrows are, however, defended against conspecifics remains somewhat of an enigma. That 70% of the burrows used by radio-collared springhare were used by only a single animal and that very few burrows were used by more than two animals suggests that springhare do display some degree of burrow territoriality. Moreover, springhare make every attempt to return to their own burrows when disturbed or pursued, ignoring others in the immediate vicinity (Smithers 1971; Skinner & Smithers 1990; pers. obs.). Scent marks, made with the pair of perineal glands located in the anogenital region or by urinating at the burrow entrance (frequently observed), may well serve to warn conspecifics that a burrow is occupied. If the burrow is, however, not frequently reused these scent marks will fade and the burrow may then be used or occupied by another animal. This is supported not only by Anderson's (1996) observation that recolonisation of the burrows of deceased animals occurred only after four to six months but also by the fact that in the present

study, no animal used a burrow within one month of it previously being used by another. The frequent burrow changes displayed by springhare may thus be to ensure that scent marks at the set of burrows used by the animal remain fresh. Regular movement between burrows may, however, also be attributed to two other factors. Firstly, animals may regularly switch burrows to escape parasites such as ticks, fleas and mites that might infest their burrows (Yahner 1978; Behrends *et al.* 1986), and secondly to avoid predators which may be attracted to the strong odour of a frequently used burrow (Behrends *et al.* 1986).

Only one new burrow was excavated during the course of this study, which is consistent with an earlier report by Butynski & Mattingly (1979) that most burrows are utilised by a succession of springhare over many years. As suggested by Butynski (1973) and Butynski & Mattingly (1979) this new burrow system was gradually extended to a five entrance system over a period of eight months. Excavation of this system was, however, initiated by one radio-collared animal and later continued by a second. Successional use of burrows appears to be a relatively common feature among animals that inhabit elaborate burrow systems (Reichman & Smith 1990).

Results presented in this study also clearly indicate that, despite large daily and seasonal fluctuations in ambient air temperature and humidity, springhare burrows provide a microclimate of stable, moderate temperature and high humidity. This is in accordance with the results obtained from numerous other burrow microclimate studies (Schmidt-Nielsen & Schmidt-Nielsen 1950; Kennerly 1964; Studier & Baca 1968; Lynch 1980; Downs & Perrin 1989; Reichman & Smith 1990). The moderate temperatures and high humidities encountered in springhare burrows have important physiological implications in terms of water and energy savings, which will be discussed in subsequent chapters on water balance and thermoregulation (Chapters 7 & 8).

Finally, the fact that burrow temperature was seasonally more stable in the burrow located under trees and bushes than in the burrow located in open grassland can, in the absence of any other obvious differences, be attributed to the additional insulation provided by the vegetation

(Geiger 1950). When compared with the burrow located in the open, the burrow located under trees and bushes was not only cooler in summer but also warmer in winter. This appears to explain springhare's preference for burrowing under trees and bushes, however, the temperature differences between the two burrows were small and are consequently of questionable biological significance. Other factors, such as the concealment provided by bushes (dark shadows) and the fact that they potentially serve as easily recognisable reference points to which springhare can move when disturbed or disorientated may be more important in this regard.

In summary, springhare in the Eastern Cape utilise a number of different burrows, which can be scattered over an area of considerable size. They frequently change burrows, seldom spending more than a few consecutive days in each and exhibit no great fidelity to any. They are generally solitary and do not appear to defend territories, although occupied and recently occupied burrows are apparently avoided by conspecifics. Males and females in the present study did not differ in the number of burrows used or in the size of the area over which these are scattered. Juveniles appear to remain in the burrows until they are 43-51 days old and females consequently lactate for at least this long. Finally, although burrow temperature appears to explain why springhare preferentially burrow under trees and bushes the temperature differences between the two burrows were small and of questionable biological significance. Consequently other factors such as that trees and bushes provide cover and can act as useful reference points may be of more importance in explaining springhare's preference for burrowing under trees and bushes.

CHAPTER 6

REPRODUCTION

6.1 INTRODUCTION

Of all the ecological and physiological aspects of springhare biology, reproduction has been the best studied and documented. Jones (1940) provided the first detailed description of the external morphology of a neonatal springhare. Since then, however, birth in captivity and early neonatal behaviour of captive born springhare have been described by Hediger (1950), Coe (1967), Rosenthal & Meritt (1973), Velte (1978) and James (1988). Detailed information on the subsequent hand rearing of juveniles is given by Rosenthal & Meritt (1973) and Velte (1978). Smith (1965) provided the first information on the reproductive organs of springhare and this was followed by a detailed description of the anatomy of the reproductive tracts of both male and female springhare from Kenya by Coe (1969). Glover (1973), however, later showed that springhare are not testicond mammals as described by Coe (1969).

Smithers (1971) provided the first real information on the reproductive ecology of springhare. He collected gravid females in every month of the year and reported on pregnancy rates in Botswana. This work was subsequently followed by four more detailed studies on the reproductive ecology of various southern African springhare populations. One in Botswana (Butynski 1979), one in the central Orange Free State of South Africa (Van der Merwe *et al.* 1980), one in south-eastern Zimbabwe (Kofron 1987) and one in the Northern Cape Province of South Africa (Anderson 1996).

The springhare placenta has also been the focus of much work. This along with the preplacenta has been examined and described by Mossman (1957), Mossman & Fischer (1969) and Owiti *et al.* (1985) while Fischer & Mossman (1969) and Owiti *et al.* (1992) have examined the foetal membranes with emphasis on their taxonomic significance.

We now know that springhare are typically monotocous, i.e. give birth to a single young, (Cable quoted in FitzSimons 1920; Smithers 1971; Butynski 1979; Van der Merwe *et al.* 1980; Anderson 1996) and opt for high individual fitness at the expense of fecundity. As yet no accurate gestation period is available but based on their observations of captive animals in zoos Rosenthal & Meritt (1973) and Velte (1978) estimate the gestation period to be 72-82 days long. Coe (1969), however, suggests a gestation of only two months, although Frazer & Huggett (1974) wrongly quote him as giving it as 360 days. No accurate information is available on the length of lactation. Based on calculations that will be discussed later, Butynski (1979) and Anderson (1996) estimated the period of lactation to be approximately 46 and 30 days respectively. During this time the body weight of the neonate increases from between 240 and 300 g (Rosenthal & Meritt 1973; Velte 1978; Coe 1969) to between 1.2 and 1.5 kg at which stage it first emerges from the burrow and is rapidly weaned (Coe 1969; Smithers 1971; Butynski 1979; Van der Merwe *et al.* 1980; Anderson 1996). By using eye lens mass to determine age, Anderson (1996) found that males and females appear to begin reaching sexual maturity at eight and 13 months, respectively. Furthermore the oldest animal collected by Anderson (1996) was approximately 88 months, or seven years and four months old, indicating that springhare are relatively long lived.

Most of the reproductive ecology has focused on the seasonality of reproduction and, despite the fact that these studies have all been conducted in strongly seasonal environments, both seasonal (Kofron 1987) and aseasonal (Smithers 1971; Butynski 1979; Van der Merwe *et al.* 1980; Anderson 1996) reproduction have been reported. Even amongst those populations that are reproductively active throughout the year there appear to be large differences in reproductive rates, with some populations having rapid consecutive pregnancies (Butynski 1979; Anderson 1996) and others not (Van der Merwe *et al.* 1980).

In the Eastern Cape nothing is known about the reproductive ecology of springhare, though based on the mild, relatively aseasonal climate and abundance of food throughout the year (Chapter 3), one might expect them to breed continuously. Unlike elsewhere in southern Africa (FitzSimons 1920; Shortridge 1934; Butynski 1973), springhare in the Eastern Cape are not

serious pests of crops or a primary food source, yet they are regularly hunted and in areas where they do come into conflict with agriculture they are often persecuted to the point of eradication. This is already thought to have occurred in some areas in this particular region of the Eastern Cape (Coetzee 1979).

Based on these observations and the previously reported differences in fecundity it is apparent that a detailed study of the reproductive ecology of springhare in the Eastern Cape is overdue. A study of this sort is not only central to understanding the ecology and physiology of springhare in the Eastern Cape but will also provide the first information on the reproductive strategy of springhare from a relatively aseasonal environment, in the extreme south of their distributional range. This information may consequently be of value for the future control and management of springhare populations in this region. The life history strategy of springhare and its evolution is also discussed.

6.2 MATERIALS AND METHODS

6.2.1 Data Collection

Ten springhare were shot every month for 12 consecutive months, from June 1994 to May 1995 on either Marlu or Thorneycroft farms (Chapter 2). These animals were shot at night from the back of a vehicle with the aid of a 1 000 000 candlepower, hand-held halogen spotlight. Dark moonless nights were best for this as the animals could be approached more closely due to the blinding and disorientating effect of the spotlight. Whenever possible animals were collected on or as close as possible to new moon thereby ensuring that the monthly samples were collected at regular intervals. As an attempt was made to collect the first ten animals encountered each night the sampling method is assumed to be random.

Most animals were shot from a distance of less than 40 m with a 12-gauge shotgun using number three or four shot. Immediately after collection each animals was weighed to the nearest 50 g, females examined to establish if lactation was occurring and the entire reproductive tract removed and fixed in 10% buffered formalin.

In the laboratory the reproductive status of each animal was assessed. Testes, cauda epididymides and seminal vesicles of the males were separated and weighed to 0.01 g. Tissue samples were taken from the middle of each testis and epididymis, fixed in 10% buffered formalin, dehydrated, embedded in paraffin wax, sectioned at 7 µm using a Leica RM2035 microtome and stained with Mallory-Heidenhain stain. These sections were then examined microscopically for the presence of spermatozoa and the mean seminiferous tubule diameter of each animal determined by measuring the diameters of 20 individual tubules with a Nikon filar micrometer eyepiece. For the purposes of this study all animals with spermatozoa in the testes and epididymides were considered to be reproductively active adults and all those without were either juveniles or reproductively inactive adults. This method is similar to that employed by Butynski & Hanks (1979) and Anderson (1996).

Adult females were distinguished from juveniles by the size and appearance of the reproductive tracts. Immature animals have small, smooth walled uterine horns whereas in mature animals the tract is much larger and the uterine walls are ribbed (Smith 1965; Butynski 1979; Anderson 1996). The occurrence of gravid females along with the weight (± 0.01 g) and location of the foetus within the reproductive tract was recorded. The length and breadth of uterine horns were measured to 0.01 mm with vernier callipers. Whenever possible the mean length and breadth of the two uterine horns were recorded, however, for gravid females and females that had one obviously distended uterine horn, most likely due to a recent birth, only the opposite uterine horn was measured. Ovaries were removed, embedded in paraffin wax, serially sectioned and stained as previously mentioned. Sections were examined for the presence of corpora lutea and the diameter of the largest Graafian follicle in each ovary was measured to 0.01 mm either with an eye piece micrometer or with vernier callipers.

Detailed rainfall and temperature data for the study period are given in Chapter 2.

6.2.2 Statistical Analysis

Chi square tests were done to determine if sex ratios were significantly different from parity, while a Mann-Whitney rank sum test was used to test for significant differences between adult

male and female body weights. One way analyses of variances were used to test for significant changes in the various adult male and female parameters measured during the 12 month period. Where the data were not normally distributed a non-parametric Kruskal-Wallis one way analysis of variance on ranks was done. Sigmastat (Jandel Scientific) was used for all statistical tests except the Chi square tests, which were performed manually. In all cases the 0.05 level of probability was accepted as indicating statistical significance.

6.3 RESULTS

6.3.1 Population Structure

In total, 120 springhare were collected over the 12 month period. Of these, 59 were males and 61 females, giving a sex ratio of 1 : 1.03 which is not significantly different from parity (χ^2 = 0.033, $P > 0.05$). Twenty six juveniles were collected and the juvenile sex ratio was 1.17 : 1 (14 males : 12 females) which is not significantly different from parity ($\chi^2 = 0.154$, $P > 0.05$) while the adult sex ratio was 1 : 1.09 (45 males : 49 females) also not significantly different from parity ($\chi^2 = 0.170$, $P > 0.05$).

The overall adult to juvenile ratio was 3.62 : 1 (94 adults : 26 juveniles) while for the females it was 4.08 : 1 (49 adults : 12 juveniles) and males 3.21 : 1 (45 adults : 14 juveniles).

There was no significant difference between adult male (3.47 ± 0.30 kg) and female (3.49 ± 0.47 kg) body weight ($t = 2099$, $P = 0.777$) and these were consequently combined to obtain a mean adult body weight of 3.48 ± 0.40 kg.

6.3.2 Males

Male springhare reach sexual maturity at a body weight of approximately 2.8 kg. Only one spermatogenically inactive animal was heavier than 2.8 kg, while no spermatogenically active animals lighter than 2.8 kg were collected. There was no overlap in the mean size of the reproductive organs of juveniles and adults although body size did overlap slightly (Table 6.1).

Table 6.1: Body size and the size of the reproductive organs of juvenile and adult male springhare.

Parameter	Juvenile (n = 14)		Adult (n = 45)	
	Mean ± 1 SD	Range	Mean ± 1 SD	Range
Body weight (kg)	2.34 ± 0.51	1.60-3.00	3.47 ± 0.30	2.80-4.00
Combined testis mass (g)	1.42 ± 0.44	0.86-2.14	38.70 ± 12.80	13.37-59.84
Combined epididymis mass (g)	0.29 ± 0.11	0.13-0.51	5.83 ± 2.25	1.05-10.37
Seminal vesicle mass (g)	0.94 ± 0.23	0.61-1.38	16.89 ± 9.59	2.39-46.24
Seminiferous tubule diameter (μm)	41.29 ± 10.06	27.90-58.30	135.42 ± 21.06	100.50-188.00

During the 12 months there was no significant change in the mean monthly masses of the combined testes (F = 1.60, P = 0.150), combined epididymides (F = 1.11, P = 0.385), seminal vesicles (H = 8.37, P = 0.680), seminiferous tubule diameter (F = 0.89, P = 0.552) and body weight (F = 0.373, P = 0.950) of adult male springhare (Fig. 6.1). With the exception of one animal that weighed 3.0 kg all animals over 2.8 kg were spermatogenically active, irrespective of the month of capture.

6.3.3 Females

Female springhare reached sexual maturity and conceived for the first time at a body weight of about 2.7 kg, a uterine horn length of 16.50-20.75 mm and a uterine horn width of 3.00-3.85 mm. Although there was no overlap in body weight of juvenile and adult female springhare, uterine horn length and width did show some overlap (Table 6.2).

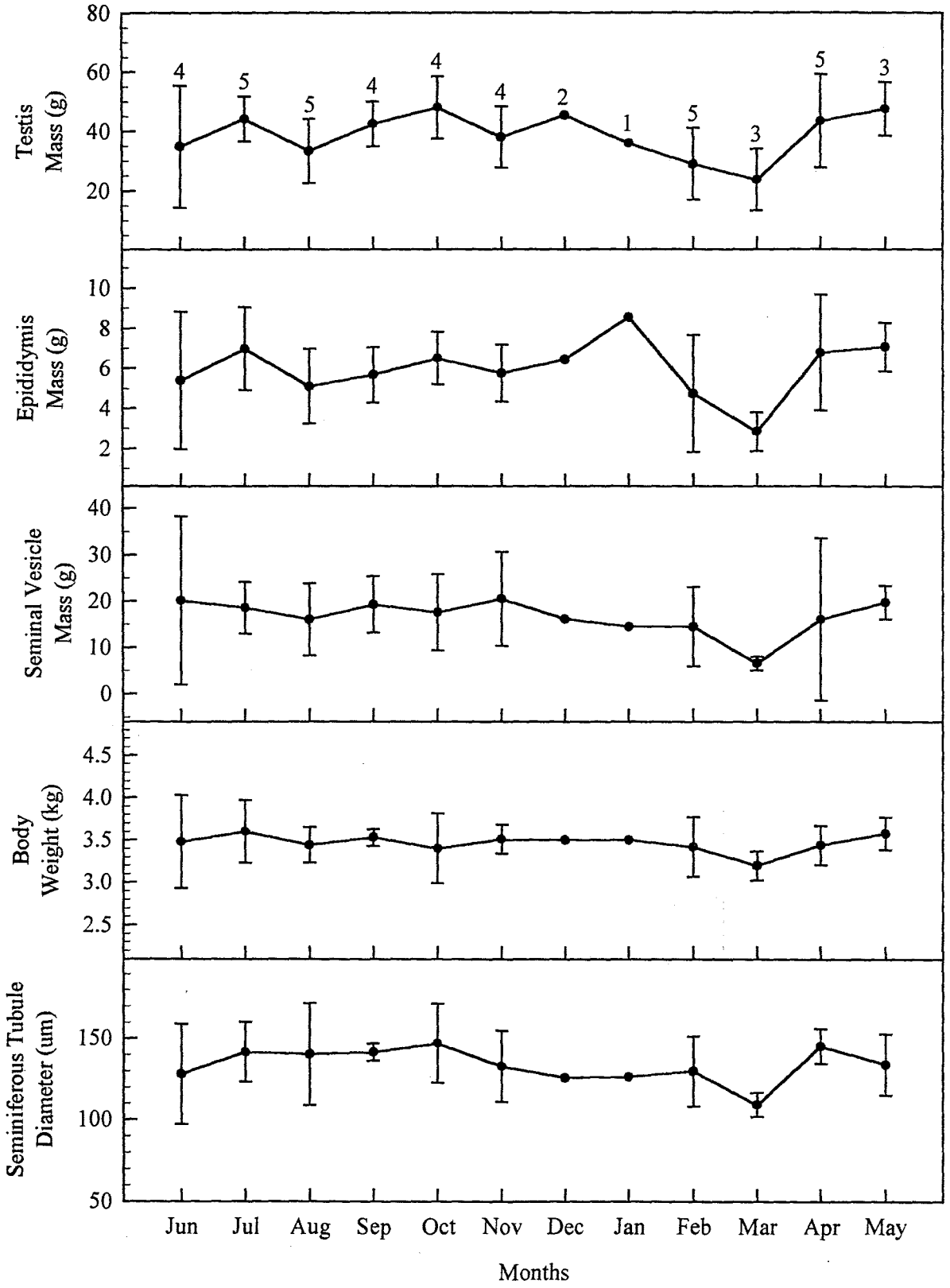

Fig. 6.1: Mean (± 1 SD) monthly adult male testis mass, epididymis mass, seminal vesicle mass, body weight and seminiferous tubule diameter. Sample sizes are given at the top and apply to all five graphs.

Table 6.2: Body size and the size of the reproductive organs of juvenile and adult female springhare.

Parameters	Juveniles (n = 12)		Adults (n = 49)	
	Mean ± 1 SD	Range	Mean ± 1 SD	Range
Body weight (kg)	2.28 ± 0.25	1.80-2.60	3.49 ± 0.47	2.70-4.50
Uterine horn length (mm)	17.15 ± 2.18	14.35-20.75	29.30 ± 5.44	16.50-38.00
Uterine horn width (mm)	2.94 ± 0.40	2.30-3.85	6.62 ± 1.16	3.00-10.00

Of the 49 adult females collected 30 (61%) were gravid, ten (20.4%) were gravid and lactating and ten (20.4%) were lactating. Nine (18.4%) of the adult females were neither lactating nor gravid. Microscopic examination of the ovaries of these nine animals, however, revealed that the ovary of one animal contained a large young corpus luteum, suggesting that it had recently ovulated and was possibly in very early pregnancy. Of the remaining eight, five had body weights between 2.7 and 3.0 kg and could thus have been sub-adults that had not yet conceived. Both ovaries of all eight animals contained at least one large (1-2 mm) Graafian follicle.

All 30 gravid animals were carrying a single foetus, 11 of which had implanted in the right uterine horn and 18 in the left. In every case a large corpus luteum was found in the corresponding ovary. The ten gravid females that were simultaneously lactating were in early pregnancy. The heaviest foetus encountered in one of these animals weighed only 53.88 g while the heaviest foetus encountered overall weighed 339.80 g and appeared to be near term. Ovaries from four of the ten lactating but non-pregnant animals also contained large young corpora lutea suggesting that they had recently ovulated and were possibly in very early pregnancy. In all 30 gravid animals collected no evidence of prenatal mortality was found.

Adult female body weight (F = 1.84, P = 0.0867), uterine horn length (F = 0.587, P = 0.8138) and uterine horn diameter (H = 14.2, P = 0.222) did not change significantly during the sample

period (Fig. 6.2). With the exception of October, when only one female was collected, pregnant animals were collected in all months (Fig. 6.3). For nine of the 12 months sampled, 50% or more of the adult females collected were gravid. Similarly lactating animals were collected in most months of the year, the exceptions being June, August and February (Fig. 6.3). With the exception of August and May juveniles, of both sexes, were collected in low but relatively constant numbers throughout the year (Fig. 6.3). Mean monthly foetal mass also did not change significantly during the course of the year ($H = 9.45$, $P = 0.490$) (Fig. 6.3). Foetal mass does peak in February, however, this may simply be due to the chance collection of the largest foetus and may not have any biological significance.

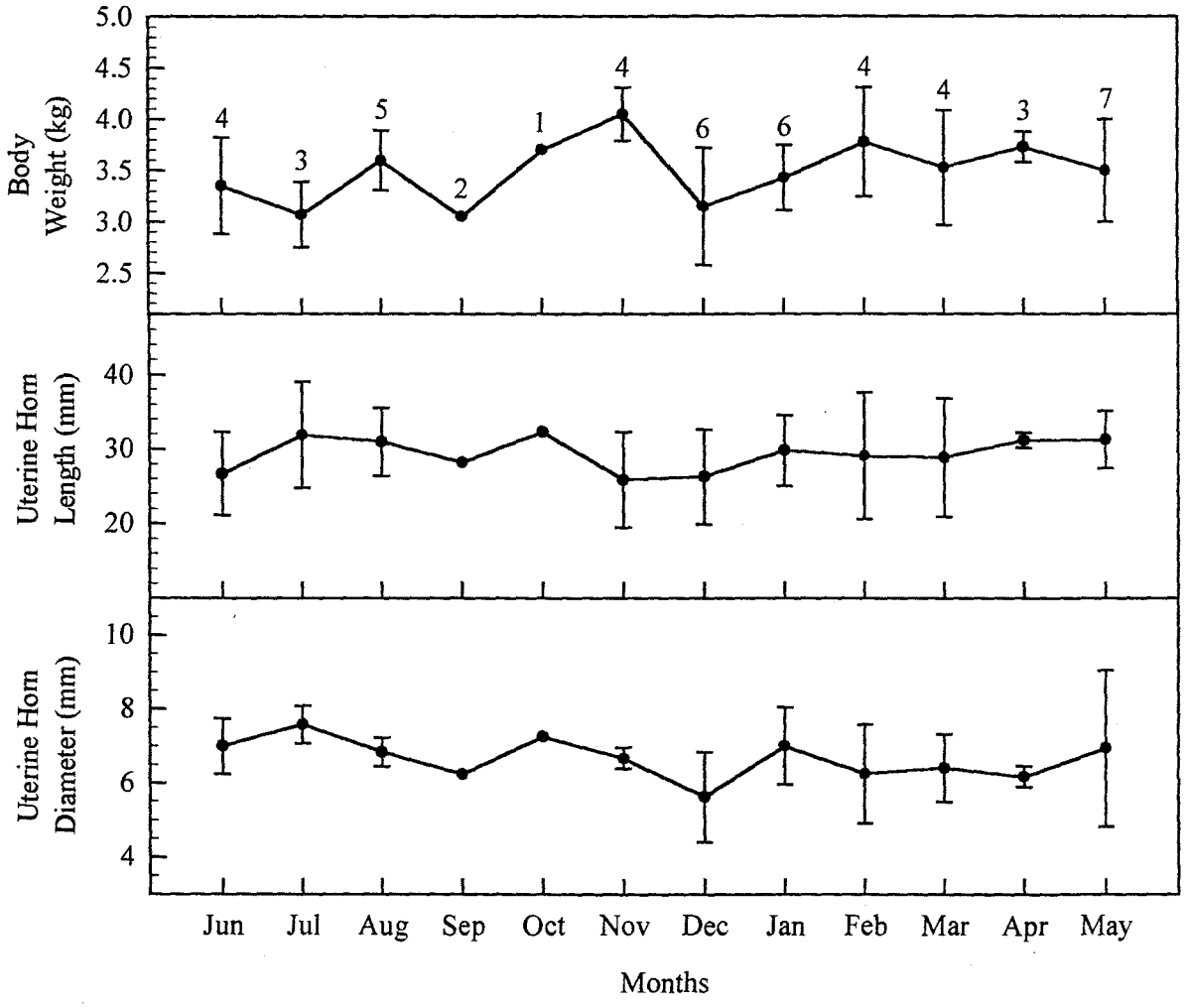

Fig. 6.2: Mean (± 1 SD) monthly adult female body weight, uterine horn length and uterine horn diameter. Sample sizes are given at the top and apply to all of the above graphs.

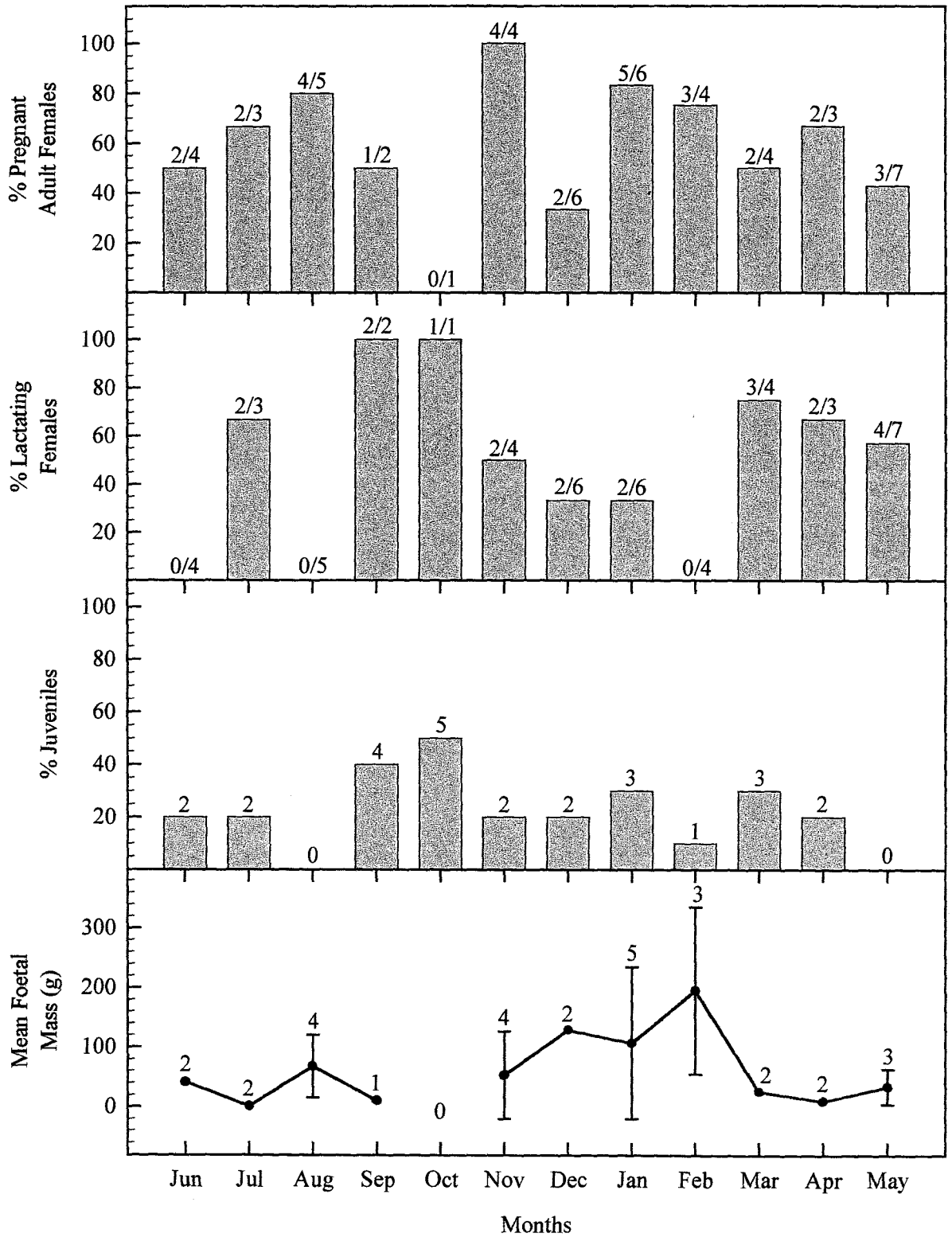

Fig. 6.3: The percentage lactating and gravid adult females, juveniles and the mean (± 1 SD) monthly foetal mass collected each month. Numbers indicate either the sample size or the actual number of adult females relative to the total number of adult females collected i.e. 2/3 = two out of a total of three adult females collected.

6.4 DISCUSSION

6.4.1 Population Structure and Sexual Maturity

Springhare population structure in the Eastern Cape is very similar to that reported for Botswana (Butynski 1979) and the Northern Cape (Anderson 1996). In all cases the sex ratio was not significantly different from parity. The overall juvenile to adult ratio in the Eastern Cape is 1 : 3.6, identical to that in the Northern Cape (Anderson 1996). In Botswana there appear, however, to be a greater number of juveniles relative to adults, 1 : 2.6 (Butynski 1979), which possibly suggests a higher fecundity or increased adult mortality there.

Male springhare in the Eastern Cape reach sexual maturity at slightly greater body weight than has previously been reported. Spermatozoa were absent from the testes and epididymides of all animals lighter than 2.8 kg in the Eastern Cape. In Botswana, however, spermatozoa were present in the testes of some males as small as 2.33 kg while all males heavier than 2.82 kg were spermatogenically active (Butynski & Hanks 1979). In the Northern Cape (Anderson 1996) and in the central Orange Free State (Van der Merwe *et al.* 1980) all males of 2.5 kg and greater were sexually mature. Despite this, results from the present study confirm previous suggestions that a combined testis mass of 5.5 g (Anderson 1996) and a right testis mass of 2.3 g (Butynski & Hanks 1979) can be used with a high degree of accuracy to separate pre- and postpubertal springhare. According to Butynski & Hanks (1979) a seminiferous tubule diameter of 117 μm can be used to separate adults from juveniles. This is very similar to what was found in the Eastern Cape where the smallest adult seminiferous tubule diameter was 100.5 μm. Anderson (1996), however, maintains that a seminiferous tubule diameter of 303.9 μm can be used with a high degree of accuracy to separate pre- and postpubertal animals. This is considerably larger than the largest adult seminiferous tubule diameter recorded in both this study and by Butynski & Hanks (1979) and may well be due to a calibration error.

Female springhare reach sexual maturity and conceive for the first time at a body weight of 2.7 kg. This substantiates previous reports by Anderson (1996) and Butynski (1979) that females in the Northern Cape and Botswana conceive for the first time at a body mass of 2.85 kg and

2.70 kg respectively. Based on dried eye lens mass the youngest postpubertal (pregnant) female encountered by Anderson (1996) was approximately 13 months old and the oldest prepubertal female collected was 24 months of age. None of the previous studies have recorded uterine horn width and diameter.

6.4.2 Seasonality of Reproduction

Neither male nor female springhare, in this population, in the Eastern Cape exhibited any seasonal atrophy or cessation of any part of the reproductive tract. Sperm were present in vast quantities throughout the year in the epididymides of males, while gravid and lactating females as well as juveniles were collected throughout the year. Furthermore there were no statistically significant changes in foetal mass during the course of the year, despite an apparent peak in February. The evidence thus shows that the reproduction of this population of springhare was largely unaffected by seasonally occurring phenomena.

This might be expected for a population inhabiting a region which is only mildly seasonal (Chapter 2), however, aseasonal reproduction has also been reported in strongly seasonal areas such as Botswana, including the Kalahari (Smithers 1971; Butynski 1979; Butynski & Hanks 1979), the Northern Cape (Anderson 1996) and the central Orange Free State (Van der Merwe *et al.* 1980). In all cases the reproductive effort was remarkably constant throughout the year. Anderson (1996), however, reports a slight peak in the number of gravid females in March, in the Northern Cape, while in the central Orange Free State the highest incidence of pregnancies was found during the winter months July and August (Van der Merwe *et al.* 1980).

This ability of springhare to reproduce throughout the year is possibly attributable to their diet and feeding behaviour. They are highly selective feeders which feed not only on grasses and stolons but also underground storage organs such as roots, rhizomes and corms (Smithers 1971; Skinner & Smithers 1990; Chapter 3). These underground food sources are essentially unavailable to most other herbivores and provide a valuable food and moisture reserve during dry periods (Chapter 3). Furthermore springhare are well adapted behaviourally and physiologically to life in arid environments (Chapter 7).

To date the only report of seasonal reproduction in springhare is that of Kofron (1987) in southeastern Zimbabwe. No animals were killed during this study which was based on hormone assays (progesterone in females and testosterone in males) of blood drawn from 123 live caught springhare. Females were gravid and gave birth to young during the wet season when food was readily available. From November 1983 to April 1984 only adults were collected. Gravid females were first collected shortly after the first heavy rains in the second half of December and births subsequently occurred in March, near the end of the wet season. Juveniles first appeared in the population sample during May and from then until mid August the population was composed of adults and juveniles, with a general trend towards an increase in juvenile weight. From late August to November the sample consisted largely of sub-adults and adults, however, two small juveniles were also collected. This observation that a small proportion of females experienced a second pregnancy during the dry season when food was scarce, along with the fact that the adult males are capable of reproducing throughout the year may suggest that this is not seasonal reproduction but rather a summer peak in reproductive effort. This summer peak in reproductive effort may also have been enhanced by the fact that 1982, 1983 and 1984, the years in which the study was conducted, were drought years in southern Africa (Kofron 1987).

According to Kofron (1987) the reason for this "seasonal" reproduction in southeastern Zimbabwe as opposed to aseasonal reproduction in other equally seasonal environments, such as the Kalahari desert, appears to lie in food availability. The study site lies adjacent to two large pools of permanent water with the result that herbivores congregate in this area during the dry season and rapidly denude it of grass. In contrast during dry periods in places such as the Kalahari herbivores migrate out of the desert in search of permanent water.

6.4.3 Reproductive Effort

As already mentioned 61% of the adult females in the Eastern Cape were gravid, 20.4% were gravid and lactating, 20.4% were lactating and 18.4% were neither gravid nor lactating. This is similar to results for the Northern Cape Province where 52% of the adult females were gravid, 17% gravid and lactating, 19% lactating and 26% neither gravid nor lactating

(Anderson 1996). Springhare in Botswana, however, appear to exhibit a much higher reproductive effort with 76% of the adult females gravid, 32% gravid and lactating and 46% lactating (Butynski 1979). This most likely explains the higher juvenile to adult ratio mentioned earlier. By contrast, in the central Orange Free State 58% of the adult females were gravid, 14.3% were lactating and no animals were collected that were simultaneously gravid and lactating (Van der Merwe *et al.* 1980). This led the authors to conclude that springhare do not have a post-partum oestrus. The group of adult animals in the present study that is neither gravid nor lactating probably includes animals whose pregnancy had been terminated early or whose unweaned young had died (Butynski 1979). It may also contain some young animals that are at puberty as well as those in very early first pregnancy and also animals that are between pregnancies and who had not mated at a post-partum oestrus.

Most of the springhare in the Eastern Cape that were simultaneously gravid and lactating were in very early pregnancy. The heaviest foetus in a lactating animal weighing only 53.88 g. No females with foetuses heavier than 59 g were lactating in Botswana (Butynski 1979), while in the Northern Cape 65% of females with foetuses less than 30 g were lactating as opposed to only 12% of females with foetuses greater than 100 g. Lactation thus appears to cease with the progression of pregnancy. This suggests that springhare do not have a post-partum oestrus but rather have rapid consecutive pregnancies. It is also important to note that an unknown proportion of the gravid females were primiparous and could consequently not possibly be lactating as well.

If springhare are reproductively active throughout the year, then the question of how many young can be born to a single female in a year remains to be answered. Butynski (1979) calculated the number of pregnancies per year that springhare could undergo by using the following equation to calculate the mean non pregnant period:

Number of gravid females / Number of adult non gravid females = Gestation period (days) / Mean non pregnant period

This calculation should, however, be treated with caution as it is based on the assumption that there is an equal likelihood of catching pregnant and non-pregnant females which, while reasonable, remains untested. The mean non pregnant period when added to the gestation period gives the mean interval between conceptions which can in turn be used to calculate the number of pregnancies per year. By using this technique it was found that springhare in the Eastern Cape can undergo roughly 2.9 pregnancies per year.

30 / 19 = 77 / mean non pregnant period

Therefore the mean non pregnant period = 49 days

Mean interval between conceptions = mean non pregnant period + gestation
= 49 + 77
= 126 days

Number of pregnancies per year = 365 / 126
= 2.9

In accordance with Butynski (1979) a gestation period of 77 days was used for the above calculation. This is based on the data of Rosenthal & Meritt (1973) and Velte (1978) who estimated the gestation period of springhare in zoos to be 80-82 days and 72-82 days respectively. Based on the duration of elevated plasma progesterone levels in a population of seasonally breeding springhare in south-eastern Zimbabwe Kofron (1987) similarly estimated the length of gestation to be approximately 79 days.

The calculated 2.9 pregnancies per year for springhare in the Eastern Cape is considerably lower than the 3.6 pregnancies per year for springhare in Botswana (Butynski 1979). By using the same equation Anderson (1996) calculated that springhare in the Northern Cape undergo approximately 3 pregnancies per year. Anderson (1996), however, substituted the wrong value for the number of adult non-gravid females and when the correct value is substituted into the equation it is found that springhare in the Northern Cape only undergo approximately 2.4

pregnancies per year. The greater number of pregnancies per year in Botswana once again possibly explains the higher juvenile to adult ratio there.

If, as calculated above, the period between conceptions is 126 days and 41% of the adults were lactating then the period of lactation must be at least 126 x 0.41 = 52 days (Butynski 1979). This is confirmed by observations of radio-tracked individuals that are thought to have given birth. These animals remained faithful to their respective burrows for periods of 43-51 days (Chapter 5). Fifty-two days is six days longer than that calculated for springhare in Botswana (Butynski 1979) and 22 days longer than that given for springhare in the Northern Cape (Anderson 1996). Anderson's (1996) calculations are, however, incorrect (because of his previous error in calculating the mean interval between conceptions) and when corrected the lactation period is only two days greater than that calculated for springhare in the Eastern Cape. Both gestation and lactation are, however, longer than expected for a similar sized rodent. The estimated gestation length of 77 days is 11 days longer than the 66 days predicted for a rodent of this size and gestation and lactation together, in the Eastern Cape, last approximately 129 days (77 + 52 = 129) which is 24 days longer than the 105 days predicted for a rodent of this size.

Log_{10} gestation and eye-opening time = 1.76 + 0.016 (Log_{10} mean body weight of sexually mature females (Eisenberg 1981)

= 1.76 + 0.016 (Log_{10} 3490)

= 1.817

Therefore gestation and eye-opening time = 66 days

Log_{10} gestation plus lactation = 1.63 + 0.11 (Log_{10} mean body weight of sexually mature females) (Eisenberg 1981)

= 1.63 + 0.11 (Log_{10} 3490)

= 2.020

Therefore gestation plus lactation = 105 days

Together this suggests a relatively long, slow gestation and lactation.

Contrary to some of the earliest reports (Lydekker and Sclater quoted in FitzSimons 1920) springhare are typically monotocous and all 30 gravid females collected in the Eastern Cape had only one foetus. Despite this twins have occasionally been collected. Smithers (1983) found one set in 104 pregnancies as did Butynski (1979) in 152 pregnancies and Van der Horst (1935) in a sample of unknown size. The set found by Smithers (1983) was in separate uterine horns and those of Butynski (1979) and Van der Horst (1935) in the same uterine horn. Cable (quoted in FitzSimons 1920), however, failed to find twins in a sample of 500 specimens of all ages and sexes from the western Transvaal, as did Anderson (1996) in a sample of 51 gravid females. Twinning thus appears to be very rare.

Implantation appears to be random and there was no significant difference between the number of implantations in the right and left uterine horns. Similar results have been reported by Smithers (1971), Butynski (1979), Van der Merwe *et al.* (1980) and Anderson (1996).

Springhare reproductive rate is also promoted by very low foetal mortality. None of the 30 gravid animals examined in the Eastern Cape showed any signs of prenatal mortality. Butynski (1979) found that prenatal death occurred before the death of the mother in only four out of 153 foetuses examined. Two of these being a set of twins. Anderson (1996) similarly reported prenatal death in only three of 50 cases examined. He states that resorption seemed to coincide with periods when most of the study area was covered in tall dry grass.

6.4.4 Birth, Lactation and Weaning

Based on data from Rosenthal & Meritt (1973) and Velte (1978) *Pedetes capensis* appears to give birth to precocial young weighing approximately 292 g. Coe (1967) similarly reports on the birth of two eastern Kenya springhare (*Pedetes surdaster*). One obviously born prematurely weighed 145 g and was almost naked while the other weighed 255 g and was fully furred. Both these animals as well as the two mentioned by Rosenthal & Meritt (1973) were born with their eyes open and with the exception of the premature one, were fully furred. Velte (1978) unfortunately does not give a description of the young. Coe (1969) similarly reports that *P. surdaster* gives birth to fully furred young weighing between 240 and 280 g.

In the Eastern Cape foetuses of up to 340 g were collected while Anderson (1996) collected foetuses up to 347 g. Furthermore, in the present study, two captive animals gave birth to healthy juveniles weighing 305 g and 325 g. The larger one was hand-reared and subsequently released. The smaller one, however, died after 21 days. At birth, both animals' ventral body surfaces were still naked and their eyes only opened at between nine and 14 days of age. It may be argued that these animals were born prematurely due to the stress of capture and captivity, however, at birth, they were considerably heavier, particularly the second, than most of those mentioned earlier. These juveniles closely resembled Jones (1940) description of a neonatal springhare. Both were, however, not as precocial as suggested by Van der Horst (1935), Hediger (1950), Coe (1967), Rosenthal & Meritt (1973), Velte (1978) and Anderson (1996).

The total mass of young carried to term (N), by a mammal, can be predicted by substituting the maternal mass (M) into the following equation.

$$N = 0.5408\ M^{0.8323}$$ (Leitch *et al.* 1959)

If the maternal mass is taken to be 3490 g, which is the mean body weight of the adult females collected in this study, then the predicted mass for newborns is 480.54 g or 14% of the mothers mass. Based on the data from this study as well as that of Rosenthal & Meritt (1973) and Velte (1978) the mean birth weight of *Pedetes capensis* was calculated to be 300 g (n = 6). This is 37.6% less than predicted and only 8.6% of the mothers mass, and suggests that the young, at least in the Eastern Cape, are in fact born altricial and not precocial as previously suggested. This is supported by the fact that the two juveniles born in captivity were not fully furred and that their eyes only opened 9-14 days after birth. Anderson (1996) attributes the small mass at birth relative to that of the mother to two possible factors. Firstly the mode of locomotion of this animal and, secondly, as a predator avoidance strategy.

The neonatal springhare remains in the burrow and as springhare have never been seen, or reported to have been seen, carrying plant material back to the burrow and no plant material has been found in springhare burrows (Butynski & Mattingly 1979; Anderson 1996; pers. obs.)

it is assumed that the neonate is completely dependent on mother's milk until it starts feeding above ground. The age at first emergence from the burrow is conservatively estimated to be 7-8 weeks since the mother lactates for at least that long. Of the 120 springhare collected in this study the smallest was a male weighing 1.5 kg. The smallest animals collected above ground in previous studies have weighed 1.473 kg (Coe 1969), 1.247 kg (Smithers 1971), 1.260 kg (Butynski 1979), and 1.050 kg (Anderson 1996). No unweaned animals were collected in the Eastern Cape, however, both Butynski (1979) and Anderson (1996) reported a very low incidence of unweaned animals i.e. juveniles with milk remains in their stomachs. Based on this low incidence of unweaned animals Butynski (1979) and Anderson (1996) suggest that there is a rapid transition from total dependence upon to complete independence from, the mothers milk. The unweaned juveniles collected ranged in weight from 1.050-1.970 kg (Butynski 1979; Anderson 1996).

6.4.5 Male and Female Sperm Plugs

Anderson (1996) reported mushroom shaped penis or sperm plugs consisting of densely packed, glutinous, active sperm in 16 out of 94 males examined. No such sperm plugs were found in freshly killed animals in the Eastern Cape. Large amounts of fresh sperm were, however, often voided when animals were shot. This later hardened in the fixative to form mushroom shaped structures surrounding the penis.

No vaginal plugs were encountered in any springhare in the Eastern Cape. Vaginal plugs have, however, previously been reported in springhare. Anderson (1996) found two out of 99 adult females with vaginal plugs which consisted of densely packed sperm. Both these animals were non-gravid and actively lactating females. Butynski (1979) similarly reported two out of 199 adult females, both of which had newly implanted blastocysts.

6.4.6 Life History Strategy

The life history strategy of springhare can be summarized as follows. Reproduction is aseasonal and a single, relatively small young is born in an altricial condition after a relatively long gestation. Lactation continues for longer than predicted for a mammal of this size and juveniles

only reach sexual maturity at between 13 and 24 months of age. Life span is relatively long and ranges between 8 years and a maximum in captivity of 14 years (Nawak & Paradiso 1983). This relatively slow drawn out reproductive strategy is rather unusual for a small mammal and is more typical of a larger mammal (Eisenberg 1981). For example, the similar sized cane rat (*Thryonomys swinderianus*), despite a long gestation, can give birth to a maximum of two litters of 1-5 individuals per year and juveniles become sexually mature after only five months (Van der Merwe 1999).

It has been suggested that this life history strategy may have evolved to minimize predation (Butynski 1979) or may be linked to springhare's bipedal mode of locomotion (Anderson 1996). Carrying one foetus, the full term weight of which is less than that predicted for mammals of this body weight, and providing care and nutrition to only one neonate may be part of a reproductive strategy evolved to minimize the female springhare's loss of fitness. Furthermore, juvenile springhare only emerge from the burrow for the first time when they are approximately half the size of the adult (≈ 1.5 kg) which is a basic predator avoidance strategy.

More recently, however, mammalian life histories have been viewed as a consequence of adult mortality rate and growth rate (Kozlowski & Weiner 1996; Harvey & Purvis 1999). In the new model, adult mortality rate sets the age at sexual maturity and a combination of age at sexual maturity and growth rate set the size at sexual maturity. Fecundity is in turn effected by factors such as the resources available, climate and the size of the offspring and in a stable population will balance juvenile mortality (Harvey & Purvis 1999).

Although there is no information available on adult mortality rates of springhare, it is likely that adult mortality is low. Saltatorial locomotion has endowed the springhare with a remarkable ability to change speed and direction of movement and this is likely to reduce the success of predators. In this respect it is interesting to note that the life history strategy of another large (≈ 1.2 kg) bipedal rodent, the giant jumping rat of Madagascar (*Hypogeomys antimena*), exhibits some similarities to that of springhare e.g. small litter size (1-2) and a delay (≈ 2 years) in the attainment of sexual maturity (Sommer 1997). In addition to their saltatorial locomotion

springhare, however, also inhabit burrows which they close behind them (Skinner & Smithers 1990), preferentially utilise flat open terrain (Chapter 3), often congregate in large groups (Chapter 3), seldom move far from the burrows on bright nights (Chapter 4), frequently change burrows and simultaneously use a number of different burrows which can be scattered over a relatively large area (Chapter 5). These are all factors which may reduce predation and adult mortality.

If adult mortality is low, then according to the model the attainment of sexual maturity may be delayed and this is indeed the case in springhare where animals only reach sexual maturity in their second year. In contrast to this cane rats reach sexual maturity at about five months (Van der Merwe 1999). Springhare fecundity is low with 2-3 litters of one young per year for perhaps nine years. The low fecundity and very small litter size probably reflect a low level of juvenile mortality and this may be a consequence of the young spending the first two months of their lives in the burrow. The low annual fecundity will also be a consequence of the relatively long life span of 14 years and also of the poor food resources which are typical of the harsh, highly seasonal, arid environments often inhabited by springhare. Aseasonal reproduction in a seasonal climate is probably linked to the diet as discussed earlier.

6.5 CONCLUSION

In conclusion, it thus appears as if springhare, throughout southern Africa, are generally not effected by seasonally occurring phenomena and are reproductively active throughout the year. This may largely be attributed to their ability to utilise underground food resources. The length of the interbirth interval and consequently the reproductive rate does, however, vary from place to place and no doubt depends on environmental conditions. In some isolated cases such as in south-eastern Zimbabwe environmental conditions may deteriorate to the point where springhare are unable to reproduce for part of the year. Unfortunately, as yet there have been no detailed studies on the reproduction of springhare from East Africa with which to compare the southern African studies. However, according to Coe (1969) there are strong indications that young are produced throughout the year in Kenya.

The overall life history strategy of springhare is rather unusual for a mammal of this size. This life history strategy has been linked to predation and to saltatorial locomotion, however, it can best be seen as a response to low levels of adult and juvenile mortality in an arid and nutritionally impoverished environment.

CHAPTER 7

OSMOREGULATION AND WATER BALANCE

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7.1 INTRODUCTION

The problems associated with life in arid areas and the various means employed by mammals to overcome these problems have previously been well reviewed and discussed (Chew 1961; Schmidt-Nielsen 1964; Bentley 1971; Macfarlane & Howard 1972; Maloiy 1972a; Prakash & Ghosh 1975; Maloiy 1979; Dawson & Pinshow 1989; Degen 1997). The major problem for most animals in arid areas is maintaining a positive water balance where there is frequently a lack of drinking water and environmental conditions that accentuate water loss by evaporation. This problem is generally overcome by reducing water loss through behavioural and/or physiological means. Water loss is, however, never completely curbed and lost water must be replaced by drinking and/or by obtaining it from food as preformed and metabolic water. In the absence of sufficient water to replace the losses animals will dehydrate and their survival will then depend on their ability to tolerate dehydration. This, in turn, depends largely on their ability to maintain a constant plasma volume (Schmidt-Nielsen 1964; Hartman & Morton 1973; Hill & Wyse 1989).

Springhare are locally abundant in arid and semi-arid areas such as the Kalahari Desert of Botswana and the Northern Cape Province of South Africa. These areas are characterised by the absence of perennial surface water and extremely variable (70%) mean annual rainfalls of ≈ 400 mm (Butynski 1984; Anderson 1996). According to Anderson (1996) springhare are completely absent from areas experiencing high (>1000 mm) or very low (<50 mm) rainfall.

Behaviourally, springhare appear to be well adapted to life in these arid environments. They avoid temperature extremes by being nocturnal and fossorial and maximise water intake by

selective feeding. Physiologically, however, very little is known about springhare and their ability to reduce water losses and tolerate dehydration. To date there has been only a single study on springhare physiology. Müller *et al.* (1979) measured metabolism, thermoregulation and heart rate of two individuals from Kenya. They concluded that springhare are more adapted to a fossorial lifestyle than to arid conditions and that they have not developed any special physiological adaptations to life in arid environments. They also maintain that springhare completely lack one of the most important adaptations to life in arid environments, namely the ability to produce highly concentrated urine. As springhare successfully inhabit arid areas and are not known to drink free water (Butynski & Mattingly 1979; Anderson 1996), even when it is available, this raises the question of how they meet their water requirements during dry seasons and prolonged droughts, which are not uncommon in the areas that they inhabit.

In the light of this apparent anomaly, the general lack of information available on the physiology of springhare, and the fact that the most remarkable adaptations to life in arid environments are found amongst the rodents, I investigated the physiological responses of springhare to water deprivation. The aim being to determining what physiological adaptations, if indeed any, enable springhare to survive in the arid areas that they do, without drinking.

7.2 MATERIALS AND METHODS

7.2.1 Capture and Care

Springhare were caught in summer on farmland (Marlu, Thorneycroft & Fairfield) surrounding the study site. They were caught on dark moonless nights by chasing them on foot with the assistance of a vehicle and spotlights. The animals were returned to the laboratory where they were housed in a large 5 x 9 m room, with an artificial burrow system in one corner, for an initial 1-2 week conditioning and acclimation period. No more than five animals were simultaneously housed in this room and very little inter-individual aggression was observed. During this period the animals were fed rabbit pellets, carrots and sweet potatoes. Although the animals were provided with water *ad lib*, there was never any evidence to suggest that they

drank any, thus confirming earlier observations by Butynski & Mattingly (1979) and Anderson (1996).

7.2.2 Experimental Protocol

Experiments were conducted in a constant environment room (22°C, 60-90% RH and 24 h D) where the animals were housed individually in rabbit cages (44 x 60 x 44 cm) modified for urine collection. Each cage was fitted with a large plastic funnel, which channeled urine into a bottle where it was collected under paraffin to prevent evaporation. A series of mesh strainers in the funnel prevented food, and faecal pellets from falling into the urine. Springhare were briefly removed for weighing (± 50 g) and daily cage cleaning. The animals were initially familiarized with the cages by placing them in the cages for 24 h, several days prior to the start of experiments. This, together with the fact that the animals were kept in the dark for the duration of the experiments, ensured that the animals were not unduly stressed. A 24 h dark regime was maintained as springhare are nocturnal and spend days in their burrows. Most animals appeared to fall asleep within 30 min of being handled.

An initial experiment was conducted on a group of eight animals. These animals were placed in the cages for an initial 24 h control period and were given both rabbit pellets (water content <10%, protein = 15%) and carrots *ad lib*. Rabbit pellets were not dried and water assimilation is assumed to be negligible at the relative humidities encountered. Urine and an initial blood sample were collected after this initial period. Blood samples (2 mL) were drawn by heparinised hypodermic syringe from the femoral veins of the hind legs, centrifuged within 10 min at 4000 rpm for 5 min and the plasma removed. Plasma and urine were subsequently frozen at -20°C until analysis. Carrots were then withheld and blood and urine samples collected after a further 24, 48, 72, and 96 h of water deprivation. The experiment was terminated at this point as the animals had almost ceased feeding and appeared to be water stressed. Subsequent analyses of the blood and urine samples collected from these animals, however, indicated otherwise and a second group of five animals was subsequently subjected to an additional 48 h of water deprivation (i.e. a total of 144 h of water deprivation). In order to minimise stress to these animals, blood and urine samples were, however, collected only after the initial 24 h control

period and then again after 120 and 144 h of water deprivation, urine being collected over the 24 hour period prior to the blood sample being taken.

Despite the fact that these animals were beginning to lose weight rapidly after 120 h of water deprivation, analyses of the samples suggested that the springhare had not yet reached their physiological limit. Consequently a third group of only three animals was deprived of water, under close scrutiny, for 168 h. Blood and urine samples this time were collected after an initial 24 h control period, after 168 h of water deprivation and again after a 24 h rehydration period during which they were given carrots *ad lib*. Following water deprivation, all animals were returned to the artificial burrow system for several days before being released at their site of capture.

7.2.3 Sample Analysis

Haematocrit was determined by drawing fresh blood into haematocrit tubes and immediately centrifuging at 4000 rpm for 5 min. Blood and urine osmolalities were measured on a freezing point depression micro-osmometer (Advanced Model 30M0). Urine and plasma sodium and potassium concentrations were measured using a Corning 410 clinical flame photometer, and plasma and urine urea concentrations were measured using a commercial test kit (Bohringer Mannheim S180) and spectrophotometer.

Data obtained from experimental animals were compared to data obtained from free-ranging springhare. Blood and urine samples were collected from five free-ranging animals killed each month from June to December 1994 as part of the reproductive study. Blood and urine samples were collected directly from the heart and bladder, respectively, as soon after death as possible, usually within 2-3 min. Blood samples were stored in heparinised tubes overnight and centrifuged early the following morning as already described. The resultant plasma was then frozen along with the urine samples for later analysis. Osmolality, sodium, potassium and urea concentrations of plasma and urine were subsequently determined as previously described.

7.2.4 Kidney Morphology

The maximum theoretical urine-concentrating ability of springhare was estimated from kidney morphology. Kidneys were collected from 25 adult animals sampled for the reproduction study and fixed in 10% neutral buffered formalin. The lengths, breadths and widths of the kidneys were measured after which they were sectioned sagitally through the *area cribrosa* and the cortical and medullary thicknesses measured to 0.01 cm using a vernier calliper. The outlines of the kidneys were then traced onto overhead transparency sheets and the cortical and medullary areas digitised and measured using computer software (SigmaScan, Jandel Scientific). Four different renal indices were subsequently used to predict the maximum urine-concentrating capacity of springhare; percent medullary thickness, relative medullary thickness, percent medullary area and relative medullary area (Brownfield & Wunder 1976).

7.2.5 Statistical Analysis

Control data were available from all three groups and were pooled. Pooling of the data was justified by the fact that there were no significant differences between the three control groups for any the variables measured (*P's* all <0.05).

As samples were collected from each animal prior to water deprivation, each animal effectively acted as its own control. Consequently, one way repeated measures ANOVA's were carried out on the first and second groups of animals and their corresponding controls. In the rare cases where the data failed to meet the assumptions required for ANOVA, the non-parametric Friedman repeated measures ANOVA on ranks was performed. In the case of the third group of animals paired *t*-tests were performed to test for significant differences between control values and those measured after 168 h of water deprivation, and between control values and those measured after rehydration. SigmaStat (Jandel Scientific) was used for all statistical tests and the 0.05 level of probability was accepted as indicating statistical significance.

7.3 RESULTS

7.3.1 Water Deprivation Experiments

7.3.1.1 Body Weight

Springhare body weight decreased steadily with water deprivation (Fig. 7.1) and was significantly different from the corresponding controls after 96 h of water deprivation (Group 1: $F = 3.63$, $P = 0.017$; Group 2: $F = 65.60$, $P < 0.001$; Group 3: $t = 4.60$, $P = 0.044$). After 168 h of water deprivation the third group of animals had lost, on average, 30% of their body weight. Although these animals still refused to drink water after 168 h of water deprivation they did eat carrots and were able to rapidly regain weight during rehydration. After 24 h of rehydration their weight, although not yet up to their initial weight, was not significantly different from it ($t = 1.34$, $P = 0.311$). All animals recovered fully without any assistance.

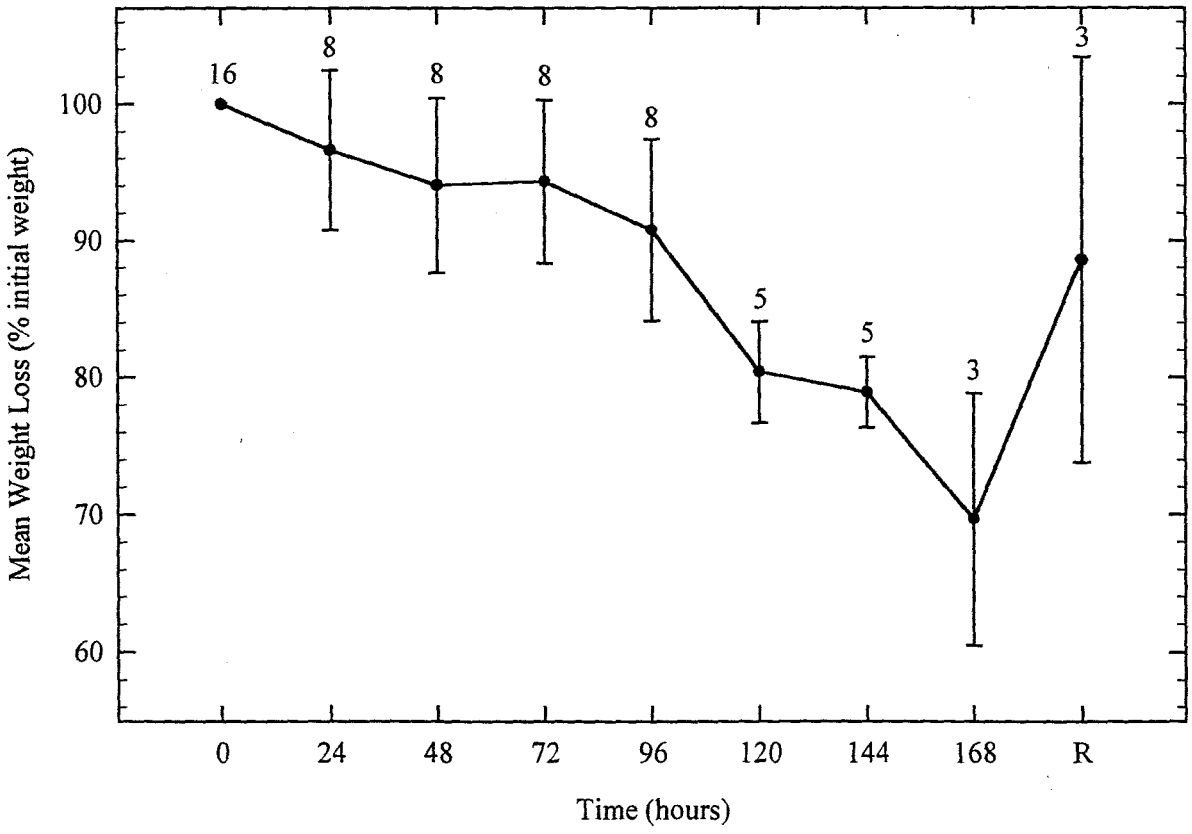

Fig. 7.1: Mean body weight loss (expressed as a proportion of initial weight ± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Numbers indicate sample size.

7.3.1.2 Urine Production

Urine production was very variable but showed an overall decrease from a mean of 73.5 mL day^{-1} to 12.5 mL day^{-1}, after 72 h of water deprivation, after which it remained at approximately this level for the rest of the water deprivation period (Fig. 7.2). Urine production decreased significantly after only 24 h of water deprivation (Group 1: $X^2 = 18.50$, $P = 0.001$; Group 2: $F = 14.60$, $P = 0.002$; Group 3: $t = 5.72$, $P = 0.029$). Urine production in the third group of springhare increased dramatically within 24 h of being fed fresh carrots and, although still only approximately 51 mL day^{-1}, was statistically indistinguishable from the controls ($t = 0.74$, $P = 0.537$).

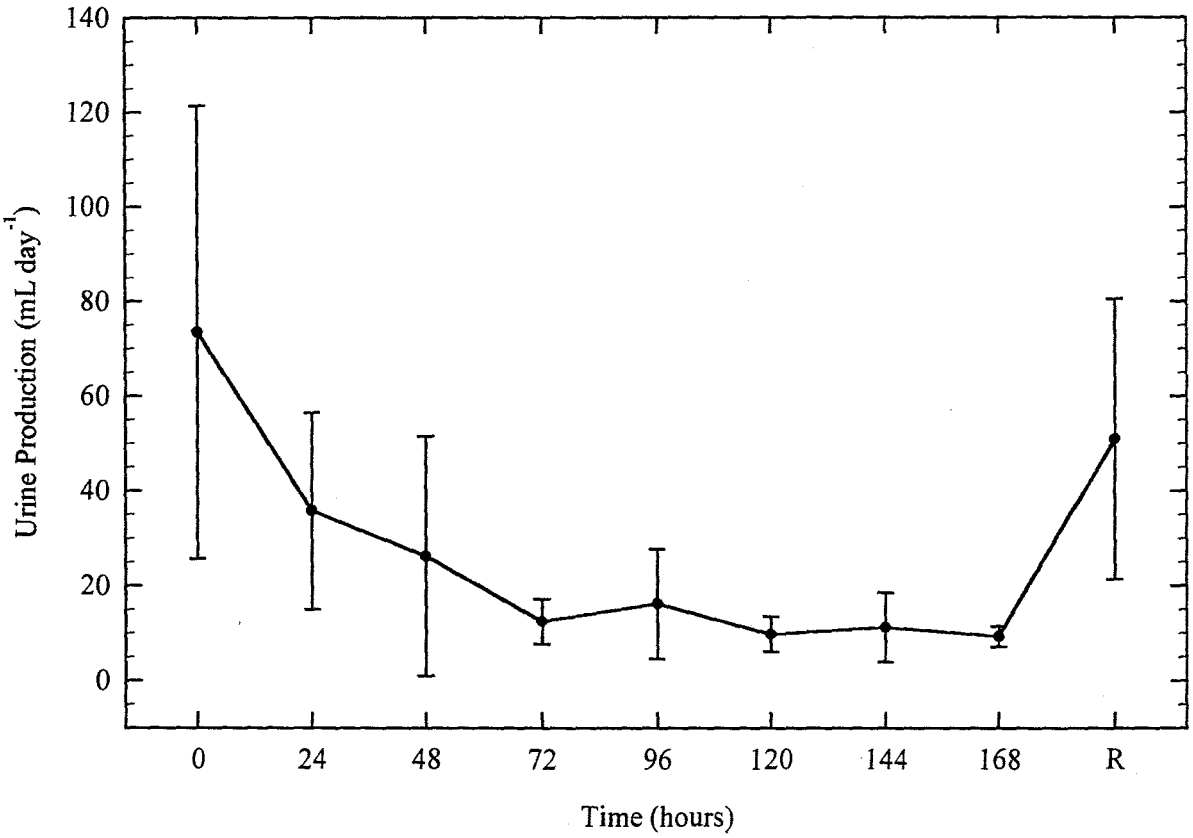

Fig. 7.2: Mean urine production (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

7.3.1.3 Haematocrit

Blood haematocrit was well regulated at 47.5 ± 3.8% throughout the period of dehydration (Fig. 7.3) and did not vary significantly from initial control values (Group 1: $F = 2.57$, $P = 0.060$; Group 2: $F = 4.28$, $P = 0.055$; Group 3: $t = -1.43$, $P = 0.290$).

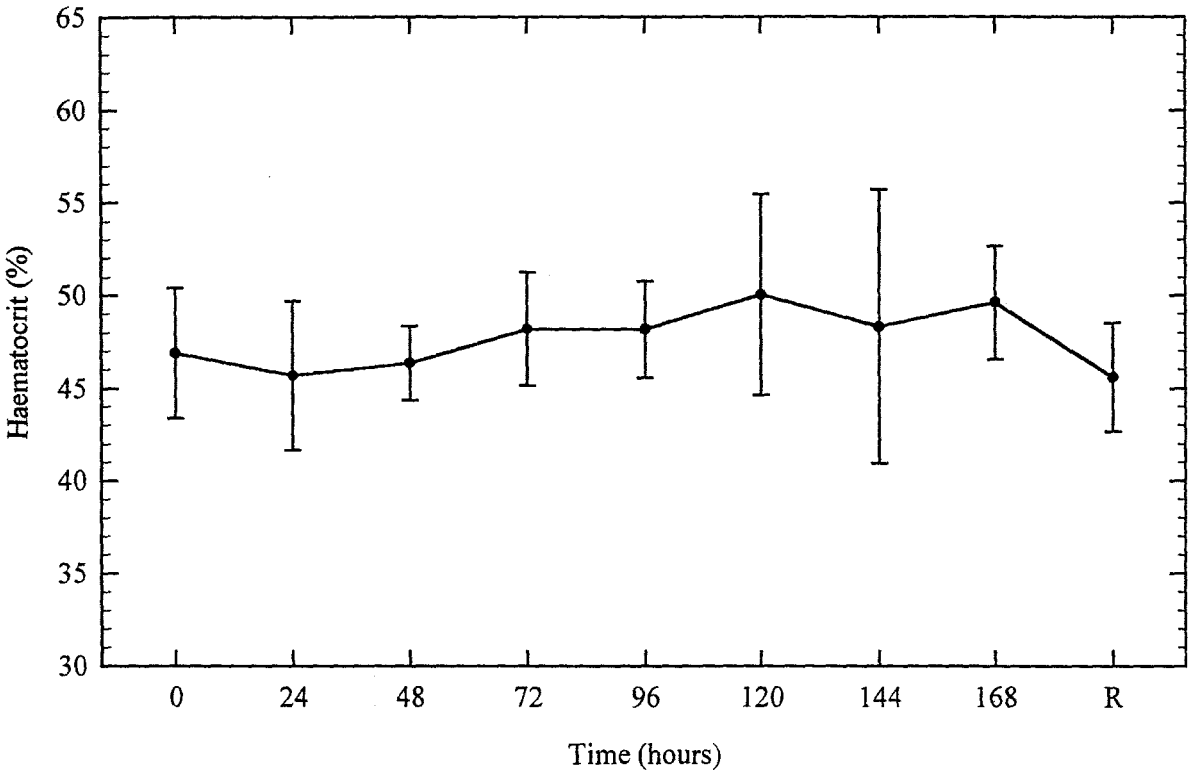

Fig. 7.3: Mean haematocrit (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

7.3.1.4 Osmolality

Plasma osmolality on the whole appeared to be well regulated (Fig. 7.4) although that of the second group of animals was slightly, but significantly, elevated from their corresponding controls after 120 h of water deprivation (Group 1: $F = 0.60$, $P = 0.665$; Group 2: $F = 18.20$, $P = 0.001$; Group 3: $t = -3.49$, $P = 0.073$). Overall, plasma osmolality ranged from an initial mean of 293 ± 12.5 mosmol kg^{-1} to 323.6 ± 7.3 mosmol kg^{-1} after 144 h of water deprivation. After 24 h of rehydration mean plasma osmolality of the third group of animals decreased from

311 mosmol kg^{-1} to 272 mosmol kg^{-1}, slightly but not significantly lower than their initial value ($t = 0.52$, $P = 0.658$).

Urine osmolality increased rapidly from 1245 ± 548 mosmol kg^{-1} to 2288 ± 254 mosmol kg^{-1} after 48 h of water deprivation, after which it remained relatively constant at 2411 ± 349 mosmol kg^{-1} for the remainder of the water deprivation period (Fig. 7.4). This was significantly higher than that measured in the corresponding controls (Group 1: $F = 22.20$, $P < 0.001$; Group 2: $F = 43.90$, $P < 0.001$; Group 3: $t = -5.02$, $P = 0.038$). The mean maximum urine osmolality recorded was 2548 mosmol kg^{-1} after 144 h of water deprivation and the maximum urine osmolality recorded from an individual animal was 3076 mosmol kg^{-1}. After 24 h of rehydration urine osmolality of the third group of animals had decreased to 1536 mosmol kg^{-1}, which was similar to their corresponding control ($t = 0.04$, $P = 0.973$).

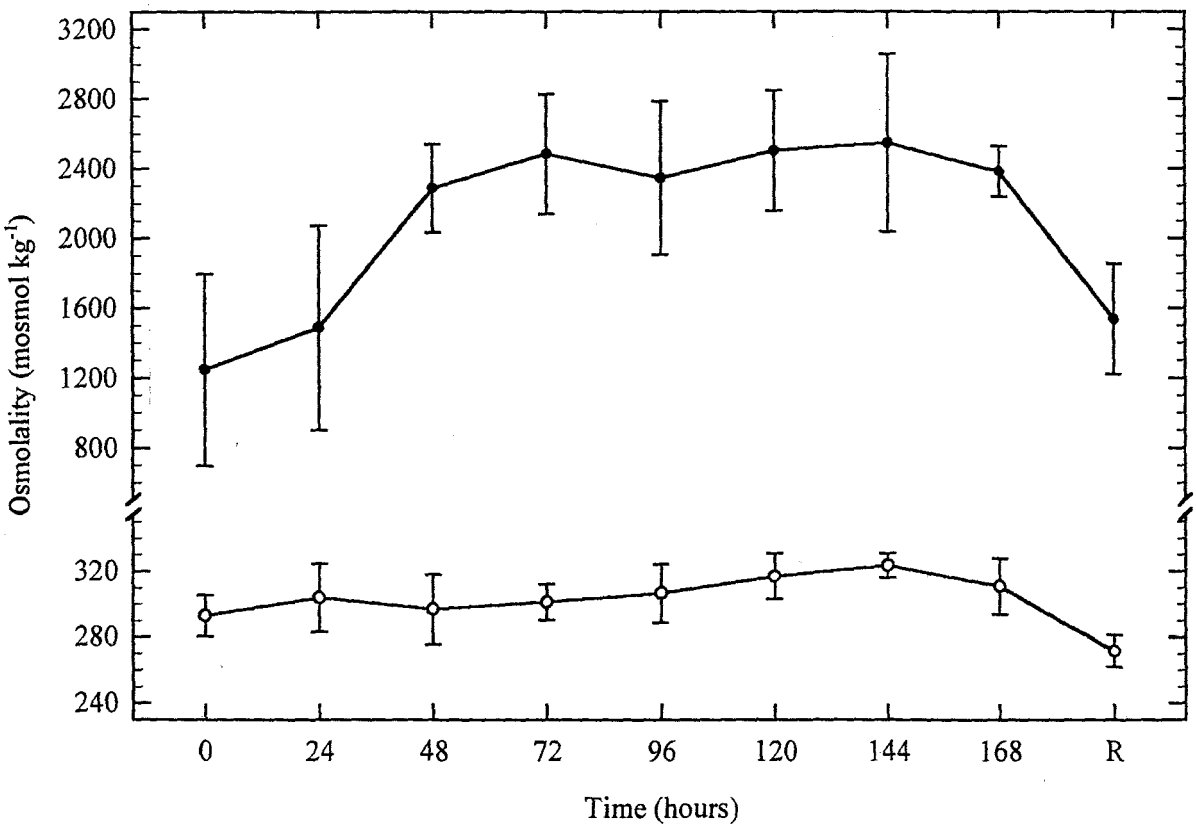

Fig. 7.4: Plasma (*open circles*) and urine (*closed circles*) osmolality (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

7.3.1.5 Sodium and Potassium

Plasma sodium and potassium were well regulated at 132.6 ± 7.4 mmol L^{-1} and 3.48 ± 0.69 mmol L^{-1}, respectively (Figs. 7.5 & 7.6) and did not vary significantly throughout the periods of water deprivation (Sodium - Group 1: $F = 0.69$, $P = 0.606$; Group 2: $F = 0.29$, $P = 0.759$; Group 3: $t = 0.50$, $P = 0.667$: Potassium - Group 1: $F = 2.17$, $P = 0.098$; Group 2: $F = 0.45$, $P = 0.653$; Group 3: $t = 2.89$, $P = 0.102$) and rehydration (Sodium: $t = 0.29$, $P = 0.802$; Potassium: $t = 0.83$, $P = 0.493$).

Urine sodium showed a slight, but not significant, increase from 145 ± 29 mmol L^{-1} to 192 mmol L^{-1} within 24 h but then remained relatively constant at 166 ± 67 mmol L^{-1} until 96 h of water deprivation. After 96 h urine sodium concentrations progressively decreased to 69 ± 5.7 mmol L^{-1} after 168 h of water deprivation. Urine sodium concentrations of the second and third group of animals (i.e. after 120 h of water deprivation) were significantly lower than their corresponding controls (Group 2: $F = 10.60$, $P = 0.008$; Group 3: $t = 4.85$, $P = 0.040$). After 24 h of rehydration mean urine sodium increased to 101 mmol L^{-1}, lower, but not significantly different from the control.

Urine potassium was highly variable. It initially averaged 266 ± 132 mmol L^{-1} but showed a significant increase after 24 h of water deprivation (Group 1: $F = 4.93$, $P = 0.004$) and peaked after 48 h at 451 mmol L^{-1}. Potassium concentrations then progressively decreased to control levels and averaged 247 ± 64 mmol L^{-1} after 168 h of water deprivation. Rehydration of animals in group 3 brought about a rapid elevation in urine potassium from 247 mmols L^{-1} to 443 mmols L^{-1}, which was not significantly different from the control ($t = 1.14$, $P = 0.372$).

7.3.1.6 Urea

Plasma urea concentrations remained quite stable at approximately 7.0 ± 3.0 mmol L^{-1} over the first 96 h hours of water deprivation (Group 1: $F = 1.17$, $P = 0.343$) (Fig. 7.7). Plasma urea concentrations of the second and third group of animals, however, were slightly, but significantly, higher than their corresponding controls and averaged 10.1 and 12.2 mmol L^{-1}, respectively, after 144 and 168 h of water deprivation (Group 2: $F = 4.80$, $P = 0.043$; Group

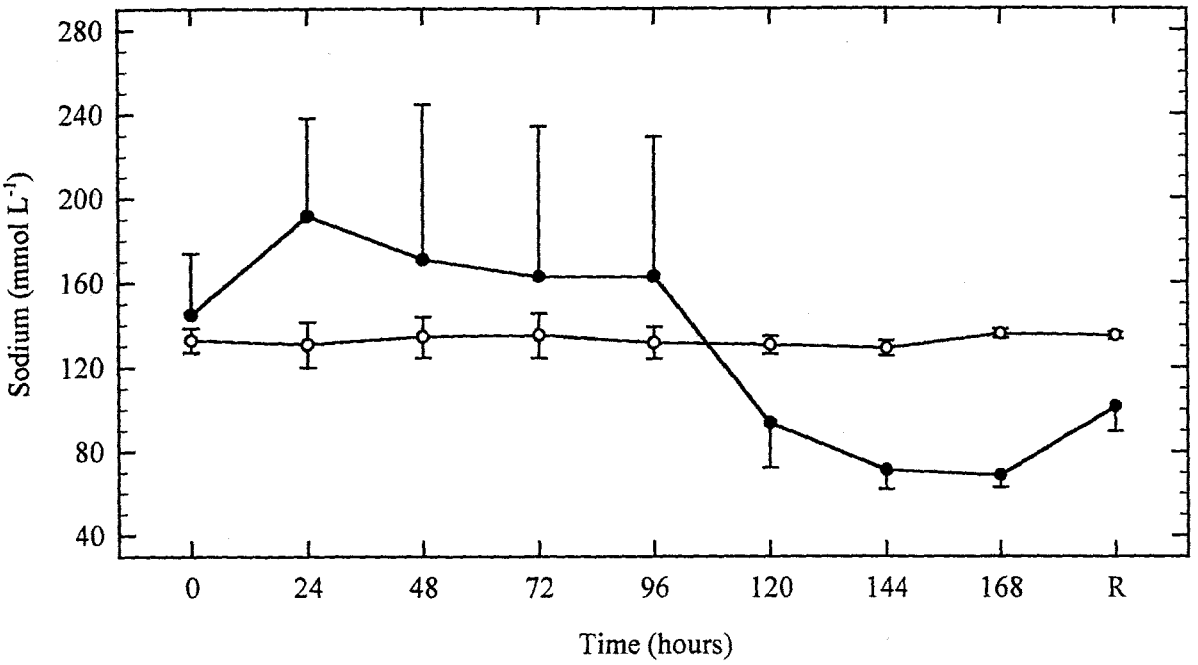

Fig. 7.5: Mean plasma (*open circles*) and urine (*closed circles*) sodium concentrations (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

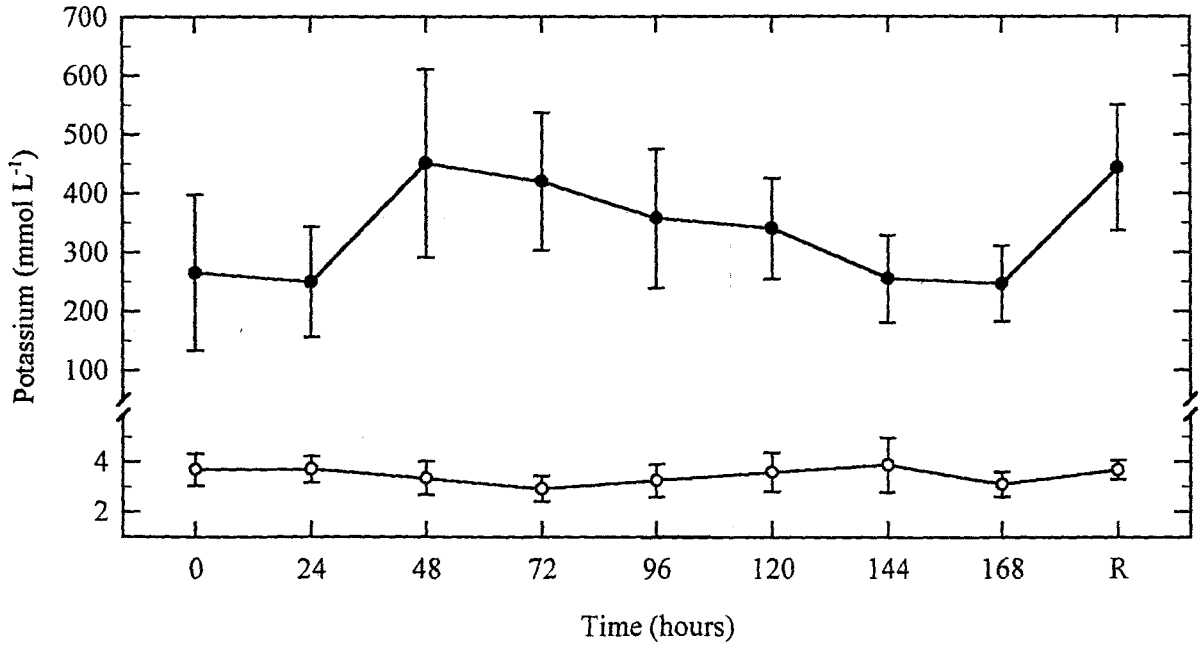

Fig. 7.6: Mean plasma (*open circles*) and urine (*closed circles*) potassium concentrations (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

3: $t = 13.40$, $P = 0.006$). After 24 hours of rehydration plasma urea concentrations decreased to 8.4 mmol L^{-1}, which was not significantly different from initial levels ($t = 1.58$, $P = 0.255$).

Urine urea concentration increased significantly during the first 48 h of water deprivation (Group 1: $F = 15.60$, $P < 0.001$; Group 2: $F = 127.50$, $P < 0.001$; Group 3: $t = 5.69$, $P = 0.030$), after which it remained relatively constant at approximately 1110 ± 286 mmol L^{-1} for the remainder of the period of water deprivation (Fig. 7.7). A mean maximum urine urea concentration of 1169 mmol L^{-1} was obtained after 168 h of water deprivation. Rehydration led to a rapid decrease in urine urea concentration within 24 h, at which stage it was not significantly different from control values ($t = 3.74$, $P = 0.065$).

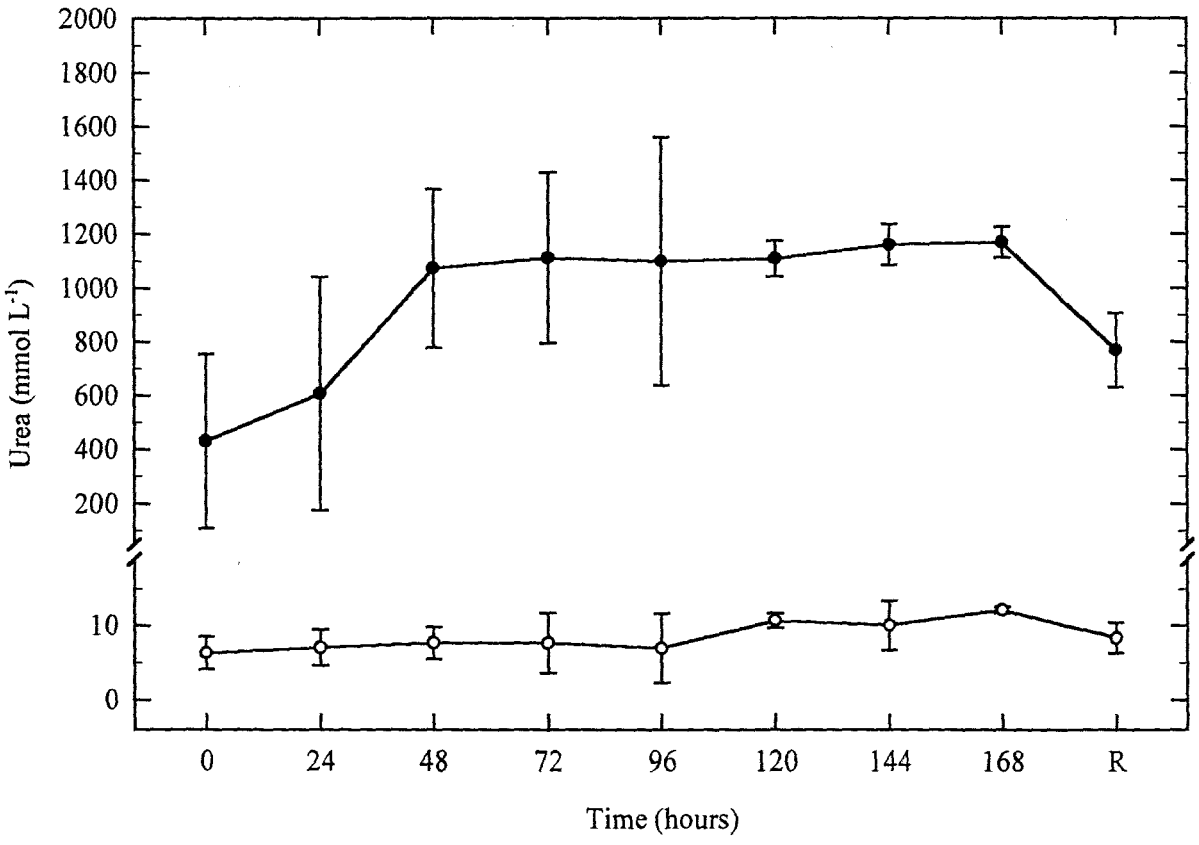

Fig. 7.7: Mean plasma (*open circles*) and urine (*closed circles*) urea concentrations (± 1 SD) of springhare during 168 h of water deprivation and 24 h of rehydration (R). Sample sizes are given in Fig. 7.1.

7.3.2 Wild Animals

Plasma sodium, urea and osmolality of springhare collected in the field showed no seasonal trends (*P's* all > 0.10) so the data for each month were pooled (Table 7.1). The mean values measured were all very similar to the control values obtained from the experimental animals. Urine potassium, urea and osmolality from animals collected in the field were highly variable (Table 7.1) but were nevertheless quite similar to values measured in the experimental animals. Plasma potassium concentrations of the free ranging animals were, however, approximately 2.5 times higher than those found in experimental animals, whereas urine sodium concentrations in springhare from the wild were only approximately one third those found in experimental animals.

Table 7.1: Mean (± 1 SD) plasma and urine concentrations of free-ranging springhare.

Parameters	Plasma	Urine
Sodium (mmol L^{-1})	134.30 ± 8.59 (n = 34)	45.6 ± 42.00 (n = 31)
Potassium (mmol L^{-1})	8.78 ± 2.41 (n = 34)	342.00 ± 161.4 (n = 33)
Urea (mmol L^{-1})	6.41 ± 2.55 (n = 34)	296.50 ± 242.3 (n = 34)
Osmolality (mosmol kg^{-1})	277.30 ± 17.50 (n = 34)	934.1 ± 474.50 (n = 34)

7.3.3 Kidney Morphology

The maximum urine-concentrating capacities of springhare, as estimated by the four renal structural indices, ranged between 2012 and 2927 mosmol kg^{-1} (Table 7.2). The estimates obtained from the relative medullary area, percent medullary area and percent medullary thickness were all very similar and suggest a maximum urine-concentrating capacity of between 2000 and 2100 mosmol kg^{-1}. The estimate obtained from the relative medullary thickness of the kidney was, however, considerably higher and indicated a maximum urine concentration of 2927 mosmol kg^{-1}.

Table 7.2: Maximum urine-concentrating capacity of springhare as predicted by various renal indices (Brownfield & Wunder 1976).

Indices	Predicted maximum urine osmolality in mosmol kg^{-1} (n = 25)
Percent medullary thickness	2012 ± 774
Relative medullary thickness	2927 ± 462
Percent medullary area	2094 ± 554
Relative medullary area	2093 ± 236

7.4 DISCUSSION

Springhare, as suggested by Müller *et al.* (1979) were not able to maintain body weight on a diet of only dry rabbit pellets and lost weight at an increasingly rapid rate. They were, however, able to survive seven days of water deprivation and tolerate a 30% loss of their initial body weight, which is twice the level that is fatal in most other mammals (Schmidt-Nielsen 1964). Man, for example, cannot recover without assistance after losing 12% of his body weight (Schmidt-Nielsen 1964). Weight lost during dehydration is due to water loss and a reduction in food intake which ultimately leads to tissue catabolism. As springhare are very messy feeders and food was often thrown out of the cages the amount of food consumed during the water deprivation experiments could not be measured. Nevertheless, it was still evident that food consumption decreased dramatically after two days of water deprivation and was negligible after six days. Small mammals commonly respond to water deprivation by reducing food intake (Ealey *et al.* 1965; Maloiy & Boarer 1971; Louw *et al.* 1972; Maxson & Morton 1974; Barboza 1993; Schoorlemmer & Evered 1993). Lowering food intake reduces the amount of water lost in the urine and faeces and less water is needed in the gut, making more available for the tissues. Lowering food intake also reduces the solute and urea load and, consequently, water needed to excrete these. A reduced food consumption may also lead to a depression of metabolism which it turn can lead to a reduced respiratory water loss (Dawson *et al.* 1983; Karasov 1983; Schoorlemmer & Evered 1993).

Springhare responded to water deprivation by immediately reducing urine production and by producing a more concentrated urine. After 72 h of water deprivation, however, urine production stabilised at approximately 12.5 mL d^{-1}. As the animals were still losing weight fairly rapidly at this point it can be assumed that they had reached their maximum urine-concentrating ability. The 12.5 mL d^{-1} of urine being produced at this stage presumably represents the minimum needed to excrete end products arising from tissue catabolism as food consumption at this point was negligible. This response has also been observed in the similar sized (≈ 3 kg) rock hyrax (*Procavia capensis*). When given water *ad lib* the mean urine production of rock hyrax varied between 42.0 mL d^{-1} and 56.5 mL d^{-1}. During dehydration, however, urine production rapidly decreased and eventually stabilised between 14.3 mL d^{-1} and 22.5 mL d^{-1} over the last five days of a nine day dehydration period (Louw *et al.* 1972). Contrary to observations in springhare and rock hyrax, however, urine production in arid-adapted merino sheep changes very little during the first 1-2 days of water deprivation and it is only after 10-12% loss of body weight that urinary water saving begins by increasing urine concentration and reducing volume (Macfarlane *et al.* 1961). Springhare and rock hyrax thus appear to reduce water loss to a minimum by rapidly responding to water deprivation.

One of the most important adaptations to arid environments is the ability of desert mammals to maintain plasma volume at the expense of other body water compartments (Schmidt-Nielsen 1964; Horowitz & Borut 1970; Hartman & Morton 1973; Hill & Wyse 1989). More mesic-adapted animals are generally poor regulators of intravascular volume (Kutscher 1968). If the intravascular volume is not protected during dehydration, water will be lost from it. This increases the viscosity of the blood and results in the heart having to work harder to circulate blood. Once blood circulatory rate is impaired, metabolic heat accumulates in the body core as it can no longer be transported to the skin where it can be dissipated to the environment. This collapse of the general circulatory system ultimately leads to a sudden rapid rise in body temperature or "explosive hyperthermia" which is fatal (Schmidt-Nielsen 1964; Hill & Wyse 1989).

Haematocrit has been shown to be a reliable indicator of plasma volume (Kutscher 1968). Springhare appear to regulate haematocrit very well and, despite a very slight increase in haematocrit with progressive dehydration, there was no significant difference between any of the treatments and their corresponding controls. Springhare thus appear to use tissue water in order to maintain vascular volume and are remarkably similar to camels in their ability to maintain plasma volume during dehydration (Schmidt-Nielsen 1964). A number of arid-adapted animals, such as merino sheep (Macfarlane *et al.* 1961), the Somali donkey, and zebu cattle (Maloiy & Boarer 1971) show significant decreases in plasma volume and increases in haematocrit when deprived of water for five days, indicating that plasma volume is less well protected. The sudden decrease in springhare haematocrit observed after 24 h of rehydration is presumably due to the sudden influx of water into the vascular compartment.

The mean maximum urine osmolality of 2422 mosmol kg^{-1} is somewhat higher than the absolute maximum urine osmolality of 2200 mosmol kg^{-1} given by Müller *et al.* (1979) for springhare. It is, however, much lower than the 3700 mosmol L^{-1} measured in dehydrated jackrabbits which are of similar size to springhare (Nagy *et al.* 1976) and also a bit lower than the mean maximum of 2800 mosmol kg^{-1} achieved by the rock hyrax (Louw *et al.* 1972). A maximum osmolality of 3088 mosmol kg^{-1} was achieved by one hyrax and this is quite similar to the 3076 mosmol kg^{-1} recorded in a single springhare. Maximum urine concentration of springhare was also well below the 4470 mosmol kg^{-1} of brown hares (*Lepus capensis*) from the Negev Desert of Israel but very similar to the maximum concentration of 2500 mosmol kg^{-1} reported for brown hares from a temperate region in southern France (Kronfeld & Shkolnik 1996). The degree to which mammals are arid-adapted is often manifest in the maximum urine osmolality that animals can produce. Most desert mammals are able to excrete urine in concentrations above 3000 mosmol kg^{-1} whereas mesic-adapted mammals tend to have maximum urine concentrations between 1000 mosmol kg^{-1} and 3000 mosmol kg^{-1} (Fig. 7.8). Springhare thus appear to fall in the upper half of the mesic-adapted range of mammals, possibly extending to the bottom of the arid-adapted range of mammals.

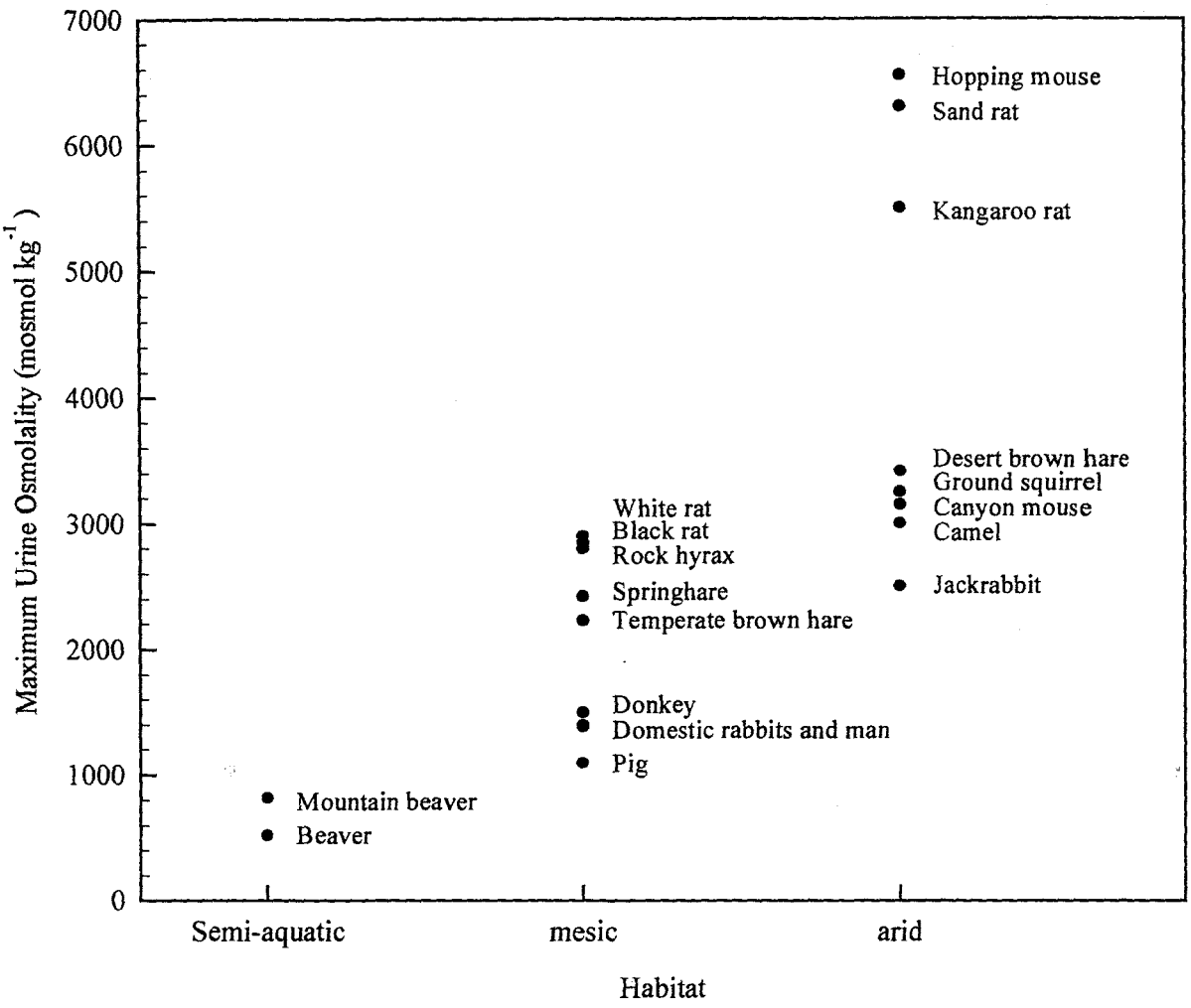

Fig. 7.8: Maximum urine-concentrating abilities of mammals living in various habitats (data from Smith 1951; Schmidt-Nielsen & O'Dell 1961; Dolph *et al.* 1962; Schmidt-Nielsen 1964; MacMillen & Lee 1967; MacMillen & Lee 1969; Norman & Baudinette 1969; Abbott 1971; Louw *et al.* 1972; Maloiy 1972b; Maxson & Morton 1974; Nagy *et al.* 1976; Kronfeld & Shkolnik 1996).

Maximum urine-concentrating ability of springhare was also estimated from kidney morphology. The concept of using renal structural indices to estimate the urine-concentrating capacity of the mammalian kidney was first introduced by Sperber (1944) who used relative medullary thickness as an index. Since then, however, percentage medullary thickness (Heisinger & Breitenbach 1969), percentage medullary area (Schmid 1972) and relative medullary area (Brownfield & Wunder 1976) have all been suggested to be good predictors of urine-concentrating ability. Brownfield & Wunder (1976) compared these four techniques and found relative medullary area to be the most accurate predictor. The maximum urine

osmolalities of 2012, 2093 and 2094 mosmol kg^{-1} predicted from the percentage medullary thickness, relative medullary area and percentage medullary area of the springhare kidney, respectively, were all similar, but low compared to the actual mean maximum urine osmolality of 2422 mosmol kg^{-1}. The maximum urine osmolality predicted from the relative medullary thickness of the kidneys was, however, 2927 mosmol kg^{-1}, which is nearer to the highest urine osmolality recorded in the study. This essentially confirms that as far as urine-concentrating ability is concerned springhare appear to fall into the range of mammals adapted to more mesic environments.

Springhare plasma osmolality showed a slight elevation with increasing water deprivation and was significantly different from controls after 120, 144 and 168 h of water deprivation. As plasma potassium and sodium are well regulated throughout the experimental period the slight increase in plasma osmolality is probably due to a combination of slight haemoconcentration, a slight increase in plasma urea concentration and an increase in divalent ions not measured in this study. This slight increase in plasma osmolality and plasma urea concentrations suggests that these animals were becoming increasingly water-stressed and that urea was beginning to accumulate in the blood as the animals could not afford to expend the water needed to excrete it. After 24 h of rehydration plasma urea returned to its initial levels. The rapid decrease in plasma osmolality after 24 h of rehydration is most likely due to the dilution effect of the sudden influx of water, which is also reflected in the haematocrit.

As already mentioned, both sodium and potassium were well regulated in the plasma throughout the water deprivation period. The maintenance of a stable plasma sodium concentration is essential for the maintenance of the volume of extracellular fluid because sodium and its anions account for 95% of the osmotic pressure of plasma and extracellular fluid (Kirchner & Stein 1994; Hill & Wyse 1989). Springhare appear to be much better ionic regulators than some other arid-adapted animals. Macfarlane *et al.* (1961), for example, have shown that merino sheep show a 5% increase in plasma sodium concentration after four days of water deprivation. Similarly, hill kangaroos (*Macropus robustus*) deprived of water for four days had plasma sodium concentrations significantly higher than kangaroos given water *ad lib*

(Ealey *et al.* 1965). Springhare also experienced no dilutional hyponatremia, as has been found in kangaroos (Ealey *et al.* 1965) and camels (Schmidt-Nielsen *et al.* 1956) after rehydration.

Urine potassium concentrations peaked after two days of water deprivation before gradually declining for the remainder of the experiment. This gradual decline in potassium concentration is assumed to correspond to the reduction in food consumption and the consequent lowering of electrolyte load. The high urine potassium concentrations as opposed to sodium concentrations are presumably because plant material generally has a high potassium and low sodium content (Potts & Parry 1964; Lloyd *et al.* 1978; McDowell *et al.* 1984; Marschner 1990). Mean urine sodium concentrations were initially only slightly higher than plasma concentrations but after four days of water deprivation dropped to below plasma concentrations indicating that sodium was being conserved. Springhare thus appear to regulate plasma osmolality by excreting potassium and preferentially conserving sodium.

Chloride, which is the most important anion, was not measured in this study. This was mainly because there was insufficient sample (particularly plasma) for chloride analyses but also because chloride, along with other negatively charged organic molecules and numerically insignificant anions, essentially balances out the predominant sodium and potassium cations. Chloride concentration thus effectively tells us nothing new.

Unlike urine sodium and potassium concentrations, which decreased with progressive dehydration, urine urea concentrations increased significantly after 24 h of water deprivation and remained at approximately 1140 mmol L^{-1} for the remainder of the experiment. Reducing food intake does not affect urine urea concentrations because nitrogen resulting from tissue protein catabolism, which increases with declining food intake, still has to be excreted. After 24 h of rehydration urine urea concentration decreased indicating the production of a greater volume of more dilute urine, whereas urine sodium and potassium concentrations increased due to the resumption of feeding. Rock hyraxes exhibited a similar response when deprived of water to that observed in springhare. There was an immediate reduction in food consumption and a decrease in urine sodium and potassium concentrations with progressive dehydration. In

contrast to springhare, however, mean urine urea concentrations of rock hyraxes increased during the first half of water deprivation then decreased during the later half (Louw *et al.* 1972). The mean maximum urine concentrations recorded for sodium, potassium and urea, during nine days of water deprivation in rock hyrax were 177 mmol L^{-1}, 494 mmol L^{-1} and 1310 mmol L^{-1}, respectively (Louw *et al.* 1972). The corresponding values obtained in springhare were 192 mmol L^{-1} for sodium, 451 mmol L^{-1} for potassium and 1140 mmol L^{-1} for urea. Springhare thus seem to be very similar to rock hyrax in their electrolyte concentrating abilities.

As expected, urine osmolality, sodium, potassium and urea concentrations of springhare collected in the field were all highly variable due to differences in the time of night at which they were collected and hence differences in feeding times and fullness of the bladder. Nevertheless, data collected from these animals were generally very similar to those of the experimental animals prior to water deprivation. Exceptions were plasma potassium and urine sodium, which were, respectively, higher and lower than in experimental animals. High plasma potassium concentration is most likely due to haemolysis of the red blood cells in the interval between collecting and processing blood samples. Samples showed visual signs of haemolysis and this typically results in an elevation in plasma potassium values because potassium is the predominant intracellular cation. Lower urine sodium concentrations may be due to the lower sodium content of natural vegetation as compared to the rabbit pellets fed to experimental animals.

In conclusion, it appears that springhare are reasonably well adapted physiologically to life in arid environments. They are good osmoregulators and closely approximate some of the true desert species in their ability to tolerate dehydration and maintain plasma volume. They do not, however, produce a highly concentrated urine, which is generally considered to be the most important adaptation to life in arid environments, yet are nevertheless able to survive seven days of water deprivation and tolerate a loss in body weight of at least 30%. Despite being very lethargic after seven days of water deprivation all animals recovered rapidly and without any assistance and physiological parameters measured were almost back to normal levels within just

24 h of being provided with fresh food. I believe the same would have occurred had the animals been released into the field without a recovery phase. During water deprivation springhare maintained a constant plasma volume and regulated plasma sodium and potassium concentrations within a narrow range. Plasma osmolality did increase due to an accumulation of urea but only after five days of total water deprivation. Water loss via urine was limited by the production of a relatively concentrated urine and by the lowered solute load achieved by a reduction in food consumption. The production of very dry faeces by springhare also contributes to water conservation. Fresh faeces collected from two animals, which had been deprived of water for 72 h, were found to have water contents of only 38% and 41%. This is comparable to that found in water stressed jackrabbits 38% (Nagy *et al.* 1976), rock hyraxes 35% (Louw *et al.* 1972), and camels 43% (Schmidt-Nielsen *et al.* 1956).

In order to maintain water balance throughout the year without drinking springhare rely on a combination of both physiological and behavioural adaptations. The most important aspects of their behavioural adaptations are burrowing, nocturnal activity and selective feeding. Burrowing is an option that is generally available to smaller animals and has been shown in various studies to provide a stable and favourable microclimate with moderate temperatures and high humidities (Schmidt-Nielsen & Schmidt-Nielsen 1950; Schmidt-Nielsen & Schmidt-Nielsen 1953; Studier & Baca 1968; Downs & Perrin 1989). Springhare burrows in the Eastern Cape have temperatures that rarely exceed 20°C and are usually saturated with water vapour (Chapter 5). This high humidity and moderate temperature effectively reduces evaporative water loss in the burrow. Feeding at night has the added advantage that the water content of food is higher due to the uptake of water vapour and possibly dew (Taylor 1968). The success of springbok in the semi-arid Kalahari of southern Africa without access to drinking water has been ascribed to the fact that they alter their diet from grass to acacia flowers in the dry season and wait until late at night to feed when the flowers have relatively high water contents from water vapour uptake (Taylor 1968; Nagy 1994). Springhare are also selective feeders often feeding on the leaf and culm bases of grasses, which have a higher water content than the rest of the plant (Chapter 3) in winter. A large part of their diet also consists of the underground

storage organs of plants such as roots, rhizomes, stolons and tubers which have relatively high water contents (Augustine *et al.* 1995; Skinner & Smithers 1990; Chapter 3).

Finally it is also important to note that the springhare used in this study were from a relatively mesic area which, although undergoing periodic droughts, has had a mean annual rainfall since 1975 of approximately 633 ± 157 mm. The animals in this study were thus not acclimatised to arid conditions and this may be of significance. Basset (1982) found that there were intraspecific differences in the urine-concentrating ability of insectivorous bats and that these differences were directly related to habitat aridity. Similarly Kronfeld & Shkolnik (1996) found that brown hares from the Negev Desert of Israel had much higher maximum urine concentrations (4470 mosmol kg^{-1} vs 2500 mosmol kg^{-1}) and only half the water turnover rate of the same species from the temperate region in southern France. The possibility thus exists that springhare from more arid regions would be able to produce a more concentrated urine and, as a result, be better adapted physiologically.

CHAPTER 8

METABOLISM AND THERMOREGULATION

8.1 INTRODUCTION

In the preceding chapter some of the behavioural and physiological adaptations that enable springhare to inhabit arid and semi-arid areas without drinking free water were examined and discussed. Since endotherms are also know to adjust their metabolic and thermal biology to unique environments (mainly through adjustments to the basal metabolic rate and thermal conductance), it was decided to examine the metabolic and thermal biology of springhare for adaptations to life in arid environments.

In the only study of springhare thermal physiology to date, Müller *et al.* (1979) examined the oxygen consumption and thermoregulatory capabilities of two individual springhare from East Africa at various ambient temperatures between 6°C and 35°C. They found these two animals to have basal metabolic rates (BMRs) that were lower than expected for a similar sized mammal (Table 8.1). Lower than expected BMRs are typical of arid-adapted mammals (McNab & Morrison 1963; Goyal & Ghosh 1983; Hinds & MacMillen 1985; Downs & Perrin 1990; Degen 1997) (Table 8.1) and are considered an alternative to the production of a concentrated urine as a means of reducing water turnover in mammals with a low water intake (McNab 1979a). Low BMRs are thought not only to reduce heat production and evaporative water loss in arid environments (Murie 1961; McNab & Morrison 1963; MacMillen 1965; Glenn 1970; Borut & Shkolnik 1974) but also to reduce energy requirements, which may be important for animals that experience periodic food shortages (Jarvis 1978; McNab 1979a; Lovegrove 1986, 1987). Low BMRs are, however, also encountered in tropical and fossorial mammals (>80 g) that are seldom if ever exposed to low temperatures (McNab 1966, 1970, 1979b) (Table 8.1). In these animals low BMRs are thought to prevent overheating in the warm humid conditions typically encountered (McNab 1966, 1979b; MacMillen & Lee 1970), but can also be

interpreted as a means of reducing gas exchange in the hypoxic and hypercapnic conditions which are characteristic of closed burrows (Darden 1972; Withers 1978; Arieli & Ar 1981).

Table 8.1: General deviations from the predicted (from weight) BMR and thermal conductance of mammals inhabiting different habitats (McNab & Morrison 1963; McNab 1966, 1970, 1979a, 1979b; Shkolnik & Schmidt-Nielsen 1976; Goyal & Ghosh 1983; Hinds & MacMillen 1985; Lovegrove 1986; Downs & Perrin 1990; Degen 1997).

Habitat	BMR	Conductance
Arid	low	low
Mesic	high	as predicted
Fossorial	low	high
Tropical	low	high
Springhare (Müller *et al.* 1979)	low	high

In addition to a low BMR, Müller *et al.* (1979) also found springhare to have a higher than expected (for a similar sized mammal) minimum thermal conductance (Table 8.1). Higher than expected thermal conductances are useful in dissipating heat and are usually found amongst mammals that are rarely, if ever, exposed to low temperatures eg. tropical (McNab 1979a; Hinds & MacMillen 1985) and fossorial mammals (McNab 1966, 1970, 1979b) (Table 8.1). Nocturnal rodents from arid habitats on the other hand typically encounter low night-time temperatures and are consequently generally characterised by having low thermal conductances (Goyal & Ghosh 1983; Hinds & MacMillen 1985; Downs & Perrin 1990; Degen 1997) (Table 8.1). That springhare have a high thermal conductance suggests that losing heat in the burrow is of greater importance than excessive heat loss when foraging at night. This combination of a low BMR and high thermal conductance led Müller *et al.* (1979) to conclude that springhare are better adapted to fossorial habits than to arid environments, which are characterised by low night-time temperatures. A low BMR in association with a high thermal conductance has, in the naked mole-rat (*Heterocephalus glaber*), clearly been shown to lead to poor body

temperature regulation, which in turn restricts these animals to a tropical distribution (McNab 1966, 1979b).

Despite the observations of Müller *et al.* (1979), springhare in southern Africa are abundant in arid areas, which are also characterised by very low night-time temperatures eg. the Northern Cape Province of South Africa (Anderson 1996) and the Kalahari Desert of Botswana (Butynski 1984). Anderson (1996) has previously reported large scale foraging of springhare at temperatures below -3 °C and temperature has in the present study (Chapter 4) been shown to have no significant effect on springhare activity. This apparent disregard for low ambient temperatures is unlikely for an animal with a very low BMR and a very high thermal conductance. In view of these observations, as well as the fact that Müller *et al.* (1979) based their observations on only two animals from an equatorial region (1-2°S latitude) an examination of the metabolism and thermoregulatory capabilities of southern African springhare (33°S) was undertaken. The objective of this chapter is consequently to provide the first detailed description of metabolism and thermoregulation in the southern African springhare and to determine what metabolic and thermal adaptations, if any, enable springhare to inhabit the arid and semi-arid areas that they do.

8.2 MATERIALS AND METHODS

8.2.1 Capture and Care

Eighteen springhare (eleven males and seven females) were caught specifically for this study on farmland surrounding the study site. Capture was effected as described previously (Chapter 7) and the animals were returned to the laboratory where they were housed, under a natural light and temperature regime, in a large 5 x 9 m room with an artificial burrow system in one corner. Animals were fed *ad lib* on commercially manufactured rabbit pellets, carrots and sweet potatoes. Drinking water was always available, though there was no evidence that the animals ever drank.

Experiments were all conducted during the autumn and winter months and were initiated only after the animals had been in captivity for at least two weeks. To ensure that animals were post-absorptive during experiments, individuals were removed from the communal enclosure and kept in a cage without food for 4-6 hours before measurements were made. All experiments were conducted during normal daylight hours when springhare are naturally inactive.

8.2.2 Energy Expenditure

Oxygen consumption was used as a measure of metabolic rate. Open-flow respirometry was used to measure oxygen consumption of each springhare at ambient temperatures (T_a) ranging from -5 to 35 °C at 5 °C intervals. Each springhare was weighed to 0.1 kg before sealing it into a rectangular, perspex metabolic chamber. An accuracy of 0.1 kg was considered sufficient as it is very difficult to weigh a largish (3-4 kg) live animal more precisely and because a precision of 0.1 kg translates into a maximum metabolic rate error of less than 5%. The dimensions of the metabolic chamber (40 x 16 x 28 cm) were made to approximate the height and width of the tunnels in natural burrow systems (Butynski & Mattingly 1979; Anderson 1996). The metabolic chamber was then placed in a darkened constant environment cabinet (± 1 °C). Air, scrubbed of water and CO_2 by passing it through tubes of soda lime and silica gel, was pumped through the chamber at a rate of 2500 mL min^{-1}. Flow rate was monitored by means of a calibrated ANAVAC FM 082-03 rotameter-type flow meter placed immediately upstream of the chamber. The flow meter was calibrated against a bubble flow meter as described by Levy (1964). A sub-sample of the chamber outlet air was drawn off for gas analysis. This air was scrubbed of both CO_2 and water vapour by passing it through a soda lime/silica gel tube before entering an Applied Electrochemistry S-3A/I O_2 analyser. The gas analyser was baselined before each experimental run by pumping dry, CO_2-free air through and adjusting it to 20.95% O_2. Any drift during the experiment was corrected using the drift correction facility on the analysis program. Chamber temperature (T_a) was monitored by means of a 26 gauge thermocouple inserted into the chamber through a rubber bung and attached to a Sensortek BAT-12 thermometer. Percentage O_2 and chamber temperature were recorded by a computer at 20 second intervals for approximately three hours using DATACAN V data acquisition software

(Sable Systems Inc., Las Vegas). Data from successful runs were stored on disk for later analyses using DATACAN V analysis software.

During the subsequent analyses of data, oxygen consumption in mL O_2 g^{-1} h^{-1} (corrected to STPD) was determined from the period of at least 10 min corresponding to the lowest stable O_2 consumption recorded during the run. Oxygen consumption was then converted to energy expenditure (J g^{-1} h^{-1}) by assuming that 1mL O_2 = 20.083 Joules (Schmidt-Nielsen 1990).

8.2.3 Body Temperature

On completion of each experimental run the animal was removed from the chamber and its rectal temperature (T_b) immediately measured at a depth of approximately 5 cm with a 26 gauge thermocouple attached to a Sensortek Bat-12 thermometer. The springhare was then returned to the communal enclosure. No animals were subjected to experiments more than once in any single 24 h period.

8.2.4 Thermal Conductance

Wet thermal conductance was calculated from individual measurements of metabolic rate and T_b by using the following equation:

$$C = MR / (T_b - T_a)$$

Where C is the wet thermal conductance measured in J g^{-1} h^{-1} $°C^{-1}$, MR is the metabolic rate in J g^{-1} h^{-1}, T_b is the body temperature (rectal temperature) in °C and T_a is the ambient temperature in °C (McNab 1980).

8.2.5 Statistical Analysis

Regression equations were calculated by the method of least squares and t-tests were used to compare means at different temperatures. Where data for the t-tests was not normally distributed the non-parametric Mann-Whitney rank sum test was used. SigmaStat (Jandel

Scientific) was used for all statistical tests and in all cases the 0.05 level of probability was accepted as indicating statistical significance.

8.3 RESULTS

8.3.1 Energy Expenditure

The results obtained clearly indicate that springhare attained basal conditions within the three hour experimental period and usually within two hours (Fig. 8.1). Lowest mass specific rates of energy expenditure were measured between 15 and 25 °C (Fig. 8.2) and this was assumed to be their thermal neutral zone (TNZ). This is supported by the fact that energy expenditure at 10 °C was significantly higher than that at 15 °C (T = 265, P = 0.048) and that energy expenditure at 30 °C was significantly higher than that at 25 °C (t = -2.15, P = 0.042). Within the TNZ energy expenditure averaged 8.62 ± 1.37 J g^{-1} h^{-1} (17 individuals with a mean mass of 2.8 ± 0.4 kg). Energy expenditure below the TNZ zone increased with decreasing T_a as described by the equation: Energy expenditure (J g^{-1} h^{-1}) = 12.63 - 0.27 T_a (r^2 = 0.99, P < 0.001). The highest mean energy expenditure (14.10 ± 2.75 J g^{-1} h^{-1}) was recorded at T_a = -5 °C, the lowest temperature to which animals were subjected. Above the TNZ, energy expenditure increased with increasing T_a, reaching a mean of 10.03 ± 1.42 J g^{-1} h^{-1} at 35 °C, the highest T_a at which springhare were measured.

At T_a = 35 °C springhare appeared to be suffering severe thermal stress and experimental runs were generally terminated as soon as possible. At 35 °C springhare lay on their backs with their limbs in the air. Blood vessels in the ears and legs were visibly dilated and animals were also observed to spread saliva over their faces and throats. As T_a decreased springhare curled up into tighter and tighter balls with the head tucked between the hind legs and the tail wrapped around the back. Shivering became increasingly apparent at low temperatures.

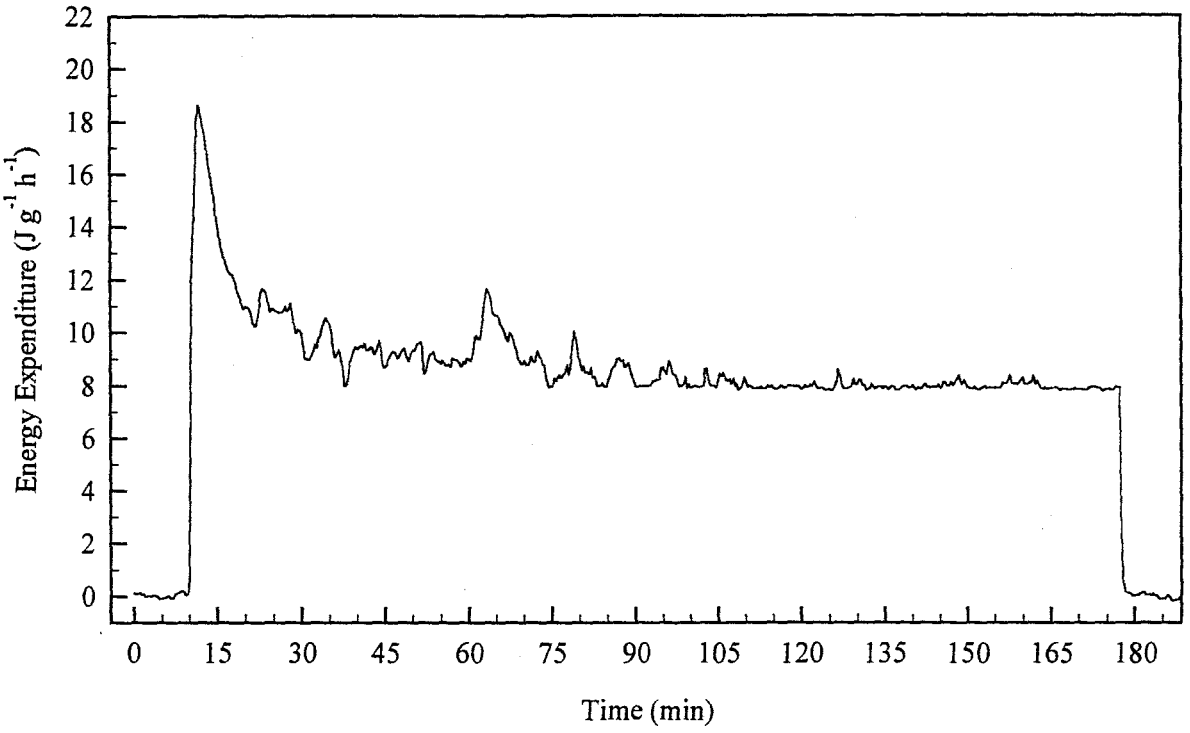

Fig. 8.1: Typical energy expenditure of a springhare during the three hour experimental period.

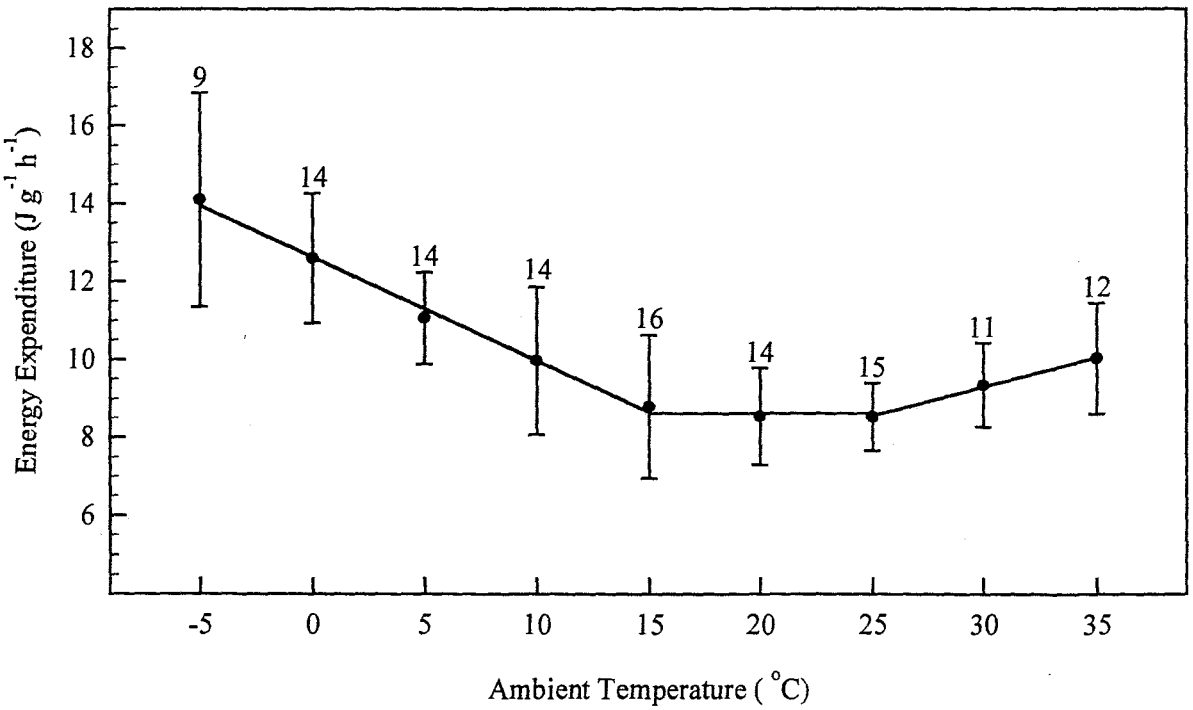

Fig. 8.2: Mean (± 1 SD) energy expenditure of springhare in relation to ambient temperature. Numbers indicate sample size.

8.3.2 Body Temperature

Body temperature was generally quite variable (Fig. 8.3). At $T_a = 25°C$ and below, T_b was independent of T_a ($r^2 = 0.55$, $P = 0.06$) and averaged $35.8 \pm 0.7°C$ (range = 34.6-36.9°C, $n = 17$). Even the lowest temperature of -5°C did not induce hypothermia. Above 25°C, however, springhare became increasingly hyperthermic and T_b approached the line of equality ($T_b = T_a$) with a mean of $38.7 \pm 0.7°C$ at 35°C. The highest T_bs were recorded at 35°C where they ranged between 37.6 and 39.9°C.

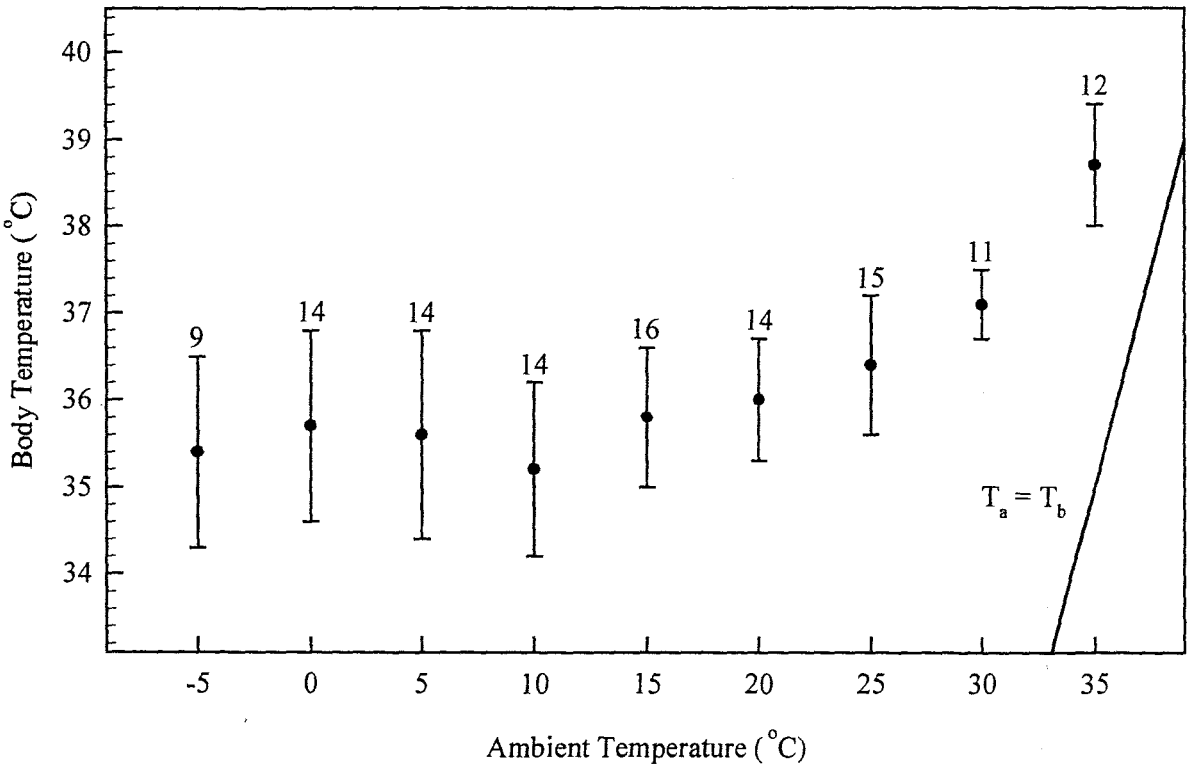

Fig. 8.3: Mean (± 1 SD) body temperature of springhare in relation to ambient temperature. Numbers indicate sample size and the solid line is the line of equality.

8.3.3 Thermal Conductance

Although wet conductance was statistically dependent on T_a at 15°C and below ($r^2 = 0.91$, $P = 0.01$), there was very little change in conductance over this temperature range and conductance remained relatively constant at 0.386 ± 0.062 J g^{-1} h^{-1} $°C^{-1}$ ($n = 17$) (Fig. 8.4).

Above 15 °C, however, thermal conductance increased rapidly with increasing T_a, reaching a mean maximum of 2.740 ± 0.506 J g^{-1} h^{-1} $°C^{-1}$ at 35 °C. The highest individual conductance recorded was 3.862 J g^{-1} h^{-1} $°C^{-1}$ at 35 °C.

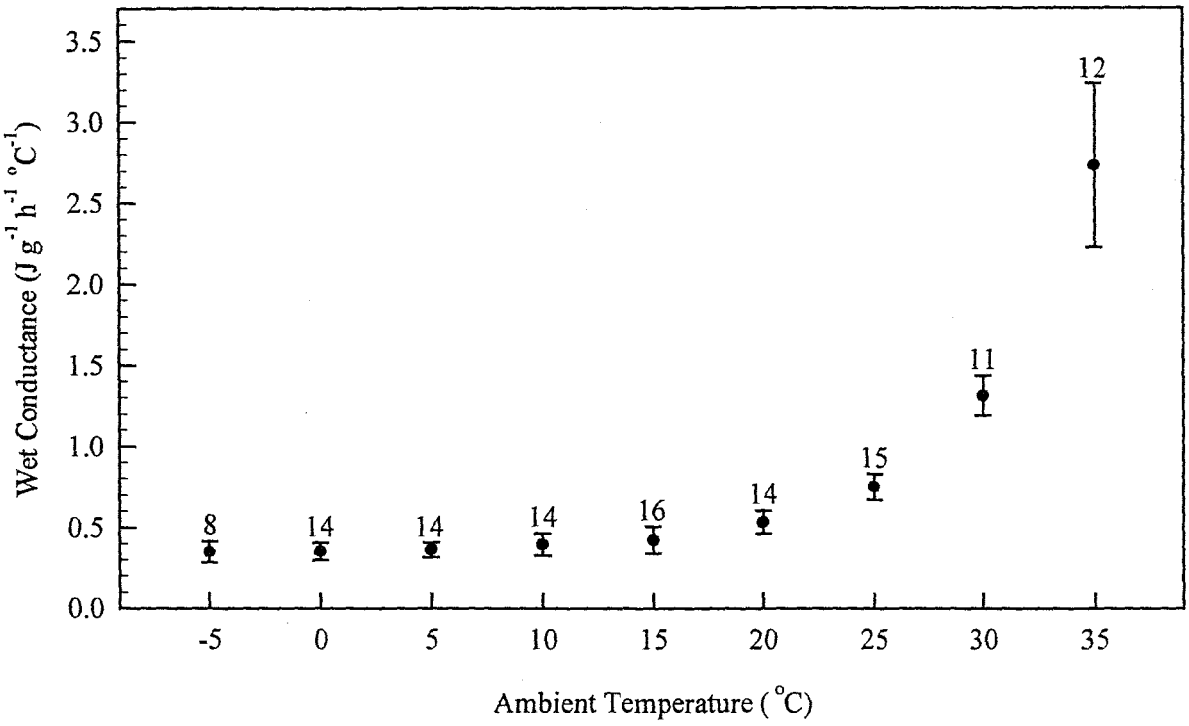

Fig. 8.4: Mean (± 1 SD) thermal conductance of springhare in relation to ambient temperature. Numbers indicate sample size.

8.4 DISCUSSION

Müller *et al*. (1979) reported BMRs of 0.32 and 0.37 mL O_2 g^{-1} h^{-1} (6.43 and 7.43 J g^{-1} h^{-1} respectively) for two East African springhare. This is only 65 and 75% respectively, of that expected for a similar sized mammal using Kleiber's (1961) equation. Despite its widespread application, Kleiber's equation has been severely criticised on the grounds that it is based on data that were insufficient in number, unrepresentative of the class Mammalia and incorrectly analysed statistically (Hayssen & Lacy 1985). Based on a much larger sample size, Hayssen & Lacy (1985) derived a new equation to describe the BMR - body

mass relationship in the order Rodentia. If this new equation is applied to the data of Müller *et al.* (1979) the two springhare are found to have BMRs only 84-97% of that expected for similar sized rodents. Although it is acknowledged that established allometric equations used in this chapter do not take into account that animals are not statistically independent because of common ancestry, these relationships are used for comparisons of BMR and thermal conductance as there are not yet any phylogenetically corrected relationships available for mammals.

Springhare in this study had a higher mean BMR (8.62 J g^{-1} h^{-1}) than that reported for East African springhare by Müller *et al.* (1979). Mean BMR in this study was 119% (range: 100-161%) of that expected for a similar sized rodent. The higher BMR in this study was also associated with a lower TNZ (15-25 °C) than that previously reported by Müller *et al.* (1979) (23-33 °C). A higher than expected BMR is typical of non-desert (mesic) rodents and suggests that springhare in this study are not very well adapted to life in arid environments (Table 8.1). Goyal & Ghosh (1983) found that non-desert rodents had BMRs that were on average 34% higher than expected. As previously mentioned, a low BMR is considered to be advantageous to animals inhabiting arid areas as it reduces energy requirements, heat production and evaporative water loss. Springhare are, however, nocturnal and spend their days in deep cool burrows (Chapter 5). As a result they seldom encounter high temperatures but are typically confronted with low night-time temperatures, particularly in winter. Although there is little or no evidence that animals from cold climates have higher BMRs than expected based on their size (Feist & White 1989) the relatively low, lower critical temperature and broad thermoneutral zone of springhare are typical adaptations to cold climates (Taylor & Sale 1969; Kronfeld & Shkolnik 1996; Degen 1997).

Mean monthly minimum T_as in the study site typically range between 16 °C in summer and 5 °C in winter with occasional sub-zero temperatures (Chapter 2). Minimum temperatures are presented as these generally occur at night when springhare are active. Mean monthly burrow temperatures on the other hand fluctuated between 22.0 °C in summer and 11.4 °C in winter (Chapter 5). Burrow temperatures in this study were generally within the thermoneutral zone

of springhare throughout the spring, summer and autumn months (Chapter 5 - Fig. 5.6). Only during the winter months of June July and August did mean burrow temperatures drop below the thermoneutral zone. Similar results have been reported for a number of mammals (Baudinette 1972; Jarvis 1978; Gettinger 1984; Degen 1997). For nine months of the year springhare thus expended no additional energy on thermoregulation in the burrow and this may explain why they do not make use of nesting materials (Butynski & Mattingly 1979; Anderson 1996). During the remaining three months mean burrow temperatures dropped below the lower critical temperature of 15°C. The lowest mean burrow temperature recorded was only 11.4°C and at this temperature metabolism is only elevated by 11% above BMR. In comparison to this, the lowest mean monthly minimum T_a encountered in the study site was 5°C and at this temperature metabolism is elevated by 31% above BMR. The relatively moderate increase in BMR at this low temperature is a reflection of low thermal conductance. At no stage did burrow temperatures reach or exceed the upper critical temperature of 25°C (Fig. 5.6) which would require active temperature regulation.

Müller *et al.* (1979) reported wet thermal conductances 120 and 155% of that expected for similar sized mammals. High thermal conductances indicate poor insulation and a high rate of heat loss at low T_as. Müller *et al.* (1979), however, used Herreid & Kessel's (1967) equation to determine the expected conductance of an animal this size. This equation is based on only 24 species, the heaviest of which weighs only 598 g and problems may consequently arise when extrapolating to body weights as large as those of springhare. If the data of Müller *et al.* (1979) are recalculated using the body weight to thermal conductance relationship of Bradley & Deavers (1980) these two springhare are found to have thermal conductances of only 86 and 111%; thereby averaging approximately 99% of the expected thermal conductance. In contrast to Herreid & Kessel's (1967) equation, that of Bradley & Deavers (1980) is based on 192 species ranging in weight from 3.5 g to 150 kg. The conclusion of Müller *et al.* (1979) that east African springhare have high thermal conductances thus appears to be unjustified.

In contrast to the observations of Müller *et al.* (1979), springhare in this study were found to have a lower than expected mean minimum wet thermal conductance. Wet thermal conductance

(calculated from individual measurements) was only 75% (range: 58-103%) of that predicted for a similar sized mammal (Bradley & Deavers 1980). A low thermal conductance reduces heat loss at low T_as and, as previously mentioned, is fairly typical for nocturnal animals exposed to low temperatures.

The differences in BMR and minimum thermal conductance between the two studies may merely be an artefact of the small sample size of Müller *et al.* (1979). These differences may, however, also be attributed to climatic differences between the study sites. The study of Müller *et al.* (1979) was conducted in Nairobi, Kenya which is located almost on the equator. Temperatures here are moderate to high throughout the year and exhibit only very slight seasonal changes, mean monthly minimum T_as typically ranging between 11 and 14°C (Thompson 1967). Springhare in the present study, however, encounter much lower temperatures and, considering that experiments in the present study were conducted during the autumn and winter months when temperatures are at their lowest, springhare in this study were presumably acclimatized to much lower temperatures than the two animals used by Müller *et al.* (1979). A number of animals acclimatized or accustomed to low temperatures have been shown to have higher BMRs, lower thermal conductances and reduced lower critical temperatures in comparison to conspecifics that are accustomed to higher temperatures. This has been illustrated in different populations of brown hares (*Lepus capensis*) (Kronfeld & Shkolnik 1996), vlei rats (*Otomys irroratus*) (Brown *et al.* 1999), black-tailed jackrabbits (*Lepus californicus*) (Hinds 1977), antelope jackrabbits (*Lepus alleni*) (Hinds 1977), white-tailed jackrabbits (*Lepus townsendii*) (Rogowitz 1990) and in different hyrax species (Taylor & Sale 1969). As the animals used by Müller *et al.* (1979) were also from a more arid region (250-600 mm of rain per year) than the animals in the present study (mean annual rainfall 631 ± 153 mm), the observed differences in BMR may also be attributed to differences in arid-adaptation. A large number of studies have shown that species or subspecies from arid environments have lower BMRs than their counterparts from less arid environments (McNab & Morrison 1963; Shkolnik & Schmidt-Nielsen 1976; Hinds & MacMillen 1985; Kronfeld & Shkolnik 1996).

As expected for an animal with a high BMR and a low thermal conductance, springhare in this study were found to be good thermoregulators at low T_as and were able to maintain T_bs averaging 35.8 ± 0.7°C at T_as ranging from -5 to 25°C. Body temperature was, however, quite variable and slightly below the 36-39°C range reported for nocturnal rodents (MacMillen 1972). Variable T_bs are, however, fairly typical of rodents in general (Hart 1971; Downs & Perrin 1990). Müller *et al.* (1979) similarly reported T_bs of 35.5-36.3°C at T_as of 6-28°C. At T_as below the lower critical temperature of 15°C conductance, and consequently heat loss, was minimal and springhare maintained T_b by increasing metabolic heat production via shivering (and possibly non-shivering thermogenesis). At these low temperatures springhare were also observed to modify their conductance behaviourally by curling up tightly thereby effectively decreasing surface area. When active at low T_as heat loss is presumably offset by the increased heat production associated with activity.

At high T_as springhare are poor thermoregulators. This is not entirely surprising as springhare rarely encounter T_as above the upper critical temperature of 25°C. At T_as above 25°C, despite a seven fold increase in thermal conductance, heat could not be dissipated as fast as it was gained and animals became hyperthermic. At these high temperatures springhare maximised conductance and heat loss by sprawling on their backs with their legs in the air. Blood circulation to the periphery, particularly the ears and legs, was also increased. At 35°C springhare were obviously heat stressed and began spreading saliva over the face and throat in an attempt to increase evaporative cooling. This behaviour has previously been reported in a number of animals including the red kangaroo (*Megaleia rufa*) (Needham *et al.* 1974) and the laboratory rat (*Rattus norvegicus*) (Hainsworth 1967). Saliva spreading is, however, used primarily as an emergency measure when T_b is near lethal levels (Schmidt-Nielsen 1964, 1990).

According to Müller *et al.* (1979) springhare do not sweat or pant effectively. This may explain their poor thermoregulatory capabilities at high ambient temperatures. Relatively poor heat loss through evaporation has also been reported in several other mammals that avoid high temperatures by being nocturnal and fossorial eg. Australian hopping mice (*Notomys alexis* and *N. cervinus*) (MacMillen & Lee 1970), *Gerbillurus* spp. (Downs & Perrin 1990), the short

tailed shrew (*Blarina brevicauda*) (Neal & Lustick 1973) and the northern pocket gopher (*Thomomys talpoides*) (Gettinger 1975), all of which are only able to dissipate a maximum of approximately 30% of their metabolic heat by evaporation. In contrast some mammals, notably those that regularly encounter high T_as, are capable of dissipating up to 100% of their metabolic heat production by evaporation eg. ground squirrels (*Spermophilus* spp.) (Hudson & Deavers 1973), the desert cottontail (*Sylvilagus audubonii*) (Hinds 1973), the jackrabbit (*Lepus californicus*) (Schmidt-Nielsen *et al.* 1965) and the rock hyrax (*Heterohyrax brucei*) (Bartholomew & Rainey 1971). Although a poor evaporative cooling capacity will promote water economy in an arid environment, it is more likely to have developed because there is no selective advantage in developing an efficient evaporative cooling mechanism when the only time a nocturnally active, diurnally fossorial rodent is likely to encounter heat stress is in the burrow where evaporation is prohibited by the high humidity (MacMillen & Lee 1970).

Finally, at high T_as springhare were able to tolerate a considerable increase in T_b. Although not significant, T_b began increasing in the upper TNZ. Müller *et al.* (1979) reported similar results for the two East African springhare. Tolerance to hyperthermia has been reported in a number of mammals including the camel (*Camelus dromedarius*) (Schmidt-Nielsen *et al.* 1957), antelope ground squirrel (*Citellus leucurus*) (Hudson 1962), black-tailed prairie dogs (*Cynomys ludovicianus*) (Reinking *et al.* 1977) and Merriam's chipmunk (*Eutamias merriami*) (Wunder 1970) and is generally interpreted as a water saving mechanism. By storing heat and allowing T_b to increase, the water that would otherwise be used to lose this heat evaporatively is saved. An elevated T_b also reduces the heat load from the environment, by reducing the temperature gradients between the animal and its surroundings, and promotes cooling by non-evaporative means such as radiation and conduction. Springhare, however, because of their nocturnal habits seldom encounter high T_as. Therefore the relatively labile T_b which reflects heat storage may rather be an adaptation to a fossorial habitat in which the possibilities for evaporative cooling during vigorous exercise eg. digging, in a warm humid burrow are limited.

In summary, springhare in this study are well adapted to a diurnally fossorial, nocturnally active lifestyle. They are poor thermoregulators at high T_as, which are seldom if ever encountered, but

are well adapted physiologically to the low night-time temperatures which are typically encountered in the arid and semi-arid areas that they inhabit. Despite the high BMR and low thermal conductance, losing enough heat in the burrow under normal resting conditions does not appear to be a problem as springhare inhabit deep relatively cool burrows in which the temperature appears never to exceed their upper critical temperature. Excess heat generated during vigorous underground exercise is, however, presumably stored and subsequently dissipated to the cool night air or to the cooler soil when subsequently resting. The higher than expected BMR is more typical of a mesic than and an arid-adapted animal but it should be borne in mind that this study was conducted on animals from a relatively mesic area and that BMRs of animals from more arid areas such as the Northern Cape Province of South Africa and the Kalahari Desert of Botswana may well be lower than expected.

CHAPTER 9

SUMMARY AND CONCLUSIONS

Springhare are large (≈ 3 kg) nocturnal, bipedal, hopping rodents that shelter in complex burrow systems during the day. They are entirely herbivorous and patchily distributed over large parts of southern and eastern Africa. Although they are extremely abundant in parts of the Eastern Cape Province of South Africa, where they also occasionally come into conflict with agriculture, little is known about their general ecology and population biology in this region. In addition, little is known about how springhare cope with the environmental conditions encountered in the arid and semi-arid areas where they frequently abound. In view of this, the objectives of this thesis were twofold;

1. to examine and describe the general ecology and population biology of springhare in the Eastern Cape and
2. to determine what behavioural and physiological adaptations enable springhare to flourish in arid and semi-arid areas, which are characterised by the absence of free-standing water and by high diurnal and low nocturnal temperatures.

9.1 GENERAL ECOLOGY

Soft sandy soils, which are suitable for burrowing, appear to be the primary habitat requirement of springhare (Skinner & Smithers 1990). The patchy distribution of these suitable substrates in turn explains the very patchy distribution of springhare within their distributional range. Springhare have, in addition, been shown to exhibit a distinct preference for flat open areas of short grass (Butynski 1984; Augustine *et al.* 1995; Anderson 1996). Springhare in this study showed a strong preference for flat, open habitat dominated by the short grass *Cynodon dactylon* and the sedge *Cyperus esculentus*. This habitat is typically found in recently disturbed (ploughed or cultivated) lands, which are subsequently left lying fallow. Both *Cynodon dactylon* and *Cyperus esculentus* are pioneer species which rapidly recolonise these areas. In

contrast to this, old disturbed (i.e. not disturbed in the preceding 15 years) and undisturbed areas, which are characterised by much taller grass species, are generally avoided. The recently disturbed areas can consequently be seen as the ecological equivalent of the pan environments of the Kalahari Desert and the Northern Cape Province (Butynski 1984; Anderson 1996), the floodplains of rivers in northern and eastern Botswana (Butynski 1984) and the short *Cynodon* and *Cynodon/Themeda* grasslands of southern Kenya (Augustine *et al.* 1995). These preferred habitats not only provide a suitable environment for predator detection and avoidance but also facilitate social interactions and provide a relatively good quality and stable food supply throughout the year. The preference of springhare for flat, open, short grass areas also means that the habitat preferences of springhare are compatible with agricultural practises such as bush removal and overgrazing by domestic livestock.

Although not quantified on a systematic basis, field observations and examination of stomach contents revealed that *Cynodon dactylon* rhizomes and *Cyperus esculentus* tubers form a major component of the diet of springhare. Large quantities of unidentified green leaf material were also consumed and there was substantial evidence of springhare feeding on *Eragrostis curvula* leaf bases. Although springhare have been reported to feed on the roots, stems, leaves, leaf bases, corms, rhizomes, fruits and seeds of a large number of species, *Cynodon dactylon* rhizomes appear to be the preferred food item throughout their distributional range (Shortridge 1934; Smithers 1971; Jacobsen 1977; Skinner & Smithers 1990; Watson 1992; Augustine *et al.* 1995; Anderson 1996; Chapter 3). There are, however, no previous reports of springhare feeding on *Cyperus esculentus* tubers. During autumn and winter, plants typically translocate reserve nutrients to the roots and leaf bases where they are stored until they are needed for growth in spring. The ability of springhare to utilise these underground food reserves ensures them of a relatively stable food and water supply even when there is not enough above-ground grazing available to support other herbivores. Field observations also indicate that springhare are highly selective and destructive feeders. Only the choicest parts of plants are eaten and when foraging for underground food sources large patches of vegetation are often laid bare.

Although springhare are often considered to be pests of chicory, which is the primary crop grown in parts of the Eastern Cape, no physical evidence of springhare feeding on chicory was found. Indeed significantly fewer springhare were encountered in camps planted with chicory than in the same camps prior to and after chicory cultivation. This is rather surprising considering the preference of springhare for underground roots and tubers. Although this may be due to the extremely bitter taste of the root, chicory is readily consumed by other grazers such as common duiker (*Sylvicapra grimmia*) and porcupine (*Hystrix africaeaustralis*). Consequently, it seems more likely that springhare's avoidance of chicory may be due to the method in which it is cultivated. Chicory is planted in parallel rows raised approximately 30 cm, thus creating an extremely uneven surface which appears to present a serious hindrance to the bipedal hopping mode of locomotion used by springhare (pers. obs.). The small amount of damage caused to chicory by springhare occurs largely around the edges of cultivated lands and is predominantly a side effect of springhare digging for *Cynodon dactylon* and *Cyperus esculentus*.

Despite their destructive and wasteful feeding habits, springhare in the study site were found to have little overall impact on the grazing available to domestic livestock, usually cattle and sheep. This is partly because of their low population densities (0.21 springhare per ha) and partly because one of the preferred food items, *Cyperus esculentus*, is not eaten by domestic livestock. If each springhare is assumed to consume approximately 162 g of wet plant material per night (Anderson 1996) then the ≈ 31 springhare in the study site consume only 34 g per hectare of wet plant material per night. The destructive potential of springhare should, however, not be underestimated. In arid and semi-arid environments, as well as in areas where preferred crops (i.e. maize, wheat, sorghum, beans, sweet potatoes, pumpkins and groundnuts) are grown or population densities are high, their destructive feeding habits can have severe consequences (FitzSimons 1920; Shortridge 1934; Butynski 1973; Kingdon 1974; Anderson 1996). Because of their low fecundity and the ease with which they can be shot at night springhare are, however, unlikely to ever pose a serious threat to agriculture. In contrast, because of their perceived conflict with agriculture and because springhare are often hunted for sport it is thought that they are now absent from some areas where they previously used to

occur in the Eastern Cape (Coetzee 1979). In Botswana springhare are not only considered a major pest species of agricultural crops but they are also considered to be one of the most important food animals for humans. According to a survey conducted by Butynski (1973) in excess of 2.5 million springhare are killed each year in Botswana for food.

In those areas where it may be necessary to manage springhare populations i.e. nature reserves and farms where their natural predators no longer occur, accurate estimates of population size are essential and these are best obtained at times when most springhare are active and visible above ground. Time of year, time of night, and level of illumination were all found to significantly affect the number of springhare active above ground. Temperature, humidity, wind and presence of dew on the other hand had no significant effect on their activity. Although wind had no significant effect and rain was not tested statistically, strong wind and heavy rain did cause springhare to return to their burrows. Springhare activity generally reaches a maximum soon after dark and remains at this level throughout most of the night, only decreasing 2-4 h before sunrise. This pattern is, however, modified by moonlight. Springhare typically respond to moonlight by reducing above ground activity, shifting their activity to dark moonless periods of the night, and by reducing their use of open space. The single nightly activity peak exhibited by springhare is not unusual for nocturnal rodents (Ashby 1972; Lockard & Owings 1974; Wolfe & Summerlin 1989), neither is moonlight avoidance, which is a fairly standard predator avoidance strategy (Lockard & Owings 1974; Kaufman & Kaufman 1982; Kotler 1984; Price *et al.* 1984; Bowers 1988; Wolfe & Summerlin 1989; Daly *et al.* 1992).

Burrows play an important part in the biology and ecology of semi-fossorial animals. Most such animals spend a large part of their day within or near their burrows and a knowledge of their burrow utilisation behaviour is consequently central to understanding their overall ecology. Contrary to earlier reports by Anderson (1996), springhare in this study were found to utilise several different burrow systems, often spread over a substantial area. In one year, for example, one individual used 27 different burrows scattered over an area of 28.5 ha. This ability to utilise a number of different burrows presumably enables springhare to range over much larger areas in search of food and potential mates than would otherwise be possible. Radio-tracking of 14

individuals showed that springhare change burrow systems on a regular basis and seldom spend more than a few successive days in each. Previously used burrows are frequently reused and previously unused burrows i.e. old burrows are also occasionally used. New burrows are, however, only rarely excavated and most burrows appear to be utilised by a succession of springhare. This is consistent with an earlier report by Butynski & Mattingly (1979) and is not unusual amongst animals that inhabit complex burrow systems (Reichman & Smith 1990). Observations made in this thesis also confirm earlier reports that springhare do not appear to defend territories (Butynski 1984; Skinner & Smithers 1990; Anderson 1996). Recently used burrows do, however, appear to be avoided by conspecifics and I propose that scent marks made by the pair of perineal glands serve to indicate burrow occupancy. Frequent burrow changes may, apart from other reasons such as predator and parasite avoidance, be a means of ensuring that these scent marks remain fresh. Although males of solitary species generally range more widely than females, male and female springhare on average utilised a similar number of burrows scattered over similar sized areas. This lack of differentiation between the sexes is, however, not entirely unusual and has previously been reported in both Merriam's kangaroo rat (*Dipodomys merriami*) and the chisel-toothed kangaroo rat (*Dipodomys microps*) (Allred & Beck 1963; Chew & Butterworth 1964; Maza *et al.* 1973; Behrends *et al.* 1986).

In addition to providing protection from predators, burrows also provide protection from unfavourable environmental conditions. Data presented in this thesis show that springhare burrows provide a stable microclimate of moderate temperatures and high humidities independent of ambient fluctuations. The thermal neutral zone (15-25 °C) of springhare was found to encompass the range of mean burrow temperatures experienced throughout the spring, summer and autumn months. Only during the winter months did mean burrow temperatures drop below their lower critical temperature of 15 °C and then only slightly so. At no stage did mean burrow temperatures exceed their upper critical temperature of 25 °C. Although springhare burrow temperatures as high as 28.4 °C have previously been reported in mid-summer by Anderson (1996) in the Northern Cape Province, these measurements were made only 50 cm from the burrow entrances and there is little doubt that at greater depths temperatures below 25 °C would be encountered. The very high humidities (100%) encountered

Aseasonal reproduction in this study, along with similar reports from highly seasonal areas such as Botswana (Smithers 1971; Butynski 1979; Butynski & Hanks 1979), the Northern Cape Province (Anderson 1996) and the central Orange Free State (Van der Merwe *et al.* 1980), suggests that springhare throughout southern Africa are aseasonal breeders. Under extreme environmental conditions reproduction may, however, occasionally be restricted to favourable parts of the year (Kofron 1987). Whilst very little is known about springhare reproduction in East Africa, the indications are that reproduction there also occurs throughout the year (Coe 1969).

Although reproduction is largely aseasonal the number of pregnancies per female per year varies considerably between populations. Springhare in Botswana undergo approximately 3.6 pregnancies per year (Butynski 1979), those in the present study 2.9 per year, those in the Northern Cape Province 2.4 per year (Anderson 1996) and those in southeastern Zimbabwe only one per year (Kofron 1987). These differences are most likely due to differences in environmental conditions and food availability and this suggest that springhare are opportunistic breeders.

I suggest that the ability of springhare to reproduce throughout the year, even in highly seasonal and arid environments such as the Kalahari Desert (Butynski 1979) can be attributed to their ability to utilise subterranean food stores such as roots, rhizomes and tubers. These underground food sources are generally not available to most other herbivores and provide a reasonably stable food and water supply throughout the year. In addition to this, springhare utilise a number of different burrow systems and this enables them to forage over very large areas.

The overall reproductive strategy of springhare involves high individual fitness at the expense of fecundity and is rather unusual for a mammal of this size. Small mammals are typically relatively short lived and produce large litters of young that grow and reach sexual maturity rapidly. In contrast to this, springhare are relatively long-lived, (up to 14 years in captivity; Nawak & Paradiso 1983), and have a slow, protracted reproductive strategy. This reproductive

strategy was previously thought to have evolved to minimise predation (Butynski 1979) or to be linked to springhare's bipedal mode of locomotion (Anderson 1996). Recent developments in the field of mammalian life history strategies and their evolution (Kozlowski & Weiner 1996; Harvey & Purvis 1999), however, indicate that the rather unusual life history strategy of springhare can best be described as a response to low levels of adult and juvenile mortality in an arid and nutritionally poor environment. Thus, although springhare are reproductively active throughout the year, they have a relatively long slow reproductive strategy which is thought to have evolved primarily in response to low levels of adult and juvenile mortality. This life history makes springhare particularly susceptible to sustained hunting pressure which can rapidly deplete populations and lead to local extinction. Although springhare are a major source of food in some parts of Africa (Butynski 1973; De Graaff 1981; Anderson 1996), their reproductive characteristics (single young, long gestation, long lactation, and slow growth of young) make them unsuitable for commercial exploitation as a food animal.

9.2 ADAPTATION TO ENVIRONMENT

Although springhare in this study were not from a particularly arid environment, springhare are known to inhabit and prosper in arid and semi-arid areas such as the Kalahari Desert (Smithers 1971; Butynski 1973, 1979, 1984; Butynski & Hanks 1979; Butynski & Mattingly 1979) and the Northern Cape Province of South Africa (Anderson 1996). These areas are typically devoid of surface water and experience large daily and seasonal fluctuations in temperature. Animals that inhabit such extreme environments usually exhibit a variety of physiological adaptations which enable them to cope with the lack of water and high temperatures. These include:

- The ability to produce a highly concentrated urine (Schmidt-Nielsen 1964; MacMillen & Lee 1967, 1969; Abbott 1971; Maloiy 1972a; Maxson & Morton 1974; Kronfeld & Shkolnik 1996; Degen 1997). This minimises water loss and is often considered to be one of the most important adaptations to life in arid environments.
- The ability to tolerate dehydration, which in turn depends largely on the ability to maintain plasma volume at the expense of other body water compartments (Schmidt-Nielsen 1964; Horowitz & Borut 1970; Hartman & Morton 1973; Hill & Wyse 1989).

- The ability to produce very dry faeces (Schmidt-Nielsen *et al.* 1956; Louw *et al.* 1972; Nagy *et al.* 1976).
- A lower basal metabolic rate (BMR) than animals from more mesic environments (McNab & Morrison 1963; Goyal & Ghosh 1983; Hinds & MacMillen 1985; Downs & Perrin 1990; Degen 1997). Low BMRs reduce energy requirements, heat production and evaporative water loss and are thought to be an alternative to the production of a concentrated urine as a means of reducing water turnover (McNab 1979a).
- A higher thermal conductance than animals from more mesic habitats (Haim & Izhaki 1993; Haim & Fairall 1986; Haim *et al.* 1987), which maximises heat loss by non-evaporative means.
- The ability to tolerate hyperthermia (Schmidt-Nielsen *et al.* 1957; Hudson 1962; Wunder 1970; Reinking *et al.* 1977), which not only minimises the amount of heat that must be lost by evaporation of water but also reduces heat load from the environment by reducing the thermal gradient between the animal and its surroundings.

To determine what physiological adaptations, if any, enable springhare to survive in arid areas without drinking, springhare were deprived of water for up to seven days and body weight, urine volume, haematocrit and plasma and urine osmolality, sodium, potassium and urea monitored. During this period springhare produced urine with a mean maximum concentration of 2548 mosmol kg^{-1} with a maximum of 3076 mosmol kg^{-1} being measured in an individual animal. This, although relatively high, is not as high as that of most desert animals which are able to produce urine in excess of 3000 mosmol kg^{-1}. It should, however, be borne in mind that animals used in this study were from a relatively mesic area and that springhare from a more arid region might well be able to produce a more highly concentrated urine. Springhare did, however, exhibit a high tolerance to dehydration and were found to be good osmoregulators capable of maintaining plasma volume during periods of water deprivation. During water deprivation springhare also minimised water loss by restricting food intake. This not only reduces the solute load but also faecal water loss. Water conservation was further augmented by the ability to produce very dry faeces i.e. with a moisture content of only 38-41%.

The metabolic and thermal biology of springhare were also examined for adaptations to life in hot, arid environments. Springhare were found to have a lower critical temperature of 15 °C, an upper critical temperature of 25 °C, a higher than expected (from mass) BMR (0.44 mL O_2 g^{-1} h^{-1}) and a lower than expected minimal thermal conductance (0.018 mL O_2 g^{-1} h^{-1} $°C^{-1}$). They were also found to be good thermoregulators at low ambient temperatures and were able to maintain a stable body temperature of 35.8 °C at ambient temperatures between -5 and 25 °C. At high ambient temperatures springhare were, however, poor thermoregulators. At temperatures above 25 °C they could not dissipate heat as fast as they gained it and became hyperthermic. At high ambient temperatures springhare were, however, able to tolerate a considerable increase in body temperature (≈ 2.9 °C above normal).

Springhare thus conform to some but not all of the predictions for arid-adapted animals. The relatively high BMR and low minimum thermal conductance can, however, be attributed to the fact that springhare are active at night when temperatures in arid areas are usually low (and can be very low) particularly in winter. In addition to this, springhare spend days in a deep, cool burrow system where the temperature never appears to exceed the upper critical temperature of 25 °C. Thus, although, springhare inhabit hot arid environments they very seldom, if ever, encounter high ambient temperatures but are usually confronted with low temperatures. Under these conditions losing excess heat generated is not a problem but excessive heat loss at night is and hence the slightly elevated BMR and low minimum thermal conductance are favourable. The relatively low, lower critical temperature and broad thermoneutral zone of springhare are also typical adaptations to cool rather than warm environments (Taylor & Sale 1969; Kronfeld & Shkolnik 1996; Degen 1997), and are consequently appropriate for a nocturnal species.

As springhare seldom if ever encounter temperatures above the upper critical temperature of 25 °C it is not surprising that springhare are good thermoregulators at low ambient temperatures and poor thermoregulators at high ambient temperatures. Efficient thermoregulation at low temperatures no doubt explains why temperature was earlier found to have no significant effect on springhare activity. The poor thermoregulatory ability of springhare at high ambient temperatures may be attributed to a poor capacity for evaporative

cooling (Müller *et al.* 1979). Although a poor evaporative cooling capacity will minimise water loss at high ambient temperatures it is more likely attributable to the fossorial habits of springhare. There is no selective advantage in developing an efficient evaporative cooling mechanism when the only time springhare are likely to encounter heat stress is in the burrow where evaporation is prevented by the high humidity (MacMillen & Lee 1970). Similarly, tolerance to hyperthermia or heat storage is usually interpreted as a water saving mechanism (Schmidt-Nielsen *et al.* 1957; Hudson 1962; Wunder 1970; Reinking *et al.* 1977) but as springhare never encounter high temperatures it is, in this case, once again rather thought to be an adaptation to a fossorial habitat in which the opportunities for evaporative cooling during vigorous exercise eg. digging, are limited. Excess heat generated during activity in the burrow can consequently be stored until it can be dissipated either to the cool night air or to the cool soil of the burrow when resting.

With the exception of peripheral vasodilation and salivation springhare exhibit no other physiological adaptations for coping with high ambient temperature, but are rather adapted to low night-time temperatures and fossorial habits. Despite this, water availability remains a problem. Springhare are, however, fairly well adapted physiologically to life in arid areas. They produce a reasonably concentrated urine, exhibit a high degree of tolerance to dehydration, are good osmoregulators capable of maintaining plasma volume over long periods of water deprivation and are able to produce extremely dry faeces. These physiological adaptations, augmented by a number of important behavioural adaptations such as burrowing, nocturnal activity, selective feeding and the ability to utilise underground food reserves, enable springhare to survive in the arid and semi-arid areas where they frequently abound.

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